



## Geographic shifts in climatically suitable areas and loss of genetic variability in *Dipteryx alata* (“Baru” Tree; Fabaceae)

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Genet. Mol. Res. 11 (2): 1618-1626 (2012)

Received October 4, 2011

Accepted January 7, 2012

Published June 15, 2012

DOI <http://dx.doi.org/10.4238/2012.June.15.11>

**ABSTRACT.** Many species are expected to suffer strong shifts in their geographic ranges due to climate changes in the next 50 years, with severe consequences for biodiversity patterns and population structure. We used here an ensemble forecast approach for obtaining species' range in which multiple species distribution models and climatic models were combined to model loss of genetic variability in Baru, *Dipteryx alata* (Fabaceae), an economically important Neotropical tree native to the Cerrado of Brazil. We estimated a series of genetic parameters (number of alleles per locus, expected heterozygosity under

Hardy-Weinberg equilibrium and mutation-drift equilibrium) for this species based on eight microsatellite loci. We then recalculated these parameters assuming that local populations in areas of low future environmental suitability will go extinct. All genetic parameters remained approximately constant up to a 50% threshold of climatic suitability in the future; after this critical threshold there is an abrupt reduction in all parameters, although the magnitude of shift is only about 10% of current values, on average. Thus, despite the shifts in geographic range and climatically suitable areas towards southeastern Brazil, our analyses do not predict a strong loss of genetic diversity in *D. alata* because of the broad tolerance of this species, which ensures large future ranges, contrasting with other Cerrado species that have been analyzed in a similar manner.

**Key words:** Climatic change; Cerrado; Geographic range shift; Microsatellites

## INTRODUCTION

Many species are expected to suffer a strong shift in their geographic ranges due to climate changes in the next 50 years, depending on their ecological tolerance and current demographic parameters, which were in turn shaped by their evolutionary history (Parmesan, 2006; Diniz-Filho and Bini, 2008). Different approaches have been used to understand how different aspects of biodiversity will be affected by these climatic changes, but most of the predictive studies on broad, macroecological scales (Kerr et al., 2007) have focused on the geographic range shifts and their implications for species' persistence. Also, as a consequence of these shifts, changes in other components of biodiversity, such as patterns in functional and phylogenetic structure, are also expected (e.g., Thuiller et al., 2011). At a lower hierarchical level, however, a more neglected issue is that these shifts may also cause a change in genetic population structure and variability, because local extinctions or reduction in fitness are not expected to be random in geographical space.

Collevatti et al. (2011) recently proposed a simple framework to understand the effects of climate change on the genetic diversity in a species, coupling species distribution modeling (SDM) (also called niche modeling or bioclimatic envelope models) and population genetic data (Alsos et al., 2009). The idea is that there will be a change in climatically suitable areas within the species, modeled by SDMs, in such a way that some local populations will become extinct or will have a strong reduction in fitness, so that overall genetic variability of the species will change (usually decrease). Because the time frame is too small (i.e., less than 100 years) it is assumed that, for slow life-history organisms, there will be very restricted dispersal towards climatically suitable regions and gene flow and no adaptation. Moreover, the changes in climate and reduction in environmental suitability will be outside the limits of current phenotypic plasticity. If these assumptions are met, local extinctions are expected, and the remaining genetic variability in the species will be ensured only by the current populations that will remain in climatically suitable areas in the future.

Here we used the approach proposed by Collevatti et al. (2011) to model loss of genetic

variability in the Neotropical Cerrado tree *Dipteryx alata* (“Baru” tree, Fabaceae). *D. alata* is a widely distributed tree species in the Cerrado biome, restricted to eutrophic and drained soils of seasonal savannas. Flowers are hermaphrodite and pollination is performed by large and medium bees of the genera *Bombus* or *Xylocopa*, or Halictidae, whereas seed dispersal occurs by mammals such as tapirs, monkeys and bats. The seed (the nuts) are important for local economies, so understanding population and range dynamics under climate change may be also important for optimizing adaptive strategies for local human communities as well (e.g., Nabout et al., 2011).

