

# Replacement patterns and species coexistence in an Andean *Araucaria-Nothofagus* forest

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## Abstract

**Questions:** Fire appears to affect both replacement patterns and coexistence of *Araucaria araucana-Nothofagus pumilio* forests in the Andean Araucarian region of south-central Chile. A quantitative assessment of coexistence in the absence of recent fires, however, is lacking. In this study, we considered the life-history attributes, time of recruitment and spatial pattern of individuals of both tree species to address the following questions. How regular has recruitment of both species been in time? Is there any temporal niche differentiation? Are the two species positively or negatively associated in space and, if so, at what scale and for what age and size classes? Is there any spatial niche differentiation?

**Location:** Andean Araucarian region of Chile, Villarrica National Park (39°35'S, 71°31'W; 1300 m.a.s.l.).

**Methods:** We stem-mapped and cored a total of 1073 trees in a 1-ha plot in a late-successional post-fire stand to examine spatiotemporal patterns of establishment. We used semivariogram modelling and the pair-correlation function to distinguish between regeneration modes and describe species interactions.

**Results:** The two species differ in their regeneration mode: whereas *A. araucana* appeared to recruit more continuously in time and space, episodic pulses of establishment were dominant for *N. pumilio*. At small scales, younger age-class stems of *A. araucana* were randomly distributed, while older age-class stems were aggregated. This was in contrast to common patterns for temperate tree species, including *N. pumilio*, following processes of self-thinning. Younger age classes of *A. araucana* were distributed independently of older trees of both species, but younger age classes of *N. pumilio* had a negative association with older conspecifics at scales similar to crown diameter.

**Conclusions:** In the absence of recent fires, it is likely that *A. araucana* would dominate the stand alone, given its greater shade tolerance, greater longevity and continuous recruitment. However, while canopy closure is still incomplete, the shade-intolerant *N. pumilio* will be able to recruit

in those open areas after seed masting and will coexist with *A. araucana*.

**Keywords:** *Araucaria araucana*; Chile; Life-history strategies; *Nothofagus pumilio*; Pair-correlation function; Semivariograms; Space as a surrogate; Villarrica National Park.

**Nomenclature:** Marticorena & Rodríguez (2003).

## Introduction

As a major force shaping composition and structure in ecosystems, disturbances influence competition and environment, substrate and resource availability (Peterson & Pickett 1995; White & Jentsch 2001), creating opportunities for tree species establishment (Veblen 1992). Fire is the dominant form of disturbance in many forest ecosystems worldwide, including the *Araucaria-Nothofagus* forests in the Andean Araucarian region of south-central Chile (Burns 1993; Veblen et al. 1995, 2005; González et al. 2005). Post-fire development of tree populations has been widely documented in the northern hemisphere in boreal (e.g. De Grandpré et al. 2000; Johnstone & Chapin 2006) and temperate subalpine forests (e.g. Sherriff & Veblen 2006; Sibold et al. 2007), but there has been little study of fire in temperate forests of South America (but see Veblen & Lorenz 1987; Burns 1993; González et al. 2005), particularly after the occurrence of fire. *A. araucana* (Molina) K. Koch (Araucariaceae) forests constitute a relict from the Tertiary; they have generally been displaced by other broadleaf species and are currently found only at sites of low productivity at high altitudes (Schmithüsen 1960; Veblen 1982). During the twentieth century, the species' distribution has been dramatically reduced following logging (Lara et al. 1999), which has caused considerable concern over