

# Araucaria Forest conservation: mechanisms providing resistance to invasion by exotic timber trees

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**Abstract** Since only 12.6% of the Brazilian Araucaria Forest remains and timber tree monocultures are expanding, biological invasion is a potential threat to the conservation of natural forest remnants. Here, we test (1) the susceptibility of Araucaria Forest to invasion by *Pinus taeda* and *Eucalyptus saligna*, (2) the efficiency of different mechanisms controlling the early establishment of these two exotic timber tree species, and (3) the potential of the native timber tree *Araucaria angustifolia* to establish successfully in ecologically-managed monocultures of *Araucaria*, *Pinus* and *Eucalyptus*. In Araucaria Forest, more than a thousand *Pinus* seeds landed annually in a hectare; however, experimentally exposed seeds were 100% removed in only 6 days. Furthermore, all experimentally transplanted seedlings of *Pinus taeda* and *Eucalyptus saligna* died in less than a year in Araucaria Forest, but not in the monocultures. Correlative evidence suggests that this mortality was associated to plant community richness, plant abundance, and soil fertility. *Araucaria angustifolia*, in contrast, showed an

establishment success in ecologically-managed tree monocultures as high as that exhibited in its natural habitat. The current resistance of Araucaria Forest to invasion by exotic timber trees is good news for the conservation of Araucaria Forest remnants and for its keystone species. The understanding of the mechanisms providing such resistance against invasion points towards management tools for minimizing future threats.

**Keywords** Brazilian Atlantic Forest · Conservation · Exotic species · Forestry · Invasibility · Management

## Introduction

Invasion of natural habitats by exotic species is the second cause of biodiversity lost on the planet (Sax et al. 2005). Exotic species modify interspecific interactions, community structure, and ecosystem processes (Vitousek et al. 1997; Lonsdale 1999; Richardson et al. 2000; Ehrenfeld et al. 2001; Le Maitre et al. 2002; Karl et al. 2005; Traveset and Richardson 2006). They also cause important impacts on human health, culture, and economy (Mack et al. 2000; Le Maitre et al. 2002).

Invasion success by exotic plant species depends on the interaction between intrinsic adaptations of the exotic species (Sax and Brown 2000; Shea and Chesson 2002; Fridley et al. 2007; Funk and Vitousek

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2007), ecological attributes of the plant community (Elton 1958; Thomsen and D'Antonio 2007), efficiency of the natural enemies (Keane and Crawley 2002; Liu and Stiling 2006), and the availability of adequate resources and environmental conditions (Davis et al. 2000; Funk and Vitousek 2007). Furthermore, propagule pressure is frequently under human control, bringing further uncertainty to the invasibility process (Rejmánek et al. 2005; Pyšek and Richardson 2006; Funk and Vitousek 2007; Vilá et al. 2007).

Exotic timber tree species used by the forestry industry commonly escape to natural habitats representing a serious world threat (Richardson 1998; Richardson et al. 2008). Exotic species of *Pinus* are well known open-habitat invaders (Higgins and Richardson 1998; Castro et al. 2002; Le Maitre et al. 2002; Matthews 2005). However, they also successfully invaded closed vegetation, such as native *Eucalyptus* forests in Australia (Williams and Wardle 2005), native forests of New Zealand (Ledgard 2001), andine forests in Patagonia, and temperate forests in northeastern Argentina (Matthews 2005). *Eucalyptus* is included in the invasive exotic species list of several countries (Higgins and Richardson 1998; Diez 2005; Lavi et al. 2005). In South Africa, at least ten *Eucalyptus* species are important invaders (Richardson 1998; Forsyth et al. 2004). In South America, invasion of *Eucalyptus* is documented in grasslands, savannas, and closed forests (Hórus 2008).

The Brazilian Atlantic Forest is one of the five richest biodiversity hotspots, containing around 20,000 plant species (Mittermeier et al. 2004; Galindo-Leal and de Gusmão Câmara 2003). Originally, it occurred from the northern state of Rio Grande do Norte to the southeast state of Rio Grande do Sul, where the community is dominated by *Araucaria angustifolia* (Bertol.) O. Kuntze, forming the so called Araucaria Forest (Ribeiro et al. 2009; Fonseca et al. 2009b). *Araucaria angustifolia* has been classified as vulnerable according to IUCN standards (Hilton-Taylor 2000) and is protected by law (National Forest Code 4771/65). The conservation status of the Araucaria Forest, itself, is critical (Fonseca et al. 2009b). Nowadays, 12.6% of the Araucaria Forest original cover remains, being mostly distributed in small fragments surrounded by different anthropogenic habitats, such as cattle fields, agriculture and exotic tree monocultures of *Pinus* and *Eucalyptus* (Ribeiro et al. 2009). The proximity of these exotic timber tree

plantations represents an additional threat to the conservation of Araucaria Forest fragments. For instance, *Pinus contorta* has invaded natural forests dominated by the native *Araucaria araucana* in the Chilean Andes (Peña et al. 2008).

Araucaria Forest fragments, on the other hand, can be the source of propagule of native species to the re-colonization of the anthropogenic matrix which can help in the restoration of this endangered ecosystem (Fonseca and Joner 2007). *Araucaria angustifolia* is able to colonize natural grasslands and cattle fields under the present climatic conditions (Behling et al. 2004). However, we have little information about its ability to re-establish populations in closed and disturbed environments (Duarte et al. 2002; Pereira and Ganade 2008). Tree monocultures, for instance, can be expected to be a harsh environment to its establishment due to alteration of the abiotic conditions (Jackson et al. 2005) and the presence of allelopathic compounds (Rizvi et al. 1999).

