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Inferring population trends of *Araucaria angustifolia* (Araucariaceae) using a transition matrix model in an old-growth forest

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Matrix population models may generate important information to prevent undesirable outcomes for endangered species. This is the case for *Araucaria angustifolia*, a Critically Endangered conifer, with little knowledge regarding its life history and trends in development over time. This study sought to investigate life-history trends of an *A. angustifolia* population in a subtropical forest in Santa Catarina, Brazil. Predictions based on the Lozenge regeneration model were established in order to determine if this model could predict changes in the species’ population dynamics: (1) the established individuals exhibit long persistence and (2) seedling and sapling abundance, as well as population descriptors, should exhibit behaviour that indicates one of the stages prescribed by the model. All *A. angustifolia* individuals were evaluated within a 5.1 ha plot at the study site over a six-year period. Lefkovitch’s transition model was used and population descriptors were calculated. Both predictions were fulfilled. The population had $\lambda = 0.9977 (0.9864 < \lambda < 1.0020; \text{CI } 95\%)$, indicating a declining stability. The basal area remained stable, whereas tree density tended to decrease, and seedlings and saplings did not promote an increase in $\lambda$. These results indicate that the population was in a phase called thinning, defined by the Lozenge model. The results led to three conclusions: recruitment seems insufficient; survival of reproductive individuals is responsible for the longevity of the population; and the predictions did not refute the Lozenge model. According to this model, the population is expected to regenerate in the future. However, the species exhibits declining stability, which aggravates the endangerment situation.

Keywords: Araucaria forest, Brazilian pine, mixed ombrophilous forest, natural regeneration, population dynamics

Introduction

Population matrix models (PMMs) have been used to develop conservation strategies (Enneson and Litzguz 2008; Portela et al. 2010; López-Mata 2013), sustainable exploitation of non-timber forest products (Schmidt et al. 2011; Venter and Witkowski 2013) and predictions of a population’s future (Crone et al. 2013). PMMs have shown both successes and failures in predicting tree population behaviour (Bierzychudek 1999; Schodelbauerová et al. 2010; Crone et al. 2013). Despite occasional model failure, PMMs are still a useful tool in elaborating conservation strategies and may be used to reduce chances of undesirable outcomes for endangered species (Crone et al. 2013). PMMs are especially important for long-lived species, because population trends are difficult to define for these species without the use of these models.

Long-lived species are either climax or pioneer species of large size (Turner 2004). In a climax species, seedlings and saplings are shade-tolerant and grow beneath the canopy layer, promoting a continuous replacement of older trees without severe disturbance regimes (Gutiérrez et al. 2008), also referred to as ‘continuous regeneration’ (Ogden and Stewart 1995). However, in long-lived pioneers, it is usual to find stands with a high density of mature trees while exhibiting complete absence of seedlings and saplings (Ogden 1985; Enright et al. 1999; Turner 2004), because saplings of long-lived pioneers are frequently shade-intolerant and are not able to grow under a dense tree canopy. In some long-lived species and canopy-dominant species, the appearance of seedlings and saplings will depend upon the occurrence of an episodic landscape-level disturbance, such as the dieback of a large number of mature trees (Boehmer et al. 2013) and landslides or wind-throw from storms (Pollmann and Veblen 2004). In other long-lived species, the appearance of seedlings and saplings will depend upon the occurrence of large-scale disturbances, as was found for *Agathis australis* in New Zealand, whose behaviour can be described by the stand replacement model called the Lozenge model (Ogden 1985; Ogden and Stewart 1995).

