



How do gap dynamics and colonization of a human disturbed area affect genetic diversity and structure of a pioneer tropical tree species?



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ABSTRACT

Pioneer tree species exhibit life-cycle characteristics and population structures that are mainly affected by natural or human disturbances. In primary forests, demographic dynamics of pioneer species may resemble those defined for a metapopulation. In early successional forests, the patterns of establishment, survival and reproduction are mainly determined by microclimate and biota modifications of the site after the human disturbance. The aim of this study was to investigate how the ecological processes and the population genetic factors associated with disturbances can affect the genetic diversity and structure of populations of a pioneer tree species: *Croton floribundus* Spreng. (Euphorbiaceae). Nuclear and chloroplast microsatellite markers were examined in plants of two size classes sampled in four gaps of primary forest and four sub-areas of early successional forest. Despite presenting similar genetic diversity levels, the genetic diversity was distributed differently between forests. The combined effects of seed dispersal and colonizations (and extinctions) were determinants of the fine-scale genetic structure of *C. floribundus*. The main finding was that human disturbances seem to boost the influence of founder effects in populations of a species with limited seed dispersal. Results suggested that gene flow by pollen was responsible for maintaining the genetic diversity within populations of *C. floribundus* in both forests, but in the early successional forest, gene flow by seeds was equally important. We conclude that gap dynamics, colonization, and pollen and seed dispersal affect the genetic diversity and structure of the pioneer species depending mainly on the number of colonizers, the number of source populations, the gene flow rates, and the level of human disturbance.

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1. Introduction

The spatial genetic structure of plant populations may vary across life stages, across generations and among different environmental conditions (Loveless and Hamrick, 1984). These changes are guided by ecological and evolutionary factors. Understanding the effects of these factors on the genetic diversity and structure of populations is important when defining strategies of forest conservation and restoration, in order to guarantee the maintenance of their evolutionary and ecological dynamics as similar as possible to the natural conditions (Ellstrand and Elam, 1993; Loveless and Hamrick, 1984).

Pioneer tropical tree species exhibit particular life histories and population structures that are mainly affected by the patchy dynamics of the tropical forests (Alvarez-Buylla, 1994; Swaine

and Whitmore, 1988; Uriarte et al., 2012). The life-cycle characteristics of the pioneer species may have significant consequences for genetic structure and evolution, mainly through frequent local extinctions and colonizations (Wade and McCauley, 1988). We might expect clear population structuring in pioneer species because the number of gap colonizers is generally small (a founder effect), and due to genetic drift that leads to the fixation of neutral genetic alleles (Loveless and Hamrick, 1984; Whitlock and McCauley, 1990; Wright, 1940). Conversely, seed banks and long distance seed and pollen dispersal could homogenize spatial genetic variation (Alvarez-Buylla and Garay, 1994; Loveless and Hamrick, 1984). In addition to these factors, genetic divergence may also be reduced by extinction and recolonization processes which can act as a form of gene flow under some conditions of metapopulation dynamics (Slatkin, 1977, 1985; Wade and McCauley, 1988; Whitlock and McCauley, 1990). Two opposite types of distribution of genetic diversity have been found in well conserved forests: nonstructured (Alvarez-Buylla et al., 1996;

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Davies et al., 2010) and genetically structured populations of adults (Born et al., 2008a; Jones and Hubbell, 2006). Nevertheless, most studies agreed with a finding of a high level of genetic diversity of the populations and a loss of genetic structure across successive life stages.

In the early successional forests where environmental conditions differ from the primary forests (Swanson et al., 2011), the pioneer trees exhibit changes in their patterns of establishment, survival, and reproduction affecting plant density and spatial distribution (Danciguer, 1996; Silvestrini and Santos, 2015; Swanson et al., 2011; Tabarelli et al., 2012). Consequently, ecological processes and evolutionary factors, such as origin and number of colonizers, competition and predation, as well as natural selection and level of gene flow, either from primary or secondary forests, could be determinant of the genetic diversity and structure of the species.

There are few studies of genetic diversity and structure of pioneer species in early successional forests (Alvarez-Buylla and Garay, 1994; Born et al., 2008b; Cavers et al., 2005; Davies et al., 2010, 2013; Franceschinelli and Kesseli, 1999; Guicking et al., 2013). The results have suggested that gene flow and the origin of populations are the determinants of the genetic patterns of diversity and structure that were found (Alvarez-Buylla and Garay, 1994; Born et al., 2008b; Cavers et al., 2005; Davies et al., 2010, 2013; Franceschinelli and Kesseli, 1999; Guicking et al., 2013). However, in some of these studies, genetic differentiation has been evaluated simultaneously among old, intermediate, and recently established populations and/or sites with different land use histories, which according to genetic theoretical models is an uninformative way to estimate genetic structure in metapopulations (McCauley et al., 1995; Wade and McCauley, 1988; Whitlock and McCauley, 1990). As a result, the effects of ecological and genetic processes such as colonization, gene flow and level of disturbance might have been underestimated or blurred. Furthermore, only a few species have been evaluated and, most of these were restricted to colonizers of large gaps while the gaps are very open, i.e., a limited range of gap-phase regeneration behaviors (Brokaw, 1987) (for example, see Alvarez-Buylla et al. (1996) and Born et al. (2008b)).

