

# What saplings can tell us about forest expansion over natural grasslands

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## Abstract

**Questions:** 1. Do the species composition, richness and diversity of sapling communities vary significantly in differently sized patches? 2. Do forest patches of different sizes differ in woody plant colonization patterns?

**Location:** São Francisco de Paula, Rio Grande do Sul, Brazil, 29°28' S, 50°13' W.

**Methods:** Three woody vegetation types, differing in structural development (patch size) and recovering for 10 years from cattle and burning disturbances, were sampled on grassland. We analysed the composition and complexity of the woody sapling communities, through relative abundance, richness and diversity patterns. We also evaluated recruitment status (residents vs. colonizers) of species in communities occurring in different forest patch size classes.

**Results:** 1. There is a compositional gradient in sapling communities strongly associated with forest patch area. 2. Richness and diversity are positively correlated to patch area, but only in poorly structured patches; large patches present richness and diversity values similar to small patches. 3. Resident to colonizer abundance ratio increases from nurse plants to large patches. The species number proportion between residents and colonizers is similar in small and large patches and did not differ between these patch types. 4. Large patches presented a high number of exclusive species, while nurse plants and small patches did not.

**Conclusions:** Woody plant communities in *Araucaria* forest patches are associated with patch structure development. Richness and diversity patterns are linked to patch colonization patterns. Generalist species colonize the understorey of nurse plants and small patches; resident species cannot recruit many new individuals. In large patches, sapling recruitment by resident adults precludes the immigration of new species into the patches, limiting richness and diversity.

**Keywords:** *Araucaria* forest; *Campos*; Diversity; Nucleation; Patchy ecosystem; Sapling community.

**Abbreviations:** PCoA = Principal co-ordinate analysis; RAI = Relative abundance index; RC = Relative cover; RF = Relative frequency; SNT = Stochastic niche theory; UNTBB = Unified neutral theory of biodiversity and biogeography.

**Nomenclature:** APG 2003; Anon. 2005).

## Introduction

Vegetation dynamics is a central issue in the ecological agenda (Cook et al. 2005). Direct periodic observation of vegetation change by means of permanent plots is the most accurate way to analyse community dynamics. Unfortunately, this approach is not always possible, especially in poorly studied environments. In those cases, static models can represent functional tools for understanding general patterns in vegetation dynamics (Pickett 1989; Cook et al. 2005). Community development is a result of structural variation along time. Pickett (1989) stressed the importance of the operational environment, i.e. the set of conditions and interactions that control system behaviour, in community dynamics modelling. In this context, knowledge of recovery patterns of communities released from disturbance regimes can be useful in order to understand long-term processes.

*Araucaria angustifolia* constitutes the main forest type on the highland plateau in south Brazil at altitudes above 500 m a.s.l. (Hueck 1972; Duarte & Dillenburg 2000). These forests often form mosaics with *Campos*, which is a natural type of grassland (Rambo 1994; Duarte et al. 2002). *Araucaria* forest expansion over grassland in southern Brazil is largely demonstrated by paleo-pollen evidence (Behling 2002; Behling et al. 2004). According to Behling et al. (2004), a change from a drier to a more moist climate that occurred 4300 years ago favoured *Araucaria* forest expansion, especially in the last millennium. These forests can now expand naturally over grassland (Rambo 1956; Klein 1960; Hueck 1972; Oliveira & Pillar 2004). However, burning and domestic cattle grazing have probably slowed, or stopped, the process (Pillar 2003; Machado 2004). In areas where cattle are extensively raised, herds use *Araucaria* forest patches for shelter, browsing and trampling the forest floor inside patches and thus preventing forest regeneration; cattle exclusion from forest patches allows successful forest species recruitment (pers. obs.).

*Araucaria* Forest expansion over *Campos* grassland occurs gradually by edge dynamics (Oliveira & Pillar 2004), or by nucleation (*sensu* Yarranton & Morrison 1974) of forest patches in the grassland (Klein 1960; Duarte et al. 2006). Recently we demonstrated the importance of shrubs and trees (particularly *Araucaria angustifolia*) in the initial establishment of forest species on grassland (Duarte et al. 2006). Nucleation is a process obviously related to area effects (Archer et al. 1988; Cabral et al. 2003; Cook et al. 2005). However, major mechanisms involved in forest patch dynamics remain unknown. In fact, Cook et al. (2005) pointed out the lack of knowledge about the influence of habitat area on community dynamics. According to the Equilibrium Theory (MacArthur & Wilson 1967), patch expansion should result in increased species richness. More recently, the Unified Neutral Theory of Biodiversity and Biogeography (UNTBB) (Hubbell 2001) stated that the area effect acts on the maximum number of individuals supported by the habitat rather than directly on the species number. Furthermore, as a forest patch expands the capacities of plant species to tolerate environmental conditions and to explore the resources should vary (Connell & Slatyer 1977; Tilman 1996, 2004). According to Cook et al. (2005), patch area is expected to be associated with major successional trends, since larger patches tend to present more accelerated ecological dynamics than smaller patches.

