

# 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

the conservation of this species (it has the status of natural monument in Chile) and has highlighted the need for a better understanding of the effects of natural disturbance on its regeneration processes (Veblen et al. 1995). In this study, the life-history attributes, time of recruitment and spatial pattern of individuals of both *A. araucana* and the co-occurring *Nothofagus pumilio* (Poeppig et Endlicher) Krasser (Nothofagaceae), in the absence of recent fires, were considered in order to gain insight into stand development and species coexistence.

The few studies conducted in the above forests have mainly focused on regeneration dynamics and successional patterns after natural disturbances (Schmidt 1977; e.g. Burns 1993), and reproduction and dispersal strategy of the species (Finckh & Paulsch 1995; Sanguinetti & Kitzberger 2008) without considering replacement patterns and coexistence of these two overstorey tree species (but see Veblen 1982). Understanding the coexistence of these species requires detailed examination centering on the mechanisms of regeneration processes and modes, and competitive interactions. Whereas spatial patterns of seed rain depend on the mechanisms of seed dispersal, those of recruitment depend on the interaction of multiple biotic and abiotic factors (Clark et al. 1999). Most of the processes that have been hypothesised to explain recruitment, species coexistence and, therefore, forest community structure (e.g. niche or neutral theory) have a strong spatial component (Williamson 1975; Wiegand et al. 2007; McIntire & Fajardo 2009). Spatial patterns of species association have been studied to infer causal mechanisms that facilitate species coexistence (Wiegand et al. 2007; McIntire & Fajardo 2009). This is based on the idea that coexistence mechanisms acting at the stand level should leave a spatial signature that could be detected and analysed (Hubbell 2001).

*A. araucana*-*N. pumilio* coexistence may be due to differences in life-history strategies relative to the occurrence and severity of fire, but the relative importance of various life-history components is unknown. The dynamics of both species are strongly regulated by fire and volcanic disturbance (Veblen 1982; González et al. 2005). Following Rowe's (1983) classification for species adaptations to fire, *A. araucana* can be considered a *resister* and *N. pumilio* an *evader* species. *A. araucana* can withstand more severe fires than *N. pumilio* (see below). When a fire takes place, it may remove seedlings, saplings and small diameter trees (<25 cm) of *A. araucana*, but most *N. pumilio* trees are killed (Burns 1993; Veblen et al. 1995).

Thus, it is expected that trees of *A. araucana* will be irregularly represented in most of the age classes, and *N. pumilio* will be represented by even-aged patches in the stand (Burns 1993; González et al. 2005; Veblen et al. 2005).

Regeneration mode – the spatial and temporal scales at which regeneration occurs in relation to disturbance (Veblen 1992; Veblen et al. 1995) – can be inferred from tree population age structures and spatial patterns, providing a first estimate of the conditions under which a species regenerates. Differences in regeneration mode may allow temporal niche differentiation and hence coexistence of two (or more) species. Resulting recruitment can be episodic or continuous at specific temporal and spatial scales (Fajardo et al. 2008). We can then assess recruitment patterns by studying spatial autocorrelation in conjunction with age. We expect a *resister* species, such as *A. araucana*, to produce and disperse seeds in a more continuous way (Wells & Getis 1999). This expectation is supported by *resister* species of the northern hemisphere like *Pinus ponderosa*, *P. jeffreyi* and *P. torreyana* (Cooper 1961; Wells & Getis 1999). If recruitment of *A. araucana* has occurred more or less continuously in time and seeds are not well-dispersed, we predict trees of similar age will be spatially clustered (showing positive spatial autocorrelation). On the other hand, we postulate that an *evader* species, such as *N. pumilio*, recruiting massively after a high-severity fire, will form more discrete, single age-class patches in the stand and will display dissimilarities in tree ages between patches.

Shade-intolerant species typically exhibit self-thinning due to light competition such that, while younger age classes may be aggregated at smaller scales, middle age classes will exhibit increasing regularity at medium scales, and mature trees will exhibit a random pattern at larger scales (e.g. Kenkel 1988; Diggle 2003; Fajardo & Alaback 2005). For *A. araucana*, regeneration dynamic studies and empirical observations indicate that it tends to establish away from mother trees, although it naturally could form all age clusters of individuals under older trees because of seed weight and poor seed dispersal (Finckh & Paulsch 1995). *A. araucana* seedlings, however, established away from older trees seem to be more successful, considering that under long-lived individuals (>700 year) they will be suppressed for most of their life (Finckh & Paulsch 1995). Therefore, if species recruitment is located near parent trees, we can expect that younger age classes could be strongly associated

with mature trees of the same species (self-replacement) or with mature trees of the other species (reciprocal replacement *sensu* Veblen 1982).

The objective of this study was two-fold. First, we examined spatial and temporal patterns of recruitment to assess how species differences in regeneration processes might contribute to species coexistence at the stand level in the absence of recent fires. Second, to detect interactions among individual trees, we tested for inter- and intraspecific associations at various spatial scales. We addressed these objectives using spatial analyses in a late-successional, post-fire stand.

