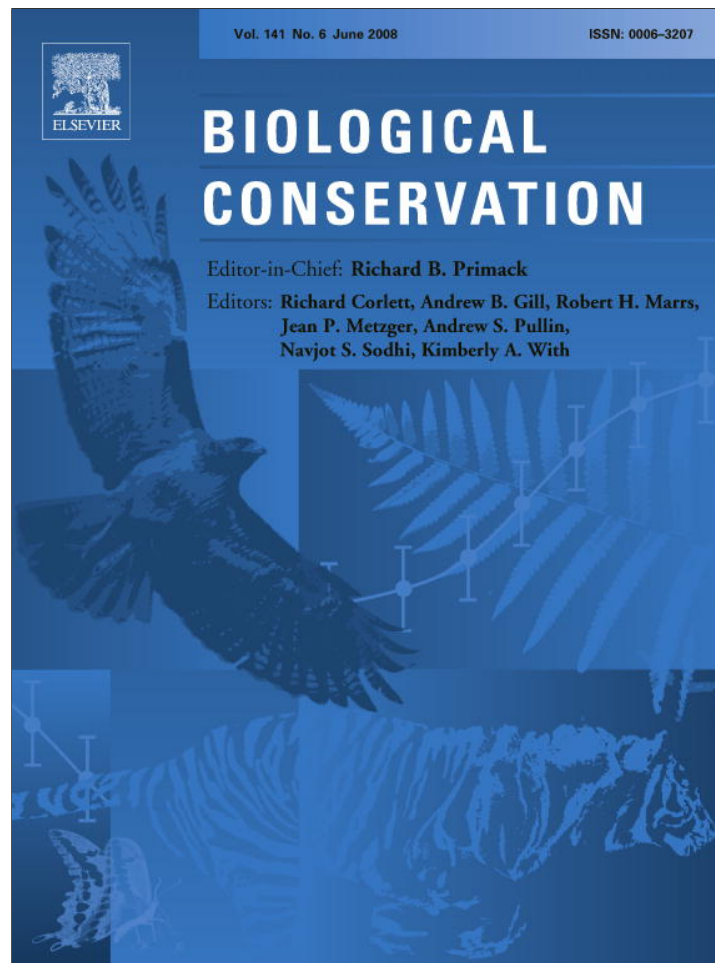


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How long does the Atlantic Rain Forest take to recover after a disturbance? Changes in species composition and ecological features during secondary succession

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ABSTRACT

We evaluated floristic and ecological changes in plant communities after disturbance in Southern Atlantic Rain Forests, in the Brazilian states of Rio de Janeiro, São Paulo, Paraná and Santa Catarina. We compiled data for 410 tree species from 18 forests ranging from 4 to 120 years after disturbance, and classified them by dispersal mode (animal vs. non-animal), successional group (pioneer vs. non-pioneer), vertical position (understorey vs. non-understorey) and geographic distribution (Atlantic Forest vs. widespread). We found that both geographical location and time since disturbance affect species distribution and β -diversity. Regression analyses showed significant, positive and strong relations ($0.26 \leq r^2 \leq 0.63$; $P < 0.05$) between fragment age and species richness, proportion of animal dispersed species, of non-pioneer species, of understorey species and with restricted distribution. Applying our data to values found in literature we predict that a forest needs about one to three hundred years to reach the proportion of animal-dispersed species (80% of the species), the proportion of non-pioneer species (90%) and of understorey species (50%) found in mature forests. On the other hand much more time is necessary (between one and four thousand years) to reach the endemism levels (40% of the species) that exist in mature forests. Our findings indicate that disturbance results in significant changes in species composition (decrease in endemic species) and ecological guilds (decrease in zoochory and in non-pioneer and understorey species), but forests can gradually recover over time spans of hundreds of years.

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1. Introduction

The Atlantic Rain Forest once covered almost all of the Brazilian coastal zones of the approximately 1,350,000 km² that existed before the Portuguese colonization in the 1500s less than 7% of the original forests remained in the early 2000s (SOS Mata Atlântica INPE, 2002). The Atlantic Rain Forest is considered a hotspot for biodiversity conservation, due to its species richness (both plant and animal species) and high

level of endemism (Myers et al., 2000). A recent study estimated that this biome is home to approximately 8000 endemic species of plants, 73 of birds, 160 of mammals, 60 of reptiles and 153 of amphibians (Myers et al., 2000). Logging and clearing the forest for agriculture have led to high levels of fragmentation and subsequent species extinctions (Morelato and Haddad, 2000).