In this study we analysed sapling recruitment patterns in *Araucaria* forest patches varying in area and scattered on a *Campos* grassland site where grazing and fire disturbances have been suppressed for ca. 10 years. Since all patches had the same time of recovery from disturbance, differences between patches in relation to vegetation recruitment patterns were expected to reveal the effect of structural development variation on post-disturbance vegetation dynamics. Our focus was on sapling communities, which are good indicators of dynamic trends of the forest woody plant communities, since they represent the net result of recent dynamics at a given site and indicate how that community is going to be in the near future. We address the following questions: 1. Do the species composition, richness and diversity of sapling communities vary significantly in differently sized patches? 2. Do forest patches of different sizes differ in woody plant colonization patterns?

## Material and Methods

### Study area

The study was conducted at the Pró-Mata Research and Nature Conservation Center (CPCN Pró-Mata). The Center has a 4500 ha area, in the town of São Francisco de Paula (29°28' S, 50°13' W), Rio Grande do Sul State, southern Brazil. The study site was on a plateau at ca. 900 m a.s.l. (Machado 2004; Oliveira & Pillar 2004) and consisted of ca. 78 ha *Campos* grassland surrounded by *Araucaria* forest in which several small forest patches occur scattered throughout the area. The climate is classified according to the Köppen system as Cfb (Dalmagro & Vieira 2005). The annual mean temperature is ca. 14.5 °C, with negative temperatures occurring from April to November (Backes 1999) and the mean annual rainfall is 2252 mm, with high rainfall levels occurring every month (Backes et al. 2000). The presence of species phytogeographically related to Austral-Antarctic and Andean floras distinguish *Araucaria* forest communities from more tropical facies of Brazilian Atlantic forests (see Rambo 1951; Waechter 2002). The most physiognomically important tree species is *Araucaria angustifolia*. Some other typical species found in those forests are *Podocarpus lamberti*, *Drimys brasiliensis*, *Dicksonia sellowiana* and several species of *Myrtaceae*, *Melastomataceae* and *Lauraceae*. Cattle grazing and burning practices were terminated in 1994, allowing increasing regeneration in the forest and more biomass accumulation and woody plant establishment in the grasslands (Oliveira & Pillar 2004).

### Sampling methods

Forest patches occurring in the grassland matrix were classified into three size classes representing different structural development stages:

**Nurse plants** (Plate 1a). *Araucaria angustifolia* individuals are preferential sites for sapling establishment on grassland (Duarte et al. 2006). Thus, we sampled all isolated *Araucaria* trees in the grassland site, considering as isolated any tree occurring without any neighbour tree or tall shrub touching its crown. Crown cover was taken as the patch size and was estimated from crown projection diameter (Table 1). All woody saplings occurring beneath the tree canopy were identified and counted, and the relative cover of each species was visually estimated using the Braun-Blanquet cover scale. We sampled 26 *Araucaria* trees from October to December 2003; two individuals were ignored since no saplings were found beneath their canopies.

**Small patches** (Plate 1b). These represent an intermedi-

ate stage of structural development, between nurse plants and large patches. We defined as forest patch any group of woody plants with at least one adult tree and accompanying shrubs, forming a continuous canopy, surrounded by a continuous herb layer (Krebs 2001; Cabral et al. 2003). A small patch is any woody vegetation lacking a clear vertical structure, generally with few adult trees and a variable numbers of woody saplings. The canopies are open, allowing grassland species to resist, to some extent, forest invasion. We estimated the total patch area as an ellipse, using the maximum length and maximum width of the patch canopy (Table 1). We sampled ten small patches in January-February 2005. All woody individuals  $> 5$  cm DBH were counted and identified, and the relative cover of each species was estimated from the basal area (Mueller-Dombois & Ellenberg 1974). Along the main axis of each patch we delimited  $1.7 \text{ m} \times 1.7 \text{ m}$  quadrats, within which all woody individuals  $< 5$  cm DBH were identified and counted; the relative cover of each species was visually estimated using Braun-Blanquet's cover scale. We surveyed ca. five quadrats per sampling unit, which represented 8% of the total area of the small patches (Table 1).

