

## Competition and dominance between angiosperms and *Araucaria angustifolia* (Bert.) O. Kuntze in the Atlantic Forest in southern Brazil



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### ABSTRACT

The dominance relationship between angiosperms and gymnosperms in natural forests has long been widely discussed, with some researchers believing that angiosperms tend to displace conifers due to competitive processes between the two species groups. The Lozenge or “temporal stand replacement” model states that a cohort of conifers is first established after a disturbance, while angiosperms establish themselves under the conifer canopy in a secondary stage that thereafter hinders conifer regeneration. This causes a drastic decline in conifer recruitment, restricting them to filling in gaps opportunistically. The objective of this study was to evaluate the competition for growth and survival between a conifer (*Araucaria angustifolia*) and two groups of angiosperms (shade-tolerant and light-demanding) in a species-rich forest using a distance-dependent competition index. We also investigated dominance among the three species groups by projecting the aboveground biomass of the groups for 50 years using an individual-tree distance-dependent growth model. We used data collected from 25 1-ha permanent plots located in the National Forest (FLONA) of Irati in southern Brazil, where all trees with more than a 10-cm diameter at breast height were identified for species and tagged, mapped, and measured. These plots have been measured every 3 years since their establishment in 2002. For diameter growth, the results indicated the araucarias were subject to severe intraspecific competition, while the light-demanding species suffered only moderate competition from the araucarias. The shade-tolerant species experienced little competition from any species group. No empirical evidence was found to support the hypothesis that competition estimates improve mortality predictions in a simple model based on stem diameter. Regarding the long-term dominance of the *Araucaria*, light-demanding, and shade-tolerant groups, the growth model indicated that araucarias will tend to dominate over the two angiosperm groups in aboveground biomass within 50 years, suggesting that this forest type follows the Lozenge model.

### 1. Introduction

Competition between angiosperms and conifers is of interest to researchers (Becker, 2000; Biffin et al., 2012; Brodribb and Hill, 1997; Coomes et al., 2005; Lusk et al., 2003), primarily because angiosperms are assumed to displace conifers in most forest types in the tropics. Some southern hemisphere studies in mixed conifer-angiosperm forests have evaluated the long-term dominance relationship between conifers and angiosperms in the long term, also known as “temporal stand replacement” or Lozenge model (Adie and Lawes, 2011, 2009a, 2009b; Claessens et al., 2006; Enright et al., 1999; Ogden, 1985; Rigg et al., 2010, 1998; Souza, 2007; Souza et al., 2008). This theory states that after a major disturbance event or disaster such as a fire or hurricane, a cohort of pioneer conifers is immediately established. In a second stage, angiosperms establish themselves under the conifer canopy, hindering

its regeneration and resulting in a drastic decline in conifer recruitment, after which the conifers are limited to opportunistically filling in the gaps left after the death of other conspecific trees. As the angiosperms move in to occupy the area, the conifers tend to go extinct, but this succession may take centuries (Claessens et al., 2006; Enright et al., 1999; Ogden, 1985).

However, in mixed conifer-angiosperm forests in the montane regions of South Africa, the inverse of the Lozenge model was seen, where the angiosperms were the first group to occupy an area after a disturbance. The area was then successively occupied by shade-tolerant late-emergent conifers (Adie and Lawes, 2011, 2009a, 2009b).

Although the Lozenge model has been most investigated in western Pacific araucarian forests such as those in New Caledonia (*Araucaria laubenfelsii*; Rigg et al., 1998; Rigg et al., 2010), New Guinea (*Araucaria hunsteinii*; Enright et al., 1999), and New Zealand (*Agathis australis*;

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Claessens et al., 2006), it has never been investigated in native Brazilian araucaria forests composed of *Araucaria angustifolia*. The two distinct scenarios for the dominance relationship between the conifers and angiosperms observed in the western Pacific and South African studies suggest different interactive processes of competition and/or facilitation between the two species groups, or perhaps differing light-demands of the conifer species under consideration.