This forest has floristic affinities with other wet forests, like those in the Amazon Basin and the Brazilian plateau

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(Leitão-Filho, 1994; Oliveira-Filho and Fontes, 2000; Scudeller et al., 2001) as well as with adjacent dry formations (Oliveira-Filho and Ratter, 1995). Despite these floristic liaisons, plant endemism levels in the Atlantic Forest can reach close to 40% (Mori et al., 1981; Guedes-Bruni and Morim de Lima, 1994; Thomas et al., 1998), which translates to a density of 8.7 endemic species for each 100 km² (Myers et al., 2000). Moreover, several species occur in low densities (Pagano et al., 1995), with narrow distributions and occur only in restricted areas (Scudeller et al., 2001). Thus each patch of Atlantic Forest has a particular flora.

The Atlantic Forest's floristics and diversity are highly variable along its area of occurrence, due to differences in latitude and historical processes (Morellato and Haddad, 2000; Scarano, 2002). In this study we focused specifically on the Southern Atlantic Forest. This is very fragmented at present, with the surviving patches located mostly in steep slopes unsuitable for agriculture or in protected areas (Leitão-Filho, 1994; Silva, 2003). A great part of remnant fragments are secondary forests regrowing after slash and burn practices during the last two centuries. The focus of the study is the secondary forests' potential to recover the former Atlantic Rain Forest.

Disturbance caused by logging strongly changes environmental conditions for plant growth and survival in tropical forests (Laurance, 1999; Laurance et al., 2002; De Walt et al., 2003; Brearley et al., 2004). Changes in temperature, humidity and light availability create new habitats that are occupied by species differing in resource requirements (Mesquita et al., 1999; Tabarelli et al., 1999). These impacts change the composition of plant communities, which start going through secondary succession (Hill and Curran, 2003; Nunes et al., 2003). In this situation not only the species composition, but also the community guilds and forest dynamics are distinctive from primary forests (Condit et al., 1995; Nascimento et al., 2005). Secondary forests are new environmental sites, where secondary succession favors the establishment of a larger proportion of pioneer and weedy species instead of the ones from mature forests (Tabarelli et al., 2004; Oliveira et al., 2004). Increase in light availability favor shade intolerant species and decrease the number of understorey species in secondary forests (Guariguata and Ostertag, 2001). All of these factors affect plant/animal mutualistic interactions, like pollination and seed dispersal (Aizen and Feinsinger, 1994), and population dynamics (Ferreira and Laurance, 1997; Laurance et al., 1998a,b; Mesquita et al., 1999).

Disturbance and subsequent successional changes also have effects on species richness and abundance (Laurance et al., 2002; Harper et al., 2005) and modify local and regional biodiversity patterns. In undisturbed areas factors such rainfall patterns, soil type and composition, latitudinal and altitudinal ranges, as well as the geographical distance between the areas cause floristic differentiation (Leitão-Filho, 1987; Oliveira-Filho et al., 2004; Oliveira-Filho and Fontes, 2000; Pyke et al., 2001; Scudeller et al., 2001; Slik et al., 2003; Peixoto et al., 2004; Santos et al., 2007). Nevertheless human impact on natural landscapes may lead species composition to a more homogeneous state (even if located more distantly), which in turn can decrease β -diversity (Shmida and Wilson, 1985). On the other hand, well pre-

served or mature forests tend to keep local floristic differentiation (De Walt et al., 2003). The understanding of the relationships between diversity patterns at a regional scale and its causes (Condit et al., 2005) is an important tool for species conservation.

In this article we investigate the effects of disturbance and subsequent successional changes on species composition and on ecological groups of species in plant communities on Southern lower slopes Atlantic Forests. Based on the compilation of data from 18 forests ranging from 4 to 120 years after disturbance, we address the following questions: (1) Is the time since disturbance or geographical location more important in causing floristic changes at a regional scale? (2) Do forests of different ages (measured by years after disturbance) show different proportions of species with particular ecological characters (e.g., dispersal mode: animal vs. non-animal; successional group: pioneer vs. non-pioneer; vertical position in the forest: understorey vs. non-understorey; as well as distributional ranges: exclusively from Atlantic Forest vs. wide-spread)? (3) Is it possible to predict the time required by the Atlantic Rain Forest to return to pre-disturbance forest conditions based on floristic and ecological changes?