The Lozenge model states that population regeneration occurs periodically through a gap-filling event that is structured into cohorts after disturbances (Ogden and Stewart 1995). After a cohort dies, which can occur up to 1,000 years after its establishment, it is replaced by a new generation. This model has three main phases: establishment, thinning and senescence. The establishment phase is marked by a rise in the population after a major disturbance, where the first seedling cohort is recruited aided by pioneer nurse plants, and the individuals’ density and biomass increases. The second stage is the thinning phase, where
the individuals’ density decreases through a self-thinning process and biomass remains constant or increases. In this phase, *Agathis australis* had a basal area up to 56 m² ha⁻¹ (Enright et al. 1999). The forest also exhibits a pattern of high-density mature trees and it is often characterised by seedling and sapling absence (regeneration gap; Enright et al. 1999). The third stage is the senescence phase, where the density and biomass of the first cohort decreases, and now a second seedling cohort begins to replace the old mature trees through a natural regeneration process. There may be small gaps and seedlings present in other phases, but no recruitment will occur until the first cohort enters the senescence phase (Ogden 1985; Ogden and Stewart 1995). The Lozenge model has also been utilised to examine the life history of *Araucaria hunteinii* in New Guinea and *A. laubenfelsi* in New Caledonia (Enright et al. 1999).

The regeneration of *A. angustifolia* populations, considered a long-lived pioneer species, can also be described by the Lozenge model (Souza 2007; Souza et al. 2008). However, previously predictions for *A. angustifolia* using the Lozenge model were tested using stem size distributions (Souza 2007), and size distributions are not always the best descriptor for population trends (Feeley et al. 2007; Virillo et al. 2011). Therefore, one might question whether this model could predict the temporal changes in descriptors of a conserved *A. angustifolia* population.

If the Lozenge model is suitable in describing the *A. angustifolia* regeneration strategy, the population dynamics predictions will suggest that a group of established individuals will exhibit longevity at a site, possibly attaining hundreds of years until senescence and death (first prediction) (Ogden and Stewart 1995). Furthermore, it is expected that the population’s growth rate, changes in biomass, and sapling abundance follow a pattern indicating its status in one of the proposed model’s three phases (second prediction).

Moreover, *Araucaria angustifolia* is one of the most endangered *Araucaria* species, as well as one of the most poorly understood regarding stand dynamics (IUCN 2013). Its distribution spans the southern part of South America (originally it covered nearly 98.96% of southern Brazil and 1.03% of Argentina; IUCN 2013), under the Araucaria Forest domain, which originally spanned an area of 25.4 Mha. *Araucaria angustifolia* has a great socio-cultural and economic importance throughout its natural distribution because it produces large edible seeds and timber (Reis and Ladio 2012). Of the original occurrence area of the Araucaria forests in Brazil, only 0.65% are legally protected (Ribeiro et al. 2009). In addition, the seeds are exploited by local seed collectors with no control throughout its area of distribution, including parks designated for its protection. Because of the man-made threats to the tree species, research on population trends are biologically important.

This study aimed to test the hypothesis of whether *Araucaria angustifolia* follows the Lozenge regeneration model. In order to test this hypothesis, two predictions were established for the model, which are stated above. Furthermore, this study also attempted to analyse population descriptors for an *A. angustifolia* population over time through a matrix model.

The study seeks to answer the following questions: What are the population trends in a developed Araucaria forest? Will the population remain stable, increase or decrease over time? Are seedling and sapling abundance important for the population’s growth rate?

**Material and methods**

**Study area and data collection**

The old growth forest used in this study is located in the Caçador Genetic Forest Reserve (CGFR), in the municipality of Caçador, state of Santa Catarina, southern Brazil. The reserve is situated between the coordinates 26°49′ and 26°53′ S and 50°59′ and 50°53′ W, with an altitude between 920 m and 1 075 m (Kurasz et al. 2008). It is a forest fragment with an area of 1 157.48 ha. The vegetation type is Mixed Ombrophilous Forest, also known as Araucaria Forest, and is found in the Atlantic Forest biome hotspot (Myers et al. 2000). The old growth forest in this study refers to a forest with numerous large long-standing trees. A plot was installed inside the old growth forest in an area with no evidence of selective logging during the past 80 years.

The target population consisted of all *A. angustifolia* individuals, from seedlings to adults within a 5.1 ha (300 m × 170 m) plot. Each individual was identified, mapped with X and Y coordinates using a topographic survey, and followed annually from 2007 to 2013 in January, totalling seven assessments in six years.

Data were collected on the life status of the individual (alive or dead), diameter at breast height (DBH) for trees with height ≥ 1.5 m, and the presence of lateral branches along the stem and total height for trees < 1.5 m. During the subsequent years from 2008 to 2013, recruits (new individuals and recently germinated individuals) were also mapped and evaluated for the same descriptors as the others. These data were used to determine to which class the individual belonged during each year.