## Methods

### *Tree species*

*A. araucana* is a dioecious, semi-shade-intolerant species whose seeds are wingless and relatively heavy (3–4 g), typically falling within a radius of 7–8 m around the mother tree (Muñoz 1984; Sanguinetti & Kitzberger 2008). Consequently, the number of seedlings establishing is normally greater near the parent tree (Finckh & Paulsch 1995). Mature *A. araucana* trees have large and thick-barked stems, buds that are protected by modified leaves (Sanguinetti & Kitzberger 2008), and crown shapes placing the foliage out of reach of surface fires (González et al. 2005; Veblen et al. 2005). *N. pumilio*, on the other hand, is a monoecious, shade-intolerant species with lighter seeds that are dispersed widely, principally by wind, and with thin-barked stems with greater susceptibility to being killed by more severe fires. Both species exhibit mast seeding, at intervals of 3–8 years for *N. pumilio* (Mascareño 1987) and about 3–4 years for *A. araucana* (Sanguinetti & Kitzberger 2008). *A. araucana* and *N. pumilio* do not exhibit vegetative reproduction, although roots and basal resprouts have been reported for *A. araucana* in their Coastal Range distribution (Schilling & Donoso 1976), and also in the Andes range as basal resprouts after severe fire events (Burns 1993; González & Veblen 2007).

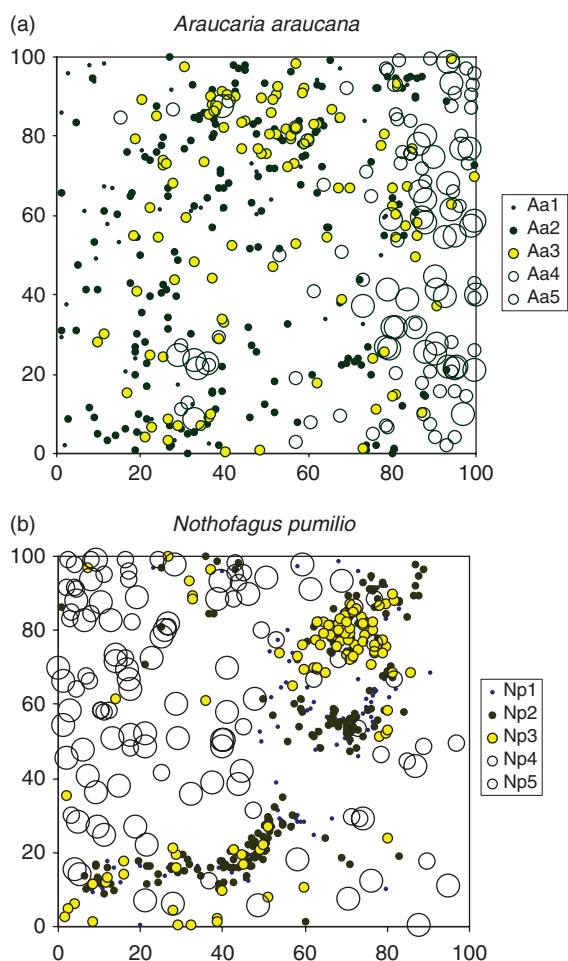
### *Study area*

The study was conducted in the foothills of Lánin Volcano in Villarrica National Park (39°35'S, 71°31'W; 1300 m a.s.l.). Our study site constitutes a subalpine mesic forest in a late-successional post-fire stand stage (*sensu* Oliver 1981). Post-fire stands of old *A. araucana*-*N. pumilio* are relatively uncommon

in the landscape as a consequence of the pervasive occurrence of fires (González et al. 2005). This type of forest is commonly located between 1000 and 1400 m a.s.l. in the Andes, in sheltered and more mesic habitats associated with less frequent but more intense fires (Veblen 1982; Veblen et al. 1995, 2005). Our study site has not been logged. Mean annual precipitation is 3150 mm, with 65% occurring in winter (between May and September), mostly as snow. Mean annual temperature is 9.3°C, with a mean monthly minimum and maximum of 4.6°C (July) and 13.9°C (February) (Puesco Meteorological Station located at 700 m a.s.l., 5 km northwest of the study area). Regionally, soils are derived from recently deposited volcanic ash that overlies Pleistocene glacial topography (Casertano 1963). Our study site is within the southern distribution of the *Araucaria-Nothofagus* forest association in Chile, where *A. araucana* dominates a rather open canopy under which there is a mixture of co-dominants, suppressed and new recruits of *A. araucana* and *N. pumilio* trees (Veblen 1982).

