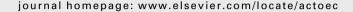


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Original article

Regeneration patterns of a long-lived dominant conifer and the effects of logging in southern South America

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ABSTRACT

The regeneration ecology of the long-lived conifer Araucaria angustifolia was studied in São Francisco de Paula, southern Brazil. We evaluated the expectations that: (i) size distribution of populations of Araucaria angustifolia, a large conifer that dominates southern Brazil's mixed forests, is left-skewed in old-growth forests but right-skewed in logged forests, indicating chronic recruitment failure in the first kind of habitat as well as a recruitment pulse in the second; (ii) seedlings and juveniles are found under more open-canopy microsites than would be expected by chance; and (iii) reproductive females would be aggregated at the coarse spatial scales in which past massive recruitment events are expected to have occurred, and young plants would be spatially associated with females due to the prevalence of vertebrate and large-bird seed dispersers. Data were collected in the threatened mixed conifer-hardwood forests in southern Brazil in ten 1-ha plots and one 0.25-ha plot that was hit by a small tornado in 2003. Five of these plots corresponded to unlogged old-growth forests, three to forests where A. angustifolia was selectively logged ca. 60 years ago and two to forests selectively logged ca. 20 years ago. For the first time, ontogenetic life stages of this important conifer are identified and described. The first and second expectations were fulfilled, and the third was partially fulfilled, since seedlings and juveniles were hardly ever associated with reproductive females. These results confirm the generalization of the current conceptual model of emergent long-lived pioneer regeneration to Araucaria angustifolia and associate its regeneration niche to the occupation of large-scale disturbances with long return times.

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1. Introduction

In forested ecosystems, large-scale disturbances like land-slides, earthquakes and slash-and-burn agriculture give rise to considerable tracts of successional forests. In contrast to the successional communities that develop following small-scale tree-fall gaps, secondary forests forming after large-scale disturbances are frequently dominated by long-lived pioneer tree species. This successional pathway seems to be a feature common to distinct tropical, subtropical and temperate forest types (Hartshorn, 1978; Swaine and Whitmore, 1988; Guariguata and Ostertag, 2001; Kennard, 2002; Kubota et al., 2005). Long-lived pioneers are shade-intolerant and depend upon disturbances for recruitment opportunities. They frequently attain large adult sizes, not rarely being emergents (Hartshorn, 1978), and present lifespans up to many centuries (Enright and Ogden, 1995).

The life-history syndrome commonly associated with long-lived pioneers seems to be related to the occupation of well-lit areas of forested ecosystems in space (as emergents), rather than time (in short-lived tree-fall gaps). This is accomplished through high growth rates associated with high maximum heights and diameters and high longevity, according to the classification of life-history traits by Easdale et al. (2007). These traits are thought to confer competitive advantage in landscapes subjected to intense and relatively large-scale disturbances (e.g., mountainous habitats) (Armesto et al., 1992; Easdale et al., 2007) that allow the establishment of cohorts in high-light microenvironments that later translate in expressive presence in the upper canopy or even as an even-aged emergent layer (Armesto et al., 1992; Enright and Ogden, 1995).

A thorough understanding of the demography of long-lived pioneers has important implications for forest community ecology and management because these species play a key role in regulating the rate of successional change (Grau et al., 1997; Mailly et al., 2000; Kubota et al., 2005). Considerable variation exists in this regard, since long-lived pioneers may retard succession by blocking the regeneration of shade-tolerant species (Kubota et al., 2005), alter the floristic composition of late-successional regenerants (Grau et al., 1997) or just reduce the time necessary for climax species to dominate the forest canopy (Mailly et al., 2000).

In the southern hemisphere conifers form an outstanding group of long-lived pioneers mostly confined to high-rainfall mountainous areas (Hill and Brodribb, 1999). Their abundance and economic value have made them a recent focus of studies on the regeneration mode and succession of the forests in which they occur (Ogden and Stewart, 1995; Enright et al., 1999; Lusk, 1999; Rigg, 2005; Souza, 2007). Although our understanding of the regeneration ecology of southern conifers is far from complete, a number of generalizations on their dispersal, recruitment requirements and microsite occupancy have been advanced in the Lozengue model (Ogden and Stewart, 1995). According to this model, cohorts of large-sized and light-demanding conifers establish following severe disturbances. They are followed by successive cohorts of smaller angiosperm species that dominate the forest understorey and suppress the recruitment of conifer seedlings,

which become restricted to multiple tree-fall gaps. Because of the high longevity and large size of adult conifers, their populations remain as dominant components of the forest biomass and architecture for long periods of time (frequently centuries), although demographically functioning as remnant populations, that lack significant constant regeneration. We investigated whether this model corresponds to the regeneration patterns of Araucaria angustifolia, a long-lived conifer that dominates the poorly studied mixed conifer-hardwood forests of the Brazilian Atlantic Forest complex.

At the beginning of the twentieth century, some 20 million hectares of Araucaria angustifolia forest existed (Guerra et al., 2002) but, as occurred in conifer-dominated temperate forests (Mailly et al., 2000), the high timber value of Araucaria angustifolia led to extensive logging of the Brazilian mixed forests in the last century, reducing them to ca. 2-4% of their former extent (Guerra et al., 2002). The selectively logged forest remnants that comprise the majority of Brazilian mixed forests present an opportunity to better assess the expectations generated by the current model of long-lived pioneer regeneration. In addition, the degraded condition of these logged forest remnants makes a deeper understanding of the regeneration ecology of Araucaria angustifolia a conservation necessity in order to achieve proper restoration and management. Despite its ecological and commercial importance, little is known of the dynamics of natural stands of Araucaria angustifolia and of the species' regeneration strategy (Veblen et al., 1995).

Specifically, we tested the validity of the following expectations:

Expectation 1: In unlogged forests, Araucaria angustifolia populations are characterized by size distributions with many large individuals and a long tail of relatively rare, small individuals. In logged stands the species' size-distributions should become more symmetric or even right-skewed, if logging activities were recent. This should reflect not only a reduction in the relative abundance of adult trees but also a marked increase of small and medium-sized individuals.

Left-skewed size distribution characterizes gap-dependent species with large fecundity, seed mortality, seedling mortality, high sapling growth and mortality rates and high proportion of recruits located in tree-fall gaps (Lorimer and Krug, 1983; Poorter et al., 1996; Coomes et al., 2003; Wright et al., 2003). A previous meta-analysis of population size-distribution of the species (Souza, 2007) seems to support this prediction, but the analyzed sites had an unknown range of logging histories.

Expectation 2: As a pioneer species, regeneration of Araucaria angustifolia should be restricted to more open-canopy microsites than expected by chance.

Canopy disturbances are known to enhance pioneer regeneration (Lieberman et al., 1995; Mailly et al., 2000). However, as a long-lived pioneer, Araucaria angustifolia probably does not continue to grow or survive long after canopy closure (Ogden and Stewart, 1995; Enright et al., 1999; Mailly et al., 2000). Hence, the species' advanced regeneration should also be found under more open-canopy conditions than expected by chance.

Expectation 3: Adult trees should be aggregated at relatively large spatial scales, that correspond to past regeneration following canopy disturbance events at scales coarser

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