Knowing the position of the trees in a forest allows studies to be conducted on neighboring trees and the competitive processes that occur among the trees (Liu and Burkhardt, 1994). We used a distance-dependent individual-tree growth model to better understand the competition existing between conifers and angiosperms and the long-term dominance interactions between these groups in native Brazilian *Araucaria* forests. Because native araucarian forests in Brazil comprise hundreds of tree species, we grouped the angiosperm species into shade-tolerant and light-demanding groups (Orellana, 2014). A third group composed solely of *Araucaria angustifolia* (Bert.) O. Kuntze—the most important species of this forest type and regarded as Brazil's most important native conifer—was set apart to evaluate the competition and dominance among the species groups over time.

## 2. Methods

### 2.1. Study area

The National Forest (FLONA) of Irati is a protected area located in southern Brazil, which extends from 25°17' to 25°25' S latitude and from 50°30' to 50°36' W longitude (Fig. 1). It was created in 1968 and has not been disturbed since. The climate in the area is humid subtropical, with no dry season. The average temperature is below 22 °C in the hottest month and above 10 °C in the coldest month; there are more than five frosts per year. The lowest recorded temperature is −9 °C in July 1975, and the average annual precipitation is 1442 mm.

According to the Brazilian soil classification system, the soils in the forest are red-yellow podzolic and dystrophic red latosol. The vegetation is classified as “montane subtropical forest” and is predominated by *A. angustifolia*. The forest fragment is presently in an advanced stage of succession and covers a total area of 1273 ha. The sampled area is comprised of 25 ha arranged in 25 contiguous 1-ha plots. These permanent plots were established in 2002 when all trees above 10 cm of diameter breast height (DBH) were measured, tagged, mapped, and identified at the species level. Since then, these measurements have been repeated in the sample area every three years.

### 2.2. Growth model

We developed an empirical distance-dependent, individual-tree growth model to predict the aboveground biomass (AGB) in natural *Araucaria* forests (Orellana, 2014). The model has a spatial resolution of 1-ha and a temporal resolution (time-step) of one year. The diameter increment, survival, and recruitment sub-models (Table 1) were fitted for each species group. The simulations were performed with the Simile visual modeling environment (Muetzelfeldt and Massheder, 2003), an efficient tool for modeling forest growth (Vanclay, 2003, 2006, 2014).

### 2.3. Grouping species

Species differ in the level of competition they exert on other species (Canham et al., 2006; Papaik and Canham, 2006; Vanclay et al., 2013). Some studies suggest that one characteristic that influences the degree of competition species exert on one another is their demand for light (Lorimer, 1983; Szwagrzyk et al., 2012). For example, some shade-tolerant species have much higher crown foliage densities than do the light-demanding species. Thus, a competition index should be calculated for each species group under study (Stadt et al., 2007).