2. Methods

The data matrix was compiled from 18 lists of tree species from phytosociological studies in the Southern Atlantic Forest (Table 1, Fig. 1). The Southern block (Rio de Janeiro, São Paulo, Paraná and Santa Catarina states) represents one of three biogeographic regions (Northern, Central and Southern blocks) in the Brazilian Atlantic Forest (Silva and Shepherd, 1986; Leitão-Filho, 1994; Thomas et al., 1998; Oliveira-Filho and Fontes, 2000; Aguiar et al., 2003). In all cases areas experienced a slash-and-burn practice or were logged before the use for pasture or subsistence agriculture. After areas had been abandoned a successional process took place resulting in the establishment of secondary forest. We chose only studies in which authors informed the forest age, i.e. how long ago the forests had been established on those abandoned lands. Nevertheless, five studies refer to "late successional forest" (Guapyassú, 1994; Silva, 1994; Melo and Mantovani, 1994; Moreno et al., 2003), for which we accepted 120 years as an estimate, following Tabarelli and Peres (2002). These 120 years old fragments are virtually the most conserved lower slope forests in the region whereas mature and undisturbed forests are located in higher altitudes. In both young and well-developed forests an additional and less important disturbance (e.g. selective cut of trees for wood or for food as the palm *Euterpe edulis*) was sometimes observed, but was not considered in the calculation of the age of the fragment. Studies included only quantitative and area delimited (plot and point-centered quadrant) surveys. Some variation in sample size (from 0.03 ha to 1 ha) and plant size was verified (Table 1), because surveys included fragments with limited area and because tree size is obviously variable in young to old growth forests. Thus we assumed that those variations were part of our aim and did not affect our results significantly. To avoid bias caused by altitudinal differentiation, we chose only areas within the range of 50–500 m elevation, a range that includes lower slope forests (IBGE, 1992).

Table 1 – General characteristics of the Southern Atlantic Forests included in this study, ordered by age

	Locality	Age (years since disturbance)	Elevation (m)	Rainfall (mm yr ⁻¹)	Species richness	Density (ind.ha ⁻¹)	Survey method (plant size)	Source
1	Antonina-PR	4	50	2500	16	3600	Plot (height ≥ 1 m)	Cheung (2006)
2	Iporanga-SP	15	230	1800	31	4306	Plot (height ≥ 2.1 m)	Torezan (1995)
3	Iporanga -SP	15	500	1800	39	1940	Plot (dbh ≥ 4.8 cm)	Aidar et al. (2001)
4	Morretes-PR	15	50	2290	24	1270	Plot (dbh ≥ 6.3 cm)	Guapyassú (1994)
5	Antonina-PR	20	60	2500	9	1890	Plot (dbh ≥ 4.8 cm)	Liebsch et al. (2007)
6	Angra do Reis-RJ	25	140	2100	62	2784	Plot (height ≥ 2 m or dbh ≥ 2.5 cm)	Oliveira (2004)
7	Iporanga-SP	25	500	1800	30	1690	Plot (dbh ≥ 4.8 cm)	Aidar et al. (2001)
8	Morretes-PR	25	50	2290	37	1690	Plot (dbh ≥ 6.3 cm)	Guapyassú (1994)
9	Iporanga-SP	36	500	1800	53	1520	Plot (dbh ≥ 4.8 cm)	Aidar et al. (2001)
10	Peruibe-SP	50	200	2000	36	1420	Plot (dbh ≥ 5 cm)	Oliveira et al. (2001)
11	Iporanga-SP	50	230	1800	69	5734	Plot (height ≥ 2.1 m)	Torezan (1995)
12	S. P. Alcântara-SC	60	300	1390	47	4966	Plot (dbh ≥ 5 cm)	Siminski et al. (2004)
13	Antonina-PR	80	60	2500	61	3006	Plot (dbh ≥ 4.8 cm)	Liebsch et al. (2007)
14	C. Goytacazes-RJ	120	250	1300	109	1250	Plot (dbh ≥ 10 cm)	Moreno et al. (2003)
15	Cananéia-SP	120	200	3000	131	2510	Plot (dbh ≥ 2.5 cm)	Melo and Mantovani (1994)
16	Antonina-PR	120	60	2500	51	1600	Plot (dbh ≥ 4.8 cm)	Liebsch et al. (2007)
17	Morretes-PR	120	50	2290	57	1405	Plot (dbh ≥ 6.3 cm)	Guapyassú (1994)
18	Morretes-PR	120	485	2290	73	2422	Point-centred (dbh ≥ 4.8 cm)	Silva (1994)

Abbreviations for the states: RJ – Rio de Janeiro; SP – São Paulo; PR – Paraná; SC – Santa Catarina.