### *Data collection*

In February 2001, we established a 1-ha plot (100 m × 100 m), with one axis perpendicular to the main direction of the slope (here <5%). To facilitate mapping, the plot was further divided into 20 smaller plots of 50 m × 20 m, and Cartesian coordinates ( $x, y$ ) were recorded with tape measures for every tree >1-m tall and >5-cm diameter at breast height (DBH), including dead stems. For each mapped tree stem, the species and DBH were recorded, and one core was taken from each mapped tree ca. 30 cm above the ground. In total, we mapped 1073 trees and extracted 987 cores (Fig. 1). In the laboratory, cores were dried, mounted and sanded with successively finer grades of sandpaper to reveal annual rings (Stokes & Smiley 1996). Rings were counted and dated to determine tree age with the aid of a stereomicroscope. For tree age determination, in cases where the pith was not intercepted, a maximum of 20 and 30 years were added for *N. pumilio* and *A. araucana*, respectively, based on Duncan's (1989) geometric procedure. No correction was applied for time required to grow to coring height. We were able to age ca. 95% of the tree cores. Five per cent of cores, especially those of older age classes, were discarded due to rotten pith or obscure rings.



**Fig. 1.** Spatial distribution of both species, *Araucaria araucana* (Molina) K. Koch and *Nothofagus pumilio* (Poepp. Et Endl.) Krasser, in a subalpine forest, Villarrica National Park, in the Andes of south-central Chile (39°35'S, 71°31'W, 1300 m.a.s.l.). Age classes for both species are represented by their quintiles,  $Aa_1$  ( $\leq 65$  years);  $Aa_2$  (66-120);  $Aa_3$  (121-180);  $Aa_4$  (181-300);  $Aa_5$  ( $> 300$ );  $Np_1$  ( $\leq 50$  years);  $Np_2$  (51-75);  $Np_3$  (76-100);  $Np_4$  (101-150);  $Np_5$  ( $> 150$ ).

#### Fitting age- and size-class distributions

We compared age distributions for both species with a negative exponential or inverse-J pattern, often assumed to represent a continuously regenerating population (Veblen 1992). To determine whether age distributions followed a negative exponential form, we fitted our empirical distributions with two functions, exponential and normal (Ricci 2005), compared relative fit using Akaike's information criterion (AIC) (Burnham & Anderson 2002) and adopted the model with the lowest AIC value.

#### Spatial analyses: linking spatial patterns to processes

##### Semivariogram modelling

Semivariograms were computed on the age of each stem-mapped individual and fitted according to semivariogram models to specific hypothesised processes (Fajardo & McIntire 2007). Empirical semivariograms are estimates of the variance of the difference between random variables at two locations (Isaaks & Srivastava 1989; Fortin & Dale 2005). The empirical semivariogram is defined as:

$$\hat{\gamma}(h) = \frac{1}{2N(h)} \sum_i [z(x_i) - z(x_i + h)]^2,$$

where  $h$  is the distance lag between sampled trees,  $N(h)$  is the number of paired comparisons at lag  $h$ ,  $z(x_i)$  and  $z(x_i + h)$  are the observed tree variable values at location  $x_i$  and  $x_i + h$  (Webster & Oliver 2001). In a semivariogram, the estimated semivariance ( $\hat{\gamma}(h)$ ) is plotted on the  $y$ -axis against lag distance ( $h$ ) on the  $x$ -axis. The nugget is the amount of variance not accounted for in the model due to measurement error plus residual variation at distances less than the shortest sampling interval. The sill, or total sample variance, is the ordinate value at which the semivariogram becomes flat. The range represents the distance beyond which samples are spatially independent (Isaaks & Srivastava 1989; Webster & Oliver 2001).

Based on current knowledge of the species life-history characteristics, we posited the following expectations. First, we postulate that continuous seed production and dispersal and seedling establishment (in time and space) will result in a monotonically increasing semivariogram (exponential or spherical type). On the other hand, a fire *evader* species, such as *N. pumilio*, is predicted to exhibit patchy regeneration with patches differing in age, resulting in a wave semivariogram with a range parameter at the same scale as distances between patches. Field observations confirmed that our 1-ha plot is large enough to contain several regeneration patches. We also considered masting species, using a nested model that was a mixture between the wave and exponential semivariogram models. We expect that a marked periodicity in seed production, and therefore recruitment, will be expressed at a shorter temporal scale than the occurrence of low-intensity fires (e.g. wave model). A wave semivariogram model depicts a strong small-scale difference in tree age that dampens with distance (neighbouring trees will differ greatly in age). Finally, we considered a model with stochastic variation (a nugget model

representing lack of spatial autocorrelation). The nugget model represents no spatial pattern at the scales we measured, suggesting that no biological process was important (the equivalent of a null hypothesis). From this semivariogram analysis, we need to note that a continuous or episodic regeneration mode is meant to represent the entire plot dataset. Also, where a larger-scale, site-level trend emerged (non-stationarity), we removed this before fitting the semivariogram model (geoR; “trend = 1st” option) (Ribeiro & Diggle 2001).