We grouped the species according to the methodology suggested by

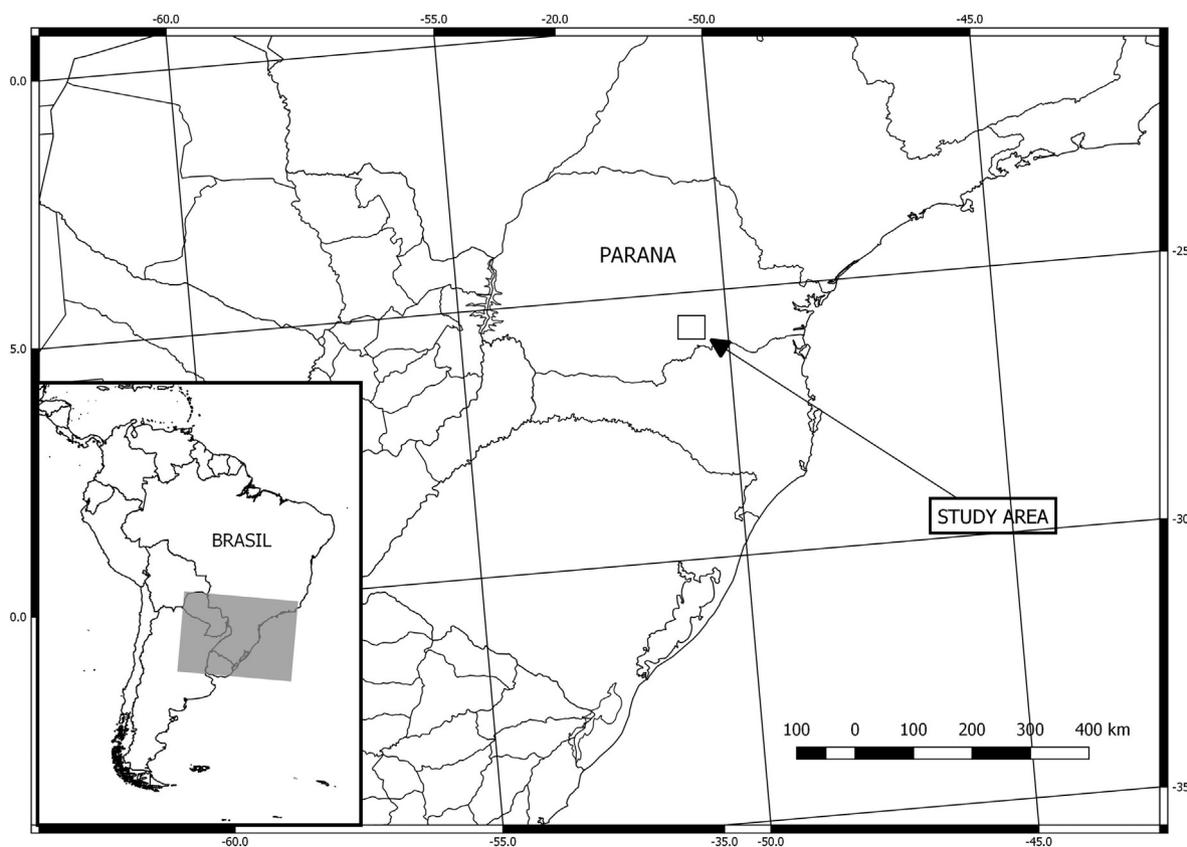


Fig. 1. Map of the study area.

**Table 1**  
Diameter increment, survival, and recruitment sub-models used in the growth model.

Function	Sub-model
DI	$\ln(DI + \alpha) = \beta_0 spp + \beta_1 DBH + \beta_2 \ln DBH + \beta_3 DBH \cdot spp + \beta_4 \ln DBH \cdot spp + \beta_5 CI$
<i>p</i>	$p = \beta_0 spp + \beta_1 DBH + \beta_2 DBH^{0.5} + \beta_3 DBH \cdot spp + \beta_4 DBH^{0.5} \cdot spp + \beta_5 CI$
N	$\ln(N + 1) = \beta_0 spp + \beta_1 Gi + \beta_2 G + \beta_3 Gi \cdot spp + \beta_4 G \cdot spp$

DI, diameter increment; *p*, probability of survival; N, number of recruited trees; *spp*, qualitative variable referring to the species group; *DBH*, diameter at breast height; *DBH.spp*, qualitative interaction between species group and *DBH*; *CI*, Hegyi competition index;  $\alpha$ , set to 0.2 to consider null and negative diameter increments and allow logarithmic transformations; *Gi*, species group basal area; *G*, plot basal area; *Gi.spp*, interaction between species group basal area and species group; *G.spp*, interaction between plot basal area and species group.

