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Native tree regeneration in native tree plantations: understanding the contribution of *Araucaria angustifolia* to biodiversity conservation in the threatened Atlantic Forest in Argentina

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Abstract Deforestation is a global process that has strongly affected the Atlantic Forest in South America, which has been recognised as a threatened biodiversity hotspot. An important proportion of deforested areas were converted to forest plantations. *Araucaria angustifolia* is a native tree to the Atlantic Forest, which has been largely exploited for wood production and is currently cultivated in commercial plantations. An important question is to what extent such native tree plantations can be managed to reduce biodiversity loss in a highly diverse and vulnerable forest region. We evaluated the effect of stand age, stand basal area, as a measure of stand density, and time since last logging on the density and richness of native tree regeneration in planted araucaria stands that were successively logged over 60 years, as well as the differences between successional groups in the response of plant density to stand variables. We also compared native tree species richness in planted araucaria stands to neighbouring native forest. Species richness was 71 in the planted stands (27 ha sampled) and 82 in native forest (18 ha sampled) which approximate the range of variation in species richness found in the native forests of the study area. The total abundance and species richness of native trees increased with stand age and time since last logging, but ecological groups differed in their response to such variables. Early secondary trees increased in abundance with stand age 3–8 times faster than climax or late secondary trees. Thus, the change in species composition is expected to continue for a long term. The difference in species richness between native forest and planted stands might be mainly explained by the difference in plant density. Therefore, species richness in plantations can contribute to local native tree diversity if practices that increase native tree density are implemented.

Key words: basal area, ecological groups, functional, logging, stand age.

INTRODUCTION

Natural forest area in the tropics and subtropics is still declining, while planted forest area is increasing (Keenan *et al.* 2015). The Atlantic Forest is a biodiversity hotspot that has been particularly affected by this process. Only about 11–16% of the original area remains today (Ribeiro *et al.* 2009) in a fragmented landscape in south-eastern Brazil, north-eastern Argentina and eastern Paraguay (Myers *et al.* 2000). Conifer plantations constitute an important land use in the Atlantic Forest region today (Simberloff *et al.* 2009). The effect of forest plantations on biodiversity is a controversial issue (Bremer & Farley 2010). The replacement of native forest by tree plantations can have negative consequences on biodiversity (Lugo 1997; Lindenmayer *et al.* 2006; Zurita 2008). On the other hand, plantations can host more species than other agro-ecosystems (Hartley 2002; Brockerhoff *et al.* 2008).

Biodiversity in forest plantations depends on stand variables as well as the availability of seed sources (Ritter *et al.* 2018). For example, the diversity of different taxa is higher in native than in non-native tree plantations (Keenan *et al.* 1999; Hartley 2002; Fonseca *et al.* 2009). Stand age is also a relevant variable; greater native tree species richness and stem density

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have been found in older than in young plantations (Keenan *et al.* 1997; Barbosa *et al.* 2009; Dummel & Pinazo 2013; Ritter *et al.* 2018). However, this relationship is not necessarily linear (Senbeta *et al.* 2002) and can vary among species that have different requirements for regeneration (Keenan *et al.* 1997; Lugo 1997; Parrotta *et al.* 1997; Selwyn & Ganesan 2009). Moreover, stand structure usually changes with time as a consequence of tree growth and the applications of silvicultural treatments which reduce the stand density (logging or thinning) (Trentini *et al.* 2017). Ritter *et al.* (2018) found a negative relationship between the density and species richness of native trees established in loblolly pine plantations, and the stand basal area (m^2 ha^{-1}), after controlling for the effect of stand age. These authors also found that, among plantations of similar age, stand basal area was a better indicator of the negative effect of planted trees on the density and species richness of establishing native tree species than the density and mean square diameter of planted trees. The negative effect of stand basal area can be changed by silvicultural treatments such as logging and thinning (Nagai & Yoshida 2006; Trentini *et al.* 2017).

Thinning in young and dense stands enhances understory plant diversity due to environmental changes associated with the reduction in basal area, as well as an increase in resource availability (Utsugi *et al.* 2006; Seiwa *et al.* 2012; Trentini *et al.* 2017). However, it has also been suggested that logging and thinning can have negative consequences on understory species richness by promoting an increase in few dominant light-demanding species (Nagai & Yoshida 2006; Barbosa *et al.* 2009). These interventions can also cause mechanical damage to native seedlings and saplings (Duncan & Chapman 2003; Trentini *et al.* 2017).

Structural changes associated with stand age can also influence dispersal processes. The colonisation of plantations by native tree species is highly dependent on seed arrival from forest remnants (Hoppes 1988; Nathan & Muller-Landau 2000; Groeneveld *et al.* 2009; Ritter *et al.* 2016). Mature stands exhibit higher habitat permeability for seed dispersers than young stands (Vespa *et al.* 2014). Studies carried out in tropical and subtropical forests found that the abundance of zoochoric tree species increases with time since disturbance in nonmanaged forests and plantations (Chazdon 2003; Tabarelli *et al.* 2010; Medeiros do Nascimento *et al.* 2014). This relationship was attributed to structural complexity, which increases with stand age, and plays an important role attracting seed dispersers (Parrotta *et al.* 1997; Vespa *et al.* 2014).