This study was developed in a mosaic landscape composed by Araucaria Forest and ecologically-managed tree monocultures of *Araucaria*, *Pinus*, and *Eucalyptus* (Fonseca et al. 2009a). Our aims were (1) to test the susceptibility of Araucaria Forest to invasion by *Pinus taeda* and *Eucalyptus saligna*, (2) to test the efficiency of different mechanisms controlling the early establishment of these two exotic timber tree species, and (3) to test the establishment success of the native keystone species *Araucaria angustifolia* in ecologically-managed tree monocultures.

## Materials and methods

### Study area

This study was carried out in the São Francisco de Paula National Forest (Brazil, 29°23'–29°27'S, 50°23'–50°25'W), a conservation unit created in 1975 with two main aims: to protect Araucaria Forest remnants and to produce timber (Schneider et al. 1989). The reserve has 1606.7 ha, located from 600 to 950 m above sea level, in a landscape previously occupied by a natural mosaic of Araucaria Forest and grasslands (Fonseca et al. 2009b). The climate is mesotermic and superumid, with mean annual rainfall of 2,252 mm and mean annual temperature of 14.5°C (Backes 1999).

The São Francisco de Paula National Forest is today a mosaic landscape composed mostly of *Araucaria* Forest remnants, monocultures of the native species *Araucaria angustifolia*, and exotic tree monocultures of *Pinus ellioti*, *Pinus taeda* and *Eucalyptus* spp. The *Araucaria* Forest is dominated by *Araucaria angustifolia* (Bertol.) O. Kuntze (Araucariaceae), but other important elements are *Podocarpus lambertii* Klotzsch ex Endl. (Podocarpaceae), *Nectandra grandiflora* Ness & Mart. Ex Nees (Lauraceae), *Ilex paraguariensis* A. St. Hill. (Aquifoliaceae), *Mimosa scabrella* Benth. (Fabaceae) and *Cryptocaria aschersoniana* Mez (Lauraceae). At the middle of the XX century, the *Araucaria* Forest was submitted to selective logging.

The National Forest adopts ecologically sustainable management practices that contrast with the intense management regimes usually adopted by the forestry industry in Brazil (Fonseca et al. 2009a). In the National Forest the monocultures are generally older (up to 60 years), tree density is lower, the stands are relatively smaller, not far away from natural forest patches, and they exhibit a more complex and diverse understory. This management practices allow the occupation of the stands by a diverse fauna of birds, mammals, leaf-litter frogs, spiders, butterflies, galling insects, soil insects, flatworms, epiphytic angiosperms, epiphytic ferns, lichens, and fruit-body producing fungi (Fonseca et al. 2009a).

### Experimental design

The work was developed in four habitats: *Araucaria* Forest (FO) and plantations of *Araucaria* (PA), *Pinus* (PP), and *Eucalyptus* (PE). For each habitat, we selected three independent 1 ha sites as replicates. In each site, 15 permanently marked points were established in a 40 × 50 m centered grid. In 2007, the stands of *Araucaria angustifolia* were the oldest ones (48, 60, and 60 years), followed by plantations of *Pinus* (*P. taeda*—35 and 39 years, and *P. ellioti*—42 years) and *Eucalyptus* sp. (13, 19, and 35 years). Land use, tree density, and thinning frequency varied among study sites.

### Studied species

The two exotic timber tree species considered in this study were *Pinus taeda* L. (Pinaceae) and *Eucalyptus saligna* Sm. (Myrtaceae). *Pinus taeda* is originally

from North America but it was introduced in Brazil in 1948 to become the main timber product in Southern Brazil. It is a fast growing tree which produces a large number of wind-dispersed seeds (5 mm long with 25 mm wide wings). *Eucalyptus saligna*, known as the Sydney blue gum, occurs originally in New South Wales and Queensland, but now it is widely distributed in the southern hemisphere. It is a fast-growing tree that can reach up to 65 m high. Their tiny wind-dispersed seeds (1.3 mm in diameter) are produced inside bell-shaped capsules being released soon after they ripe.

We also investigated the establishment performance of *Araucaria angustifolia* O. Kuntze (Araucariaceae), an ecologically dominant native species which was widely used by the timber industry for many decades. *Araucaria angustifolia* is a wind-pollinated, dioecious gymnosperm tree that can reach up to 50 m in height. Its reproductive cycle extends for 20–24 months, but the production of their large (7 g) and nutritious (70% of endosperm) seeds concentrates on the southern hemisphere winter (Mantovani et al. 2004). Considering that during this season most angiosperms are not reproducing, its seeds are essential as feeding resource for a large number of rodents, medium size mammals and birds (Job and Vieira 2008). In periods of intense seed production, secondary dispersion seems to be the main mechanism of its recruitment (Solórzano-Filho 2001). Based on its relevance to the local fauna, some authors have classified *Araucaria angustifolia* as a keystone species (Pereira and Ganade 2008).

### The environmental setting

**The density of naturally established saplings** (height < 1.5 m) of *Pinus*, *Eucalyptus*, and *Araucaria* were determined by complete surveys of the 50 × 40 m grids.

**Plant community richness and abundance** were determined by the complete survey of six randomly allocated plots (10 × 10 m) per site. Woody plants with circumference at the breast height (cbh) ≥ 15 cm where recorded in the whole plot, while plants with cbh < 15 cm and height > 1 m where sampled in half the plot.

**Canopy openness (%)** was determined for each one of the 15 permanently marked points by hemispherical photographs taken with a FC-E9 Nikon digital

camera associated with Coolpix 5400 Fisheye lens. The camera was positioned in a 50 cm high tripod, with the lens facing the sky, horizontally aligned with the magnetic South. All photographs were taken in February 2007, during 5 days, between 9 a.m. and 5 p.m., under cloudy conditions. Photographs were treated with the program Gap Light Analyser (1999). The threshold was adjusted manually for each photograph to obtain the best fit between the original and the working image (Frazer et al. 2001).