**Large patches** (Plate 1c): We used data available from Machado (2004), who sampled five large forest patches in the grassland matrix between 2002 and 2003 (Table 1). These patches presented high structural development when compared to nurse plants and small patches, since they had a structured tree layer, a well-defined shrub layer, and a herb layer consisting exclusively of forest species. The author used  $5 \text{ m} \times 5 \text{ m}$  quadrats to sample woody individuals  $> 5$  cm DBH, and small quadrats ( $1.7 \text{ m} \times 1.7 \text{ m}$ ) delimited within larger quadrats to sample individuals  $< 5$  cm DBH. Relative cover of species was visually estimated using Braun-Blanquet's cover scale. Since our interest was only on forest woody species, we ignored non forest species and recalculated relative abundances based only on forest species. We surveyed ca. 72 quadrats per sampling unit, which accounted for 11% of the total area of the large patches (Table 1).

To verify whether any bias in the analyses would

**Table 1.** Mean area of nurse trees and forest patches and sampling effort of sapling communities in forest patches at different structural development stages in natural grassland, São Francisco de Paula, RS, southern Brazil. SE = standard error.

Patch size class	n	Mean area ( $\text{m}^2$ ) $\pm$ SE	
		Total area	Surveyed area
Nurse plants	24	$35.9 \pm 5.2$	$35.9 \pm 5.2$
Small patches	10	$195.3 \pm 37.9$	$15.3 \pm 1.7$
Large patches	5	$1899.6 \pm 255.7$	$209.8 \pm 6.4$

(a)



(b)



(c)



**Plate 1.** Nurse plants and forest patches in natural grassland in São Francisco de Paula, RS, southern Brazil. **a.** *Araucaria angustifolia* trees scattered in grassland. **b.** A small forest patch. Note the lack of a well-defined shrub layer below tree canopies. **c.** A large forest patch. Photographs: L.S. Duarte (2005).



arise from the fact that small forest patches were surveyed 1-2 years later than nurse plants and large forest patches, we used additional data on the sapling community structure beneath the same nurse trees, which were re-surveyed in 2005 at the same time as the small forest patches (L.S. Duarte unpubl.). We computed Euclidean distances between nurse trees in October-December 2003 and similar distances between the same nurse trees in January-February 2005. We performed a Mantel test (Mantel 1967) for the correlation between these two matrices ( $r = 0.37$ ) and found it highly significant ( $P < 0.01$ ), which indicates similar sapling community structure beneath the nurse trees in both years. Therefore, the comparison between nurse trees and small forest patches was not biased. By extension, we assumed that large patches were similarly stable at this time scale.

We described each sampling unit by the abundance of forest woody saplings, i.e. species dispersed from the surrounding forest. For this we measured a relative abundance index (*RAI*), computed from the relative frequency (*RF*) and relative cover (*RC*):

$$RAI = \frac{(RF + RC)}{2} \quad (1)$$

In this way a data matrix describing communities (sampling units) by the relative abundances of sapling species (variables) was used for the analyses.

To analyse the recruitment status of each species, individuals  $\geq 5$  cm and  $< 5$  cm DBH were assembled into two size classes, respectively, as presumed adult tree-shrubs (hereafter simply called *adults*) and as saplings. For each species in each patch size class (nurse plants, small patches and large patches) we counted (1) the number of sampling units with co-occurrence of adults and saplings of the species and (2) the number of sampling units with occurrence only as adults or (c) only as saplings; and then a Jaccard similarity index was computed as  $J = a/(a+b+c)$ . To be considered *resident* in a given patch size class, a species must be present in both adult and sapling classes in at least one sampling unit ( $J > 0$ ). Species present only as saplings, or not occurring simultaneously in the same units as saplings and adults, were considered *colonizers*. Species occurring only as adults in the same patch size class were considered *non-recruiter* species. Thus, for each patch size class, we obtained a set of residents, colonizers and non-recruiters. Undetermined species were removed from the analyses.