Araucaria Forest is a forest type in the Atlantic Forest from South America (Rambo 2000), where the main canopy tree is *Araucaria angustifolia* (Bertol) Kuntze. Araucaria trees were harvested for wood production, and the forest was transformed for agriculture and cattle ranching in the last century (Sebbenn *et al.* 2003). Because of such land use changes, only about 17.2% the forest's original area remains (Ribeiro *et al.* 2009). In Argentina, there are about 16 500 ha of araucaria commercial plantations, which are managed for wood production. An important question is to what extent native tree plantations can be managed to reduce biodiversity loss in a highly diverse and vulnerable forest region. Functional traits or groups are useful for discriminating species with different requirements for regeneration in tropical forests (Laurans *et al.* 2012). The functional approach could help to understand regeneration dynamics in forest plantations. Atlantic Forest tree species have been split along a gradient from pioneer shade-intolerant trees to late successional shade-tolerant trees (Carvalho 2003). Irrespective of the successional assumptions underlying such classification, species in a given group can be similar in the requirements for regeneration. Traits such as wood density and seed mass tend to increase from pioneer to climax groups such ecological classification reflects a functional gradient from shade intolerant to shade tolerant species (Medina M., unpubl. data, 2015).

We evaluated the effect of stand age and time since last logging on native tree regeneration in planted araucaria stands that were successively logged over 60 years, as well as the differences between ecological groups in response to stand variables. We specifically predicted that total abundance and species richness of native trees increase with stand age and time since last logging, but that different trends are expected for different ecological groups. The abundance of pioneer species is expected to decrease with stand age and time since last logging. In contrast, the abundance of nonpioneer species is expected to increase with stand age and time since last logging at rates decreasing from early successional to late successional and climax species. Finally, we expected that native tree species richness in the native tree plantation converges on the species richness of nearby Atlantic Forest remnants with time.

METHODS

Study area

This research was carried out in 'Campo Anexo Manuel Belgrano' (CAMB) north-eastern Misiones Province, Argentina, at 26°04′02″S and 53°45′00″W (Fig. 1). Mean annual precipitation is 2100 mm, evenly distributed throughout the year. Mean annual air temperature is 21°C, with monthly average of 26°C in January and 16°C in July. Frost events occur sporadically (Cabrera 1976). Soil is lateritic and was

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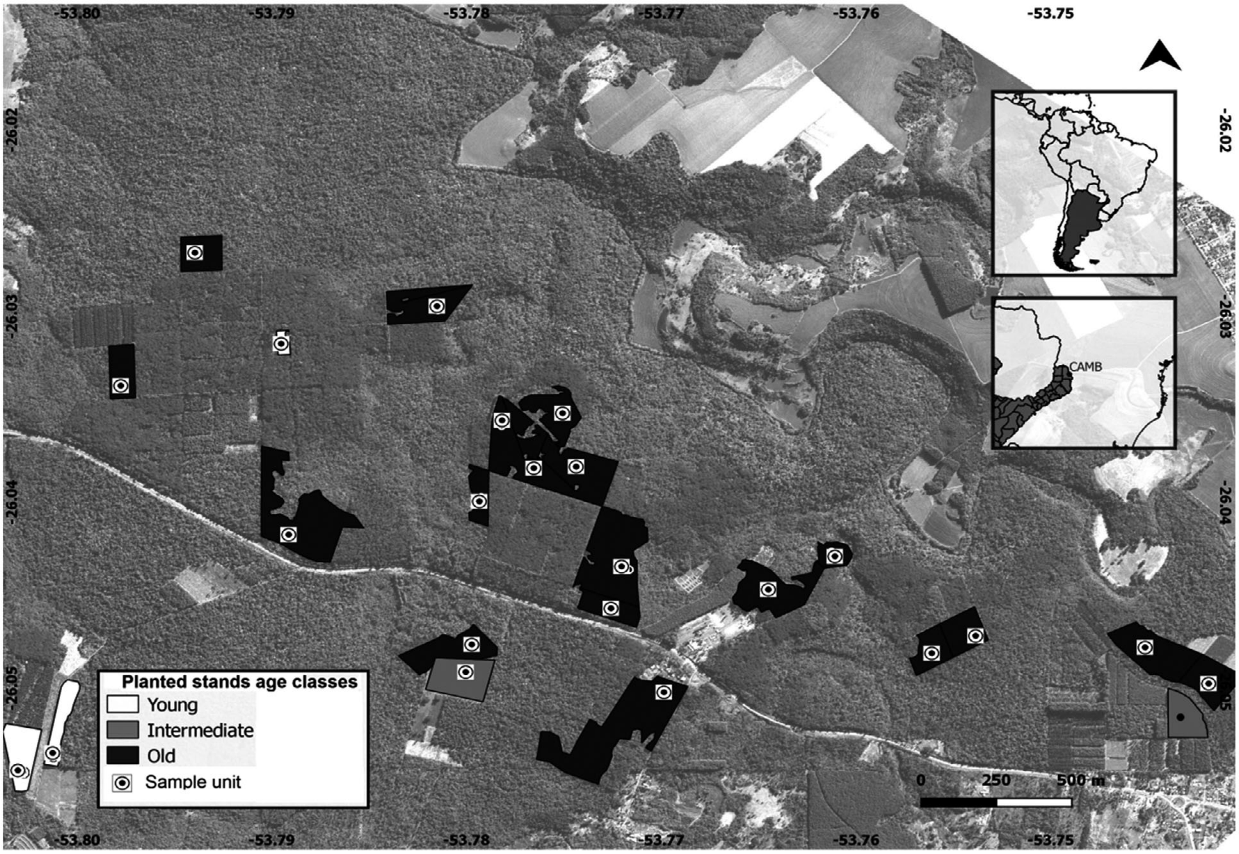

