



# Genetic diversity of *Ceiba pentandra* in Colombian seasonally dry tropical forest: Implications for conservation and management

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## ABSTRACT

Seasonally dry tropical forests (SDTFs) are one of the most degraded vegetation types worldwide and in Colombia < 10% of the original cover remains. This calls for urgent conservation measures and restoration efforts. Understanding the genetic diversity and structure of tree species is crucial to inform not only conservation measures, but also sourcing of planting materials to ensure the long-term success of tree planting efforts, particularly in light of climate change. We assessed the genetic diversity distribution and structure of *Ceiba pentandra* from twelve representative locations of SDTF in Colombia, and how they may have been shaped by past climatic changes and human influence. We found three different genetic groups which may be the result of differentiation due to isolation of the Caribbean region, the Upper Cauca River Valley and the Patía River Valley in pre-glacial times. Range expansion of SDTF during the last glacial period, followed by more recent range contraction during the Holocene can explain the current distribution and mixture of genetic groups across contemporary SDTF fragments. Most of the sampled localities showed heterozygosity scores close to Hardy–Weinberg expectations. Only two sites, among which the Patía River valley, an area with high conservation value, displayed significantly positive values of inbreeding coefficient, potentially affecting their survival and use as seed sources. While the effects of climate change might threaten *C. pentandra* populations across their current distribution ranges, opportunities remain for the *in situ* persistence of the most genetically diverse and unique ones. Based on our findings we identify priority areas for the *in situ* conservation of *C. pentandra* in Colombian SDTF and propose a pragmatic approach to guide the selection of appropriate planting material for use in restoration.

## 1. Introduction

Seasonally dry tropical forest (SDTF) is one of the most endangered ecosystems worldwide (Miles et al., 2006). More than 60% of its original area has already been lost, and the remaining SDTFs experience high levels of fragmentation and are little protected (Miles et al., 2006;

Sánchez-Azofeifa et al., 2013). SDTFs occur in nearly all continents, but more than half (54.2%) of its surface area is found in South America where it has been an important focus for human settlement throughout history (Sánchez-Azofeifa et al., 2005; Miles et al., 2006). Colombian SDTFs occupy an intermediate position between Central and South American dry forests. They are, however, severely degraded and the

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remaining fragments are located in the Caribbean coastal area and in the Cauca, Magdalena, Chicamocha and Patía river valleys (Pennington et al., 2000; Pizano and García, 2014). These fragments contain biological elements from Caribbean and Mesoamerican SDTFs in the north and from the Andes, Brazil and southern South America in the south (Pizano and García, 2014; Banda et al., 2016). Previous research has shown that floristic differences between Caribbean and Andean SDTF in Colombia may be mirrored by the population genetic structure of tree species distributed across the different fragments (Thomas et al., 2017b).

The current genetic structure of many tropical tree species has been strongly influenced by past changes in climate. Under adverse climate conditions, a species might suffer range contraction through which spatially isolated populations undergo genetic differentiation (Thomas et al., 2015). On the other hand, more favorable climate conditions might boost range expansion and lead genetically differentiated populations to meet again in convergence zones. The two most recent climate events that are classically believed to have influenced the genetic structure of tree species from SDTF are the late Pleistocene cool and dry glacial period and climate warming during the Holocene. During the last glacial period, and especially the last glacial maximum, neotropical SDTFs are likely to have had more extensive and largely contiguous distributions (Pennington et al., 2000; Moggi et al., 2015) which may have facilitated dispersal and gene flow among species populations (Crooks and Sanjayan, 2006). Changes in climate during the warming Holocene led to contraction of SDTF eventually forming the spatially isolated fragments known today. These processes of SDTF expansion during the last glacial period and contraction in more recent times is known as the dry forest refugia hypothesis (Prado and Gibbs, 1993; Pennington et al., 2000; Mayle, 2004). Individual tree species responded to these changes in past climates in idiosyncratic ways. Evidence from paleodistribution modelling and population genetic studies in multiple SDTF tree species supports the dry forest refugia hypothesis (Caetano et al., 2008; Vitorino et al., 2016; Thomas et al., 2017b), but the opposite effect (range contraction during the last glaciation followed by range expansion) has also been reported (de Melo et al., 2016).

The post-glacial isolation of tree species populations in different SDTF fragments is likely to have initiated process of genetic differentiation. However, it seems to have been too short to be detected in the current genetic structures of SDTF tree species (but see Moreira et al., 2015). An increasing body of evidence suggests that the formation of different genetic groups in SDTF tree species may predate the late Pleistocene (Caetano et al., 2008; Collevatti et al., 2012; Vitorino et al., 2016; Thomas et al., 2017b). SDTF fragments currently dispersed throughout South America are relatively old remnants which may have persisted since the Neogene (Burnham and Carranco, 2004; Côrtes et al., 2015).