We estimated empirical semivariograms for each species individual's age, and fitted them to each of the five theoretical models (Cressie 1985): nugget, exponential, spherical, wave and nested (wave-exponential). Formulae can be found elsewhere (e.g. Fajardo & McIntire 2007). Empirical semivariograms were estimated using the geoR package (Ribeiro & Diggle 2001) of the statistical software R 2.6.2 (R-Foundation, 2004, R: A Language For Statistical Computing, Vienna, Austria, <http://www.R-project.org>). Semivariogram model fitting was also done in R. We used weighted least squares to fit these models and selected among the best models using the small sample adjustment to the  $AIC_c$  (Burnham & Anderson 2002). The absolute magnitude of the differences in  $AIC_c$  between alternate models provides an objective measure of the strength of empirical support for the competing models (Burnham & Anderson 2002). When the difference in  $AIC_c$  between two models is  $>2$ , the model with the lowest  $AIC_c$  is considered to have larger empirical support. The assumptions for the expected results to be reliable are a constant mortality rate for both species at all ages after the occurrence of fire, and no vegetative reproduction.

#### *Second-order effects spatial point pattern analyses*

Both species spatial structures were also compared with uni- and bivariate spatial point pattern analyses using the pair-correlation function (Wiegand & Moloney 2004; Wiegand et al. 2007). We sought to, first, assess the spatial autocorrelation found in the semivariogram modelling analysis (univariate tree-tree interactions), and second, to establish the intra- and interspecific spatial distribution and thus test the expectations already formulated (bivariate tree-tree interactions). For both cases, we used the pair-correlation function (Stoyan & Stoyan 1994; Wiegand et al. 1999; Wiegand & Moloney 2004), which is based on the distribution of distances between pairs of mapped

points (in this case, stems). For bivariate tree-tree interaction purposes, groups of points are classified according to some categorical variable (e.g. age class, species, survivorship), and therefore can be compared and their spatial association inferred. We classified the individual trees of each species population into five age classes representing their quintiles. For *A. araucana*, the age classes were:  $Aa_1$  ( $\leq 65$  years),  $Aa_2$  (66-120),  $Aa_3$  (121-180),  $Aa_4$  (181-300) and  $Aa_5$  ( $> 300$ ); for *N. pumilio* age classes were  $Np_1$  ( $\leq 50$  years),  $Np_2$  (51-75),  $Np_3$  (76-100),  $Np_4$  (101-150) and  $Np_5$  ( $> 150$ ).

To determine the spatial distribution of the two species age classes we used the pair-correlation function. For homogeneous patterns the pair-correlation function can be interpreted as the expected density of points (i.e. trees) at distance  $r$  from an arbitrary point, divided by the intensity  $\lambda$  of the pattern (Stoyan & Stoyan 1994). The pair-correlation function,  $g(r)$ , is derived from Ripley's  $K$ -function [ $g(r) = (2\pi r)^{-1} dK(r)/dr$ ] (Ripley 1977), where both are related to the cumulative distribution function and probability density function of distances between pairs of points (Stoyan & Penttinen 2000; Diggle 2003). Values of  $g(r) > 1$  indicate that interpoint distances around  $r$  are more frequent, and values of  $g(r) < 1$  that they are less frequent, than they would be under complete spatial randomness (CSR). A transformation,  $O(r) = \lambda g(r)$ , the  $O$ -ring function (Wiegand & Moloney 2004), allows straightforward interpretation of local neighbourhood density and is therefore used instead of the pair-correlation function. To reveal significant second-order effects (age classes interactions) in the univariate patterns (i.e. uniformity, aggregation), we compared the observed pattern with Monte Carlo envelopes originated from the analysis of 99 simulations of a null model. Ninety-nine simulations correspond to the 99% simulation envelope (Stoyan & Stoyan 1994). Our null model was of a CSR based on the pattern of a specific age class. In a CSR situation, any point of the pattern has an equal probability of occurring at any position in the study area, and the position of the point is independent of the position of any other point (Wiegand & Moloney 2004). A positive deviation from CSR confidence envelopes indicates aggregation at scale  $r$ , and a negative deviation implies regularity. From the semivariogram modelling analysis we found that age spatial autocorrelation fades away beyond ca. 20 m (semivariogram range) and we therefore calculated the pair-correlation function for all 10 age classes up to scales of 20 m. Finally, we also used a goodness-of-fit test (GOF) (Diggle 2003) along with the

simulation envelope method for inference in order to avoid the occurrence of Type I error (Loosmore & Ford 2006). This GOF test summarizes the scale-dependent information contained in the pair-correlation function into a single test statistic  $u_i$  that represents the total squared deviation between the observed pattern and the theoretical result across the distances of interest (see Wiegand et al. 2007).

