



Molecular evidence of cryptic speciation, historical range expansion, and recent intraspecific hybridization in the Neotropical seasonal forest tree *Cedrela fissilis* (Meliaceae)

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ABSTRACT

Molecular phylogeography can lead to a better understanding of the interaction between past climate events, large-scale vegetation shifts, and the evolutionary history of Neotropical seasonal forests. The endangered timber tree species *Cedrela fissilis* is associated with seasonal forests and occurs throughout South America. We sampled *C. fissilis* from 56 sites across the species' range in Brazil and Bolivia and obtained sequence data for nuclear and chloroplast DNA. Most specimens (149 out of 169) exhibited intraindividual polymorphism for the nuclear internal transcribed spacer (ITS). Cloning and an array of complementary sequence analyses indicated that the multiple copies of ITS were functional paralogs – concerted evolution in *C. fissilis* appeared to be incomplete. Independent Bayesian analyses using either ITS or cpDNA data revealed two separate phylogenetic lineages within *C. fissilis* that corresponded to populations located in separate geographic regions. The divergence occurred in the Early Pliocene and Late Miocene. We argue that climate-mediated events triggered dispersal events and split ancestral populations into at least two large refugial areas of seasonal forest that were located to the east and west of the present day Cerrado. Upon recent climate amelioration, formerly isolated lineages reconnected and intraspecific hybridization gave rise to intraindividual polymorphism and incomplete concerted evolution in *C. fissilis*.

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1. Introduction

Interest in Neotropical seasonal forests is growing because they are important areas of endemism (Prado, 2000; Pennington et al., 2006) and are threatened by high rates of deforestation due to urban expansion, conversion to agricultural use, and forest fires (Steininger et al., 2001; Fundação SOS Mata Atlântica and INPE, 2009). Moreover, little is known about their evolutionary history. Seasonal forests occur in areas that experience a severe dry season (up to five consecutive months), or in areas where precipitation shows little fluctuation, but where winter temperatures (<15 °C) cause physiological drought (Veloso et al., 1991; Oliveira-Filho and Fontes, 2000).

Although seasonal forests are disjunct in their distribution across the Neotropics (Fig. 1), distant blocks of such forest are related floristically (Bigarella et al., 1975; Ab'Saber, 1977). Where they do occur, seasonal forests are often intermingled with patches of other types

of vegetation, which include evergreen forests, savannas, and shrublands (e.g., Pennington et al., 2000; Killeen et al., 2006; Oliveira-Filho et al., 2006). Despite their geographical proximity to other vegetation types, Neotropical seasonal forests contain many phylogenetically unrelated species that are absent from evergreen forests and savannas in neighbouring areas (Prado, 2000; Pennington et al., 2006). The 'Pleistocenic Arc' hypothesis (Prado and Gibbs, 1993) explains these patterns by suggesting that present-day seasonal forests are relicts formed by vicariance of a much larger, single formation that covered South America during the Pleistocene. An alternative hypothesis suggests that rare long-distance dispersal of seasonal forest species might explain the disjunct distribution of floristically related blocks (Gentry, 1982; Mayle, 2004).

The disjunct distribution of seasonal forests at the continental scale, as well as their often patchy distribution at regional scales, suggests that these forests are spatially and temporally dynamic. Indeed, seasonal forests have both contracted (Carnaval and Moritz, 2008; Carnaval et al., 2009) and expanded (Auler et al., 2004; Mayle, 2004) in response to climatic changes during the Quaternary period (Ledru et al., 2007). These shifts in vegetation were triggered by cy-

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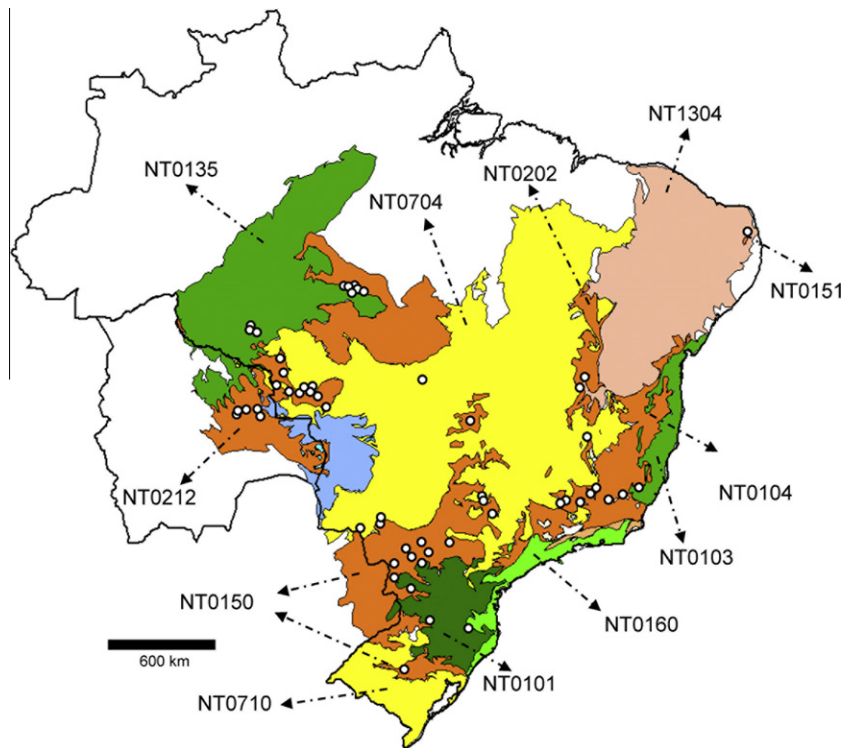