Alder et al. (2002), which defines ecological groups according to the position of the individual tree species on a two dimensional graph plotting the average diameter increment (cm/yr) against the 95th percentile (DBH sorted in ascending order) of the diameter distribution (Alder et al., 2002). To prevent bias, the 95th percentile was used to represent the adult tree rather than the maximum observed size (King et al., 2006). Alder's approach clustered species into six ecological groups: understory, subcanopy, shade-tolerant upper canopy, light-demanding upper canopy, pioneer, and emergent. For our study, we grouped the species into shade-tolerant and light-demanding groups following Alder's approach (Orellana et al., 2017, 2016).

Stadt et al. (2007) reported that for evaluating competition, using separate shade-tolerant and light-demanding species groups is more effective than considering all of the species together. Using Alder's categories, we defined the shade-tolerant group as the understory, subcanopy, and shade-tolerant upper-canopy, and the light-demanding group as the pioneer, emergent, and light-demanding upper-canopy groups. *Araucaria angustifolia* was the sole member of a third group, representing the conifers.

The study area has over 120 recorded angiosperm species, but many have only one or few observations. The 106 angiosperm tree species with more than 10 observations were grouped into the shade-tolerant and light demanding groups, while species with fewer than 10 recorded individuals were assigned to a group based on the light requirements for the species as described in the literature.

#### 2.4. Competition

Competition among trees reduces diameter growth and increases the probability of mortality (Weiskittel et al., 2011). Researchers have used a variety of methods to assess the effects of competition on tree growth, and the most common ones involve the use of regression models (Canham et al., 2004). We used the Hegyi competition index to assess the level of competition among species groups and its effect on diameter growth and survival (Hegyi, 1974). Instead of using a fixed search radius around the subject tree to define the trees that are effectively competitors (e.g. Hegyi, 1974; Béland et al., 2003; Contreras et al., 2011; Das et al., 2011), we took into account that the search radius varies depending on the diameters of the competitor and subject trees and the distance between them (Vanclay et al., 2013). The competition calculations included only those trees within the plot whose competitor trees were known. With three species groups, nine possible competition scenarios can occur among the groups, as shown in Table 2.

The Hegyi competition index was parameterized for each competition scenario to assess the existing competition between the three groups. We used Simile to calculate the competition index, a simulation software that facilitates the efficient calculation of distance-dependent competition indices (Vanclay, 2006).

**Table 2**

Competition scenarios under which intra- and intergroup competition can occur.

Scenario	Cause competition		Suffer from competition
1	Shade-tolerant	→	Shade-tolerant
2	Shade-tolerant	→	Light-demanding
3	Shade-tolerant	→	<i>Araucaria angustifolia</i>
4	Light-demanding	→	Shade-tolerant
5	Light-demanding	→	Light-demanding
6	Light-demanding	→	<i>Araucaria angustifolia</i>
7	<i>Araucaria angustifolia</i>	→	Shade-tolerant
8	<i>Araucaria angustifolia</i>	→	Light-demanding
9	<i>Araucaria angustifolia</i>	→	<i>Araucaria angustifolia</i>

**Table 3**

*Araucaria angustifolia* and the main species representing the two angiosperm species groups in order of abundance.

Groups	(No. of spp.) Family	Mean $\Delta d$ (cm)	<sup>a</sup> Max <i>DBH</i> (cm)	<sup>a</sup> N·ha <sup>-1</sup>
<b>1. Shade-tolerant</b>	<b>(43)</b>	<b>0.196</b>	<b>73.53</b>	<b>375.28</b>
<b>Angiosperms</b>				
<i>Ocotea odorifera</i> (Vell.) Rohwer	Lauraceae	0.141	56.34	49.84
<i>Ilex paraguariensis</i> A. St.-Hil.	Aquifoliaceae	0.199	43.77	47.40
<i>Nectandra grandiflora</i> Nees	Lauraceae	0.213	64.14	32.64
<b>2. Light-demanding</b>	<b>(63)</b>	<b>0.338</b>	<b>155.97</b>	<b>78.08</b>
<b>Angiosperms</b>				
<i>Cedrela fissilis</i> Vell.	Meliaceae	0.348	82.60	14.52
<i>Ocotea puberula</i> (Rich.) Nees	Lauraceae	0.299	86.58	12.60
<i>Ocotea diospyrifolia</i> (Meisn.) Mez	Lauraceae	0.271	69.07	8.88
<b>3. <i>Araucaria angustifolia</i></b> <b>(Bertol.) Kuntze</b>	<b>Araucariaceae</b>	<b>0.417</b>	<b>121.44</b>	<b>41.32</b>

Mean  $\Delta d$ , mean diameter increment (cm/yr); Max *DBH*, maximum diameter at breast height (cm).