The bivariate pair-correlation function,  $g_{12}(r)$ , can be defined as the expected number of pattern two points within distance  $r$  of an arbitrary pattern one point, divided by the intensity  $\lambda_2$  of pattern two points. When different age classes were spatially analysed, we effectively assumed that both age classes represent sequential events in time, therefore the pattern of the younger age class did not influence the development of the pattern of the older age class, but the opposite may have been true (i.e. the older age class may influence the development of the younger age class). The appropriate null model for this biological situation needs to consider the antecedent condition (Wiegand & Moloney 2004). In our case, for example, this means that for investigating the spatial association between mature *A. araucana* trees ( $Aa_5$ , pattern one) and saplings ( $Aa_1$ , pattern two) an appropriate null model (stochastic process) for testing negative or positive associations would be to randomize the locations of the saplings (because they could potentially be found in the entire study area) and to keep the locations of the mature trees fixed. When relatively similar age classes were compared (e.g.  $Aa_1-Np_1$ ), we used the null model that the two age classes have independent spatial distributions (Goreaud & Pélissier 2003; Wiegand & Moloney 2004). In this case, both patterns were randomly located and the toroidal shift null model was used. We used Monte Carlo simulations of the stochastic process underlying the specific null model for construction of simulation envelopes. Each simulation generates a  $g_{12}(r)$  function, and we computed approximate 99% simulation envelopes from the highest and lowest values of the function taken from the 99 simulations of the null model. Values from  $g_{12}(r)$  located outside of these simulation envelopes are considered to be a significant departure from the null model. Accordingly, we also used a GOF test to join the simulation envelope method (see above). The whole set of expectations and spatial analyses used, including semivariograms, are summarized in Table 1. All the spatial point pattern analyses were done with the grid-based software Programita (Wiegand & Moloney 2004).

## Results

### General demography

*A. araucana* and *N. pumilio* were the only two dominant species: a total of 467 and 520 individuals  $\text{ha}^{-1}$  was mapped, respectively (Fig. 1). The tree ages ranged from 33 to 465 (median value of 117 years) for *A. araucana*, reaching a basal area of  $35.02 \text{ m}^2 \text{ ha}^{-1}$ ; and from 19 to 472 (median value of 67.5 years) for *N. pumilio*, with a total basal area of  $26.39 \text{ m}^2 \text{ ha}^{-1}$  (more details in Appendix S1). These tree age and basal area ranges confirm the late-succession post-fire status of the stand. We compared the frequency distributions of tree age and size classes to models often assumed to represent a continuously regenerating population, and for both species, data proved to be best fitted by a normally shaped age distribution and not by a negative exponential or inverse-J pattern; i.e. most of the trees did not belong to relatively younger age classes (Fig. 2a). The age-class distribution is normal for both species, with most tree ages around 80 and 150 years for *A. araucana* and around 55 and 80 years for *N. pumilio*. However, when size classes were analysed, they proved to be best fitted by a negative exponential or inverse-J pattern; i.e. most of the trees belonged to relatively smaller size classes (Fig. 2b). We did not map trees shorter than 1 m and thinner than 5 cm DBH, which may explain the departure from an inverse-J pattern in the age-classes distributions. Competition processes may explain the difference between age- and size-classes distributions, i.e. trees confined to lower size classes because of strong asymmetric competition. As an aside, age figures and distributions, particularly for *N. pumilio*, are in accordance with figures characterizing a late-successional post-fire stand, e.g. *N. pumilio* individuals older than 300 years (González et al. 2005).

### Semivariograms

Spatial autocorrelation of individual tree ages was strong for both species; i.e. the computed semivariograms were significantly different from the nugget spatial model, suggesting that stochastic processes are not the main determinants of the spatial structure of both species populations (Table 2, Appendix S2, Fig. 3). For *A. araucana*, the exponential semivariogram model was the best-fit model describing the spatial autocorrelation of tree ages (lowest AICc,  $w_j = 0.8518 \sim R^2$ , Appendix S2); i.e. *A. araucana* trees of similar ages were neigh-

**Table 1.** Null and alternative models, analyses and expectations used to investigate the spatial structure of the two dominant tree species, *Araucaria araucana* and *Nothofagus pumilio*, in a subalpine forest in the Villarrica National Park, in the Andes of south-central Chile (39°35'S, 71°31'W, 1300 m a.s.l.). Notes: SPP stands for spatial point pattern analysis; †the five age classes are species-specific and represent quintiles of each age distribution.