Fig. 1. Location of sampled planted stands in 'CAMB-EEA Montecarlo', north-eastern Misiones, Argentina. Young stands: <30 years; intermediate: 30–50 years; old: 50–67 years.

classified as Kandiudult, in a flat to hilly topography (Panigatti 2010). The canopy of the native forest is dominated by *A. angustifolia* followed by *Balfourondendron riedielanium* (Engl.) Engl (Cabrera 1976). Species of *Nectandra* and *Ocotea* dominate in the middle strata, while common subcanopy species are *Ilex paraguariensis* A. St.-Hil and *Myrsine balansae* (Mez) Otegui (Cabrera 1976). Woody bamboos, shrubs, vines, ferns and nonvascular plants form the lowest vegetation strata in this forest type.

A total of 450 ha of the area have been afforested with *A. angustifolia* for wood production and germplasm conservation in 105 stands in the CAMB experimental station. The afforested stands are surrounded by 1000 ha of native forest which has remained unlogged since 1955. In planted araucaria stands, chemical control of leaf-cutting ants was applied for the first two years after planting, while weeds were mechanically controlled for 20 years. Stands followed a similar temporal trend in tree density: initial densities were about 1000 trees per hectare. They were logged approximately every 15 years leaving a little more than 50% of standing trees each time, which is the usual management of commercial araucaria plantations in the region. The number of trees removed each time was not recorded, but it can be reasonably assumed that all stands were subjected to similar intensities of logging. Logging dates were taken from the records of the experimental station.

Vegetation sampling and stand variables

We selected 23 stands to represent the available range of stand age (13–67 years), time since last logging (2–30 years) and an appropriate spatial distribution. However, a balanced distribution of different combinations of stand age and time since last logging was not available. The selected stands exhibited at least 20% native forest cover in a 300 m radius circular area around the sampled stand, and were planted on sites previously covered by native forest. Mean stand area was 6.3 ha (0.8–14.1 ha).

The sample unit consisted of four 300-m^2 circular plots (9.78 m radius) located at the corners of a 30-m side square. This array of four circular plots better captures the spatial variability than a single plot of the same area (Kangas & Maltamo 2006). Each sample unit was located at least 20 m from the edge of the stand. In each sample unit, we recorded the diameter at 1.30 m height (DBH) of every individual tree stem greater than 5 cm DBH, by DBH and tree species. When it was not possible to identify sampled stems, plant parts were collected for later identification.

Every planted araucaria tree in a plot was recorded by DBH to estimate plantation density (trees ha^{-1}) and stand basal area (m^2 ha^{-1}). The same sampling scheme was applied in 15 native forests near araucaria planted stands. Native forest formed a continuous matrix in which araucaria planted stands were embedded. Sampled native forest stands were located no further than 100 m away from a sampled araucaria planted stand to avoid the influence of a potential spatial variation on the comparison of species richness. Species richness of araucaria plantation and native forest was estimated using species accumulation curves for individuals greater than 5 cm in DBH.

Ecological groups

The ecological group of each species was taken from Carvalho (2003): pioneer (P), initial secondary (IS), late secondary (LS) and climax (C) species. Dispersal groups were defined as zoochoric or nonzoochoric (anemochoric and other dispersal modes) based on the dispersal modes reported by Carvalho (2003).

Data analysis

Abundance (total individuals in each sample unit consisting of four plots at corner of each square) and species richness (number of species in each sample unit) were estimated for each stand. We calculated the abundance per ecological group as the number of individuals of each ecological group in each sample unit. The same procedure was applied for dispersal groups.

Species richness, abundance and the abundance per ecological group were used as response variables in three different general linear models (GLMs). These variables were counts, and therefore, we assumed a Poisson distribution using a 'log' link function. We also used binomial GLMs with link 'logit' to analyse the variations in the ratio between the abundance of zoochoric and nonzoochoric individuals. Quantitative predictors were the density of araucaria, basal area of araucaria, stand age and time since last logging.

We tested the correlation between predictors using the Pearson correlation coefficient (*r*). We followed the criterion recommended by Dormann *et al.* (2013) to avoid collinearity in the linear models. These authors recommend selecting one of two explanatory variables if the absolute correlation coefficient between them is larger than 0.7. We fitted GLMs including different combinations of the explanatory variables based on the hypothesis we were testing, rather than using automatic procedures. The best models were selected based on the Akaike information criterion (Burnham & Anderson 2002). Using fitted models, we predicted total species richness, total abundance and the abundance per ecological group for a simulated stand between 20 and 70 years after plantation which was logged every 15 years. Since the available stands made balanced combination of explanatory variables not possible, exploratory analysis of raw data and fitted values was used to avoid spurious interpretations as recommended by Zuur *et al.* (2010).

