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Spread of a Brazilian keystone-species in a landscape mosaic

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Abstract

Changes in land use often threaten the existence of ecologically and economically important plant species. We studied patterns of colonization of *Araucaria angustifolia* (Araucareaceae) in a man-made landscape mosaic composed of patches of exotic and native tree species in southern Brazil. We investigated patterns of population structure, spatial distribution, understory vegetation density, seed dispersal and seed consumption in three replicates of the following four vegetation types: *Araucaria* forest, *Araucaria* plantation, *Pinus* plantation and *Eucalyptus* plantation. For measurements of population structure and spatial distribution we sampled all individuals present in two 100 m × 10 m transects, divided in 5 m × 5 m plots, randomly placed in all habitats. Individuals were classified into four height classes: seedlings (≤50 cm); juvenile 1 (>50 cm and ≤2 m); juvenile 2 (>2 m in height plus ≤10 cm DBH); adult (DBH > 10 cm). The dispersion index used was ID = variance/mean. Vegetation cover was measured in all sites by counting the number of times the vegetation touched a pole in 10 5 m × 5 m plots randomized along the two transects installed in each replicated site. Four groups of seeds were offered to seed predators at high (60) and low (10) densities in each site. Seed consumption was monitored over a 14 days period during which all seeds had been consumed. Naturally dispersed seeds were counted and monitored over a 2-month period. Seed bite marks were used to identify seed predators. We found 863 individuals of *A. angustifolia* in all vegetation types. The number of regenerating individuals was similar among vegetation types even though *Araucaria* forest and *Araucaria* plantation areas sustained a higher number of reproductive adult trees. Patterns of spatial distribution of seedlings and juveniles did not differ between vegetation types. The density of the understory vegetation cover was negatively correlated with the number of regenerating individuals. We recorded 1103 naturally occurring seeds while only 5 were confirmed present in the exotic plantations. Seed consumption increased at lower seed density and was high at all sites tending to be greatest at the *Araucaria* forest sites. We conclude that *A. angustifolia* colonizes native and exotic vegetation types. Biotic barriers such as seed dispersal and seed consumption may influence patterns of colonization of this keystone-species in the studied landscape mosaic.
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Keywords: *Araucaria angustifolia*; Seed predation; Seed dispersal

1. Introduction

Alterations in vegetation cover due to land use changes contribute to the loss of biodiversity as well as to the diversification of the environmental mosaic that shelters this diversity (Vitousek, 1994). The impact on the fauna and flora caused by the substitution of native areas by human altered areas is still poorly understood (Lomolino and Perault, 2000). Changes in vegetation cover may alter environmental conditions at different spatial scales, affecting plant population dynamics, which are in many cases regulated by spatial heterogeneity (Oliveira-Filho et al., 1994; Law et al., 2001). Plant populations of great economic and ecological importance have suffered significant reductions in abundance due to the loss of natural habitat and their constraints for colonizing new kinds of habitats created by man (Benitez-Malvido, 1995; Scariot, 1999; Fonseca, 2001; Bruna and Kress, 2002; Peres et al., 2003).

The Brazilian-pine, *Araucaria angustifolia* (Bertol.) Kuntze (Araucariaceae), is a species of great economic and ecological importance which became vulnerable due to habitat reduction, intense wood exploitation and frequent disturbances of its regeneration by cattle (Giannotti et al., 1980; Longhi and Faehser, 1980; Soares, 1980; Backes and Nilson, 1983). *A. angustifolia* is a keystone-species, since it produces a large amount of highly-nutritious seeds during autumn and winter, periods of great fruit scarcity in this forest (Reitz et al., 1988;

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Backes, 1999; Solórzano-Filho, 2000). Some predators of these seeds can stock them, or carry them to potential germination sites, at some distance from the parent tree (Kindel, 1996). Therefore, predators can act as secondary seed dispersers, increasing the overall spatial dispersion of this species (Janzen, 1970; Kindel, 1996; Westcott and Graham, 2000).