**Soil fertility of** each site was determined by six randomly chosen soil samples (10 cm depth) extracted with a 10 cm diameter soil auger bucket. Phosphorus and potassium concentration ( $\text{mg}/\text{dm}^3$ ) were determined by the Mehlich method; aluminum, calcium, magnesium ( $\text{cmol}_c/\text{dm}^3$ ), and manganese ( $\text{mg}/\text{dm}^3$ ) were extracted by  $\text{KCl}$   $1 \text{ mol L}^{-1}$ ; zinc and copper were extracted with  $\text{HCl}$   $0.1 \text{ mol L}^{-1}$ ; sulfur was extracted with  $\text{CaHPO}_4$   $500 \text{ mg L}^{-1}$ ; boron was extracted with hot water. Argil (%) was determined by the aerometer method. Soil pH was measured in water solution 1:1. Soil analyses were performed in the Soil Laboratory of the Universidade Federal do Rio Grande do Sul. For more methodological details, see Pavan et al. (1996).

#### Seed rain

In order to test how seed rain varied among habitats, 12 seed traps were installed in each study site. Traps were arranged along three 25 m distant parallel transects (50 m long), containing four equally spaced traps. Each trap consisted of  $1 \text{ m}^2$  plastic mesh (2 mm) installed one meter above the soil with the aid of wood steaks. Every 4 weeks, all traps were visited and the seeds were collected. In laboratory, the number of seeds of *Pinus* and *Araucaria* in each trap was determined. Since we fail to generate trustful data on the seed rain of *Eucalyptus saligna*, because their tiny seeds could not be efficiently separated from the leaf debris, these results are not provided. The number of seeds per hectare per year, was estimated as  $(x + 1) \times (10000/12)$ ,  $x$  being the number of seeds captured in the 12 seed traps along the year.

#### Seeds removal

In order to test how seed removal varied among habitats, 10 seeds of each species were experimentally

offered in each one of the 15 permanently marked points in each study site. Seeds were exposed in 15 cm diameter plastic dishes. The experiment was set up in July 2007 and the number of seeds remaining was recorded daily until all seeds were removed. Since we verified that rain spells were washing away *Eucalyptus saligna* seeds from the plastic dishes, making their final fate uncertain, these results are not provided.

#### Seedling survival

In order to test how seedling survival varied among habitats, we recorded the fate of transplanted seedlings of *Pinus taeda*, *Eucalyptus saligna*, and *Araucaria angustifolia* along 1 year. In May 2006, 60 healthy seedlings of each species were selected, ranked by size (height, number of branches, and number of leaves), and randomly allocated in 12 blocks of five seedlings in a way to minimize differences among blocks. One block of each species were then randomly allocated to the 15 marked points in each study site. From June 2006 to May 2007, we recorded monthly whether each seedling was dead or alive.

#### Seedling growth and biomass

In June 2007, we recorded the height (nearest mm) and the number of leaves of all surviving saplings. Also, all plants were collected and their total dry biomass, as well their root and shoot components, were determined to the nearest 0.1 g.

#### Statistical analysis

Among habitat differences in the number of naturally established saplings of *Pinus taeda*, *Eucalyptus saligna*, and *Araucaria angustifolia*, plant community richness and abundance, as well as the percentage of canopy openness were tested with one-way ANOVA, followed by Tukey post hoc test. Homogeneity of the variances and normality were tested by Levene's and Kruskal–Wallis tests, respectively. Multi-Response Permutation Procedure (MRPP) implemented in PcOrd (McCune and Mefford 1997) was used to test for differences in soil quality among habitats. The two first axis of a principal component analysis (PCA) were used to synthesize differences in soil quality among sites.

General Linear Model was used to test if the pattern of seed rain among habitats varied among species (*Pinus taeda* and *Araucaria angustifolia*). The full model contained the explanatory variables habitat, sites within habitat, species, and the interaction habitat  $\times$  species. We tested the interaction between habitat  $\times$  species using the error model as the denominator of the  $F$ -test. Differences among habitat were tested independently for each species by one-way ANOVA. Before analysis, seed rain data were transformed as  $\text{Log}_{10}((x + 1) \times (10000/12))$  in order to be expressed as number of seeds per hectare (in  $\text{Log}_{10}$  scale). Homogeneity of the variances and normality were tested by Levene's and Kruskal–Wallis tests, respectively.

Repeated measure ANOVA was used to test for differences on the dynamic of seed removal among habitats. The number of seeds remaining intact in each point (10–0) was used as independent variable. The full model contained the explanatory variables habitat and site within habitat (between subject) together with time, the interaction time  $\times$  habitat, and the interaction time  $\times$  site within habitat. The factor habitat was tested against the variation of site within habitat. The interaction time  $\times$  habitat was tested against the interaction time  $\times$  site within habitat.

Differences on seedling longevity among species and among habitats were tested by survival analyses (Systat 2004). Simple and stepwise multiple logistic regressions were used to test how seedling survival was affected by plant community richness and abundance, canopy openness (log), and the PCA axes soil 1 and soil 2. Model simplification was done by a recursive backward elimination procedure (Crawley 2005). One-way ANOVA were carried out to test differences in plant height (m), number of leaves, plant biomass, and shoot/root ratio among habitats for each study species. Due to the high mortality rates, individuals were used as replicates.

All analyses were performed in Systat 11 (Systat 2004), except when stated otherwise.

## Results

### Natural recruitment and the plant community

Naturally established saplings of *Pinus taeda* and *Eucalyptus saligna* were not found in Araucaria Forest.

