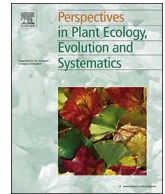




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## Research article

# From inland to the coast: Spatial and environmental signatures on the genetic diversity in the colonization of the South Atlantic Coastal Plain



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## ABSTRACT

The process of colonization and range expansion to novel environments involves both demographic and selective processes that can be traceable in the genetic diversity of the organisms. Nevertheless, it can be difficult to disentangle the signatures of the demographic and selective in the current genetic diversity of the populations. In this work, we use a landscape genetics framework to investigate the association of spatial and climatic variables with the genetic diversity and differentiation patterns of wild *Petunia* populations involved in a process of coastal colonization during the last 400 thousand years. Over 300 individuals from 17 populations were genotyped using ten microsatellite loci. Our results suggest that the genetic diversity is higher in populations located at the center of the species range with a decline toward the edges, and that gene flow follows an inland-to-coastal and central-to-peripheral dynamic that parallels the colonization history of this coastal lineage. We identify high levels of genetic differentiation between inland and coastal populations. As part of the inland-coastal genetic differentiation, we find signals of isolation by environment associated with differences in extreme temperature regimes. The differentiation of edge populations along the coast is associated with precipitation seasonality. Our results are robust to controls for spatial and historical divergence in the observed genetic differentiation. We conclude that the ecological differentiation process during the colonization of the South Atlantic Coastal Plain (SACP) was likely facilitated by genetic enrichment resulting from gene flow from central to marginal populations, as well as by rapid allele fixation resulting from serial founder effects during the range expansion along the coast.

## 1. Introduction

Investigations of diverging lineages that occupy regions with different ecological conditions enable researchers to understand how biotic or abiotic constraints can shape patterns of genetic differentiation across the geographic range of a species (Orsini et al., 2013). The distinction between isolation by distance (gradual genetic differentiation across populations as a product of limited dispersal), isolation by colonization (clear differentiation patterns resulting from founder effects), and isolation by environment (differentiation resulting from restricted gene flow between populations inhabiting different environments by selection against dispersers or by preference to remain in a particular environment due to local adaptation) is particularly challenging due to the superimposition of their respective signals in the genetic data (Ferchaud and Hansen, 2016; Laurent et al., 2016). For example, when

a species colonizes a region with new ecological conditions, genetic divergence can be enhanced by the reduction of gene flow related to the spatial separation, as well as by selection against maladapted migrants.

The complex interplay of spatial and ecological processes in determining the spatial distribution of a species can be assessed using a landscape genetics framework (Balkenhol et al., 2016; Manel et al., 2003). Landscape genetics is a field that has been developing rapidly due to the increasing sophistication of molecular methods and statistical analyses, as well as the growing availability of spatial ecological data (Manel and Holderegger, 2013; Storfer et al., 2010, 2007). Several factors may have an impact on the interpretation of the influence of space and environment on the genetic differentiation. These factors include the type of genetic marker used, the geographical range of the focal species, and the methods used to detect gene flow with respect to environmental gradients.

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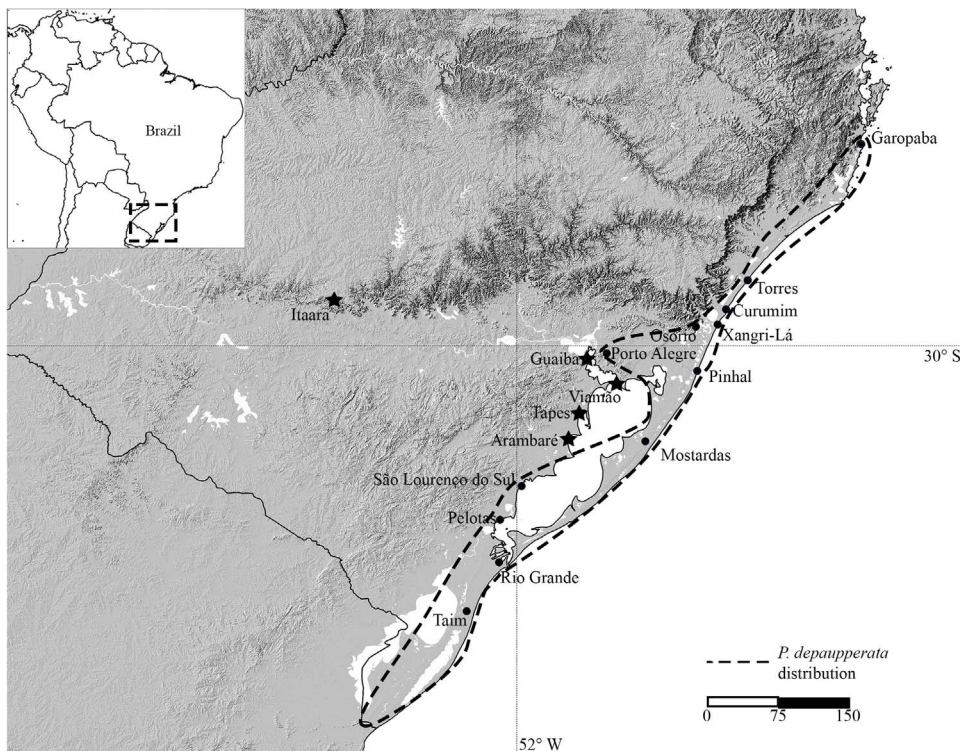
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**Fig. 1.** (A) Sampling sites of *P. integrifolia* (stars) and *P. depauperata* (circles) populations included in this study. The full geographical range of *P. depauperata* is also indicated. The localization of the study area within South America appears is inset at the upper-left corner.