We estimated the number of species in planted araucaria stands and native forest surrounding the stands from species accumulation curves based on cumulative sampling units and cumulative individuals. Species richness of planted araucaria stands and native forest was compared based on the confidence intervals calculated for each accumulation curve. We used the function 'specaccum' in R package 'vegan' (Oksanen *et al.* 2018) with the method 'exact' for survey site accumulation and 'rarefaction' for individual accumulation curves.

RESULTS

Native tree species richness in planted araucaria stands and native forest

We recorded a total of 71 species and 59 genera belonging to 27 families in planted araucaria stands (2.7 ha sampled; Appendix S1). In the native forest, we recorded 82 species and 56 genera belonging to 30 families (1.8 ha sampled). Five families Fabaceae, Myrtaceae, Rutaceae, Euphorbiaceae and Lauraceae accounted for at least 70% of the sampled individuals in planted araucaria stands and native forest (Table 1).

Table 1. Plant species richness by family in planted araucaria stands and native forest

Family	Native forest	Planted araucaria stands
Fabaceae	14	14
Myrtaceae	7	5
Rutaceae	5	5
Euphorbiaceae	5	4
Lauraceae	5	3
Sapindaceae	4	3
Salicaceae	5	5
Solanaceae	2	4
Boraginaceae	3	3
Meliaceae	4	2
Apocynaceae	3	2
Araliaceae	2	2
Bignoniaceae	2	2
Sapotaceae	2	2
Ulmaceae	2	2
Aquifoliaceae	2	1
Annonaceae	1	1
Asteraceae	1	1
Erythroxylaceae	1	1
Malvaceae	1	1
Melastomataceae	1	1
Myrsinaceae	1	1
Nyctaginaceae	1	1
Simaroubaceae	1	1
Symplocaceae	1	1
Urticaceae	1	1
Araucariaceae	1	0
Polygonaceae	0	1
Rosaceae	0	1
Arecaceae	1	0
Lamiaceae	1	0
Moraceae	1	0
Rubiaceae	1	0

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Zoochory was the most frequent dispersal syndrome (about 68%). Among the nonzoochoric species, a total of 20% were anemochoric. Pioneer species accounted for 23% of species found in planted araucaria stands, while 33% were initial secondary, 39% were late secondary, and 6% were climax. About 90% of sampled native trees ranged between 5 cm and 20 cm in DBH.

About 70% of the tree species we found in the native forests were also found in planted araucaria stands. Species accumulation curves reflected lower species richness in planted araucaria stands than in native forest when they were based on species–area and species–individual accumulation (Fig. 2).

Native tree abundance and species richness as a function of stand variables

The density of araucaria was higher in young than in mature planted stands because of successive logging, while basal area exhibited the opposite trend (Appendix S2). Since the density of araucaria and stand age were negatively correlated ($r = -0.76$, $P < 0.05$), we performed GLM with the stand basal area of araucaria, stand age and time since last logging. The density and species richness of establishing trees increased with stand age (Table 2). However, the abundance and species richness remained almost constant 30–40 years after plantation establishment (Fig. 3). Species richness in stands logged less than 5 years before sampling was more variable (0–28 species) than in those logged more than 5 years before sampling (20–31 species; Fig. 3) which was also apparent in the plot of plant density and species richness as a function of planted stand age.

A positive effect of stand age and time since last logging on plant abundance and species richness was found for species grouped as initial secondary, late secondary and climax (Table 3). On the other hand, the abundance of pioneer species was negatively affected by time since last logging but no effect of stand age was observed. A negative effect of stand basal area on plant density was only observed for late secondary species. The zoochoric/nonzoochoric ratio decreased with stand age and time since last logging (Table 3). Modelled data also reflected that total abundance and species richness, and the abundance of early secondary trees, recovered about 5 years after logging (Fig. 4), but the abundance of late secondary and climax trees took a longer time to recover after logging.

DISCUSSION

Native tree species richness in planted araucaria stands and the native forest

The number of tree species found in planted araucaria stands (71 species) indicates that an important proportion of the species present in native forests can establish and grow in long-living plantations. The native forests exhibited higher species richness (82 species) than that estimated in a larger sampling of forest composition in the study area in which 64 species were found for trees ≥30 cm DBH (Moscovich *et al.* 2010), probably because smaller trees were included in our sampling (>5 cm DBH). Moreover, studies in forest remnants in different conservation stages in the Atlantic Forest in Argentina reported