<sup>a</sup> Data from last survey.

### 3. Results and discussion

The mean diameter growth, maximum size (DBH), and density (number of trees per hectare) of the three main species in each group are shown in Table 3, sorted in decreasing order of abundance. There were almost five times as many individuals in the shade-tolerant group as in the light-demanding group. On average, however, the diameter increment of the light-demanding species was larger than that of the shade-tolerant species. *Araucaria angustifolia* had the greatest diameter increment, with rates twice those of the shade-tolerant species.

#### 3.1. Competition among species groups

The fitted parameters for the diameter increment and survival sub-

**Table 4**  
Fitted parameters for the diameter increment and survival sub-models for the gymnosperm (*Araucaria angustifolia*) and two angiosperm groups.

Sub-model	Variable	Groups			
		G1 (n = 18938)	G2 (n = 6041)	G3 (n = 1224)	
$\Delta d$	$\beta_0$	-1.1759**	0.1070	-1.7121**	
	DBH		-0.0002	-0.0187**	
	ln DBH	0.1119**	0.0884	0.7797**	
	C3, C6	0.0042	0.0042	0.0042	
	C1, C2, C4, C7	-0.0104**	-0.0104**	-0.0104**	
	C5, C8		-0.0295**	-0.0295**	
	C9			-0.0532**	
	$p$	$\beta_0$	1.4126*	-0.4330	-4.0490
		DBH	-0.0793*	0.0279	-0.1240
DBH <sup>0.5</sup>		0.7805*	0.0726	1.9430*	
C1		-0.0179			

$\Delta d$ , diameter increment;  $p$ , probability of survival;  $\beta_0$ , estimated parameter; DBH, diameter at breast height; C1–C9, competition scenarios as defined in Table 2; G<sub>1</sub>, shade-tolerant angiosperms; G<sub>2</sub>, light-demanding angiosperms; G<sub>3</sub>, *Araucaria angustifolia*; n, number of observations used to parameterize the diameter increment sub-model; CI, Hegyi index calculated for each competition scenario among the species groups.

\*  $p < 0.05$ .

\*\*  $p < 0.01$ .

models used in the growth model are shown in Table 4, as well as the fitted parameters for the competition index among groups (Ci) for each competition scenario (Table 2). The parameters for the competition indices (adjusted for each competition scenario) with similar values were combined to predict the growth competition.

### 3.1.1. Growth competition

In all cases in which the adjusted competition parameters were negative, they were significant at the 1% level ( $p < 0.01$ ), indicating that competition for diameter growth is present among the species groups. The magnitude of the competition parameters (C1–C9; Table 4) indicates the level of competition among species (Canham et al., 2004), which in this research means among species groups. For example, in the three scenarios under which the shade-tolerant angiosperms suffer from competition (C1, C4, and C7), as well as when the light-demanding angiosperms experience competition from the shade-tolerant group (C2), the growth competition was low (fitted parameter = -0.0104). The intragroup competition in the light-demanding species (C5) and the competition suffered by the light-demanding species from araucarias (C8) was only moderate, although the level of competition was approximately three times (fitted parameter = -0.0295) that of the low-competition scenarios (-0.0104; C1, C2, C4, and C7). The magnitude of the adjusted parameter for Scenario 9 (*Araucaria* → *Araucaria*) indicates that araucarias suffer from severe intraspecific competition, with a fitted parameter approximately five times (-0.0532) that of the low-competition scenarios (-0.0104; C1, C2, C4, and C7).