*Pinus taeda* were found in one stand of *Eucalyptus* ( $N = 29$  saplings in  $2,000 \text{ m}^2$ ) and one stand of *Araucaria* ( $N = 1$ ) while saplings of *Eucalyptus saligna* were only found in one stand of *Eucalyptus* ( $N = 48$ ). In contrast, saplings of *Araucaria angustifolia* were found in all 12 sites. Furthermore, the density of *Araucaria angustifolia* saplings in Araucaria Forest ( $23.7 \pm 10.2$  [SE] saplings in  $2,000 \text{ m}^2$ ) was not significantly different to that found in plantations of *Araucaria* ( $24.3 \pm 16.8$ ), *Pinus* ( $5.7 \pm 1.2$ ), and *Eucalyptus* ( $26.3 \pm 0.7$ ,  $F_{[3,8]} = 0.95$ ,  $P = 0.460$ ).

Plant community was richer in Araucaria Forest ( $53 \pm 3.5$  [SE] species) and plantation of *Araucaria* ( $47.3 \pm 3.8$ ) than on plantations of *Pinus* ( $29 \pm 1.5$ ) and *Eucalyptus* ( $26 \pm 13.3$ ), these differences being marginally significant ( $F_{[3,8]} = 3.45$ ,  $P = 0.072$ ). Plant abundance was higher in plantations of *Araucaria* ( $405.7 \pm 26.8$  individuals) and Araucaria Forest ( $375.3 \pm 56.3$ ) than on plantations of *Pinus* ( $177.3 \pm 25.3$ ) and *Eucalyptus* ( $168.3 \pm 51.7$ ), these differences being highly significant ( $F_{[3,8]} = 8.86$ ,  $P = 0.006$ ).

### Differences in the abiotic environment among habitats

Canopy openness was lower in Araucaria Forest ( $13.57\% \pm 0.1$  [SE]) and plantation of *Araucaria* ( $14.99\% \pm 0.20$ ) when compared to plantations of *Eucalyptus* ( $20.46\% \pm 3.58$ ) and *Pinus* ( $16.67\% \pm 0.74$ ), however these differences were not significant ( $F_{[3,8]} = 2.65$ ,  $P = 0.121$ ).

The soil nutrient composition of Araucaria Forest differed from the soils found in plantations of *Araucaria* (MRPP, observed delta = 0.357, expected delta = 0.500,  $T = -2.593$ ,  $P = 0.023$ ) and *Pinus* (MRPP, observed delta = 0.341, expected delta = 0.500,  $T = -2.236$ ,  $P = 0.032$ ). Principal Component Analysis indicated that Araucaria Forest had lower pH levels and lower concentrations of potassium, calcium, magnesium, manganese, as well higher concentration of aluminum, boron, phosphorus, and sulfur when compared with the monocultures. The first axis of a PCA, named Soil 1, explained 36.86% of the total variance of the soil data, being positively associated with the availability of potassium (0.938), calcium (0.913), magnesium (0.894), manganese (0.798), and pH (0.754). The second axis, named Soil 2, explained 25.08% of the variance, being positively related to pH



(0.642) and negatively related to aluminum ( $-0.601$ ), boron ( $-0.921$ ), phosphorus ( $-0.730$ ), and sulfur ( $-0.576$ ).

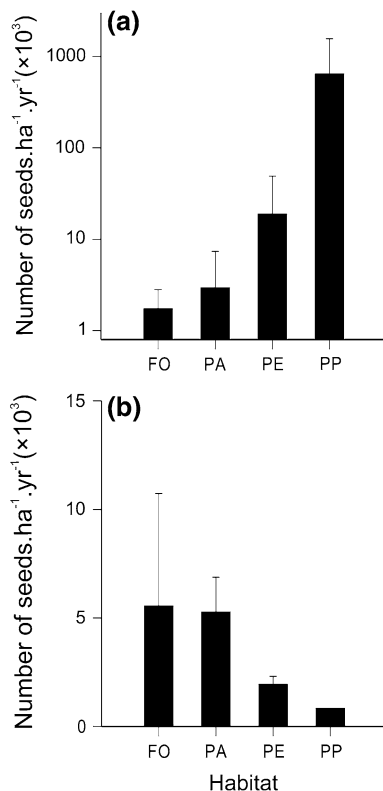
### Seed rain

The pattern of seed rain among habitats varied significantly between species ( $F_{[3,8]} = 21.06$ ,  $P < 0.001$ ; Fig. 1). The wind-dispersed seeds of *Pinus* were able to reach all four habitats, despite being more abundant in plantations of *Pinus* and *Eucalyptus* ( $F_{[3,8]} = 17.9$ ,  $P < 0.001$ ). In Araucaria Forest, *Pinus* arrived at a rate of  $1,111 \pm 555$  [SE] seeds  $\text{ha}^{-1}$  -  $\text{year}^{-1}$  (Fig. 1a). The number of seeds of *Araucaria angustifolia* collected in the seed traps along the year did not varied significantly among habitats ( $F_{[3,8]} =$

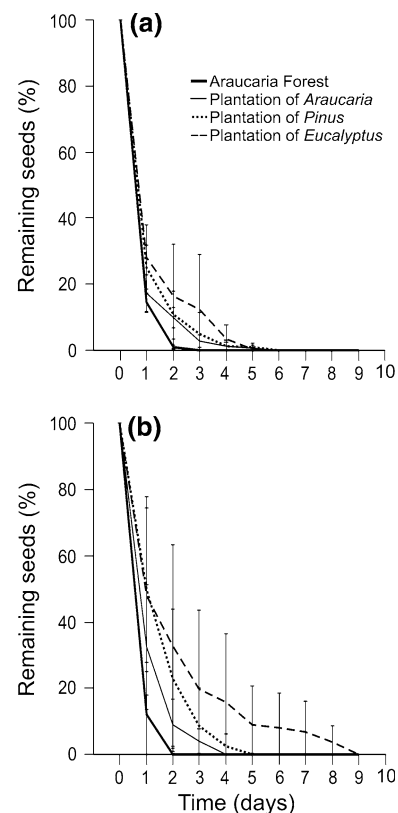
$3.21$ ,  $P = 0.083$ ; Fig. 1b), despite being absent from the traps located in the plantations of *Pinus*.