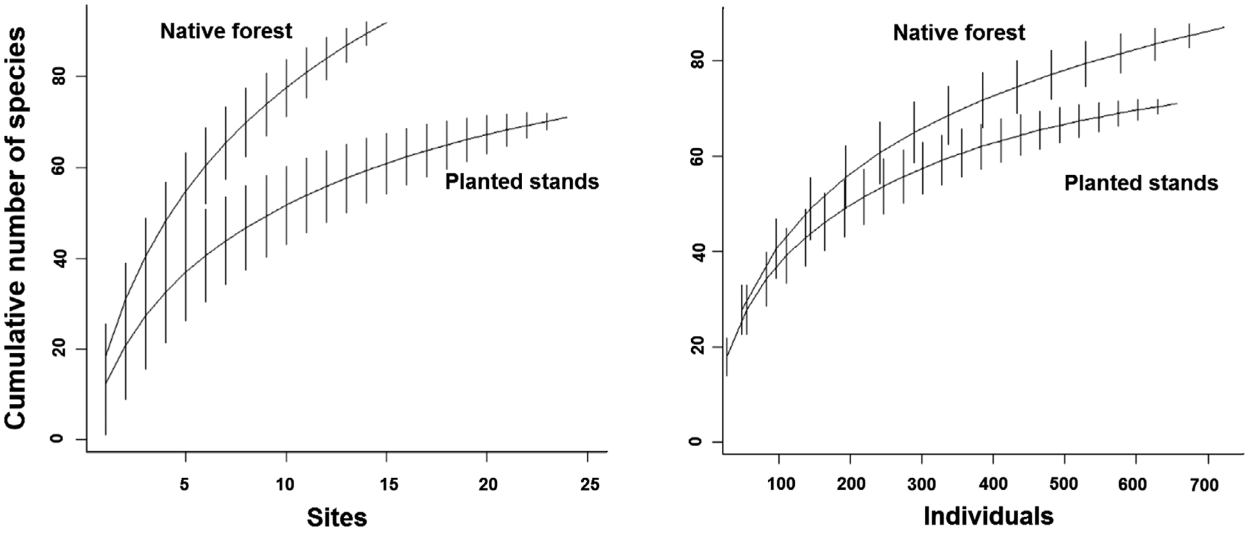

Fig. 2. Rarefaction curves for native trees greater than 5 cm DBH in araucaria planted stands and in native forest.

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Table 2. Mean plant abundance and species richness per stand age-class, ecological group and dispersal mode

		Plant abundance (plants per sample unit)		Species richness (species per sample unit)	
Age range (years)	Ecological group	Zoochoric	Nonzoochoric	Zoochoric	Nonzoochoric
17–19 (*n* = 3)	Pioneer	11 (7–15)	7 (4–9)	1 (1–2)	1 (0–2)
	Initial secondary	12 (8–17)	3 (0–7)	1 (0–1)	1 (0–1)
	Late secondary	6 (2–11)	1 (0–2)	1 (0–1)	1 (0–1)
	Climax	0	0	0	0
33–37 (*n* = 2)	Pioneer	6 (2–10)	5 (1–8)	1 (0–2)	1 (0–2)
	Initial secondary	34 (18–50)	17 (7–27)	10 (5–15)	5 (2–7)
	Late secondary	15 (12–18)	3 (0–6)	5 (0–10)	2 (1–3)
	Climax	6 (2–10)	2 (0–4)	1 (0–2)	1 (1–1)
52–67 (*n* = 18)	Pioneer	18 (14–23)	4 (0–6)	2 (0–3)	1 (0–2)
	Initial secondary	29 (16–37)	11 (5–14)	7 (3–12)	5 (1–8)
	Late secondary	15 (12–26)	4 (0–7)	4 (3–4)	3 (0–8)
	Climax	1 (0–3)	9 (6–13)	2 (2–2)	2 (0–3)

n, number of stands; minimum and maximum abundance and richness are indicated between parentheses.