The South Atlantic Coastal Plain (SACP; Fig. 1; Fig. A.1, Appendix A) is a flat and continuous open coastal formation occupied mostly by large coastal lakes. Extending over approximately 600 km NE-SW in southern Brazil and Uruguay, SACP is crossed by only two perennial water channels and it is the largest coastal plain in South America (Tomazelli et al., 2000; Weschenfelder et al., 2010). The SACP was formed during oscillatory sea level transgressions and regressions caused by the glacial-interglacial cycles over the past 400,000 years. Each transgression-regression cycle led to the formation of a sand barrier running parallel to the coast (barrier-lagoon systems I–IV, Tomazelli et al., 2000; Tomazelli and Dillenburger, 2007; Fig. A.1, Appendix A). Due to this well-characterized history of cycles of exposure and flooding during the glacial and interglacial periods, it can be assumed that most organisms inhabiting this coastal plain, colonized it, and are expanding into and adapting to this new environment during the Pleistocene-Holocene period. The SACP therefore represents a promising model for the understanding of recent colonization processes.

Coastal environments offer particular climatic and edaphic conditions, such as salt exposition, temporal flooding, and seasonal or permanent strong winds. Additionally, the shape of coastal habitats is inherently linear, thereby conditioning the distribution of the taxa restricted to these regions. Moreover, global climatic changes can strongly affect the availability of suitable habitats for coastal organisms over time (Hoegh-Guldberg and Bruno, 2010; Reyer et al., 2013). Several studies have addressed the phylogeographical patterns of coastal organisms (Lopes et al., 2013; Mäder et al., 2013; Ramos-Fregonezi et al., 2015) and their distributional and demographic responses to climate change (Weising and Freitag, 2007; Turchetto-Zolet et al., 2016). Others have discussed physiological and molecular approaches to examine specific mechanisms of adaptation to saline environments (Lowry et al., 2009; Zhu, 2001). The study of the colonization of saline environments involving sister inland-coastal lineages through the characterization of genetic diversity and gene flow in relation to spatial and ecological variables could be important to understand the adaptation to saline environments from an evolutionary point of view.

The aim of this study was to identify genetic signatures related to the recent coastal colonization process of a lineage of the *Petunia* genus (Solanaceae) to the SACP from a continental ancestor. To achieve this, we characterized the genetic diversity and structure of coastal populations and used a landscape genetics approach to examine alternative spatial and ecological drivers of genetic differentiation and gene flow in coastal populations. We specifically addressed the following questions: (1) Do historical and current gene flow explain current patterns of genetic diversity and structure? (2) Do environmental conditions constrain the gene flow between SACP populations?

## 2. Materials and methods

### 2.1. Study system

*Petunia integrifolia* subsp. *depauperata* (hereafter *P. depauperata*) is a diploid ( $2n = 14$ ), prostrate annual herb, with purplish flowers pollinated by the solitary small bee species *Callonychium petuniae* (Wittmann et al., 1990), and also likely by other species of the genus *Leioproctus* and *Calliopsis* (Ando et al., 2001; Gübitz et al., 2009), and dry dehiscent capsules that produce hundreds of tiny seeds with no dispersion mechanism. Ando et al. (2001) analyzed one population from São Lourenço do Sul and concluded that this taxon is self-incompatible. Accounting for the reproductive traits of *P. depauperata* seed dispersion seems to be more limited than pollen dispersion. However, secondary seed dispersion by wind might be an important gene flow promoter in *P. depauperata* due to the strong wind potential in the SACP. There are no studies about gene flow in *P. depauperata*, but *P. axillaris* (a hawkmoth pollinated species) have been found pollen dispersal distances until 1013 m (Turchetto et al., 2015a).

*P. depauperata* is restricted to open sandy grasslands, dunes and rocky outcrops of lakeside or marine environments along the SACP. The *P. depauperata* lineage likely diverged around 400 thousand years ago (kya) from populations of its closest relative, *P. integrifolia* subsp. *integrifolia* (hereafter *P. integrifolia*) (Ramos-Fregonezi et al., 2015), a taxon that is widespread in inland subtropical grasslands and belongs to the *P. integrifolia* complex (Longo et al., 2014) that in previous

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