### Seed removal

All *Pinus taeda* seeds were removed by the sixth day of the experiment (Fig. 2a). Removal rates of *P. taeda* seeds were similar among habitats (Repeated measure ANOVA; Habitat,  $F_{[3,8]} = 0.97$ ,  $P = 0.454$ ) and exhibited similar temporal patterns (Interaction Time  $\times$  Habitat,  $F_{[12,32]} = 0.92$ ,  $P = 0.543$ ). In Araucaria Forest, 82.7% of the seeds of *Pinus taeda* were removed within 24 h. The removal rate of *Araucaria angustifolia* seeds was similar among habitats (Repeated measure ANOVA; Habitat,  $F_{[3,8]} = 0.95$ ,  $P = 0.463$ ) and had similar temporal dynamics (Interaction Time  $\times$  Habitat,



**Fig. 1** Seed rain, expressed as the number of seeds estimated to land annually in one hectare, of **a** *Pinus* and **b** *Araucaria angustifolia* in Araucaria Forest (FO) and plantations of *Araucaria* (PA), *Pinus* (PP), and *Eucalyptus* (PE). Notice the log-scale for *Pinus*. Vertical lines enclose  $\pm 1$  SE. The number of seeds per hectare per year, was estimated as  $(x + 1) \times (10000/12)$ ,  $x$  being the number of seeds captured in 12 seed traps ( $1 \text{ m}^2$ ) along 1 year



**Fig. 2** Percentage of seeds of **a** *Pinus taeda* and **b** *Araucaria angustifolia* that remained intact along the seed removal experiment in Araucaria Forest (thick line), and in plantations of *Araucaria* (thin line), *Pinus* (dotted line), and *Eucalyptus* (dashed line). Vertical lines enclose  $\pm 1$  SE

$F_{[21,56]} = 0.99$ ,  $P = 0.485$ ; Fig. 2b). In 24 h, 74.5% of *Araucaria angustifolia* seeds were removed.

### Seedling survival

All *Pinus taeda* seedlings died in Araucaria Forest within a period of 10 months (Fig. 3a). Mean seedling longevity of *Pinus taeda* varied among habitats (Survival Analysis, Mantel,  $\chi^2 = 24.96$ , g.l. = 3,  $P < 0.001$ ), being lower in Araucaria Forest (7.1 months) when compared to plantations of *Pinus* (8.3 months), *Araucaria* (13 months), and *Eucalyptus* (15.7 months).

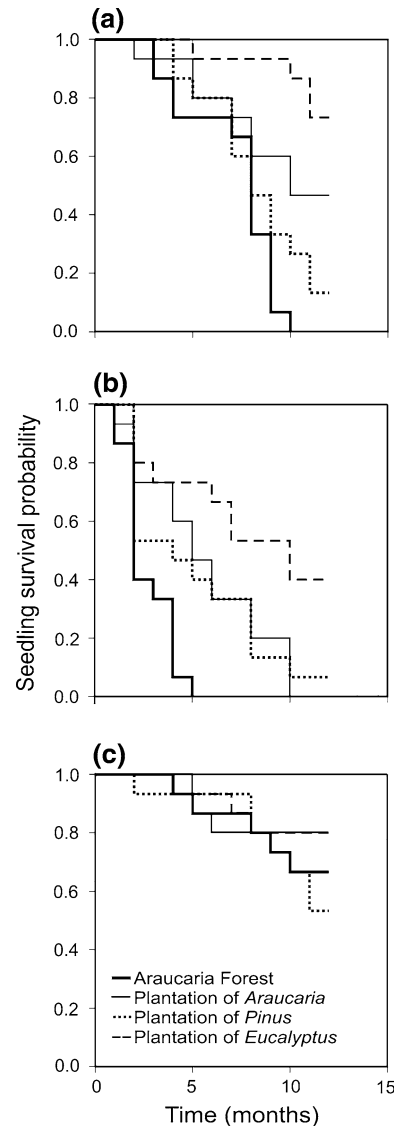
Likewise, all *Eucalyptus saligna* seedlings died before 5 months in Araucaria Forest and before 10 months in plantations of *Araucaria* (Fig. 3b). Mean seedling longevity of *Eucalyptus saligna* varied among habitats (Survival Analysis, Mantel,  $\chi^2 = 23.55$ , g.l. = 3,  $P < 0.001$ ), being lower in Araucaria Forest (2.7 months) when compared to plantations of *Pinus* (5.3 months), *Araucaria* (5.5), and *Eucalyptus* (9.3 months).

*Araucaria angustifolia*, in contrast, established successfully in all habitats (Fig. 3c). Its mean seedling longevity did not differ significantly among habitats (Survival Analysis, Mantel,  $\chi^2 = 2.60$ , g.l. = 3,  $P = 0.457$ ), varying between 10 and 11 months.

Overall, mean seedling longevity for *Eucalyptus saligna* (5.6 months) and *Pinus taeda* (9.0 months) was lower when compared to *Araucaria angustifolia* (13.4 months), this difference being highly significant (Survival Analysis, Mantel,  $\chi^2 = 66.4$ , g.l. = 2,  $P < 0.001$ ). After 1 year, only 11.7% of the *Eucalyptus saligna* seedlings and 33.3% of the *Pinus taeda* seedlings were alive. In contrast, 73.3% of the seedlings of *Araucaria angustifolia* survived the first year.