The adjusted competition parameter values in the scenarios where the araucarias suffer from competition with the shade-tolerant (C3) and light-demanding (C6) groups (0.0042) indicate that the presence of angiosperms among neighboring araucarias does not affect the diameter growth of the conifer. In fact, its positive sign in these scenarios suggests that araucarias tend to benefit in growth when angiosperms are neighboring them, but this is not conclusive, as the value did not meet the minimum 5% level of significance ( $p > 0.05$ ). Facilitation among species when assessing distance-dependent competition indices has been observed in other studies (Forrester et al., 2011; Vanclay, 2006), and Stadt et al. (2007) identified additional interactions such as amensalism, neutralism, and commensalism among species in boreal forests. Certainly, these interactions among species or groups of species also occur in species-rich forests.

The evidence for angiosperms facilitating gymnosperms found in this study corroborates a study by Peterson and Squiers (1995) that evaluated the competition between a gymnosperm (*Pinus strobus*) and an angiosperm (*Populus grandidentata*). Although they conducted clonal experiments in their research, the results demonstrated that *Pinus* sp. trees tend to have more diameter growth when they are adjacent to *Populus* sp. Furthermore, the intraspecific competition for the *Pinus* sp. was high. Taken together, these results agree with those in this study pertaining to the competitive processes between gymnosperms and angiosperms.

In contrast, Vanclay et al. (2013) found only modest intraspecific competition for *Araucaria cunninghamii* growing in mixed plantings with *Flindersia brayleyana*. They additionally reported the angiosperm imposed severe competition on the *Araucaria* spp. The differing results for these conifer-angiosperm forests suggest that the interactive processes inherent to facilitation or competition between conifers and angiosperms might indicate the dominance of one of these two groups in the long term, the focus of discussion of the Lozenge, or “temporal stand-replacement,” model.

### 3.1.2. Competition for survival

Relative to survival, the independent competition variables were insignificant after the adjustments ( $p > 0.05$ ), with only one incidence of intra-group competition (shade-tolerant → shade-tolerant), which had the expected negative fitted parameter value. There are two possible reasons for the small contribution made by competition to the survival sub-model adjustments: (1) the competition among the shade-tolerant, light-demanding, and *Araucaria* groups was not strong enough to cause tree mortality; or (2) the competition index used did not accurately represent the competition for survival among the groups.

Working in natural *Picea abies* forests, Castagneri et al. (2008), found that while the dependent and independent competition indices contributed minimally in evaluating the competition effect on tree mortality in a low density plot, the indices contributed in plots with higher densities, especially those indices related to total tree height, crown area, and distance between trees. In our study, the only scenario in which competition was likely present between groups was when the shade-tolerant group suffered intragroup competition. Even so, the variable produced no significant adjustments to the models, although it was included in the survival sub-model (Table 4).

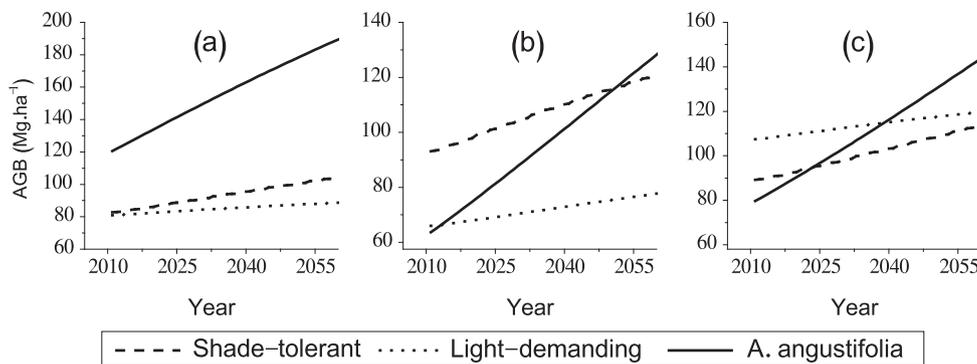
Asymmetric competition indices have been widely included in models of mortality, but no published studies have investigated whether one-sided competition (asymmetry) situations effectively represent these predictions (Peltoniemi and Mäkipää, 2011). Although it has been shown that shade-tolerant species compete with light-demanding species in diameter growth, we found no studies evaluating the effects of competition between these two species groups with regard to survival.