### Data analyses

We carried out a Principal Co-ordinates Analysis (PCoA) of sampling units to detect the principal axes of variation of sapling communities and their association with patch size. The data were previously log-transformed and the ordination was based on Euclidean distances between sampling units. Stability of the ordination axis was evaluated through bootstrap resampling (Pillar 1999). Additionally, we analysed the association between the main axes of PCoA scores and the patch size through linear regression analysis (Sokal & Rohlf 1981). For this analysis we used the residuals of a regression of PCoA scores on the surveyed area, instead of the original scores themselves, since there was a significant positive correlation between patch size and sampling effort ( $r = 0.89$ ,  $P < 0.01$ ). This procedure allowed us to remove the effect of varying sampling effort in different patch size classes.

We evaluated the complexity of sapling communities for each sampling unit using richness and diversity indexes, based on the Rényi generalized entropy formula (see Anand & Orlóci 1996):

$$H_\alpha(S) = \frac{1}{1-\alpha} \log \sum_{j=1}^q p_j^\alpha, \quad \text{in bits} \quad (2)$$

where  $q$  indicates the number of components (species) of the system  $S$  (community),  $p_j$  is the proportion of the species  $j$  in the community and  $\alpha$  is the order of entropy. Most frequently used diversity indexes, such as Shannon's, are special cases of Rényi entropy. When  $\alpha$  tends to 1, Rényi entropy equals Shannon's entropy. When  $\alpha = 0$ , the entropy value does not take into account the variation in the proportion of different species in a given community, and behaves as a richness index. Anand & Orlóci (1996) pointed out that the effect of varying species  $p$  (the equitability effect) is only stabilized when an order of entropy much higher than Shannon's ( $\alpha \approx 1$ ) is used, and suggested  $\alpha = 12$  as a good entropy order. Thus, we adopted the entropy orders 0 and 12 for richness and diversity analysis, respectively.

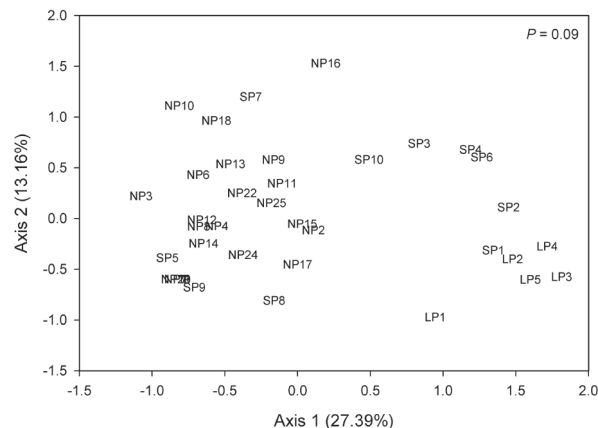
To evaluate the association between richness (or diversity) and patch size, we also used the residuals of a regression of richness (or diversity) on the surveyed area, to remove the effect of the sampling effort. Based on these residuals we computed Euclidean distances between sampling units, to verify differences in richness and diversity between the patch size classes. For this we used an ANOVA with randomization testing, using sum of squares between groups (Qb statistics) as the test criterion (Pillar & Orlóci 1996). In the cases when analyses of variance indicated significant differences between groups, we performed contrast analyses to verify which groups differed from others (Pillar &

Orlói 1996). The significance of contrasts was evaluated through randomization, in a similar way as in the variance analyses (Pillar & Orlói 1996). The same approach was used to evaluate the differences between the mean abundance and the mean species number proportion of resident and colonizer species in different forest patch classes.

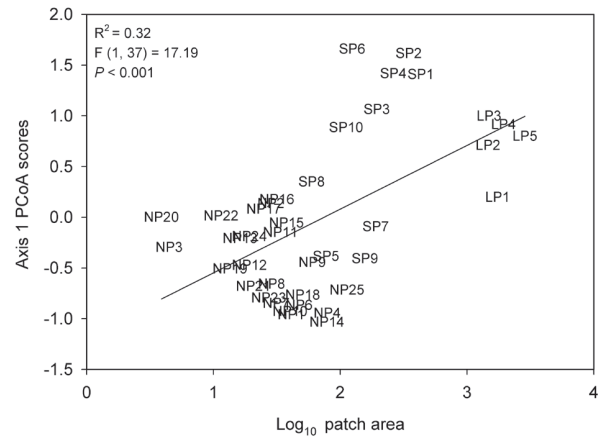
Regression analyses were carried using the SigmaStat 3.11 software (Anon. 2004). All other analyses were performed using the MULTIV 2.3.17 (Pillar 2004) statistical software.