**Data analysis**

A Lefkovitch matrix model (LMM) (Lefkovitch 1965) was used to estimate the population’s longevity and growth rate, as well as the population trends and the role of seedlings and saplings in population growth. This method was adapted from age-based matrix models, developed mainly for animals (Leslie 1945). The LMM does not require knowledge of the individual’s age, but requires the population’s division into different stages or classes (Lefkovitch 1965).

Therefore, individuals were classified into five categories: (1) seedlings (SE) were post-germinated individuals without any lateral ramifications; (2) juvenile I (J1) were individuals with height < 1.5 m, possessing lateral ramifications; (3) juvenile II (J2) were individuals with height ≥ 1.5 m and DBH < 10 cm; (4) immature (IM) were individuals with DBH ≥ 10 cm and < 29.2 cm; and (5) potentially reproductive (PR) were individuals with a probability >50% of being in the reproductive phase, taking into consideration DBH ≥ 29.2 cm. This DBH was estimated according to the diometric relationship with the reproductive phase established in Paludo et al. (unpublished data).
for the CGFR. The relationship was expressed by the following equation:

\[
DBH = \ln((1 - P)^{-1} - 1) + 7.61299 \cdot 0.26070^{-1}
\]

where \( \ln \) is the natural logarithm, \( P \) is the probability of an individual being in the reproductive phase, and \( DBH \) the diameter at breast height.

In old and large trees \( DBH \) measurements are susceptible to errors such as expansion or contraction of bark thickness induced by atmospheric conditions or simply due to random errors. Initially, in order to avoid such problems, a regression between size and year was calculated, which generated an equation with the coefficients \( (b - DBH \) growth rate) for each individual. Secondly, during each year, the size of each individual was estimated through the calculated regression. This procedure allowed for the estimation of the size of each individual every year, and reduces variations as well as random errors between size measurements.

It is important to note that for \( A. \) angustifolia, seed quantity was slightly correlated to the size of the reproductive tree measured \( (r = 48\% \) for basal area and \( r = 58\% \) for height; Mantovani et al. 2004).

Transition probabilities for each class were stasis (remaining within the same class; \( S \)), advancing classes (\( G \)) or death (\( D \)). Those probabilities were calculated using the observed data and class criteria for each year. Afterwards, five matrices were assembled, one for each annual transition between 2008 and 2013. Fecundity was estimated as the number of seedlings found in 5.1 ha, divided by the number of PR and multiplied by the category’s stasis for the specified year (Caswell 1989). The transition matrix used for the analysis was generated with the transition elements specified year (Caswell 1989). The transition matrix used for the analysis was generated with the transition elements specified year (Caswell 1989).

Results

During the study the population showed an average of 113 (22 individuals ha\(^{-1}\)) SE, 136 (27 individuals ha\(^{-1}\)) J1, 107 (21 individuals ha\(^{-1}\)) J2, 99 (19 individuals ha\(^{-1}\)) IM and 144 (28 individuals ha\(^{-1}\)) PR within 5.1 ha, totaling 117 individuals ha\(^{-1}\). The generated transition matrix was summarised in the population’s life cycle (Figure 1). In the study area, only the seeding process produced new individuals. In this unlogged site, no resprouting individuals or vegetative propagation were recorded. Female PR produced seeds that generated SE and sometimes J1. A seed could only generate a J1 when the individuals grew fast and grew ‘branches’ prior to the first census after the seeds fell.

The mortality rates (\( D \)) for the categories PL, J1, J2, IM and PR were, respectively, 0.795, 0.196, 0.064, 0.022 and 0.003. The transition between categories followed a similar

\[
D = 1 - S - G
\]

The long-term population growth rate was estimated by calculating the population’s finite growth rate (\( \lambda \)), using the dominant eigenvalue of the matrix (Caswell 1989). Confidence intervals with 95% probability were constructed for this value using bootstrap resampling and the percentile method (Caswell 1989). To compute the percentile method, each category had its individual frequency fixed, and the transitions (\( S, G \) or \( D \)) were randomly selected over 100 000 times with replacement (Maloney 2011). When no death appeared in a class within the randomly selected matrices, a mortality rate of 0.001 was assigned. In each iteration a randomly selected fecundity value was assumed from a set containing five field-observed values \( (n = 5; \) from 2008 to 2013). The elasticity analysis was used to access the relative participation of each transition element in \( \lambda \).

