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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 Burkhart, 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

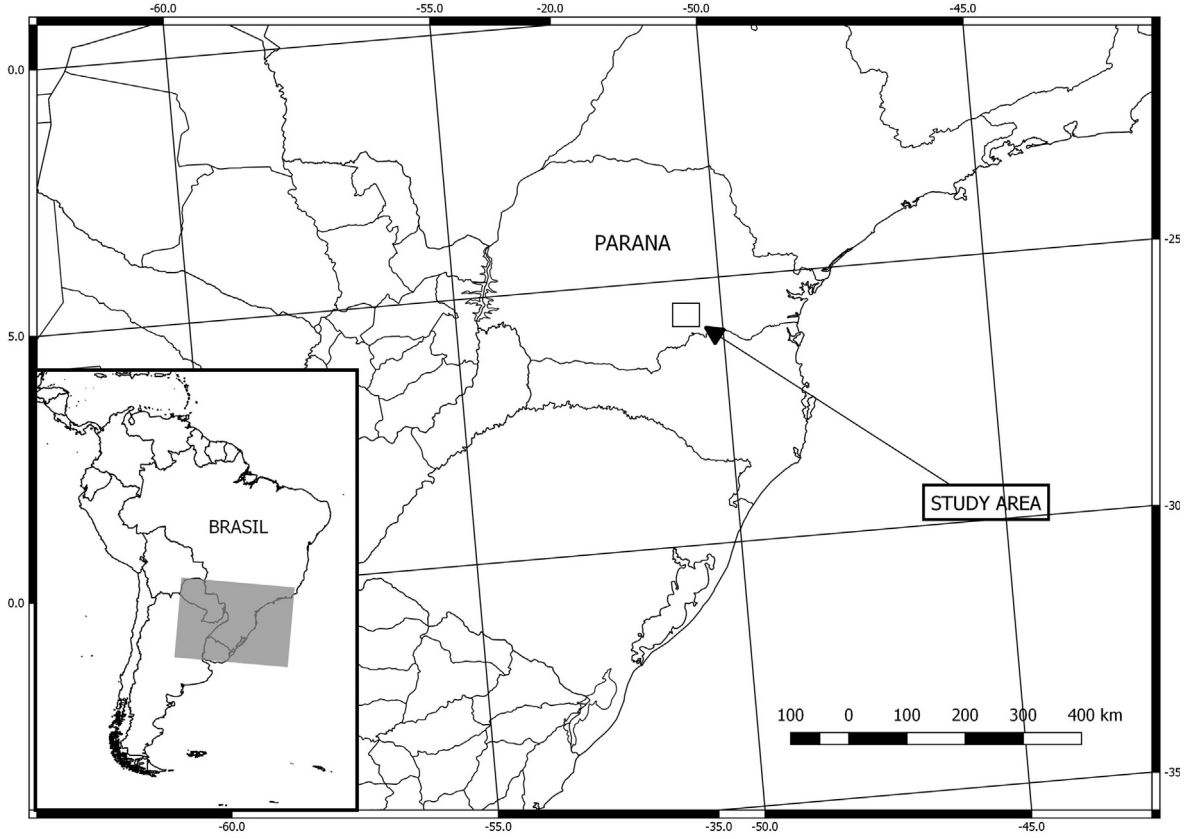

Fig. 1. Map of the study area.