## Results

A detailed description of sapling communities is shown in Table 2. Undetermined species removed from analyses (taxonomic noise) represented < 1% of the total variance in each vegetation type (Table 2). We found a species pool common to all patch size classes, made up of nine species i.e. *Araucaria angustifolia*, *Drimys brasiliensis*, *Gordonia acutifolia*, *Ilex microdonta*, *Lamanea ternata*, *Miconia hyemalis*, *Myrsine lorentziana*, *Psidium cattleianum* and *Siphoneugena reitzii*. This species group accounted for 91% of relative abundance beneath *Araucaria* nurse plants. In small patches and large patches, those species still remained with, respectively, 69% and 59% of relative abundance (Table 2). Moreover, they represented 43% of species in small patches and 18% in large patches (Table 2). Nurse plants did not present any exclusive species beneath their canopies, while small patches presented just one species (Table 3). On the other hand, large patches presented 33 exclusive species. Most of the exclusive species found in large patches were colonizers (Table 3).

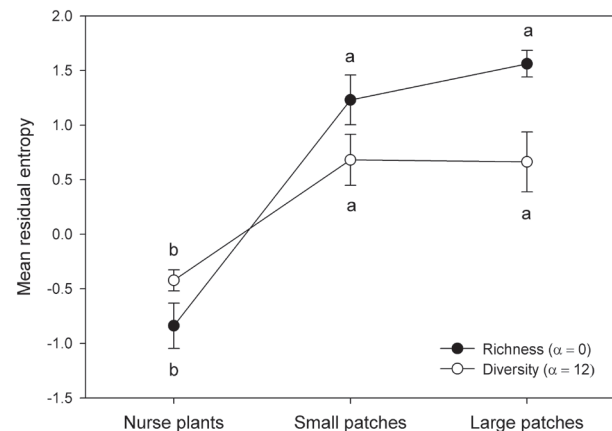


**Fig. 1.** PCoA ordination of sapling communities in forest patches at different structural development stages in natural grassland, São Francisco de Paula, southern Brazil. NP = nurse plants, SP = small patches, LP = large patches. *P* value for axis 1 generated by bootstrap resampling.



**Fig. 2.** Association between the first PCoA ordination axis and patch size in natural grassland, São Francisco de Paula, southern Brazil. NP = nurse plants, SP = small patches, LP = large patches.

Ordination analysis of sapling communities indicated a significant gradient along the first ordination axis (Fig. 1). While lower scores were associated with *Araucaria* nurse trees, higher scores were related to large patches. Small patches had an oscillating distribution; while some small patches were positioned close to the nurse plants, others showed greater proximity to large patches. This gradient along the first ordination axis was characterized by an increase in *Myrcia retorta*, *M. guianensis*, *Drimys brasiliensis*, *Daphnopsis fasciculata*, *Miconia cinerascens*, *Siphoneugena reitzii*, *Vernonia discolor* and *Ilex microdonta*. Those species were



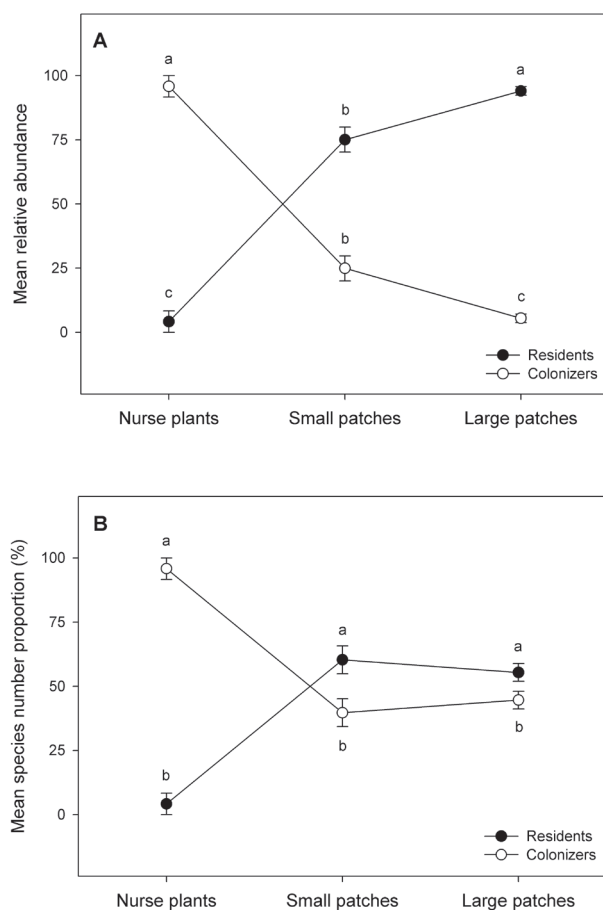
**Fig. 3.** Richness and diversity patterns in three forest patches, at different structural development stages, in natural grassland, São Francisco de Paula, southern Brazil. Mean values calculated on residuals of a regression of richness or diversity on sampling effort. Lines crossing mean values are standard errors. Mean richness/diversity values followed by the same letter do not differ significantly between patch size classes ( $\alpha = 0.05$ ).