Therefore, we encourage the investigation of other competition indices to assess the competition between species groups in modeling survival in species-rich forests. Although tedious, only rigorous testing of the different methodologies that have been proposed for determining competition indices will prove which of these is the most effective (Miina and Pukkala, 2000).

### 3.2. The Lozenge model

We simulated three different scenarios in terms of the initial density within a plot, where either the shade-tolerant species, the light-demanding species, or the araucarias had the higher initial AGB density. This analysis aimed to identify whether gymnosperms or angiosperms would dominate over time, the primary point of discussion in the Lozenge Model. The gymnosperms were represented by *A. angustifolia*, while the angiosperms were represented by the shade-tolerant and light-demanding species groups.

The araucarias tended to surpass the angiosperms in growth and dominate the AGB density by the end of the fifty-year simulations under



**Fig. 2.** Fifty-year projections of the above-ground biomass (AGB) for the shade-tolerant, light-demanding, and *Araucaria angustifolia* groups. The araucarias achieved dominance under three different initial density conditions: (a) higher araucarian AGB density; (b) higher shade-tolerant species AGB density; and (c) higher light-demanding species AGB density.

all three initial density situations (Fig. 2). The dominance of the araucarias over the angiosperms may reflect that the *Araucaria* forests in southern Brazil follow the Lozenge model (Souza, 2007; Souza et al., 2008), in which the araucarias initiate the forest succession process and, in a second stage, the angiosperms become established in the lower strata, hindering the regeneration of the conifers. According to this model, in the future, the conifers should tend to succumb after the death of mature emergent individuals in the upper strata.

These results corroborate those from simulations of the same study area performed with a distance-independent individual tree-growth model (Orellana et al., 2016), in which the emergent species (including *A. angustifolia*) tended to grow for approximately 200 years regardless of forest density. Considering the oldest *A. angustifolia* trees in the study area are approximately 300-years old (Stepka, 2012), this suggests the first araucaria saplings were established after a disturbance 300 years ago and that the cohort will continue to grow for another 200 years. After this ~500-year period (since the first *A. angustifolia* saplings became established), the biomass growth of the oldest araucaria trees will tend to stabilize. According to the Lozenge model, the tendency for the conifers to succumb would occur in the following stage, and the angiosperm biomass would then be more likely to dominate the area.

Claessens et al. (2006) described the same pattern when analyzing *Agathis australis* (another conifer in the family Araucariaceae that is endemic to New Zealand) where they found that after a disturbance, the light conditions favored the establishment of an *A. australis* cohort. In the second stage, approximately 400 years later, the *A. australis* biomass remained the same despite a lack of recruitment from the seedling pool, because lateral growth of the surrounding individuals filled the gaps. A cohort senescence phase occurs after 400–800 years, where the biomass declines and tree density is further reduced to a limited number of large trees because of the decline in recruitment opportunities.