We used an ensemble forecast approach for obtaining species’ range in which multiple SDMs and climatic models were combined (Marmion et al., 2009; Diniz-Filho et al., 2009a, 2010a,b; Nabout et al., 2010). We then obtained a series of genetic parameters (number of alleles per locus, expected heterozygosity under Hardy-Weinberg equilibrium (HWE) and mutation-drift equilibrium) for the entire species, which were recalculated assuming that local population in areas of low future environmental suitability will become extinct. This approach is then equivalent to evaluating the amount of phylogenetic diversity lost if endangered species or critical regions for conservation (i.e., hotspots) are lost in the near future (Purvis et al., 2000; Sechrest et al., 2003; Diniz-Filho, 2004).

## MATERIAL AND METHODS

We obtained a total of 448 occurrences of *D. alata* throughout the Brazilian Cerrado (Figure 1A), which were recorded in a grid with 6240 cells of 0.5° latitude/longitude covering South America. These occurrences were modeled as a function of eight climatic variables from WORLDCLIM (maximum temperature of the warmest month, minimum temperature of coldest month, annual temperature range, mean minimum temperature, annual precipitation, precipitation of wettest month, precipitation of driest month, precipitation standard deviation), for the current time and then projected for 2050, for three different coupled Atmospheric-Oceanic Global Circulation Models (AOGCMs; CCCma, CSIRO, HadCM3).

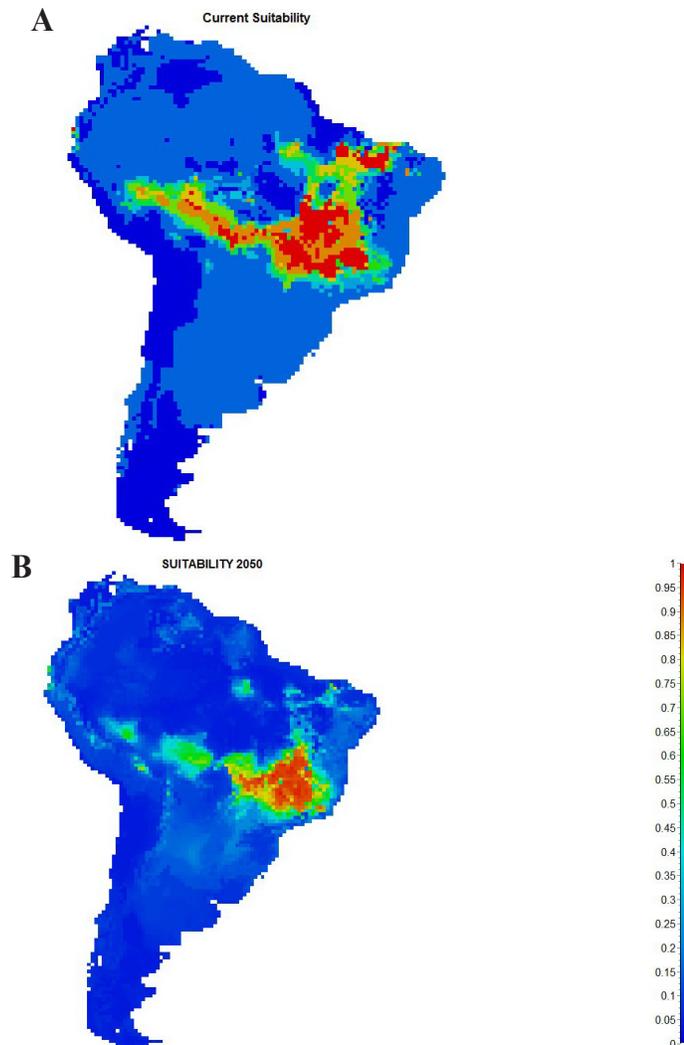
Occurrences were modeled using six different SDM techniques (Elith and Graham, 2009) and independently projected into future AOGCMs. The methods used were BIOCLIM, Euclidian, Gower and Mahalanobis distances, GARP and MAXENT. For each of these methods, models were built using 255 combinations of the 8 climatic variables, each one tested using 50 cross-validations using True-Skill statistics (models with TSS <0.7 were excluded) (Allouche et al., 2006). The maps for different variable combinations and cross-validation were used to calculate expected frequencies of occurrences for each of the 18 combinations of SDM method and AOGCM. These maps were then compared using principal component analysis (PCA), and variance components of a two-way ANOVA of these sources (i.e., SDM methods and AOGCMs) were obtained based on PCA loadings (see Araújo and New, 2007; Diniz-Filho et al., 2009a, 2010a, for details of ensemble forecasting approach).