The structure and spatial distribution of a population is a result of the influence of abiotic and biotic factors on plant establishment, growth, mortality and reproduction (Silvertown, 1982; Augspurger, 1984; Forget, 1991; Hutchings, 1997; Cintra, 1998). The distribution of species in age classes may indicate a growing, stable, or declining population (Silvertown, 1982). Moreover, populations may be arranged in three basic spatial distribution patterns: (1) random, when individuals are randomly distributed and establishment is not limited; (2) uniform, when the individuals are evenly distributed in space, reflecting possible intraspecific competition and (3) grouped, when the individuals are spatially related due to certain environmental characteristics such as seed dispersal, concentrated resource distribution and safe sites (Begon et al., 1996; Ricklefs, 1996). Some studies demonstrated that spatial patterns in plant species depend on the spatial scale or size class considered (Augspueger, 1983; Oliveira et al., 1989; Oostermeijer et al., 1996; Fonseca, 2001). However, once these variables are taken into account, the population structure, as well as the spatial distribution, may indicate the capacity of a population to grow, disperse and use environmental space (Hanski and Simberloff, 1997). Therefore, variations in population structure and spatial distribution are expected to occur in an environmental mosaic, since each mosaic unit offers different environmental conditions for plant establishment, survival and reproduction.

Factors such as light availability, soil humidity and vegetation structure have frequently explained the spatial distribution of plant species at the environmental micro- and meso-scales (Primack et al., 1985; Buschbacher and Serrão, 1988; Gerhardt, 1993; Oliveira-Filho et al., 1996; Gray and Spies, 1997). Schwarz et al. (2003) suggested that, when the influence of abiotic factors is not clear, biotic factors can be considered as important forces defining species abundance and distribution. This influence occurs mostly through changes in the processes responsible for plant population dynamics such as pollination, seed dispersion and consumption (Forget, 1991; Aizen and Feinsinger, 1994; Restrepo et al., 1999; Mustajärvi et al., 2001).

Seed consumption and dispersion can be key processes defining seedling establishment and spatial distribution of plant populations in different scales (Howe and Smallwood, 1982; Schupp, 1993; Chambers and Macmahon, 1994; Hulme, 2001; Hansson, 2002). Plant species may reach long distances when seeds are dispersed by bats, birds and other small animals (Fleming and Heithaus, 1981, Wunderle, 1997; Holbrook and Smith, 2000; Westcott and Graham, 2000). Moreover, large animals such as Tapirs, can influence plant spatial distribution at the meso-scale (Fragoso et al., 2003). According to the model proposed by Janzen (1970) and Connel (1971), once the seed is dispersed, seed predation intensity can be related to seed density and distance from the parent tree. Thus, habitat alterations that modify adult density such as the creation of forest plantations could change the way seed consumption and dispersion influence juvenile spatial distribution.

This study investigates the colonization pattern of *A. angustifolia* and the factors that influence such pattern in an environmental mosaic composed of different kinds of exotic and native vegetation types: *Araucaria* forest, *A. angustifolia* plantations, *Pinus* plantations and *Eucalyptus* plantations. More specifically this work aims:

(1) To investigate possible differences in population structure, spatial distribution at varying spatial scales, seed dispersion and seed consumption of *A. angustifolia* among vegetation types of this environmental mosaic.
(2) To verify the influence of understory vegetation density on the regeneration of *A. angustifolia* populations in this environmental mosaic.
(3) To discuss how biotic processes such as seed dispersion and seed consumption could influence the colonization of *A. angustifolia* populations in this environmental mosaic.

2. Methods

2.1. Study area

The study was performed in the São Francisco de Paula National Forest (FLONA-SFP) in the municipality of São Francisco de Paula, State of Rio Grande do Sul, Brazil (29° 02′S to 50° 23′W). The region is located 912 m above sea level, with an average yearly temperature of 14.5 °C. Negative temperatures may occur from April to November. Rainfall is high during all months, being in average 2252 mm year^{-1} (Backes, 1999).

The FLONA-SFP encompasses an area of 1606 ha, and is classified as a Conservation Unit of Sustainable Use. Seventeen percent of the area is planted with *Pinus*, 1% with *Eucalyptus* and 23% with *A. angustifolia* for wood production. Although 44% of the area is covered by native *Araucaria* forest, this forest is discontinuous and interspersed by tree plantations, comprising an environmental mosaic (Fig. 1).

2.2. Studied species

A. angustifolia (Bertol.) Kuntze (Araucariaceae) is a gymnosperm of austral origin that defines the features of the Araucaria Forest. This species is distributed throughout most altitudinal regions in south and southeast Brazil (Reitz and Klein, 1966; Backes, 1999). *A. angustifolia* is a wind pollinated dioecius plant, its female strobilus maturing time occurs mostly between April and June and its cone (10–20 cm diameter) produces 10–150 seeds or pine nuts (Reitz et al., 1988). After maturation, seeds are dispersed primarily by autochory. The dehiscence is caused by the weight of the seed that falls from the branches of the parent tree, where sometimes the seed may be launched up to 20 m from the adult tree's crown (Solórzano-Filho, 2000). Events of secondary dispersion also occur

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