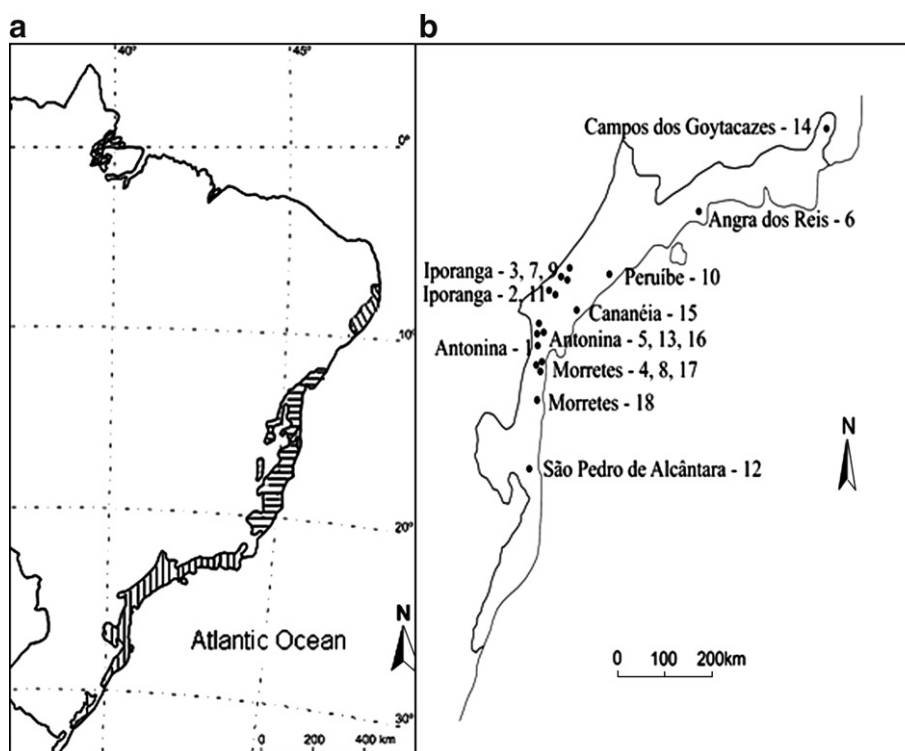


Fig. 1 – The Atlantic Forest in Brazil. (a) Diagonal lines: Northern Atlantic Forest; horizontal lines: Central Atlantic Forest; vertical lines: Southern Atlantic Forest. (b) Localization of the 18 Southern Atlantic Forests compared for this study. From: IBGE (1992) and Tabarelli and Peres (2002).

Despite their fairly wide geographical range (~7° latitude), all the areas are under similar climates, being tropical, rainy and wet and without a dry season following Köppen's classification.

A list of species was organized and checked for nomenclatural updates, and the undetermined species were excluded from the analysis (18% of the species). The remaining 410 tree species were classified by the following characters:

1. Dispersal modes: the species were categorized as animal-dispersed or non-animal-dispersed (wind or other abiotic vector), following Pijl (1972).
2. Successional group: the species were categorized as pioneers (with populations established in gaps or under full sunlight) or non-pioneers (with populations established under shade), following Swaine and Whitmore (1988).
3. Vertical position: the species were categorized as understorey (biggest trees up to 8 m tall at maximum) or non-understorey (biggest trees more than 8 m tall), following Guilherme et al. (2004) and Oliveira-Filho et al. (2004).
4. Distributional range: the species were categorized as exclusively from Atlantic Forest or widespread, when occurring also in other types of vegetation than the Atlantic Forest.

Both the placement of each species in these guilds and verification of recent synonyms were checked in herbarium collections (UPCB), literature (Flora Neotropica, Flora Ilustrada Catarinense, Flora Fanerogâmica de São Paulo), websites (Instituto Agronômico de Campinas-SP and Missouri Botanical Garden), as well as other compilations (Isernhagen, 2001; Oliveira-Filho et al., 2005). A small proportion (<0.05%) of 410 species has no information about guilds and was not considered in the analysis. Family classification followed APG II (APG, 2003).

In order to verify if differences in species composition among fragments could be explained by the time since last disturbance or geographical position we constructed two matrices. The main matrix contained the binary data from the occurrence of 410 species and the second matrix the latitude, longitude, species richness and age data from the 18 sites. We performed a Detrended Correspondence Analysis (DCA) using PC-ORD 5.0. Like other correspondence analyses, DCA ordines both species and sample units simultaneously. Nevertheless, it is better in cases where samples are very variable as no assumptions about the distribution of sample units and species in environmental space are necessary (McCune and Grace, 2002). The significance of correlation coefficients generated by DCA was checked for different confidence intervals, considering $\alpha = 0.05$ (Zar, 1999).