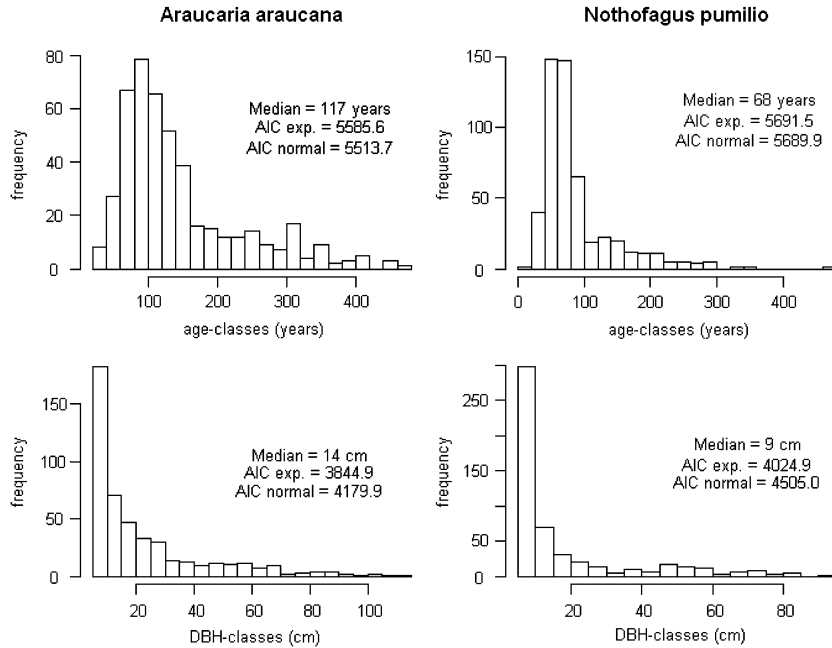
Analysis	Null model	Alternatives	Expectations
<b>Univariate</b>			
<b>Semivariograms</b>			
Tree ages autocorrelation $i, j = \text{absolute tree age}$			
$Aa_i$	Complete absence of spatial autocorrelation (nugget semivariogram)	1. Increasing positive spatial autocorrelation (exponential semivariogram); 2. Negative spatial autocorrelation (wave semivariogram); 3. Interrupted positive autocorrelation (nested semivariogram)	1. Gradual recruitment in time and space; 2. Strong shift in recruitment in time and space; 3. Gradual recruitment in space but not necessarily in time, e.g. seed masting
$Np_j$			
<b>SPP</b>			
Tree age classes† $i = 1, 5, j = 1, 5$			
$Aa_i$	Complete spatial randomness (CSR) of $Aa_i$ or $Np_j$	1. Aggregated pattern; 2. Regular pattern	1. Trees form patches (microsite effect, lack of competition); 2. Avoidance of trees (competition effect)
$Np_j$			
<b>Bivariate</b>			
<b>SPP</b>			
Conspecific tree age class comparison $i = 1, 5, j = 1, 5$			
$Aa_i$ versus $Aa_{i-1}$	Younger conspecifics are independently associated with older ones at small scale (antecedent condition: pattern $Aa_i$ fixed, randomization of pattern $Aa_{i-1}$ )	1. Younger age classes aggregated around older age class trees (self-replacement); 2. Repulsion of younger age class trees compared to older age class trees	1. Facilitation, gradual recruitment in time and space; 2. Shade avoidance, masting years
$Np_j$ versus $Np_{j-1}$			
Heterospecific same tree age class comparison $i = 1, 5, j = 1, 5$			
$Aa_i$ versus $Np_j$	$Aa_i$ is independently associated with $Np_j$ at small scale and vice versa (independence: pattern $Aa_i$ and $Np_j$ are randomly shifted as a whole)	1. Both species age classes are positively spatially associated; 2. Both species age classes are negatively spatially associated	1. They share similar niche requirements, especially for younger age classes; 2. They differ in niche requirements
$Np_j$ versus $Aa_i$			
Heterospecific different tree age class comparison $i = 1, 5, j = 1, 5$			
$Aa_i$ versus $Np_{j-1}$	$Np_{j-1}$ is independently associated from $Aa_i$ at small scale and vice versa (antecedent condition: pattern $Aa_i$ fixed, randomization of pattern $Np_{j-1}$ )	1. Younger $Np$ age classes aggregated around older $Aa$ age class trees (reciprocal replacement); 2. Repulsion of younger $Np$ age class trees compared to older $Aa$ age class trees	1. Facilitation, shelter of younger individuals; 2. Competition, allelopathy
$Np_j$ versus $Aa_{i-1}$			

bours, and therefore the recruitment has occurred more continuously in time and space. For *N. pumilio*, the nested (i.e. wave and exponential) semivariogram model was the best-fit model describing the spatial autocorrelation of tree ages (lowest AICc,  $w_i = 0.9691 \sim R^2$ ; Appendix S2). Although, a general positive spatial autocorrelation for *N. pumilio* is evident, some discontinuity (wave part of the nested semivariogram) needs to be recognized. Ranges of around 20 m characterise both best-fitting semivariograms species ages, which give an estimate of the mean diameter patch size. Recruitment pulses more associated with masting years may be responsible for this discontinuity in the spatial autocorrelation.