The Lozenge model as applied to mixed conifer-angiosperm forests was based on studies of light-demanding gymnosperms (mainly in New Zealand and New Caledonia), and they included some species within the *Araucaria* family (Rigg et al., 1998; Enright et al., 1999; Claessens et al., 2006; Rigg et al., 2010). However, the ecology of *A. angustifolia* is not well understood. Some authors have suggested that this tree species is a pioneer (Carvalho, 2002; Klein, 1960; Reitz and Klein, 1966), and studies examining varying light intensity have shown that the araucaria seedlings have a higher photosynthetic and growth capacity in the shade than under direct light (Franco and Dillenburg, 2007; Inoue et al., 1979). Other authors disagree that it should be classified as a pioneer (Heringer and Jacques, 2001; Ntima, 1968), while still others regard it as a long-lived pioneer species (Souza et al., 2008). There is some consensus among researchers that the pioneer species in the *Araucaria* forests in southern Brazil are angiosperms and that *A. angustifolia* is a secondary species (Amarante et al., 2007; Catharino et al., 2006; Fowler et al., 1999; Lamprecht, 1989) that, when present, indicates a late stage of succession (Longhi et al., 2006).

If the hypothesis that *A. angustifolia* is a pioneer species is accepted, then one can state that the Brazilian *Araucaria* forest follows the

Lozenge model. However, if the species is secondary, then it does not follow the Lozenge model, but rather an alternative inverse model such as that found in the montane forests in South Africa, where the first group to occupy an area after a disturbance is the angiosperms. The area would then be successively occupied by shade-tolerant late-emergent conifers (Adie and Lawes, 2011, 2009a, 2009b). Under these conditions, the araucarias should successfully regenerate in the long term.

*Podocarpus latifolius* was the dominant conifer tree species in the canopy strata (dbh > 10 cm) in the South African study, with 205 stems/ha and a basal area of 9.9 m<sup>2</sup>/ha. In our study, *A. angustifolia* trees (dbh > 10 cm) averaged 41.32 stems/ha (Table 1) and covered a basal area of 8.1 m<sup>2</sup>/ha. Although the number of stems per hectare is considerably lower in the native Brazilian *Araucaria* forests, the tree diameters are larger than those of the trees in the South African montane forests, as indicated by the similar conifer basal areas in the two study areas.

The main discrepancy found between the African and South American conifer-angiosperm forests is that the conifer also dominated the regeneration strata in the African forests. This is completely different from the Brazilian araucaria forests because regeneration in mature stands of *A. angustifolia* is rare (Caldato et al., 1996; Longhi et al., 2018; Rosa et al., 2016; Vicente-Silva et al., 2016), although the species can successfully regenerate under increased light levels (Souza et al., 2008). Mature stands dominated by *A. australis* in New Zealand have also shown a low capacity for conifer regeneration (Ogden et al., 1987).

It is important to highlight that little is known about the regeneration of *A. angustifolia* under different disturbance regimes or the forest succession over time in this forest type. This is primarily due to the different levels of anthropogenic impact, either from the seed collection for human consumption that discourages regeneration, or the illegal logging of large trees, which hinders comparative studies in different areas. Therefore, we encourage more studies to further extend our understanding of *A. angustifolia* regeneration under different disturbance levels.

#### 4. Conclusion

This study provides insights into the effects of competition on the growth and survival of araucarias and shade-tolerant and light-demanding angiosperms in a species-rich forest at an advanced stage of succession. The Hegyi index that we employed to represent the competition among species groups has contributed greatly to understanding competition in terms of growth in size. For the diameter increment, the results indicated that there is high intraspecific competition among the araucarias, and light-demanding species suffer from moderate competition, both intra-specifically and with *Araucaria*. In contrast, competition exerted over the shade-tolerant species by the shade-tolerant, light-demanding, and *Araucaria* groups is low, and light-demanding species experience little competition from the shade-tolerant species.

We found that competition caused no significant mortality among the species groups as defined. Two hypotheses were proposed to explain this: first, the effect of competition was not strong enough to cause mortality among the species groups as we defined them; and second, the Hegyi competition index may poorly reflect the competition existing among these species groups. We therefore encourage other studies to use distance-dependent competition indices to assess the effects of competition on the survival of species or species groups within species-rich forests.

The simulations showed that over the next 50 years, the araucarias are expected to be dominant over the two angiosperm species groups (shade-tolerant and light-demanding). This indicates that the araucarian forests predominating in southern Brazil follow the Lozenge model.

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