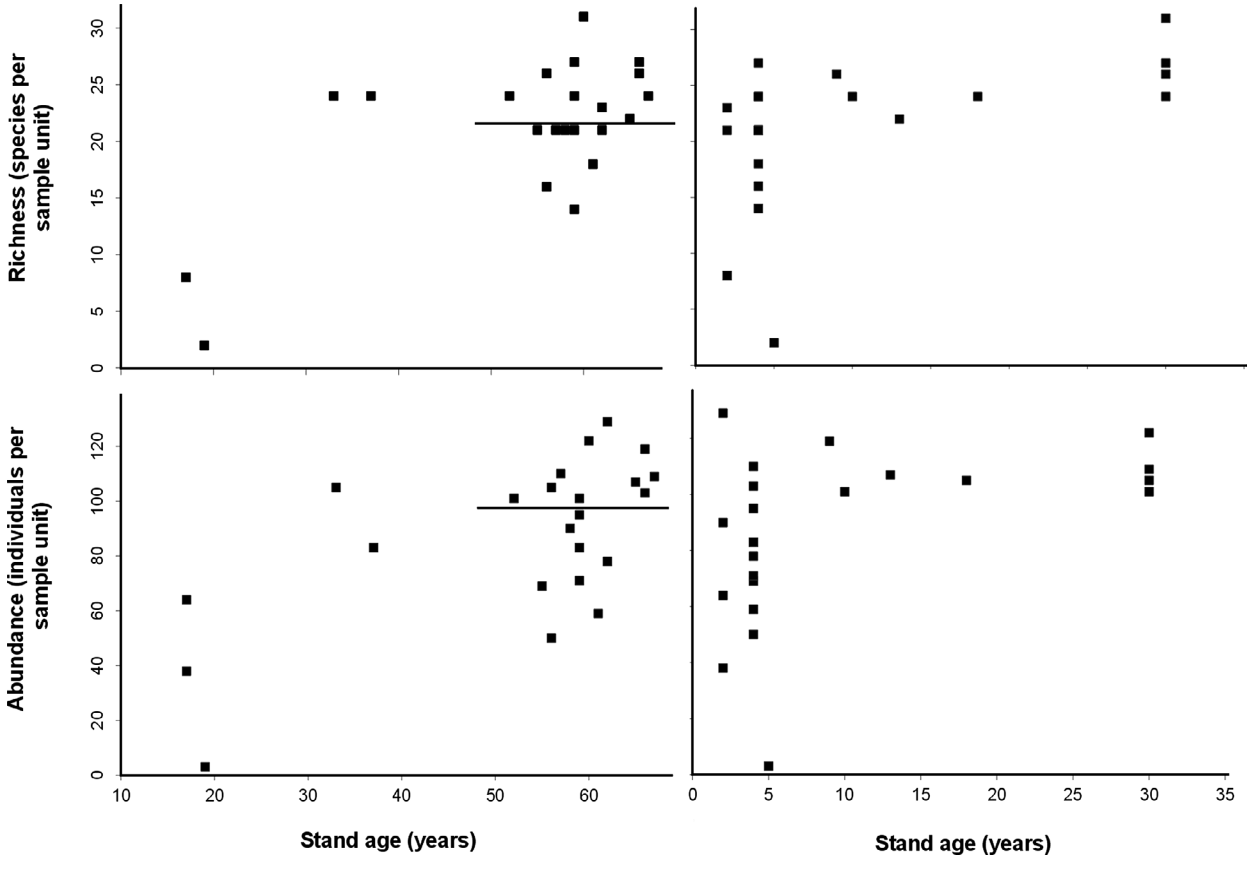

Fig. 3. Species richness and plant abundance of native trees established in araucaria planted stands as a function of stand age and time since last logging. Old stands (filled squares), intermediate stands (empty squares) and young stands (empty circles). Mature stands below the horizontal line were logged at most 5 years before sampling.

tree species richness (>10 cm DBH) ranging between 72 and 89 species (Placci *et al.* 1992; Placci & Giorgis 1993; López Cristóbal *et al.* 1996). Therefore, our studied native forest and planted araucaria stands approximate both the higher and the lower native tree species richness in the study area.

Table 3. Final generalised linear models for different dependent variables

Response variable	Parameter	Estimate	*Z*	*P*
Total species richness	Intercept	−0.098773	−0.163	0.8702 NS
	Time since last logging	0.008604	2.009	0.0446*
	Stand age	1.772972	5.047	4.49-07***
Total abundance	Intercept	1.865171	6.744	<1.54e-11***
	Time since last logging	0.008332	3.984	6.76e-05***
	Stand age	1.477120	9.151	<2e-16***
Zoochoric/nonzoochoric ratio	Intercept	1.579722	5.762	8.33e-09***
	Time since last logging	−0.018741	−3.736	0.000187***
	Stand age	−0.011298	2.356	0.018463*
Pioneer abundance	Intercept	0.0701	43.20	<2e-16***
	Time since last logging	−0.0296	−4.57	4.89e-06***
Initial secondary abundance	Intercept	0.22566	0.445	0.65666
	Time since last logging	0.010008	2.821	0.00479**
	Stand age	0.775543	6.054	1.41e-09***
Late secondary abundance	Intercept	−2.697737	−2.628	0.00858**
	Time since last logging	0.028396	5.516	3.46e-08***
	Stand age	1.328472	5.260	1.44e-07***
	Basal area	−0.013707	−2.082	0.03738*
Climax abundance	Intercept	−3.838688	−2.479	0.013166*
	Time since last logging	0.030920	4.262	2.03e-05***
	Stand age	1.317157	3.415	0.000638***

All models were fitted with Poisson distribution except for the zoochoric/nonzoochoric ratio, for which the binomial distribution was used. NS, not significant; *P*, probability of *Z*; *Z*, *z*-scores for inference on parameters. *$P < 0.05$; **$P < 0.01$; ***$P < 0.0001$.

The species accumulation curves calculated for native forest and araucaria plantations exhibited smaller differences when compared based on the same number of individuals than they exhibited when compared based on the same number of samples. This suggests that the difference in species richness between native forest and araucaria plantations might be at least partially explained by the difference in the density of establishing trees.

Native tree abundance and species richness as a function of stand variables

Few stands under 35 years old were available in the study site, but our results are clearly in agreement with the relationships between stand age and native tree establishment found in other studies (Keenan *et al.* 1997; Barbosa *et al.* 2009; Dummel & Pinazo 2013; Ritter *et al.* 2018). Stands older than 30 years exhibit higher species richness and higher abundance of late secondary trees than younger stands, which were dominated by pioneer or early secondary trees. Such variation in the abundance of functionally different native trees was also observed in forest plantations in Australia (Keenan *et al.* 1997). Different causes might be involved in such changes. First, the older stands had longer time for the colonisation and establishment by new tree species than younger stands. Second, stand structure changes with time, due to tree growth, mortality and logging, increasing the environmental heterogeneity. The establishment of species differing in ecological requirements can be promoted by changes in stand structure along the age. However, total native tree abundance and species richness remain almost constant 30–40 years after plantation. Similar results were found in araucaria plantations in Brazil (Barbosa *et al.* 2009). The total abundance and species richness might tend to increase slowly with stand age as the result of different trends in the abundance of different ecological groups, that is different species accumulation rates are expected between ecological groups. Early secondary tree species tend to increase in abundance 3–8 times faster than climax or late secondary tree species. The species richness of late secondary or climax tree species might need longer time than early successional tree species to approximate the stable state. The change in species composition may therefore continue for a long term.