#### Spatial point pattern analyses

*A. araucana* and *N. pumilio* were, in general, significantly clumped at most of the spatial scales

(Table 3). When analysed at different age classes, surprisingly, we found that the youngest age class of *A. araucana* ( $Aa_1$  e.g. saplings and juveniles) was randomly distributed, while mature trees ( $Aa_5$  and  $Aa_4$ ) were significantly clumped ( $P < 0.05$ ). This is contrary to what we found for *N. pumilio* and to what it is established for spatial pattern dynamics of most temperate tree species. When conspecifics age classes were compared, we mostly found a significantly positive spatial association for *A. araucana* between contiguous age classes (e.g.  $Aa_5\_Aa_4$ ,  $Aa_4\_Aa_3$ , etc.), which is in accordance with a continuous recruitment of individuals in time and space (monotonically increasing exponential semivariogram, see above). This is also somewhat similar for *N. pumilio*, where only younger age classes exhibited a significantly positive spatial association (e.g.  $Np_3\_Np_2$ ,  $Np_2\_Np_1$ ). Younger trees of *N. pumilio*, however, showed a significantly negative spatial association when compared to mature trees ( $Np_5$ ,  $Np_4$ ,



**Fig. 2.** Tree age and size (DBH) distributions for *Araucaria araucana* and *Nothofagus pumilio* in a subalpine forest in the Villarrica National Park, in the Andes of south-central Chile (39°35'S, 71°31'W, 1300 m a.s.l.). AIC stands for Akaike information criterion for both normal and exponential fitting curves.

**Table 2.** Model coefficients and AIC<sub>c</sub> values for describing tree age spatial autocorrelation for both *Araucaria araucana* and *Nothofagus pumilio* in a subalpine forest in the Villarrica National Park, in the Andes of south-central Chile (39°35'S, 71°31'W, 1300 m a.s.l.). For nested model parameters only: (\*) corresponds to the wave part of the nested model; (†) corresponds to the wave part of the nested model. Note that the nested model is a combination of wave and exponential models. Best models correspond to AIC<sub>c</sub> values in bold.

Model coefficients							
Species	Models	Nugget	Sill*	Range*	Sill†	Range†	AIC <sub>c</sub>
<i>A. araucana</i>	Exponential	1957.385	3304.149	20.325			<b>160.798</b>
	Nested	1615.949	3221.277	21.309	443.166	3.081	164.217
	Spherical						
	Wave	1751.065	3077.549	5.464			189.212
<i>N. pumilio</i>	Nugget	4822.933					187.383
	Exponential	- 584.214	2496.823	12.847			178.435
	Nested	- 2679.309	2658.355	16.690	2057.300	4.486	<b>171.446</b>
	Spherical						
	Wave	- 590.535	2327.967	2.067			189.023
	Nugget	1754.697					188.211

Fig. 4) up to 20 m, which implies self-replacement (continuous mode *sensu* Veblen 1992) is not the predominant regeneration mode.

Older trees of *A. araucana* (*Aa*<sub>5</sub>) mainly established negative associations with younger age classes of *N. pumilio* at small scales and had significantly negative associations at larger scales (>4 m) with older trees of *N. pumilio* (*Np*<sub>5</sub>) (Table 4, Fig. 4). Younger age classes of *A. araucana* were independently associated with older trees of both

species, while younger age classes of *N. pumilio* had a negative association with older trees of *A. araucana* (although not significant) and with *N. pumilio* at scales <5-6 m (e.g. crown diameter effect). These findings imply that neither self- nor reciprocal replacement regeneration modes are acting on these two species. Intermediate age classes of *N. pumilio* and *A. araucana* (e.g. *Aa*<sub>4</sub>-*Np*<sub>2</sub>, *Aa*<sub>4</sub>-*Np*<sub>3</sub>, *Aa*<sub>3</sub>-*Np*<sub>3</sub>) displayed significant positive associations with each other at scales larger than 5-6 m (Table 5, Fig. 4).

