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Disentangling landscape effects on population genetic structure of a Neotropical savanna tree

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ABSTRACT

Geographical patterns of genetic variation and population structure and their relationship with habitat loss and fragmentation have been investigated at distinct scales and extents using spatially explicit statistics. Here, we analyzed population genetic structure of *Dipteryx alata* (Fabaceae; the baru^o tree), an economically important tree widely distributed in Central Brazil that is endemic to the Cerrado^o (savanna) biome, relating population genetic divergence with broad-scale landscape patterns. Genetic divergence among 25 populations, estimated based on eight microsatellite loci for a total of 644 individuals, was correlated with landscape features using several forms of Mantel tests (standard Mantel correlations, Mantel correlograms, partial correlations, and multiple regression). Patterns of genetic divergence are significantly correlated with human-driven landscape features of habitat loss and fragmentation, after taking into account isolation-by-distance and historical effects of range expansion after the last glacial maximum. Our findings present important implications for the conservation of this species, because interruption of gene flow by habitat loss and fragmentation jeopardize the persistence of population in the medium- and long term due to disruption of demographic patterns, increased endogamy, and recruitment problems.

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Introduction

Geographical patterns of genetic variation and population structure have been investigated at distinct scales and extents using spatially explicit statistics, in different research programs, ranging from the analysis of fine-scale population genetic structure up to broad-scale phylogeographical patterns (see Epperson 2003; Guillot et al. 2009; Diniz-Filho & Bini 2012; Wagner & Fortin 2013 for overviews). In all cases, spatial analyses allow for the inference of ecological and evolutionary mechanisms underlying the patterns and, at the same time, may be informative in respect to helping to establish effective strategies for biodiversity conservation within species (e.g., Diniz-Filho & Telles 2002; Escudero et al. 2003; Diniz-Filho et al. 2012a).

At more local and regional scales, several studies have focused on inferring processes underlying population structure related to spatial constraints on dispersal and gene flow (Epperson 2003). Moreover, it is possible to relate these dispersal processes to landscape characteristics, including natural features and human-induced modifications related to habitat loss and fragmentation, as proposed by the new research program in landscape genetics (Manel et al. 2003; Manel & Holderegger 2013).

The Cerrado is one of the world's conservation hotspots, mainly due to a high level of endemism for plants, adapted to the long dry season, including several tree species whose fruits have commercial importance for local economies. Most of them may be considered endangered due to habitat loss and climate changes (e.g., Nabout et al. 2012). One of these economically important Cerrado species is *Dipteryx alata* Vogel (Fabaceae), popularly known as the "baru" tree, a widely distributed large tree species endemic to the biome, usually restricted to seasonal savannas habitats and growing in eutrophic and drained soils ("cerradão"). The species is hermaphroditic, and pollination is mainly performed by large- and medium-sized bees. Seeds have a very woody endocarp, with edible nuts that are eaten and dispersed by mammals, such as bats and monkeys, and are a source of raw material for small- and middle-sized food industries, playing an important role in the local economy of Central Brazil.

Previous analyses with *D. alata* revealed spatial patterns in genetic variation both at local and regional scales (Collevatti et al. 2010, 2013; Diniz-Filho et al. 2012b) and that, at least in part, this structure may be related to human occupation and habitat fragmentation in the Cerrado (Soares et al. 2008). Spatial autocorrelation analyses (Collevatti et al. 2010) showed the spatial genetic structure at local scales, as expected by considering the ecological and life history traits of the species. Our current knowledge of broad-scale genetic diversity and population structure in *D. alata* shows that the species possess a strong spatial structure in genetic differentiation, following an IBD-like pattern coupled with range expansion after glacial maximum for distinct loci (Diniz-Filho et al. 2012b).

Here, we analyzed the broad-scale genetic population structure of *D. alata*, associating patterns of variation with landscape features, using an explicit landscape genetics framework (the "link approach", as recently defined by Wagner

& Fortin (2013). Our goal was to investigate, in more detail, how broad-scale patterns of population genetic divergence due to range expansion and isolation-by-distance in deep time are disrupted by recent constraints to gene flow caused by intense human occupation of the Cerrado biome.

Materials and methods

Genetic data

We estimated genetic variation for a total of 644 individuals sampled in 25 localities (populations hereafter) in the Cerrado region, with sample sizes varying from 13 to 32, at distinct points covering most of the range of *D. alata* (Fig. 1). Individuals were genotyped using eight microsatellite loci, following Soares et al. (2012). The variation in these eight loci was used to estimate pairwise allelic divergence (q) obtained from an analysis of variance of allele frequencies, among all populations and for pairwise comparisons (see Holsinger & Weir 2009). These values of q were transformed into Slatkin's linearized form ($F_{ST}/[1 - F_{ST}]$) to improve linearity in the relationships and allow a better link with theoretical expectations. For simplicity, these values will hereafter be referred to only as F_{ST} .

Landscape data and metrics

Land use data was obtained from the vegetation cover maps of the Brazilian biomes in the 1:250.000 spatial scale, by visual interpretation of compositions of bands three, four, and five of Landsat 7 ETM+ images from the year 2002 (see www.mma.gov.br). We used the basic classification that differentiated natural vegetation (forests, savannas, and natural grasslands) from anthropic land cover classes (including agriculture, pasture lands, urban, and mining areas). The polygons were converted into a raster image with resolution of approximately 100 m (0.001°).

We then created lines connecting all pairs of populations and, around these lines, we created "corridors" with variable widths. However, fragmentation metrics across widths were highly correlated (i.e., $r > 0.90$), so results were presented only for the 10.0 km corridor width. We considered each of the corridors as a landscape connecting pairs of populations and quantified landscape metrics of the natural vegetation for each of these landscapes, using Fragstats 4.1 (McGarigal et al. 2002), by means of the following commonly used landscape metrics (Metzger 2003; Table 1). Each of these metrics allowed for calculating a pairwise matrix that could be spatially analyzed and compared with the genetic divergence matrix.

Mantel tests

Patterns in genetic distance and correlations with landscape data were analyzed using several forms of the Mantel test of matrix correspondence (see Diniz-Filho et al. 2013 for a review). These include simple Mantel tests correlating two matrices, Mantel correlograms describing patterns across distinct classes of connectivities, and multiple regression of distance

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