The abundance of pioneer tree species did not exhibit an association with stand age. However, the abundance of such trees sharply increased after logging and then declined over time, irrespective of stand age, which is in contrast with the trends of other ecological groups. Logging reduced total plant density and species richness as is apparent in raw data as well as in the predicted values from GLM. Logging promotes an increase in light availability and air temperature (Trentini *et al.* 2017) as well as an

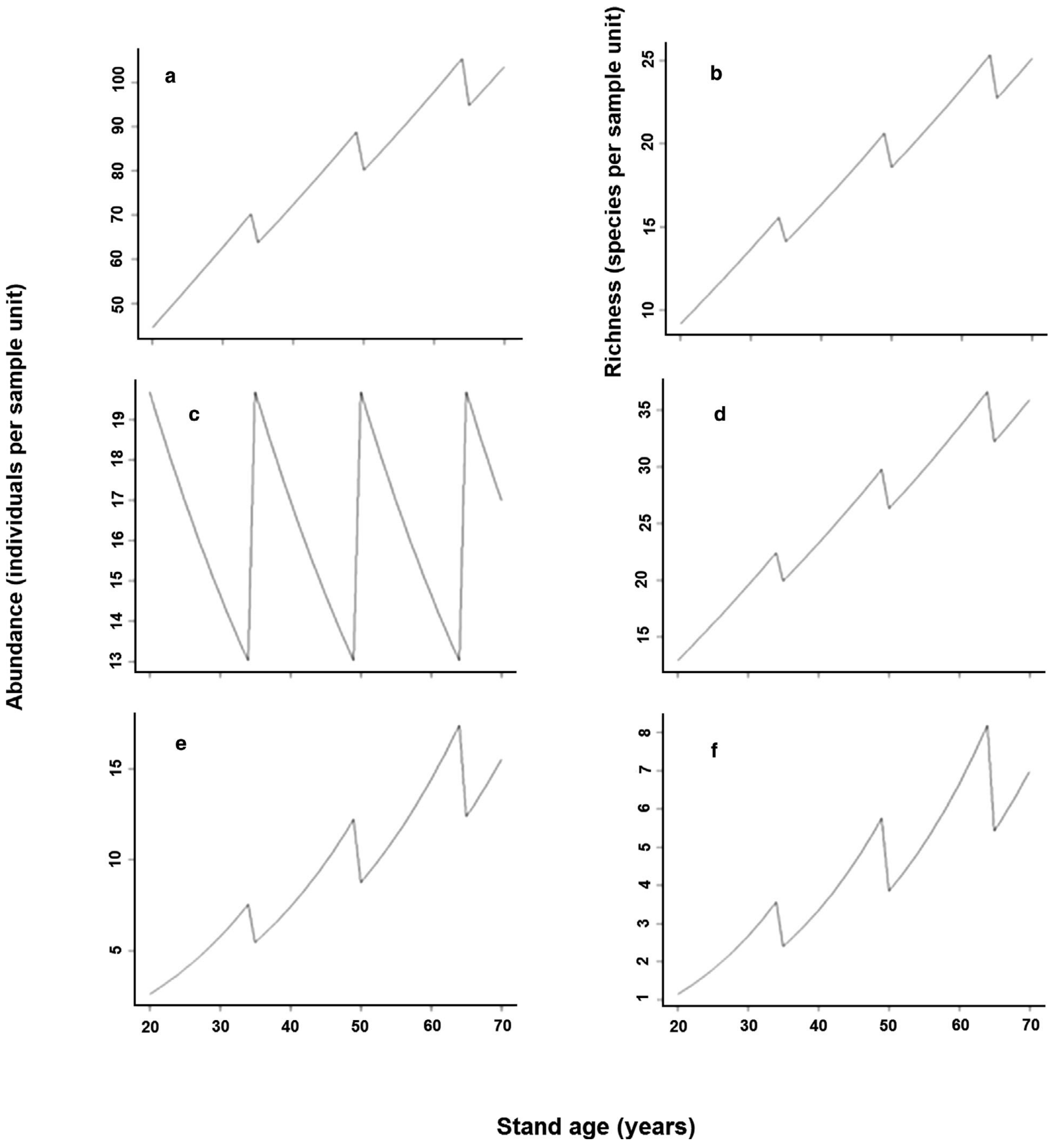

Fig. 4. Predicted values from the models fitted for total plant abundance (a), species richness (b) and the abundance for each successional group (c: pioneer species, d: early secondary species, e: late secondary species, f: climax species) for a simulated stand 20–70 years old, logged every 15 years.

increment in soil temperature and a reduction in litter accumulation (Utsugi *et al.* 2006; Seiwa *et al.* 2012). In such environmental conditions, light-demanding species are usually more efficient than shade-tolerant ones and are able to establish and grow faster (Campanello *et al.* 2011; Seiwa *et al.* 2012). Three of the most abundant pioneer trees in araucaria stands are well-known light-demanding, fast-growing, short-lived, small trees (*Cecropia pachistachya* Trécul., *Solanum granulosum-leprosum* Dunal, *Trema micrantha* (L.) Blume) which commonly establish from seed germination after thinning in recently thinned loblolly pine plantations in the study area (Ritter *et al.* 2016; Trentini *et al.* 2017).