### Ecological factors affecting seedling establishment

Simple logistic regressions indicated that the establishment of seedlings of *Pinus taeda* was positively affected by canopy openness (log) ( $11.052 \pm 4.018$ ,  $t = 2.75$ ,  $P = 0.006$ ) and PCA axis soil 1 ( $0.797 \pm 0.307$ ,  $t = 2.592$ ,  $P = 0.01$ ), and negatively affected by plant richness ( $-0.06 \pm 0.021$ ,  $t = -2.853$ ,  $P = 0.004$ ). However, a multiple stepwise logistic regression indicated that the establishment of seedlings of *Pinus taeda* was positively related to the PCA axis



**Fig. 3** Survival probability curve of experimentally transplanted seedlings of **a** *Pinus taeda*, **b** *Eucalyptus saligna*, and **c** *Araucaria angustifolia* in Araucaria Forest (thick line) and in plantations of *Araucaria* (thin line), *Pinus* (dotted line), and *Eucalyptus* (dashed line)

soil 1 ( $1.148 \pm 0.42$ ,  $t = 2.76$ ,  $P = 0.006$ ) and negatively related to plant richness ( $-0.079 \pm 0.024$ ,  $t = -3.21$ ,  $P = 0.001$ ); plant abundance, axis soil 2, and canopy openness (log) being excluded from the minimal adequate model (Log-likelihood = 21.05, g.l. = 2,  $P < 0.001$ , MacFadden's Rho-squared = 0.276).

For *Eucalyptus saligna*, simple logistic regressions indicated that its establishment was positively affected

by canopy openness (log) ( $56.735 \pm 30.327$ ,  $t = 1.87$ ,  $P = 0.061$ ), and negatively affected by plant richness ( $-0.228 \pm 0.106$ ,  $t = -2.152$ ,  $P = 0.031$ ) and plant abundance ( $-0.003 \pm 0.009$ ,  $t = -3.005$ ,  $P = 0.003$ ). However, in the stepwise multiple logistic regression only plant abundance affected negatively the seedling establishment of *Eucalyptus saligna* ( $-0.028 \pm 0.009$ ,  $t = -3.00$ ,  $P = 0.003$ , MacFadden's Rho-squared = 0.513).

Establishment of seedlings of *Araucaria angustifolia* was not significantly affected by any of the environmental variables, both when analyzed independently in simple logistic regressions or together in the stepwise multiple logistic regression model.

### Seedling performance

After 1 year, seedlings of *Pinus taeda* that remained alive in plantations of *Araucaria*, *Pinus*, and *Eucalyptus* exhibited the same height, number of leaves, biomass, and shoot/root ratio (Table 1). One-year old

saplings of *Eucalyptus saligna* that were alive in plantations of *Pinus* and *Eucalyptus* were also similar in relation to height, number of leaves, biomass, and shoot/root ratio (Table 1). For *Araucaria angustifolia*, all plant performance traits were similar between *Araucaria* Forest and the three tree monocultures (Table 1).

### Discussion

*Araucaria* Forest has been exposed for many decades to a high propagule pressure exerted by *Pinus* and *Eucalyptus*, but so far it has been able to resist against this threat. This high resistance is not only corroborated by our experimental results, but also by the very low number of invasion records in the literature (Zalba et al. 2009) and in the Inter-American Biodiversity Information Network (IABIN) database for exotic invasive species (I3N, Hórus 2008). Similar resistance to invasion has been recently documented

**Table 1** Seedling performance of *Pinus taeda*, *Eucalyptus saligna*, and *Araucaria angustifolia* in *Araucaria* Forest and plantations of *Araucaria*, *Pinus*, and *Eucalyptus*

	Araucaria Forest	Plantation of <i>Araucaria</i>	Plantation of <i>Pinus</i>	Plantation of <i>Eucalyptus</i>	<i>F</i>	<i>df</i>	<i>P</i>
<i>Pinus taeda</i>							
Plant height (cm)	–	29.96 ± 4.00	30.75 ± 5.85	31.75 ± 1.40	0.123	2,17	0.885
Number of leaves	–	150.0 ± 34.9	59.0 ± 52.0	151.8 ± 17.6	1.431	2,17	0.266
Plant biomass (g)	–	1.188 ± 0.313	1.033	2.017 ± 0.497	0.787	2,15	0.473
Shoot/root ratio	–	6.194 ± 0.769	4.374	4.352 ± 0.498	2.257	2,15	0.139
Number of survivors	0	7	2	11			
<i>Eucalyptus saligna</i>							
Plant height (cm)	–	–	28.50	34.50 ± 3.13	0.525	1,5	0.501
Number of leaves	–	–	44	28.7 ± 7.1	0.673	1,5	0.449
Plant biomass (g)	–	–	0.221	0.807 ± 0.194	1.304	1,5	0.305
Shoot/root ratio	–	–	3.623	4.252 ± 0.913	0.068	1,5	0.805
Number of survivors	0	0	1	6			
<i>Araucaria angustifolia</i>							
Plant height (cm)	19.58 ± 0.76	17.93 ± 0.67	19.71 ± 0.57	19.50 ± 1.01	1.172	3,40	0.332
Number of leaves	169.6 ± 19.8	187.3 ± 17.7	211.4 ± 26.4	195.4 ± 19.1	0.650	3,40	0.588
Plant biomass (g)	1.042 ± 0.156	1.048 ± 0.098	1.071 ± 0.115	1.239 ± 0.118	0.629	3,40	0.601
Shoot/root ratio	2.682 ± 0.429	2.770 ± 0.288	2.765 ± 0.206	2.075 ± 0.186	1.454	3,40	0.242
Number of survivors	10	12	10	12			

Values are mean ± 1 SE



for *Nothofagus glauca* Forest from the coast of Chile against the exotic timber tree *Pinus radiata* (Bustamante and Simonetti 2005), and for *Nothofagus/Austrocedrus* Forest from Isla Victoria (Argentina) threatened by the presence of a large range of exotic conifers and broad-leaved timber tree species (Simberloff et al. 2003).