Genetic data for *D. alata* consisted in microsatellite markers analyzed for 25 widely distributed local populations, encompassing most of species’ geographical range (Figure 1B). A total of 644 individual trees were genotyped for 8 microsatellite loci (Collevatti RG, Telles MPC, Nabout JC, Chaves LJ, et al., unpublished results). These data were used to calculate genetic parameters that are surrogates for the total amount of polymorphism and genetic diversity currently found in *D. alata*. Thus, for distinct levels of cuts of future climatic suit-

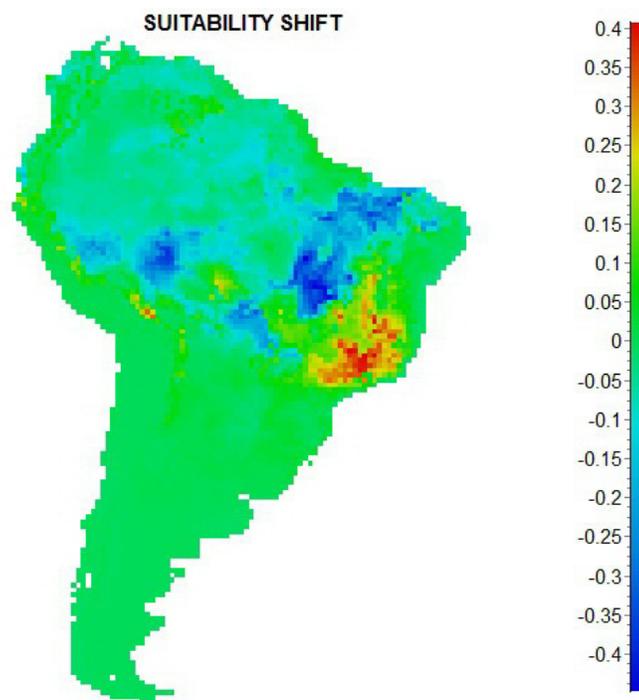


## RESULTS

The ensemble forecasting approach shows that *D. alata* will shift its geographic range from Central towards Southeastern Brazil in 2050 (Figure 2), so that most of the current species' range will show a negative shift in climatically suitable areas (Figure 3) (Diniz-Filho et al., 2009b; Marini et al., 2009). The first principal component of estimated frequency of occurrence maps explained 74.3% of the variation, so that most SDM methods and AOGCMs tended to reveal the same patterns of range shift. Even so, the variance components of the two-way ANOVA showed that, on average, 95% of the variation among these maps was due to SDMs used and not due to uncertainties in AOGCMs.