**Table 2.** Abundance of forest woody species in sapling communities at different forest development stages in natural grassland, São Francisco de Paula, southern Brazil. NP = nurse plants, SP = small patches, LP = large patches. Taxonomic noise is the percent of total variance associated with non-identified species.

Species	Family	Mean relative abundance (%)		
		NP	SP	LP
<i>Araucaria angustifolia</i>	Araucariaceae	4.17	1.14	3.85
<i>Cabralea canjerana</i>	Meliaceae	-	-	0.12
<i>Casearia decandra</i>	Salicaceae	-	-	0.61
<i>Calyptranthes grandifolia</i>	Myrtaceae	-	-	< 0.01
<i>Clethra uleana</i>	Clethraceae	-	-	0.10
<i>Daphnopsis fasciculata</i>	Thymelaeaceae	-	0.60	16.16
<i>Dicksonia sellowiana</i>	Dicksoniaceae	-	-	0.29
<i>Drimys brasiliensis</i>	Winteraceae	1.07	2.41	9.03
<i>Erythroxylum cuneifolium</i>	Erythroxylaceae	-	-	0.03
<i>Eugenia uruguayensis</i>	Myrtaceae	-	-	0.12
<i>Ficus luschnathiana</i>	Moraceae	-	-	0.01
<i>Gordonia acutifolia</i>	Theaceae	1.38	2.47	0.08
<i>Ilex brevicuspis</i>	Aquifoliaceae	-	-	0.14
<i>Ilex dumosa</i>	Aquifoliaceae	7.57	1.02	-
<i>Ilex microdonta</i>	Aquifoliaceae	0.35	0.67	2.65
<i>Ilex paraguayensis</i>	Aquifoliaceae	-	-	0.11
<i>Inga lentiscifolia</i>	Fabaceae	-	-	0.01
<i>Lamanonia ternata</i>	Cunoniaceae	0.38	0.63	0.02
<i>Leandra laevigata</i>	Melastomataceae	-	-	0.02
<i>Leandra sublanata</i>	Melastomataceae	-	-	0.92
<i>Matayba elaeagnoides</i>	Sapindaceae	-	0.16	0.11
<i>Miconia cinerascens</i>	Melastomataceae	-	3.93	3.17
<i>Miconia hyemalis</i>	Melastomataceae	11.67	10.98	6.95
<i>Miconia sellowiana</i>	Melastomataceae	-	-	< 0.01
<i>Mollinedia elegans</i>	Monimiaceae	-	-	0.02
<i>Myrsine coriacea</i>	Myrsinaceae	-	1.60	0.54
<i>Myrceugenia euosma</i>	Myrtaceae	0.08	-	1.26
<i>Myrcia guianensis</i>	Myrtaceae	-	5.02	3.25
<i>Myrcia hartwegiana</i>	Myrtaceae	-	-	0.23
<i>Myrsine lorentziana</i>	Myrsinaceae	68.14	43.81	29.17
<i>Myrceugenia miersiana</i>	Myrtaceae	-	-	0.32
<i>Myrceugenia myrcioides</i>	Myrtaceae	-	-	0.13
<i>Myrcia retorta</i>	Myrtaceae	-	9.25	3.27
<i>Nectandra grandiflora</i>	Lauraceae	-	-	0.01
<i>Ocotea corymbosa</i>	Lauraceae	-	-	0.02
<i>Ocotea elegans</i>	Lauraceae	-	-	0.03
<i>Ocotea indecora</i>	Lauraceae	-	-	0.01
<i>Ocotea porosa</i>	Lauraceae	-	-	0.11
<i>Ocotea puberula</i>	Lauraceae	-	-	0.08
<i>Ocotea pulchella</i>	Lauraceae	-	-	2.60
<i>Piptocarpha axillaris</i>	Asteraceae	-	-	1.36
<i>Piptocarpha notata</i>	Asteraceae	-	-	0.50
<i>Podocarpus lamberti</i>	Podocarpaceae	-	-	0.47
<i>Psidium cattleianum</i>	Myrtaceae	2.01	4.03	0.42
<i>Rollinia rugulosa</i>	Annonaceae	-	-	0.42
<i>Roupala brasiliensis</i>	Proteaceae	-	0.16	0.09
<i>Rudgea parquioides</i>	Rubiaceae	-	0.11	0.21
<i>Sapium glandulatum</i>	Euphorbiaceae	-	0.46	0.42
<i>Siphoneugena reitzii</i>	Myrtaceae	1.77	3.20	6.99
<i>Solanum johannae</i>	Solanaceae	-	-	0.03
<i>Solanum pseudoquina</i>	Solanaceae	-	-	0.04
<i>Solanum variabile</i>	Solanaceae	-	1.27	0.09
<i>Tibouchina sellowiana</i>	Melastomataceae	-	-	0.30
<i>Vernonia discolor</i>	Asteraceae	-	3.36	2.10
<i>Vitex megapotamica</i>	Lamiaceae	-	-	0.46
<i>Weinmannia paulliniifolia</i>	Cunoniaceae	-	0.76	-
<i>Xylosma pseudosalzmannii</i>	Salicaceae	-	-	0.37
<i>Zanthoxylum rhoifolium</i>	Rutaceae	-	-	0.03
Sub-total		98.58	97.04	99.85
Non-identified species		1.42	2.96	0.15
Total		100.00	100.00	100.00
Taxonomic noise		0.82	0.12	0.02