Whether *Pinus* and *Eucalyptus* will become an important threat for Araucaria Forest is a matter of speculation. However, considering that both genera have successfully invaded many closed-forests around the world (Richardson 1998; Matthews 2005; Williams and Wardle 2005), it is not wise to rule out the possibility that the invasibility process in Araucaria Forest is still in the “lag phase” (Theoharides and Dukes 2007). Indeed, many temperate studies have shown that several decades can pass between the first introduction of an exotic species and its spread, although some studies suggest that the lag phase can be substantially shorter in the tropics (Daehler 2009). Independent of the future outcome of this invasibility process, this study allows us to understand the ecological mechanisms that are now acting to provide Araucaria Forest resistance against invasion by *Pinus* and *Eucalyptus*. As a corollary, one is able to understand under which conditions windows of opportunities for the invasive process can be opened.

#### The mechanisms of resistance

The propagule pressure of *Pinus* and *Eucalyptus* in the original geographic area of Araucaria Forest is intense. In the three most southern states of Brazil, where most Araucaria Forest fragments are located, tree monocultures occupy a total of 469 thousand hectares, being present in the region for many decades (Bracelpa 2008). In the mosaic landscape of the São Francisco de Paula National Forest, Araucaria Forest remnants and stands of *Pinus* and *Eucalyptus* occur side by side (Fonseca et al. 2009a). Yearly, more than a thousand wind-dispersed *Pinus* seeds, plus a non-quantified number of *Eucalyptus* seeds, land on a single hectare of Araucaria Forest. However, despite the good opportunity for the invasive process to be launched, no saplings of *Pinus* and *Eucalyptus* were found naturally regenerating inside the Araucaria Forest fragments. This strongly suggests that ecological factors others than seed rain limitation is controlling the resistance of Araucaria Forest to invasion.

Several ecological hypotheses were proposed to explain why exotic species sometimes are able to successfully invade natural habitats and sometimes are not, such as the Natural Enemy Release Hypothesis (Keane and Crawley 2002; Liu and Stiling 2006), the Species Diversity Hypothesis (Elton 1958; Thomsen and D’Antonio 2007), and the Resource Fluctuations Hypothesis (Davis et al. 2000; Funk and Vitousek 2007). Our study suggests that the outcome of the invasibility process can be determined simultaneously by multiple factors and that these factors can act differently along the ontogeny of the invader species.

At the seed stage, predation was by far the most important factor explaining the low performance of *Pinus taeda* in Araucaria Forest. In less than a week, all experimental seeds were predated in the spot or disappeared. Mammal surveys conducted in the same landscape showed that the local abundances of small rodents are particularly high (Fonseca et al. 2009a). Experimental studies conducted in different Araucaria Forest remnants and in different years invariably have indicated high rates of seed predation (Guglielme and Ganade 2006; Pereira and Ganade 2008; Iob and Vieira 2008). The main seed predators are generalist rodents, such as *Oligoryzomys nigripes* Olfers, 1818, *Akodon montensis* Thomas, 1913, and *Delomys dorsalis* Hensen, 1872, that can reach very high local populations in Araucaria Forest fragments but also in monocultures of *Araucaria*, *Pinus*, and *Eucalyptus* (Vieira et al. 2006; Fonseca et al. 2009a). Most seeds removed by those animals are either predated immediately or consumed afterwards (Iob and Vieira 2008). Also, some granivorous birds act as post-dispersal seed predators, and can potentially contribute to the Araucaria Forest resistance to invasion (Sick 1997). Dispersion of the native *Pinus sylvestris* from Spain mediterranean forest to wetlands is also limited by seed predation (Castro et al. 1999, 2002). In Isla Victoria, Argentina, the invasion of five species of *Pinus* has been suggested to be limited by biotic interactions, as seed predation by birds and rodents (Nuñez et al. 2008).

At the seedling stage, in contrast, field observations fail to record the presence of herbivores and pathogens that could explain the strong mortality rates exhibited by *Pinus taeda* and *Eucalyptus saligna* in Araucaria Forest. In winter, coccids fed on leaves of *Pinus taeda* seedlings, but they did not cause any death. Also, generalist leaf-cutting ants of

the genus *Atta*, that can have a strong impact on *Araucaria* seedling survival (Zanini et al. 2006), were rarely recorded in the 12 studied sites. The lack of specialized natural enemies is predicted by the Natural Enemy Release Hypothesis (Keane and Crawley 2002), however, this force was not enough to ensure the establishment success of *Pinus* and *Eucalyptus* in Araucaria Forest.

According to Elton's Hypothesis, richer communities are less susceptible to invasion by exotic species because in such environments, plant-plant competition by light, nutrients and water would be intense (Elton 1958). However, recent studies have been controversial about positive (Levine 2000; Naeem et al. 2000; Kennedy et al. 2002; Fargione and Tilman 2005; Thomsen and D'Antonio 2007) and negative (Stohlgren et al. 1999, 2003; Levine 2000; Pauchard et al. 2003; Collins et al. 2007) effects of species richness on ecosystem resistance to invasion. In our study, plant richness and plant abundance were negatively related to the survival of *Pinus* and *Eucalyptus*, even when soil and light availability were controlled for. This suggests that plant-plant competition plays an important role determining Araucaria Forest resistance to invasion.

The Resource Fluctuations Hypothesis states that temporal and spatial variation in resource availability can create windows of opportunity to invasive species (Davis et al. 2000; Funk and Vitousek 2007). Empirical studies suggest that communities on richer soils are more likely to be invaded (Lonsdale 1999; Stohlgren et al. 1999; Howard et al. 2004; Fridley et al. 2007). Our results indicate that *Pinus* survival depends positively on the availability of potassium, calcium, magnesium, and manganese, being also favored by basic soils. As those conditions were not present in Araucaria Forest, this can be an additional factor explaining why *Pinus taeda* failed to invade this natural environment.