Indicators of the species longevity were also calculated using each class size divided by the class’s average growth rate, suggesting the possible amount of time that an individual tree could remain in the class (Rigg et al. 2010).

Basal area was used as an approximation to biomass measurement in order to verify increases or decreases in biomass for the second prediction. The basal area was calculated for 2007 and 2013, and a confidence interval was constructed using 100 000 randomly selected iterations for the same amount of individuals in a population corresponding to the year in question. According to the asymmetric distribution of this descriptor, a non-parametric comparison test was used (Zar 2010). A two-sample Wilcoxon test (Zar 2010) was used for non-paired samples.

Analyses were performed using the R software (R Core Team 2012), in association with the popbio package (Stubben and Milligan 2007).

Figure 1: Population life cycle of Araucaria angustifolia at the Caçador Genetic Forest Reserve, Santa Catarina State, Brazil. The circles represent the different stages (SE = seedling, J1 = juvenile 1, J2 = juvenile 2, IM = immature, PR = potentially reproductive). The horizontal lines represent stage advancement, the lower lines represent permanence within a class and the upper lines represent fecundity accompanied by their respective probabilities of occurrence between each census, determined by the six annual censuses in a 5.1 ha plot.
pattern of reduction, where the larger the size the lower the transition rates (Figure 1).

The population’s growth rate ($\lambda$) was 0.9977, close to 1 (95% CI: 0.9864 < $\lambda$ < 1.002; CI based on 100 000 bootstrap resampling). The distribution of $\lambda$ values obtained through bootstrap resampling is shown in Figure 2. Elasticity was mainly distributed in the stasis of PR individuals, and secondly in the stasis of IM individuals, with a low participation from other transitions (Table 1).

The growth in height for J1 was 0.0436 m y$^{-1}$. Whereas the growth in DBH for J2 was 0.0952 cm y$^{-1}$, for IM it was 0.110 cm y$^{-1}$ and for PR it was 0.419 cm y$^{-1}$. The time given by the ratio between growth rate and size for each category was 29.5 years for J1 (considering that individuals of age 1 year have a 0.20 m height), 105.0 years for J2, 174.5 years for IM, and 286.9 years for PR. In total, the time between germination until the current moment for the largest individual (149.4 cm) in the plot was estimated to be 595.9 years.

The population’s basal area in 2007 was 12.1 m$^2$ ha$^{-1}$ (CI 95% using the percentile method: 9.9–14.4 m$^2$ ha$^{-1}$), and for 2013 it was 12.8 m$^2$ ha$^{-1}$ (CI 95% using the percentile method: 10.6–15.2 m$^2$ ha$^{-1}$). The distribution of $\lambda$ values obtained for 2013 it was 12.8 m$^2$ ha$^{-1}$, $0.110$ cm y$^{-1}$ years was not significant ($\lambda < 1$ (95% CI: 0.9864–1.002), the present population in Santa Catarina, this population had a recruitment rate of 0.75 individuals y$^{-1}$ adult$^{-1}$, which can be contrasted to A. laubenfelsii whose average rate was 104 individuals y$^{-1}$ adult$^{-1}$ and $\lambda$ consistently >1 (Rigg et al. 2010). Araucaria muelleri had an average rate of 0.585 individuals y$^{-1}$ adult$^{-1}$, with $\lambda$ close to 1 (Enright et al. 2013). In contrast, for Carya glabra in the USA, even with recruitment of 18.5 individuals y$^{-1}$ adult$^{-1}$, the projection indicated a population decline (Evans and Keen 2013). With the exception of A. muelleri, which shows one of the highest known survival rates (Enright et al. 2013), it can be concluded that the number of recruits for A. angustifolia is low relative to other studies, indicating that these rates may be insufficient to guarantee the maintenance of adult individuals in the population. Some of the causes for this may be the high demand for A. angustifolia seeds by humans (IUCN 2013) and small rodents (Iob and Vieira 2010).