Fig. 1. Locations of populations of *Cedrela fissilis* (white dots) included in this study and their associated vegetation formations. Terrestrial ecoregions (Olson et al., 2001) included the following: NT0101, Araucaria moist forests; NT0103, Bahia coastal forests; NT0104, Bahia interior forests; NT0135, Madeira-Tapajós moist forests; NT0150, Paraná-Paraíba interior forests; NT0151, Pernambuco coastal forests; NT0202, Atlantic dry forests; NT0212, Chiquitano dry forests; NT0704, Cerrado. Ecoregions NT1304 (Caatinga), NT0710 (Uruguayan savanna), and NT0160 (Serra do Mar coastal forests) are shown for reference purposes. Colour code: orange, seasonal forests; green, moist evergreen forests; yellow, savanna; pink, scrubland. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

cles of alternating cool–dry and warm–wet climates during the last 2 million years of the Pleistocene (Whitmore and Prance, 1987), and possibly earlier (Mayle, 2004; Pennington et al., 2004). The interaction between past climate events, large-scale vegetation shifts and the evolutionary history of plant lineages that are characteristic of seasonal forests remain poorly understood.

Cedrela (Meliaceae) is a tree genus that probably evolved in seasonal forests. *Cedrela* is a Neotropical, monophyletic genus whose diversification started in the Oligocene and Early Miocene and intensified in the Late Miocene and Early Pliocene (Muellner et al., 2010). At present, most of the 17 species of *Cedrela* have restricted distributions in seasonal forests of Central and South America; two species, *Cedrela odorata* and *C. fissilis*, are widespread and occur in both moist evergreen forests and seasonal forests (Muellner et al., 2009). The IUCN Red List (IUCN, 2010) categorizes *C. odorata* as ‘Vulnerable A1cd+2cd’ and *C. fissilis* as ‘Endangered A1acd+2cd’ species. Recent molecular studies have identified three genetically distinct entities in *C. odorata* that are morphologically indistinguishable (Muellner et al., 2009).

Cedrela fissilis Vell. (Meliaceae), which is known commonly in Brazil as ‘cedro branco,’ is a valuable timber species that has long suffered from overharvesting. *Cedrela fissilis* occurs throughout South America (Pennington et al., 1981), but its presence in Central America (Costa Rica and Panama) is uncertain (Pennington and Muellner, 2010). In Brazil, *C. fissilis* is associated with seasonal forests, but it also occurs in forest–savanna ecotones, gallery forests, and moist evergreen forests that are adjacent to seasonal forests (Carvalho, 1994). Large canopy trees occur at low densities (1–3 trees/ha) in old-growth forests of Southern Brazil (Carvalho, 1994). In secondary forests, densities of *C. fissilis* are often much higher (Smith, 1960). *C. fissilis* exhibits a number of traits that favour cross-pollination and long-distance gene flow and are

important to its biogeography. These traits include: protogynous dichogamy; asynchronous floral anthesis among both inflorescences of the same tree and individuals; pollination by moths and bees; and wind-dispersed seeds that are released from high in the forest canopy (Carvalho, 1994).

It is likely that an understanding of the evolutionary history of seasonal forests in the Neotropics will benefit from investigation of the molecular phylogeography of plant species (e.g., Caetano et al., 2008; Oliveira et al., 2010). Molecular phylogeographic studies on *Carapichea ipeacacuanha* (Rubiaceae), an understory shrub with a disjunct distribution in seasonal forests, have suggested the long-term persistence of the species in the Atlantic range. In contrast, the colonization of the Amazonian range by *C. ipeacacuanha* seems recent, and probably occurred from a single parental source after a strong genetic bottleneck (Oliveira et al., 2010). In *C. ipeacacuanha*, the internal transcribed spacer (ITS) was found to exhibit intraindividual polymorphism in a range-dependent manner. Intraspecific hybridization in the Atlantic range led to specimens with multiple, functional copies of ITS, as well as pseudogenes, whereas specimens in the Amazonian range, with a single lineage, lacked polymorphisms in ITS (Queiroz et al., 2011). *Cedrela fissilis* and *C. ipeacacuanha* are codistributed throughout much of the range of *C. ipeacacuanha* and it is plausible that the two species, although differing with respect to several life history traits and ecological requirements, could have experienced a common history of climatic changes. We anticipated that molecular data from *C. fissilis* would be even more informative than those of *C. ipeacacuanha* because of the widespread distribution of the former relative to the latter species: *C. fissilis* occurs in many areas (Carvalho, 1994) where *C. ipeacacuanha* is absent (Oliveira et al., 2010).

In this study, we explored the evolutionary history of seasonal forests through molecular analysis of nuclear and chloroplast

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