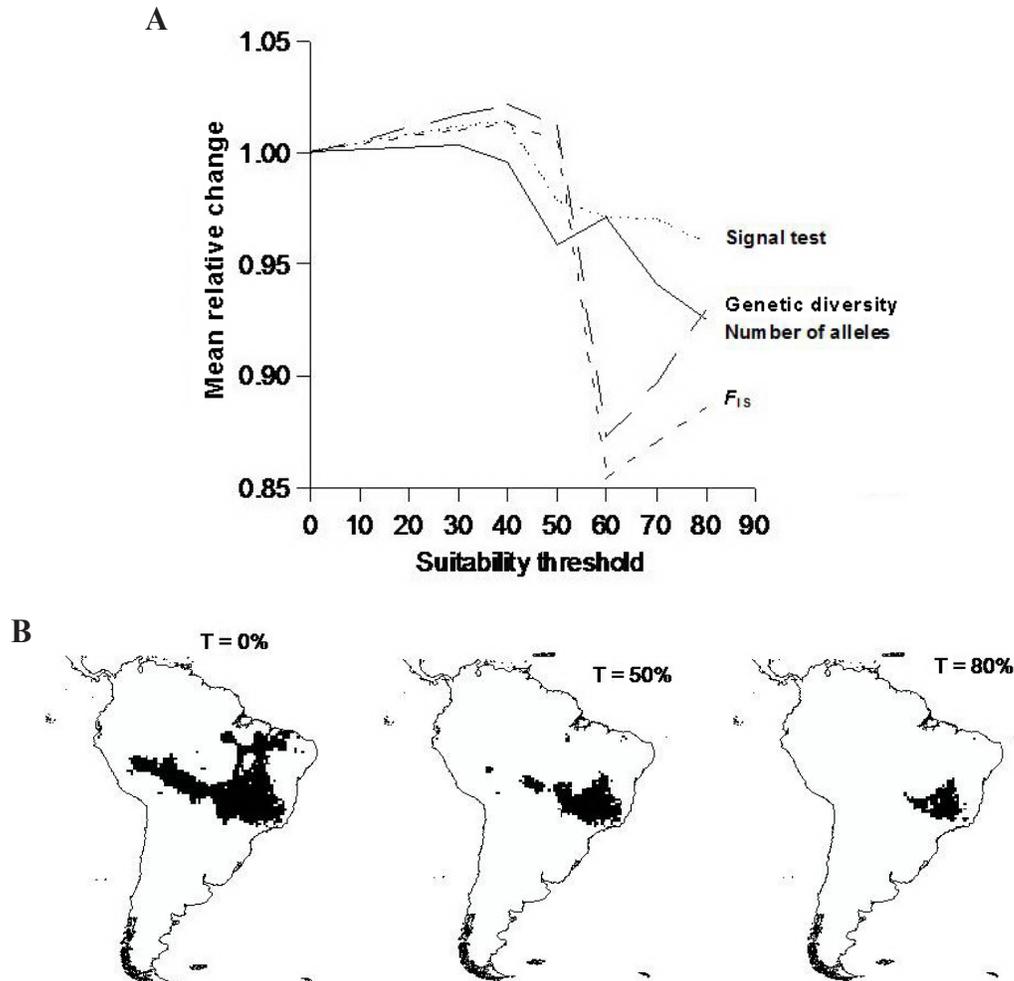
**Figure 2.** Ensemble forecasting of climatically suitable regions for *Dipteryx alata* modeled by SDM (A) and projected for 2050 using 3 AOGCMs (B).



**Figure 3.** Shifts in climatically suitable regions between current time and in 2050 for *Dipteryx alata*, according to ensemble SDMs.

The changes in the climatically suitable areas in *D. alata* implied a reduction in species' range, and consequently, local extinctions of local populations are expected, changing the genetic parameters. For example, overall genetic diversity (i.e., expected heterozygosity) across 8 loci was 0.5 for all local populations (i.e., in current environment, or assuming that populations will be able to persist in all environmental suitabilities in 2050), and will slowly drop to around 0.45 when local populations will be able to persist in regions with suitabilities higher than 80%. This implied a loss of only about 10%, and the same reasoning was applied to all other genetic parameters (Figure 4).

Overall, all genetic parameters calculated remained approximately constant up to a 50% threshold, which is the minimum by assuming a majority consensus of frequency of occurrences, and are shown comparatively in terms of percentage of reduction at increasingly climatically suitability levels (Figure 4). However, beyond this critical threshold, there was an abrupt reduction in all parameters, although the magnitude of shift was only about 10% of the current values, on average. The strongest shift occurred for  $F_{IS}$ , which will drop a bit more than 10% and will show a cut-off when suitability needed for persistence of local populations drops below 50%. Therefore, reduction in the number of local populations will tend to slightly decrease endogamy. On the other hand, the signal-test for mutation-drift equilibrium remained more or less constant, with little shifts. There was a wide variation of shift direction and magnitude among loci for each parameter, and these trends are actually usually driven by two or three alleles within each locus.