**Finite population growth rate ($\lambda$) and longevity**

For the A. angustifolia population in Santa Catarina, this study found a $\lambda$ close to 1 ($\lambda = 0.9977$, CI$_{95\%}$ = 0.9864–1.002), but with a large concentration of values <1 (Figure 2). In two populations of A. laubenfelsii in New Caledonia, which is also a long-lived pioneer, a $\lambda$ consistently >1 (from 1.013 to 1.184) was found (Rigg et al. 2010). Furthermore, in New Caledonia in four A. muelleri populations, the average $\lambda$ was 1.0020, varying from 0.9955 to 1.0039, with all CI values including the value 1 (Enright et al. 2013). For the species A. hustinii and A. cunninghamii in New Guinea, $\lambda$ values ranged from 1.055 to 1.010, respectively (Enright et al. 1995). The first prediction (a group of established individuals will exhibit longevity at a site, possibly reaching hundreds of years until senescence and death) is confirmed by the $\lambda$ found for A. angustifolia, plus the time given by the ratio between growth rate and class size of 595.9 years, where the species exhibits high longevity. When only considering the demographic rates ($\lambda = 0.9977$, CI$_{95\%}$ = 0.9864–1.002), the present population will persist for a long time at the study site, unless affected by a catastrophic event. As an example of the species longevity, a deterministic projection of $\lambda$ for the studied population indicates that 50% (59 individuals ha$^{-1}$) of individuals (117 individuals ha$^{-1}$) would remain for 301 years, and 10% (12 individuals ha$^{-1}$) for 999 years.

### Table 1: Elasticity matrix calculated from an average transition matrix of an A. angustifolia population in a forest area in Santa Catarina State, southern Brazil. The data were obtained from seven annual censuses in a 5.1 ha plot (170 m x 300 m). SE = seedling, J1 = juvenile 1, J2 = juvenile 2, IM = immature, PR = potentially reproductive.

<table>
<thead>
<tr>
<th>Category at time</th>
<th>SE</th>
<th>J1</th>
<th>J2</th>
<th>IM</th>
<th>PR</th>
</tr>
</thead>
<tbody>
<tr>
<td>time $t+1$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SE</td>
<td>0.000003</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>J1</td>
<td>0.000320</td>
<td>0.001866</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>J2</td>
<td>0</td>
<td>0.000485</td>
<td>0.006348</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>IM</td>
<td>0</td>
<td>0</td>
<td>0.000485</td>
<td>0.016860</td>
<td>0</td>
</tr>
<tr>
<td>PR</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.000485</td>
<td>0.972661</td>
</tr>
</tbody>
</table>
unsuitable microsites or some other process that has not been studied or was not considered, because this was not the objective of the present study. It is possible that the low recruitment is the first ‘bottleneck’ of A. angustifolia regeneration; this aspect should receive more attention and additional research is needed to explain the main causes of this pattern.

Moreover, in the present study, the recruitment elasticity and transition elements of the classes PL, J1 and J2 were low. Longevity in the studied population is due to the already initially established trees in the PR category (Table 1), which possess a low mortality rate and may remain for a long time within the population. The concentration of elasticity in the last class’s stasis is an expected pattern for forest tree species (Watkinson 1997) and for long-lived conifers (e.g. Kwitt et al. 2004; Enright et al. 2013), which may indicate a possible characteristic of long-lived species for model matrices. Meanwhile, according to the \( \lambda \) distribution values obtained through iterations (Figure 2), \( \lambda \) is basically determined by the annual mortality rate of the PR individuals. A value of \( \lambda > 1 \) (for \( t = 1 \) year) was observed only in iterations where no PR died (Figure 2a). In iterations where at least one PR individual died, \( \lambda \) was always less than 1 (Figure 2b and c), and the peaks in the simulation distributions coincide with the number of dead PR individuals (Figure 2a–c). This result indicates that the random selection of individual transitions in all of the other categories did not cause variations in \( \lambda \) greater than those caused by the deaths of the PR. Araucaria angustifolia seedlings and saplings were present at the study site (about 70 individuals ha\(^{-1}\)), but the results indicate that the seedlings and saplings were insufficient to completely replace the deaths of the PR individuals in the observed conditions. Random selection generated different transition rates for each class and, even then, this did not promote significant increases in \( \lambda \). Given that the number of recruits per year was low compared with other species, such results suggest a regeneration failure in the current conditions. According to Turner (2004) for a long-lived pioneer species, the regeneration categories might be absent when referring to a mature stand.

