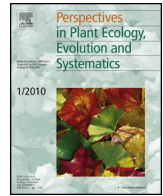




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Research article

Environmental drivers of diversity in Subtropical Highland Grasslands



Michel J.F. Barros^a, Gustavo A. Silva-Arias^a, Jeferson N. Fregonezi^a,
 Andreia C. Turchetto-Zolet^a, João R.V. Iganci^b, José Alexandre F. Diniz-Filho^c,
 Loreta B. Freitas^{a,*}

^a Department of Genetics, Universidade Federal do Rio Grande do Sul, PO Box 15053, 91501-970 Porto Alegre, RS, Brazil

^b Department of Botany, Universidade Federal do Rio Grande do Sul, Av. Bento Gonçalves 9500, 90509-9000 Porto Alegre, RS, Brazil

^c Department of Ecology, Universidade Federal de Goiás, Campus II, 74001-970 Goiânia, GO, Brazil

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ABSTRACT

The aim of this study was to identify major bioclimatic variables associated with the diversity patterns of plant genera and the contribution of elevations in highly diverse areas of the Subtropical Highland Grasslands (SHG), which form mosaics with *Araucaria* forests. We selected three plant genera that have diversified, in part, within the Neotropical SHG: *Adesmia* (Fabaceae) and *Calibrachoa* and *Petunia* (Solanaceae). We delimited the major high elevation areas of the region and calculated the taxonomic diversity for these taxa in each area. Ecological Niche Models (ENMs) were used to predict the distribution of each taxon and to project it to the Last Glacial Maximum (LGM), allowing searching for stable areas. Those stable areas were then compared to areas with high diversity levels. We explored the spatial occurrences and the multivariate contribution of environmental factors to differentiate among the *Araucaria* forest and the SHG. Finally, we examined the correlations between the environmental variables and the molecular and taxonomic diversity. Niche stability was directly linked to diversity and positively correlated with altitude. Although some niche aspects differed subtly, the predicted distributions of grassland and forest taxa were not different at larger scales. Two of the four studied areas were suggested by the ENMs to be high-relevant sites for conservation studies and the maintenance of diversity.

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Introduction

Biodiversity is a result of ecological features and evolutionary processes that drive the species distribution patterns in time and space (Safford, 1999; Sklenář et al., 2011; Fregonezi et al., 2013). Condamine et al. (2012) encouraged the combination of multiple datasets based on ecological traits, species distribution, fossil records, genetic diversity, and paleogeography, together with paleoclimatic studies, to better understand what determines the spatial patterns of species diversity at distinct hierarchical levels.

Grassland biomes are a major component of global biodiversity, and several of these grasslands harbor high levels of endemism (Fisher and Robertson, 2002; Safford, 2007; Iganci et al., 2011; Sklenář et al., 2011; White et al., 2011) and genetic diversity (Jakob et al., 2009; Lorenz-Lemke et al., 2010; Palma-Silva et al., 2011; Sede et al., 2012; Fregonezi et al., 2013). The southern Brazilian subtropical grasslands have been highlighted as threatened by habitat loss

and fragmentation (Iganci et al., 2011) due to severe and long-term human disturbance, including the over use of fire and cattle grazing, spreading of agriculture in large areas, and the introduction of alien species (Pillar and Quadros, 1997; Zalba and Villamil, 2002; Behling and Pillar, 2007; Overbeck et al., 2007; Gieselmann et al., 2013). Additionally, the area is experiencing rapid and intense expansion of invasive tropical woody plants (Zalba and Villamil, 2002; Behling and Pillar, 2007).

The identification of priority areas for conservation and modeling species diversity distribution in the Neotropics may be difficult due the lack of information on geographic locations, mainly for rare species (Kamino et al., 2011). Therefore, linking broader ecological-evolutionary processes to current diversity patterns based on model taxa would help to recognize major areas for conservation studies. Especially, taxa with a well-established taxonomy, known evolutionary history, and relatively comprehensive and comparable distribution datasets are suitable for identifying those diversity patterns (Eldon et al., 2013).

In arctic and alpine environments, climate variables strongly affected vegetation survival and drove species diversity distribution patterns. However, the effects of freezing were less intense or

* Corresponding author. Tel.: +55 51 3308 6731; fax: +55 51 3308 9823.

E-mail address: loreta.freitas@ufrgs.br (L.B. Freitas).

sometimes absent in most tropical and broadly defined temperate climates (Bliss, 1962). In the Neotropics, the Andean Cordillera strongly influenced evolutionary processes in both highland and lowland flora (Antonelli et al., 2009). Although the highland plateaus in southern Brazil are lower than the highest altitudes of the Andean Cordillera, an Andean origin is attributed to several plant groups inhabiting the Brazilian highland grasslands (Safford, 1999; Sklenář et al., 2011; Iganci et al., 2013); some of the Andean biomes and the niches from the Subtropical Highland Grasslands (SHG) have similar temperature and humidity conditions (Safford, 1999). Some taxa, mostly represented by species with island-like distributions (Lorenz-Lemke et al., 2010), reflect the history and differentiation of grasslands since their allopatric origin can be attributed to the geographical isolation of vegetation, related to forest expansion–retraction cycles (Fregonezi et al., 2013).