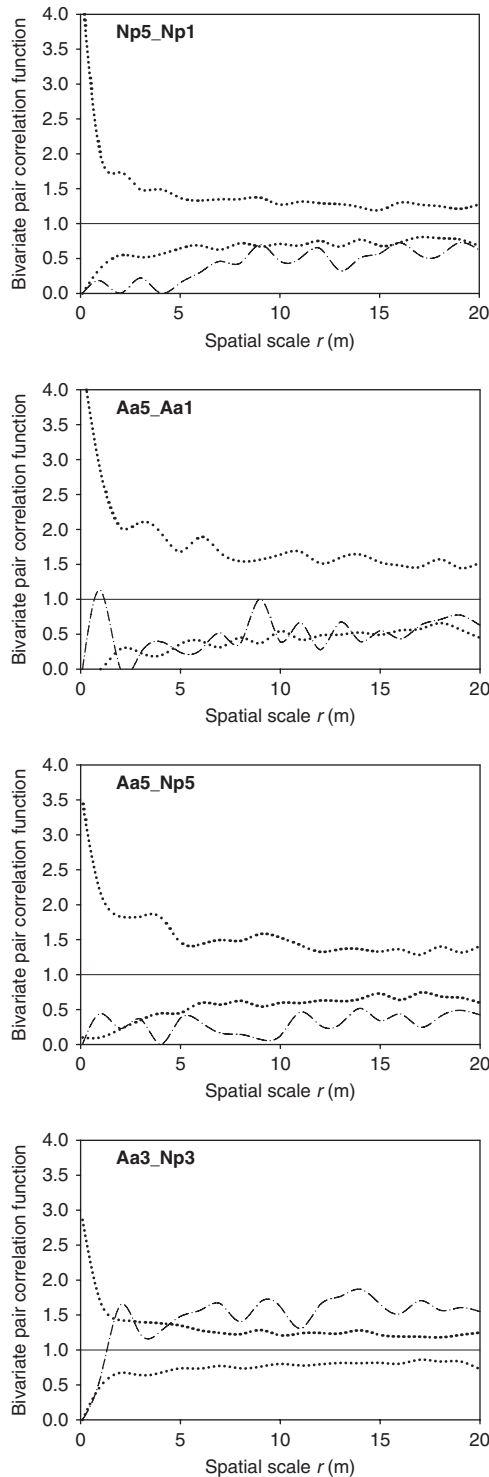


This difference in recruitment mode, consistent with our semivariogram analysis, helps in confirming a probable coexistence mechanism through temporal niche differentiation. In our study site, a late-successional post-fire stand, a primary severe

fire likely promoted initial establishment, particularly for *N. pumilio*. Results here suggest that subsequent establishment of *N. pumilio* (but not necessarily of *A. araucana*) was restricted to open areas and good years of seed production. Small-scale surface fires may also promote recruitment after seed masting years, explaining peaks of regeneration, particularly for *N. pumilio*. For these results to be reliable we assumed weak competition between individuals. Although the spatial structures found did not show evidence of interspecific competition, we cannot discard the idea. Study of neighbour growth rates should shed some light on this potential phenomenon.

We found a pattern of significant aggregation for younger (< 50 years) *N. pumilio* individuals. This clustering of younger age classes is consistent with models of patch dynamics stand development in other temperate forests (Watt 1947; Williamson 1975; Veblen 1985; Fajardo & de Graaf 2004; Fajardo & Alaback 2005). Younger age classes of *N. pumilio* were never positively associated with mature trees (e.g. *Np5*, *Np4*) of either species (under their canopy), consistent with shade-intolerance (Veblen 1982; Veblen et al. 1996). Furthermore, older age classes of *N. pumilio* were randomly distributed, consistent with commonly observed spatial patterns for temperate tree species due to density-dependent mortality (self-thinning), mediated through competition for resources (e.g. light), suggesting that the original aggregated distribution changes first to regularity and then randomness (e.g. Kenkel 1988; Szwagrzyk & Czerwczak 1993; Fajardo & Alaback 2005).

*A. araucana* stems exhibited aggregated spatial patterns at small scales for older age classes, while younger age classes were not significantly aggregated, but randomly distributed, a feature that may be more likely for shade-tolerant species. This is contrary to the spatial distribution exhibited by



←  
**Fig. 4.** Examples of significant small-scale interactions between different age classes, *Np5* (>150) versus *Np1* (≤ 50 years) and *Aa5* (> 300) versus *Aa1* (≤ 65 years), and different species, *Aa5* (> 300) versus *Np5* (> 150), and *Aa3* (121-180) versus *Np3* (76-100) in a subalpine forest in the Villarrica National Park, in the Andes of south-central Chile (39°35'S, 71°31'W, 1300 m a.s.l.). The bivariate pair-correlation function  $g_{12}(r)$  over scale  $r$  show the  $g_{12}$  function of the data (dash-dot line) and the simulation envelopes (dotted lines) being the fifth-lowest and fifth-highest values of the Monte Carlo simulations of the null model (conditional antecedent for *Np5*–*Np1* and *Aa5*–*Aa1*, spatial independence for *Aa5*–*Np5* and *Aa3*–*Np3*).





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## Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Density (trees ha<sup>-1</sup>), basal area (m<sup>2</sup> ha<sup>-1</sup>), relative density, relative basal area and relative importance value for live trees > 5 cm DBH in an 1-ha mapped plot in an *Araucaria araucana* and *Nothofagus pumilio* subalpine forest in the Villarrica National Park, in the Andes of south-central Chile (39°35'S, 71°31'W, 1300 m a.s.l.).

**Appendix S2.** Summary of AIC<sub>c</sub> selection models, Akaike differences ( $\Delta_i$ ), and Akaike weights ( $w_i$ ) for describing tree age spatial autocorrelation for both *Araucaria araucana* and *Nothofagus pumilio* in a subalpine forest in the Villarrica National Park, in the Andes of south-central Chile (39°35'S, 71°31'W, 1300 m a.s.l.).

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