The observed and modelled data also reflect that total plant density, species richness and the

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abundance of early secondary tree species recovered about 5 years after logging. Logging negatively affected the height-growth rate of native trees because stems are broken by mechanical operations, thus reducing the abundance of trees greater than a given size (5 cm DBH in this study). Consequently, species richness of trees is also reduced because, as observed in the rarefaction curves, species richness strongly depends on plant abundance. Moreover, pioneers establish immediately after logging, increasing the competition with established nonpioneer trees. On the other hand, logging increases resource availability. Similar results have been found in a forest plantation in Uganda (Duncan & Chapman 2003). In that study, plant abundance and species richness decreased immediately after logging because of sapling injuries or mortality. Nevertheless, 5–6 years after logging, stands reached similar or higher values than before logging because of seed germination, coppice and root sprouts (Duncan & Chapman 2003). Therefore, logging may induce negative short-term, but positive or zero, medium or long-term effects on plant density and species richness.

We found a far greater variation in plant density and species richness among planted stands which were logged less than 5 years before sampling than in those logged more than 5 years before sampling. This can reflect differences in the severity of the mechanical injury induced by logging, which was not assessed in this study. This finding highlights that research is needed to understand the effects of different kinds of harvest to increase the survival and growth of nonpioneer trees.

Our results suggest that species classified in different ecological groups exhibit functional differences related to their requirements for regeneration. The araucaria plantations of different ages and time since last logging constitute a heterogeneous environment where functionally different species can establish. Most of the establishing tree species were also found in the surrounding native forests (57/71), and the species which were only found in plantations or native forest tended to exhibit functional differences. Tree species establishing only in plantations were mainly pioneer or initial secondary (10/14), while for those species only found in native forests, the ratio was lower (10/25). Probably older or unmanaged planted araucaria stands are needed for the establishment of more late secondary and climax tree species.

We found that zoochory was the most frequent dispersal mode among the tree species in the araucaria plantations that we studied. This result supports the observations in other forest plantations in the study area (Barbosa *et al.* 2009; Dummel & Pinazo 2013; Vespa *et al.* 2014) as well as in other tropical and subtropical plantations (Denslow & Moermond 1985; Keenan *et al.* 1999). However, the abundance of zoochoric tree species decreased with stand age and time since last logging. Probably, young araucaria planted stands are as frequently used by dispersers as old ones (Barbosa *et al.* 2009). Two characteristics of araucaria trees can make them attractive for dispersers and could increase seed arrival. First, it is a canopy emergent tree and develops a large horizontal crown, effectively used as perches by birds (Zanini & Ganade 2005; Duarte *et al.* 2006). Second, araucaria produces large, highly nutritious seeds which are largely consumed and dispersed by birds and small mammals (Santos *et al.* 2002). In addition, araucaria plantations older than 10 years provide useful habitat for a near-threatened bird characteristic of native araucaria native forest (Pietrek & Branch 2011).

In summary, we found that stand age and logging shaped plant density and species richness in araucaria plantations and that ecological groups exhibited specific responses to such factors. Logging promoted a fast positive response of pioneer trees irrespective of the stand age, while nonpioneer groups increased in abundance at different rates with stand age, were negatively affected by logging and recovered at different rates. Araucaria plantations can increase the contribution to local tree diversity, especially, if the mechanical damage to established native tree species during harvest operations is reduced with appropriate planning of logging roads and directional felling of cut trees.

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Conceptualization-equal, formal analysis-lead, investigation-lead, methodology-equal, software-equal, writing-original draft-equal: M.M. Conceptualization-equal, formal analysis-equal, investigation-equal, writing-review & editing-equal: M.P.F. Conceptualization-equal, funding acquisition-equal, project administration-equal, writing-review & editing-equal: J.F.G. Conceptualization-equal, supervision-equal, writing-review & editing-equal: P.I.C. data curation-equal, investigation-equal: L.J.R. Data curation-equal, funding acquisition-equal, writing-review & editing-equal: M.P.F. Conceptualization-equal, funding acquisition-equal, methodology-equal, project administration-equal, supervision-equal, writing-review & editing-equal: M.F.A.

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SUPPORTING INFORMATION

Additional supporting information may/can be found online in the supporting information tab for this article.

Appendix S1. Species, and ecological groups, recorded in 23 planted araucaria stands (2.7 ha sampled) and native forest (1.8 ha sampled).

Appendix S2. Stand variables for 23 planted araucaria stands.

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