To establish models that could predict the amount of time a secondary forest needs to return to pre-disturbance standards we performed regression analyses (Zar, 1999) between the ages of the areas and the proportion of species that belong to each of the four guilds. The same analyses were made using the proportion of individuals from each species in each fragment. We also tested linear and logistic models, adjusting the curves according to the best value of r^2 (Zar, 1999). An additional test (Spearman's correlation) was performed between the guilds (proportion of species) in order to investigate putative associations among variables and their effect on the regressions (Zar, 1999).

From these models we calculated the time that a disturbed forest needs to return to pre-disturbance characteristics. Here we considered literature information about the percentage of species expected in a mature tropical forest (or specifically to the Atlantic Rain Forest) in terms of zoochoric species (80%, according Howe and Smallwood, 1982), non-pioneer species (90%, Tabarelli and Mantovani, 1999), understorey species (50%, Silva, 1994; Tabarelli and Mantovani, 1999) and endemic

species (40%, Mori et al., 1981; Guedes-Bruni and Morim de Lima, 1994; Thomas et al., 1998). These expected proportions were used in each linear or logarithmic model generated from regressions to estimate the time, in years, for the forest to recover. Since these values from the literature are estimates we also calculated a time range considering a change in 5% above and below the base value. As an example, for zoochoric species we calculated the number of years during which a secondary forest could reach 80% of zoochorous species (according to the proportion expected in literature), and therefore we also considered 85% and 75% of species (5% above and below the base value). The same method was used to estimate the proportion of non-pioneer, understorey and endemic species.

3. Results

The total checklist showed a strong variation among the floristic composition of the sites, as well as among the species character (BC-Supplementary material).

3.1. Variation in floristic composition

The DCA produced a homogeneous diagram (Fig. 2) represented by axis 1 (eigenvalue = 0.50; length of gradient = 2.84) and axis 2 (eigenvalue = 0.36; length of gradient = 2.85). The axis 1 represents latitude ($r = -0.63$, $P < 0.001$) and longitude ($r = -0.56$, $P < 0.001$) that are the more important variables causing differences in species composition. Axis 2 represents forest age ($r = -0.45$; $P = 0.03$) that is also an important factor in species distribution.

3.2. Relations among species richness, ecological characters and time after disturbance

Species richness (from 9 to 275 species) and the proportions of animal-dispersed species (all $\geq 56\%$), non-pioneer species (from 19% to 87%), understorey species (6–54%) and endemic

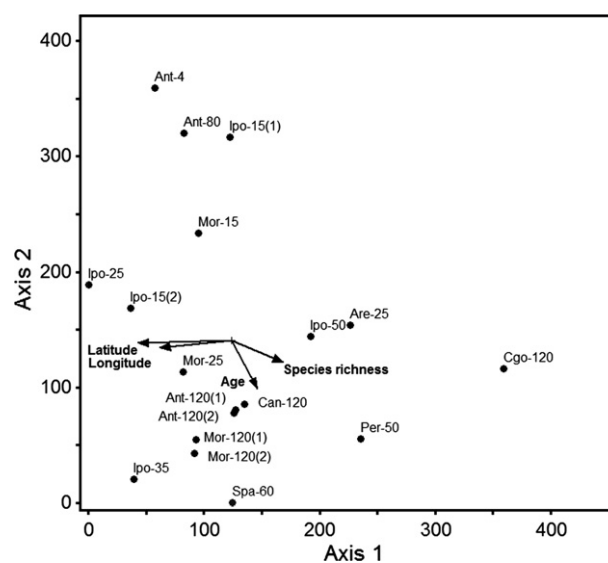


Fig. 2 – Axis 1 and 2 of the Detrended Correspondence Analysis (DCA) applied to 18 Southern Atlantic Forests. The area numbers are the same as shown in Table 1.