**Figure 4.** A. Proportional reduction of genetic parameters at increasingly level of cut-off in minimum climatic suitability needed for ensuring persistence of local population in 2050. B. The projected range of *Dipteryx alata* in 2050 is shown at three of these levels.

## DISCUSSION

The consensus map obtained using the ensemble forecasting approach reveals that *D. alata* will shift its geographic range in climatically suitable areas from Central towards South-eastern Brazil in 2050, which is a common pattern for Cerrado species (Siqueira and Peterson, 2003; Diniz-Filho et al., 2009b; Nabout et al., 2010). However, because of the wide distribution of species and the relatively homogenous climate throughout its range, even if species will be able to persist only in highly suitable regions (e.g., with occurrence frequencies above 80%), there will not be a very drastic reduction in range size, and only a few of the current local populations will be lost. Consequently, reductions in genetic variability within species will

not be so drastic, being around 10%.

The patterns reported here contrast with recent results for other Cerrado species; the “Pequi” tree (*Caryocar brasiliense*), in which climatic change will drive a stronger reduction in geographic range (also from Central towards Southeastern Brazil) and a more drastic change in genetic parameters will be observed (Collevatti et al., 2011a). The strongest effect on *C. brasiliense* under climate change was then expressed as a strong bottleneck detected by the Wilcoxon test of mutation-equilibrium drift, a completely different pattern when compared to that observed for *D. alata* reported here.

For *D. alata*, although the number of local populations is much larger than the one used by Collevatti et al. (2011b), the variability detected by the microsatellite loci reveals a relatively low variability in *D. alata* (e.g., as compared with the observed for *C. brasiliense*). This was attributed to strong population bottlenecks for the species in the recent past, which were corroborated by coalescent analyses and hindcast projections of the SDMs using paleoclimatic data (Collevatti RG, Telles MPC, Nabout JC, Chaves LJ, et al., unpublished results) and also explains the low level of genetic variability in *D. alata*, despite its wide geographic range. Moreover, this also explains why no shifts in mutation-drift equilibrium were detected here, even if just a few local populations remained after strong reductions in range shift due to persistence in highly suitable climatic regions. The slight decrease in endogamy ( $F_{IS}$ ) is most likely due to Wahlund effect because of the high differentiation among populations in *D. alata* (Collevatti RG, Telles MPC, Nabout JC, Chaves LJ, et al., unpublished results).

Thus, despite the shift in geographic range size and climatically suitable areas towards Southeastern Brazil and the expected downward shift in the genetic parameters, the analyses performed here do not show a strong loss of genetic diversity in *D. alata*. Even so, it is important to realize that these results are mainly due to the relatively low current genetic variability of the species, probably associated with recent population bottlenecks. In this case, climatic shifts can have more serious adaptive consequences, and further investigations are necessary to avoid a false indication of high probability of persistence of this species based on a low relative level of loss of genetic diversity. Also, more complex models, involving dispersal in SDM and more realistic processes of local extinctions and habitat loss, as well as taking into account phenotypic plasticity, adaptations and mutations, must be developed to give a better picture of the future of this Cerrado species.

## ACKNOWLEDGMENTS

Our research program integrating macroecology, molecular ecology and conservation genetics has been continuously supported by several grants from CNPq, CAPES, FUNAPE, and Systema Naturae Consultoria Ambiental Ltda., and more recently by MCT/CNPq grants and fellowships to the research network GENPAC (Geographical Genetics and Regional Planning for natural resources in Brazilian Cerrado; projects #564717/2010-0, #563624/2010-8) and Núcleo de Excelência em Genética e Conservação de Espécies do Cerrado - GECER (PRONEX/FAPEG/CNPq; CP 07-2009).

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