Light can represent a limiting factor to invasion of shade intolerant plants in closed forests. *Eucalyptus* is considered shade intolerant, showing lower photosynthetic activity under shade conditions (Luttge et al. 2003). In this study, *Eucalyptus saligna* seedlings had higher probability to survive under open canopy. However, canopy openness was excluded from the minimum adequate multiple regression model in favor of plant abundance. Since plant abundance and canopy openness are negatively correlated ( $r =$

$-0.684$ ,  $P = 0.014$ ), light limitation can be an additional factor explaining the resistance of Araucaria Forest to *Eucalyptus* invasion. In areas where Araucaria Forest is subjected to selective logging, or to other types of structural disturbances, we expect windows of opportunity to invasion can be opened (Davis et al. 2000; Kota et al. 2007).

In conclusion, Araucaria Forest currently resists invasion by exotic fast growing woody species. This resistance is achieved through a fine balance defined by top-down forces and direct plant-plant interactions that modifies the availability of limited resources. However, it is not safe to assume that Araucaria Forest will remain free from such exotic timber tree invaders forever (Simberloff et al. 2002; Daehler 2009). Natural and anthropogenic disturbances can open opportunities to invaders by altering the processes that are actually bringing resistance to the Araucaria Forest. For instance, forest fragmentation can potentially alter the population of small rodents and the survival rate of *Pinus* and *Eucalyptus* seeds. Also, selective logging of Araucaria Forest can increase the incidence of gaps and the availability of light, eventually biasing plant-plant competition towards the exotic species. In principle, efforts to conserve the integrity of the Araucaria Forest remnants can help maintaining intact its resistance to invasion (see Kennedy et al. 2002).

#### *Araucaria angustifolia*: re-gaining the lost ground

The Araucaria Forest that occurs in the highlands of southern Brazil is a relatively young formation that replaced natural grasslands only in the Late Quaternary (Behling et al. 2004; Behling and Pillar 2007). That expansion coincided with warmer and wetter conditions that replaced the colder and highly seasonal climate that prevailed for more than 40 thousand years. Nowadays, where Araucaria Forest patches and natural grasslands occur in a mosaic landscape, *Araucaria angustifolia* and other associated species are still expanding over grasslands (Duarte et al. 2006; Overbeck et al. 2007). Here, we demonstrated that *Araucaria angustifolia* is able to re-colonize and re-establish a population of juveniles inside ecologically-managed monocultures of *Araucaria*, *Pinus* and *Eucalyptus*.

*Araucaria angustifolia* is a dominant Araucaria Forest species, comprising up to 92% of the total

basal area (Souza 2007). The production of seeds is intense ( $117\text{--}427\text{ kg ha}^{-1}\text{ year}^{-1}$ ), but varies considerably among patches and among years (Guerra et al. 2002; Solórzano-Filho 2001; Mantovani et al. 2004). In 2007, the production of *Araucaria angustifolia* seeds was not very high in several of the Araucaria Forest studied sites. Nevertheless, we verified that a reasonable number of Araucaria seeds reached successfully several exotic monoculture stands. We attribute this high level of dispersal success to the presence in the National Forest of healthy populations of two long distance travelers, *Amazona pretrei* (Psittacidae) and *Cyanocorax caeruleus* (Corvidae). The latter has been considered by the local population as the main disperser of Araucaria seeds (Anjos 1991; Solórzano-Filho 2001). Although we have shown that dispersed seeds face extremely high predation rates, natural recruitment of *Araucaria angustifolia* does occur inside the monocultures.

The large seeds ( $\pm 7\text{ g}$ ) of *Araucaria angustifolia* germinate as soon as they are exposed to adequate water conditions, transferring its energy, compressed under the form of starch, to the young seedling (Duarte and Dillenburg 2000). Green house experiments indicate that once the roots and the first leaves are produced young saplings are able to survive well under full- and medium-light conditions (Duarte and Dillenburg 2000). In this study, we demonstrate that experimentally transplanted seedlings of *Araucaria angustifolia* are able to survive equally well in ecologically-managed tree monocultures and Araucaria Forest. This corroborates the suggestion that the recruitment of *Araucaria angustifolia* is not light limited (Duarte et al. 2002). Phenotypic plasticity of *Araucaria angustifolia* seedlings in response to deep shade (10% of total solar radiation) has been demonstrated in green house conditions (Duarte and Dillenburg 2000). In the mosaic landscape of the São Francisco de Paula National Forest, however, experimentally transplanted seedlings showed no difference between habitats in plant height, number of leaves, total biomass, and shoot/root ratio. This reinforces the view that *Araucaria angustifolia* has the potential to re-gain its lost ground in both open and closed environments.

According to the Brazilian Forest Code (4771/65), *Araucaria angustifolia* trees are protected by law and once established they cannot be extracted without

permit. In the São Francisco de Paula National Forest, establishment of *Araucaria angustifolia* inside ecologically-managed tree monocultures is considered to be desirable to increase the connectivity among its natural populations. In Chile, monocultures of *Pinus radiata* were considered habitat reservoir to some native species, as *Cryptocaria alba* (Guerrero and Bustamante 2007). The fact that *Araucaria angustifolia* has proved to be able to invade closed environments is also positive for its re-establishment in secondary forests and abandoned old fields. In fact, due to recent environmental awareness in Brazil, many areas inside the Atlantic Forest domain, that were temporarily occupied by an array of economic activities, are now turning to secondary forests (Ribeiro et al. 2009).

The resistance against invasion by the timber trees *Pinus taeda* and *Eucalyptus saligna* represents good news to the conservation of Araucaria Forest remnants located both on biological reserves and private land. This resistance seems to be insured by a complex mechanism involving natural enemies, plant-plant interactions, and the interplay between ecophysiological adaptations of the invaders and the abiotic environment. We highlight that, although *Araucaria angustifolia* is today under threat, it has the potential to expand its actual narrow geographic range if proper management is insured.

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