The reasons for such a failure were not evaluated in the present study and are not sufficiently known for A. angustifolia. Although A. angustifolia seedlings and saplings are able to live under low light availability (Duarte et al. 2002), the results of the present study showed negligible transitions between classes. Several hypotheses can be formulated to help explain the regeneration failure, for example (1) the slow growth of individuals with low light availability and (2) damage to and death of trees caused by a wide range of herbivores (Crawley 1997). For Carya glabra, herbivory was indicated to be responsible for regeneration failure (Evans and Keen 2013). Drake et al. (2012) suggest that regeneration failure for A. araucana in Chile, which has characteristics similar to those of A. angustifolia, was possibly due to seed predation, low production of reproductive individuals and/or competition with fast-growing species.

Lozenge regeneration model

The basal area for the A. angustifolia population between 2007 and 2013 did not demonstrate significant differences. Schaaf et al. (2006) found an increase from 11.3 to 16.47 m\(^2\) ha\(^{-1}\) during a 21-year period for A. angustifolia, in a forest without clear-cutting, but with previous exploitation before the first survey. Considering the predominance of \( \lambda \) values < 1, the maintenance of basal area overtime, and the low participation of regeneration in \( \lambda \), the second prediction (it is expected that the population’s growth rate, changes in biomass, and sapling abundance follow a pattern indicating its status in one of the proposed model’s three phases) is not rejected, because it is possible to identify the population in the thinning phase of the Lozenge model.

It is expected that the population's future behaviour also will follow the Lozenge model, because the predictions constructed using the Lozenge model (Ogden and Stewart 1995) were able to predict the established behaviour. If this were to happen in practice, the population would gradually pass into the next phase, which will occur when the current adult population enters into senescence. Concurrently with senescence, the appearance of a large number of seedlings and saplings sufficient to form a new group of reproductive individuals is expected. However, to expect a new group to re-establish from senescent individuals may seem counter-intuitive. Boehmer et al. (2013) observed a similar situation for Metrosideros polymorpha in Hawaii, where episodic regeneration, denominated ‘waves of regeneration’, were found, even though the adult population was already in senescence.

The Lozenge model can be accepted for A. angustifolia, with hopes that in the future regeneration will appear in the population. Nonetheless, the present data suggests that the current regeneration is insufficient in this study area in Santa Catarina, and strong pressure exists on this species overall. In the twentieth century, at least 30 M\(\text{m}^3\) of A. angustifolia lumber was produced from native forests (Carvalho 2010), and currently the pressure on the species’ future is caused via by excessive seed collection (IUCN 2013). Collection occurs across the entire Araucaria forest area, with no locations being free of collection. Moreover, only 0.65% of Araucaria forests in Brazil are legally protected (Ribeiro et al. 2009). All these factors lead to greater risk of species extinction, especially since the species distribution is in a country that has recently approved changes in legislation that increase the reduction of native forest areas (Nazareno et al. 2011). Further studies should focus on the causes of the low number of individuals in the first developmental classes and the reasons for a limited entry of individuals.

Conclusion

The native population of A. angustifolia studied tends towards a very slow decline in the number of individuals, defined here as declining stability. The decline occurs because of the low recruitment of new individuals, and seedlings and saplings do not grow to the reproductive stage at rates that are equal or higher than the rate of deaths of the reproductive individuals. Nonetheless, the decline is very slow, and is closer to stability because the individuals in the reproductive stage exhibit expressive longevity.

However, the predictions regarding the Lozenge model were confirmed, and the results did not refute the hypothesis
that regeneration of *A. angustifolia* follows this model. Thus, the model predicts that regeneration should occur in the future, when the population enters into the next phase, i.e. senescence.

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