Since the arrival of humans to South America, and especially after the onset of the European colonization, all Colombian SDTF fragments have been influenced to varying extent by anthropogenic disturbance. Today, < 10% of the original SDTF cover in Colombia remains (Sánchez-Azofeifa et al., 2013; Pizano and García, 2014). Fragmentation of populations of tree species that are characterized by low densities, slow growth rates and long generation times, reduces effective population sizes, which in turn increases the risk of inbreeding and genetic drift, as documented for several species of SDTF such as *Samanea saman* (Cascante et al., 2002), *Tabebuia ochracea* (Moreira et al., 2009) and *Caryocar brasiliense* (de Melo et al., 2012). Over the longer term this might lead to loss of genetic diversity and eventually lead to extinction of local populations and concomitantly the loss of ecosystem services (Aguilar et al., 2008). Population genetic footprints of anthropogenic disturbance on populations of tree species in Colombian SDTFs are expected to be most marked in relicts located in the upper Magdalena, Chicamocha and Patía rivers due to their notable geographical isolation and associated constrained gene flow (Sarmiento,

1975; Pizano and García, 2014; Vergara, 2015). Understanding the genetic diversity and structure of tree species is crucial to inform not only conservation measures (Kageyama et al., 2003; Vieira-Blanco et al., 2007), but also sourcing of planting materials to ensure the long-term success of tree planting efforts, particularly in light of climate change (Breed et al., 2013; Thomas et al., 2014, 2017a; Prober et al., 2015).

Here we assess the genetic diversity and structure of the tree species *Ceiba pentandra* across twelve representative locations of SDTFs in Colombia in light of past climate change. In line with the findings of similar studies in tree species from neotropical SDTFs, we hypothesize that the formation of genetic groups in *C. pentandra* predates the late Pleistocene and that the species experienced range expansion during the Last Glacial Maximum (LGM), leading to the admixture of different genetic groups in convergence zones. We expect LGM range expansion to have been followed by range contraction during the Holocene, resulting in an ensemble of forest fragments characterized by the presence of one or more genetic clusters. Furthermore, we investigate potential signals of human disturbance and fragmentation on the genetic profiles of sampled localities, and assess the predicted impact of climate change on their *in-situ* persistence. Based on our findings we identify priority areas for the *in situ* conservation of *C. pentandra* in Colombian SDTFs and propose a pragmatic approach to guide the selection of appropriate planting material for use in tree planting efforts.

## 2. Methods

### 2.1. Study species

*Ceiba pentandra* (L.) Gaertn (Malvaceae) is a pantropical habitat generalist species which is a characteristic element not only of SDTFs, but also wetter vegetation types, including tropical rainforest (Baker, 1965; Zotz and Winter, 1994). The species has become popular for its potential for reforestation of degraded areas and plywood production (Brondani et al., 2003; Celis and Jose, 2011). From an ecological point of view, *C. pentandra* fulfils an important role in protecting SDTFs soils due to the species' low nutritional requirements, high tolerance to competition and drought and its ability to regrow after disturbances (Lobo et al., 2005; Celis and Jose, 2011; Sorngmenyenye-Abengmeneng et al., 2016). For instance, Paloma-Lozano (1994) showed *C. pentandra*'s higher capacity to establish in deteriorated soils of very low fertility and shallow depth compared with other native species in a SDTF in South America. However, despite these useful traits remaining *C. pentandra* populations are gradually diminishing in different parts of the world (Quesada et al., 2004; Sorngmenyenye-Abengmeneng et al., 2016).

In Colombia, *C. pentandra* is present in most SDTF regions. However, due to expected negative impacts of habitat loss on the species' conservation, it has been included in the strategic plan for the conservation of plants in the country (Pizano and García, 2014). To date, there are no genetic studies of SDTF populations in Colombia to guide the development of effective genetic conservation measures, jeopardizing its sustainable management and safeguarding in the long term.

### 2.2. Genetic analyses

#### 2.2.1. Field sampling

Between July 2014 and June 2015, we collected young and healthy leaves of 97 reproductive individuals of *C. pentandra* in 12 sampling sites which are representative of the current distribution of SDTF remnants in Colombia (Table 1). Except for the locality of Tatacoa (TAT), the diameter at breast height (DBH) of all trees was measured. Sampled trees were separated by at least 50 m to avoid sampling of highly genetically related individuals. Field sampling was guided by suitability maps based on occurrence data obtained from botanical collection records (see below). All biological material was collected in collaboration with the Instituto Alexander von Humboldt following the

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