more abundant in large patches. Regression analysis indicated a significant association between patch area and the first axis scores of PCoA, after accounting for the effect of sampling effort (Fig. 2).

Small and large patches presented higher richness and diversity mean values than nurse plants; however, they did not differ from each other, after accounting for the effect of sampling effort (Fig. 3). Beneath *Araucaria* nurse plants, sapling communities were constituted mostly by colonizer species, both in abundance and species number proportion terms (Fig. 4a, b). Large patches presented the highest abundance of resident species and the lowest abundance of colonizers, while small patches had intermediary values between nurse plants and large patches (Fig. 4a). Nonetheless, small and large patches did not differ in relation to the proportions of resident and colonizer species (Fig. 4b).



**Fig 4.** Recruitment patterns of resident and colonizer species at different forest development stages, in natural grassland, São Francisco de Paula, southern Brazil. **A.** Mean relative abundance; **B.** Species number proportion. Values are means and lines crossing mean values are standard errors. Mean values followed by different letters differ significantly between patch size classes ( $\alpha = 0.05$ ).

**Table 3.** Species distribution in sapling communities in forest patches, at different structural development stages, in natural grassland, São Francisco de Paula, southern Brazil.  $N_T$  = Total species number;  $N_E$  = Exclusive species number. Percent values in parentheses refer to the proportion of exclusive species in the total number of species.

Site	$N_T$	Exclusive species		
		$N_E$	%	
			Residents	Colonizers
Nurse plants	9	0	0	0
Small patches	23	1 (4%)	0	4
Large patches	56	33 (59%)	18	82

## Discussion

Our study indicated that the recruitment of woody saplings in *Araucaria* forest patches released for ten years from a secular disturbance regime was strongly associated with the structural development of the patches. We observed a positive relationship between patch area and species richness, a result very similar to other studies (e.g. Archer et al. 1988; Cabral et al. 2003; Cook et al. 2005). However, this pattern was only evident when we compared *Araucaria* nurse plants with small and large patches. Despite large patch areas being ca. ten times larger than small patches, richness and diversity did not differ significantly between those patch types, which is contrary to the classical species-area positive association (MacArthur & Wilson 1967). The UNTBB (Hubbell 2001) states that species richness is a function of the maximum number of individuals ( $J$ ) supported by a given habitat patch (the zero-sum dynamics). Since  $J$  is spatially dependent on the patch size, the UNTBB prediction is that large patches must present higher species richness than small patches, which was not observed. Unfortunately, we did not have any information on the carrying capacity of the patches, which would have allowed us to evaluate zero-sum dynamics in the present study. Nonetheless, the UNTBB also predicts that whenever a habitat patch comes closer to its specific  $J$  value, the probability of any dead individual being replaced by a new immigrant species ( $m$ ) must decrease.