Croton floribundus Spreng. (Euphorbiaceae) is a shade intolerant, fast-growing pioneer tropical tree species (Gandolfi et al., 1995; Lorenzi, 1992) that is widespread and equally distributed in canopy gaps of different size and age in primary forests, colonizes over extended time, i.e., colonization process can persist for years after gap formation, and is abundant in early successional human disturbed forests (Silvestrini and Santos, 2015). This broad gap-phase regeneration behavior is particularly important for genetic studies because it allows us to analyze a species that occupies more heterogeneous environments, and thus, it is exposed to more diverse selection pressures. Besides this, *C. floribundus* does not seem to follow the same long-distance seed dispersal patterns of other genetically well-studied pioneer species that have shown high gene flow rates (Alvarez-Buylla and Garay, 1994; Born et al., 2008a; Guicking et al., 2013; Litrico et al., 2005). *C. floribundus* is pollinated by flies and wind (Passos, 1995), which implies a long distance pollen dispersal and high rates of gene flow (Hamrick and Nason, 2000), but has seeds dispersed short distances by autochory (explosive seed dispersal) (Lorenzi, 1992). Thus, a fine-scale study of genetic diversity and structure of this species using both nuclear and chloroplast markers may help to elucidate how these mechanisms of dispersal, with opposite effects on gene flow rates, affect the distribution of the genetic variation in its populations. Analysis of both nuclear and chloroplast markers can also be helpful for investigating effects of the colonization process on the genetic structure among populations by means of cyto-nuclear linkage disequilibrium estimates (Fields et al., 2014).

In addition, a comparison between populations located in primary and early successional forests and a detailed analysis of the

fine-scale genetic structure among life stages or size classes could shed light on what factors determine the patterns of genetic diversity and structure in this species. The knowledge of such aspects of pioneer species is essential for understanding the effects of human disturbance and of successional processes in tropical forests, which in turn is important for forest conservation, management and restoration.

In this study, we evaluated the genetic diversity and structure of the pioneer tree *C. floribundus* between two size classes and among populations located in a primary forest and in an early successional Brazilian forest. Specifically, we attempted to answer the following questions: (1) Do the genetic diversity and fine-scale genetic structure of *C. floribundus* differ between primary and early successional forests? (2) Are there changes in the genetic diversity and structure between size classes in these forests? (3) Is there a correspondence between the genetic structure of populations in the primary forest and their spatial distribution in the gaps? (4) How do ecological processes and genetic factors associated with natural and human disturbances affect the genetic diversity within and among populations in the species?

2. Materials and methods

2.1. Study site

The study was conducted within a 10.24 ha permanent plot (Rodrigues, 2005) in a primary forest at Caetetus Ecological Station (CES) and in an early successional forest adjacent to the state reserve at Torrão de Ouro Farm, Gália/Alvinlândia, Brazil (Fig. 1) (22°20'–22°30'S; 49°40'–49°45'W). The regional climate corresponds to Köppen's "Cwa" mesothermic type, that is, humid subtropical with a dry winter (Rodrigues, 2005; Tabanez et al.,

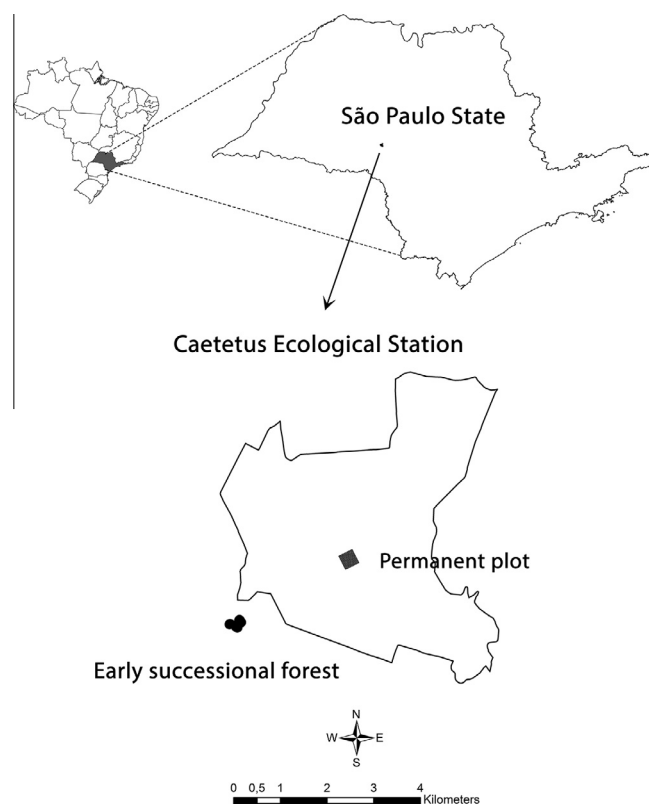


Fig. 1. Map of the region of Caetetus Ecological Station, São Paulo, Brazil showing the location of the permanent plot in the primary forest and the adjacent early successional forest at Torrão de Ouro Farm.

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