Most of the evidence on grasslands and forest distribution dynamics from the Last Glacial Maximum (LGM; ~21,000 years ago) and the extrapolations for climate changes in the SHG is pollen-based (Behling, 2002; Behling and Pillar, 2007). However, it is difficult to distinguish between temperature and precipitation changes based on pollen data alone. Using complementary methods to define this distinction is necessary (Weijers et al., 2007). Ecological Niche Models (ENMs) are adequate to infer the effects of climate changes on taxa distributions since the LGM (Waltari et al., 2007; Carnaval and Moritz, 2008) and have successfully allowed the identification of stable distribution areas (Terrible et al., 2012). Even though some caution is required (Collevatti et al., 2013), using ENMs associated with phylogeographic approaches allow the identification of Quaternary climatic stable areas as centers of genetic diversity (Waltari et al., 2007; Carnaval and Moritz, 2008; Jakob et al., 2009; Vera-Escalona et al., 2012). Additionally, this combined approach could predict macroecological patterns, such as species diversity and abundance (Peterson et al., 2011; Rangel and Loyola, 2012).

Pleistocene climate cycles have been suggested as potential drivers of genetic diversity distribution patterns for some taxa from

SHG (Lorenz-Lemke et al., 2010) and this reinforces the necessity of correlating genetic diversity patterns with bioclimatic variables, aiming to identify ecologically stable areas during the Quaternary. The climate in SHG is subject to seasonal low temperatures, including frosts and snowfall (Pezza and Ambrizzi, 2005). Records of fire as a recurrent trait since ca. 7400 yr BP suggest the influence of human occupation in the region (Behling and Pillar, 2007). The SHG form mosaics with the *Araucaria* forest, which is characterized by the dominant presence of *Araucaria angustifolia* (Bertol.) Kuntze. In a general sense, this forest belongs to the Atlantic Forest Domain and is under the influence of tropical and subtropical humid climate, without pronounced dry seasons (Duarte et al., 2012). Phylogeographic and phylogenetic analyses for taxa present in the SHG (Lorenz-Lemke et al., 2010; Fregonezi et al., 2013; Iganci et al., 2013) have suggested the importance of forest expansion and retraction during the Pleistocene, in establishing geographical plant distribution and molecular diversity.

Furthermore, public interest in better understanding the biodiversity and genetic resources is increasing due the imminent extinction risk of species as a consequence of environmental pollution, climate changes, and habitat fragmentation and destruction (Picó and Groenendael, 2007; White et al., 2011). These imminent risks are even higher for fragile habitats such as SHG. Therefore, to search for major ecological traits that drive diversity patterns within the SHG, we aimed to answer three questions: (1) Which sites are the most diverse within the SHG studied, and how are the taxonomic and molecular diversities distributed among those areas? (2) What is the correlation between the variance of abiotic variables, such as climate and altitude, and the SHG taxonomic and molecular diversities in major areas? (3) How do the niche conditions and predictions of the SHG contrast with those of the *Araucaria* forest since the LGM? We aimed to investigate diversity patterns and conservation priority areas in the SHG, to correlate factors that potentially drive taxonomic and molecular diversity in the SHG, and to identify potential relationships between the grasslands and the *Araucaria* forest niches since the LGM climatic period. We coupled

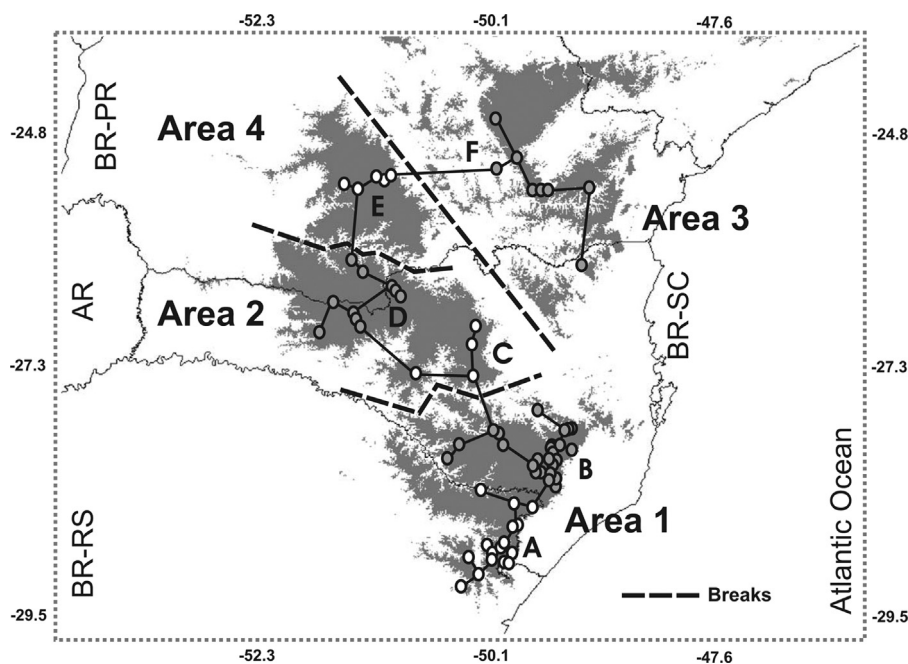


Fig. 1. The SHG region in the southeastern part of South America and the locations of the individuals studied. The locations are shown over a threshold of 900 m.a.s.l. This threshold was consistent with plant distribution and avoided incorporation of different lowland habitats or species in sampling. Based on the altitude, four areas (from 1 to 4) and breaks among these units can be distinguished, which are represented by dashed lines. Areas were the sampling units used to calculate the diversity variables, which were used to develop the linear correlation analyses (Table 3). Caps letters (A–F) correspond to plastid haplogroups of *Petunia*; BR-RS—Rio Grande do Sul Brazilian state; BR-SC—Santa Catarina Brazilian state; BR-PR—Paraná Brazilian state; AR—Argentina.

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