Nucleation dynamics involves the increased recruitment of new individuals by mature resident species (Yarranton & Morrison 1974; Cook et al. 2005). The more intense this process is, the more rapidly the number of individuals in the patch should tend to  $J$ , and patch colonization by new species must be progressively prevented as  $m$  decreases (see Fargione et al. 2003). Thus, richness patterns observed in this study probably reflected differences between patches in respect to their receptiveness for colonizer species. Post-disturbance

colonization by new species was favoured beneath *Araucaria* nurse plants and in small patches, when compared to large patches, since nurse plants and small patches had few adult plants capable of recruiting new individuals (high  $m$  probability). Instead, large patches possessed well structured shrub/tree communities, making the intense recruitment of new individuals by resident species possible, and precluding a more pronounced establishment of new colonizers (low  $m$  probability).

We found that small and large patches had similar diversity values. However, the components of diversity were distinct when we compared small and large patches. In small patches, colonizer species were more abundant than in large patches, which contributed to the increase of diversity. The low abundance of colonizers in large patches reduced diversity values, although both patch types presented a similar species number proportion of residents and colonizers (close to a 1:1 ratio), which suggested that the colonization by new species was not limited by seed dispersal from continuous forest. Anjos & Boçon (1999) found a positive association between *Araucaria* forest patch area and the number of frugivorous bird species present in the patches. Thus, a more pronounced seed rain in the well-structured large patches might be expected, since those patches have more appeal to a large amount of vertebrate dispersers than the poorly structured nurse plants and small patches. Disperser attraction might possibly counterbalance the negative effect of resident recruitment.

According to the Stochastic Niche Theory (SNT) proposed by Tilman (2004), the colonization of forest patches by immigrant species might be explained by a niche-based mechanism, in which the probability of a colonizer to survive until maturity depends on its capacity to explore the resources left available by the resident species. In other words, colonizers must not show overlapping niche characteristics related to establishment with resident populations. In this study we found that most species established beneath *Araucaria* nurse plants were also abundant in small and large patches. Those generalist species occurred in a broad set of environmental conditions, from the very open and grassy understorey of *Araucaria* nurse plants to the darker understorey of large patches. In small and large patches, they accounted for a considerable part of resident sapling populations. Our results showed that in small patches, where resident saplings were less abundant than in large patches, colonizer sapling communities were constituted mainly by generalist species. In large patches, more than 90% of relative abundance was constituted by resident saplings of generalist species. Nonetheless, most colonizers were exclusive species, totally absent in poorly structured patches. If colonizers presented distinct ecological requirements in relation to

resident species, we could hypothesize that SNT was also operating in nucleation dynamics. Perhaps woody species colonizing large patches allocate more energy to seed reserves than those generalist species, to be more competitive and successfully occupy the few spaces left by the residents (Foster & Janson 1985; Moles & Westoby 2004). A large amount of evidence indicates that seed size: number ratio represents an important trade-off for plants, being closely associated with differential capacities of survival (investment in reserves) or dispersal (investment in seed number) of the species, across a vast variety of habitats (Leishman 2001; Leishman & Murray 2001; Moles & Westoby 2004). It remains to be tested.

We live in a changing world, where a global tendency for increased woody plant abundance on grasslands ecosystems has been suggested (Archer et al. 1988). Nonetheless, studies focusing on forest nucleation in grassland landscapes are scarce, especially in less developed countries. Brazilian *Araucaria* forest is one of the most threatened (and less well known) ecosystems in South America. *Araucaria angustifolia* itself is considered a threatened species (Hilton-Taylor 2000). Thus, ecologists focused on this marvellous landscape must use approaches that optimize the evaluation of environmental processes and mechanisms involved in its structure and dynamics in short-term studies. Nucleation is a very complex phenomenon, and long-term monitoring studies on *Araucaria* forest sites are lacking. Thus, static models should be used as functional tools for understanding ecological patterns in this ecosystem (see Pickett 1989). We also need to propose long-term studies to confirm or dismiss the hypotheses generated by static models. What can saplings tell us about forest dynamics? First, sapling dynamics represent an excellent tool for studying forest dynamics, since sapling communities show how the present community is working, and how the near-future community is going to work. Our study showed the major trends in woody plant colonization in *Araucaria* forest patches varying in structural development and recovering from secular disturbance. Second, working with saplings instead adults is less time consuming. This point is very important for studies with conservation purposes. Last, but not least, our methodological approach raised some important questions about the ecological mechanisms underlying forest patch colonization: Are colonizer species ecologically distinct from the residents? Does seed dispersal by vertebrates affects plant colonization in forest patches? We hope to answer these and other questions in future studies.



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