Table 2 – Total tree species richness and percentages of species guilds (\pm SD) of the Southern Atlantic Forests included in this study

Age (years since disturbance)	Studied sites (n)	Species richness	Zoochoric species (%)	Non-pioneer species (%)	Understorey species (%)	Endemic species (%)
4	1	16	75	19	6	13
15	3	31.3 \pm 7.5	72 \pm 4.6	54.4 \pm 5.3	32 \pm 7.8	10.3 \pm 4.9
20	1	9	56	22	22	0
25	3	42.7 \pm 16.3	76.7 \pm 12.7	65.8 \pm 21.3	42.9 \pm 0.7	14.4 \pm 7.2
36	1	53	75	70	38	11
50	2	52.5 \pm 23.3	83.8 \pm 4.5	76.4 \pm 9.7	43.8 \pm 4.6	16.7 \pm 4.6
60	1	47	87	85	54	24
80	1	61	85	87	50	20
120	5	84 \pm 34.2	82.7 \pm 3.8	79.1 \pm 7.2	44.2 \pm 8.3	24.5 \pm 3.9

species (0–24%) varied among all forest ages (Table 2). The species richness was a function ($r^2 = 0.54$, $F_{1,17} = 18.19$, $P = 0.0007$) of the time after disturbance (Fig. 3a). The proportion of animal-dispersed species was positively related to time since disturbance ($r^2 = 0.26$, $F_{1,16} = 5.4$, $P = 0.034$, Fig. 3b). Also, there was a greater variability among younger fragments than among older fragments. The lowest proportions of animal-dispersed species (56%) were those found in areas around 20 years old, while the 60 year-old forests have approximately 85%. The same pattern was found when we analyzed the proportions of individuals, instead of species ($r^2 = 0.62$, $F_{1,14} = 21.22$, $P = 0.0005$, 1 missed outlier), with one exception: the four years old forest (area 1), with 84% individuals that are animal-dispersed. From the model it was possible to estimate that a forest needs 65 years (range: 23–178 years) to achieve a proportion of 80% of animal-dispersed species.

The proportions of non-pioneer species also increased in older areas ($r^2 = 0.59$, $F_{1,17} = 23.86$, $P = 0.0002$, Fig. 3c). They represented approximately 18% of the species in young forests (although a great variation was detected among young areas) up to about 85% in mature ones. This pattern was stronger when the individuals were analyzed ($r^2 = 0.79$; $F_{1,14} = 51.87$; $P < 0.0001$, 1 missed outlier), when up to 95% of the individuals in a 120 years old forest (area 15) belong to non-pioneer species. According to the model the forest needs about 157 years (range: 116–206 years) to regain this character (90% of species).

The proportion of understorey species increased in older forests ($r^2 = 0.49$, $F_{1,17} = 15.99$, $P = 0.0007$, Fig. 3d). Younger areas (up to 20 years) showed 6–30% of understorey species, while in older ones (50–120 years old) these raised up to 44–54%. This pattern was stronger when the individuals were analyzed ($r^2 = 0.78$, $F_{1,14} = 346.65$, $P < 0.0001$, 1 missed outlier), with up to 80% of understorey individuals. It was calculated that 167 years (range: 88–317 years) are necessary to reach the expected levels for mature forests (50% of species).

Regarding the geographic distribution of the species, younger areas showed higher proportions of widespread species. In fact, the 20 year-old forests had no species exclusive to the Atlantic Forest. In older forests, these proportions reached 30%. Thus, species exclusive to the Atlantic Forest showed a positive relation with time after disturbance ($r^2 = 0.63$, $F_{1,116} = 26.43$, $P = 0.0001$, Fig. 3e). The proportions of individuals of species exclusive to the Atlantic Forest also increased

in older areas ($r^2 = 0.76$, $F_{1,13} = 39.12$, $P < 0.0001$, 2 missed outliers), with up to 37% of the individuals in one of the 120 years forests (area 17). From the regression it was possible to estimate that 1987 years (range: 860–4592) are necessary after a disturbance to reach the percentage of endemism that occur in mature forests (40%).

3.3. Relations between guilds

The proportion of animal-dispersed species had a significant relation with the proportion of non-pioneer species ($r_s = 0.78$, $P < 0.0001$), with the proportion of understorey species ($r_s = 0.61$, $P = 0.0063$), and with the species restricted to the Atlantic Forests ($r_s = 0.60$, $P = 0.008$). Pioneer species were correlated to non-understorey species ($r_s = 0.52$, $P = 0.025$) and to widespread species ($r_s = 0.78$, $P < 0.0001$). The understorey species were correlated to non-pioneer species ($r_s = 0.52$, $P = 0.025$) and to species restricted to the Atlantic forest ($r_s = 0.54$, $P = 0.019$).

4. Discussion

The comparative analyses among the 18 areas in the southern Atlantic Forest showed that disturbance and subsequent secondary succession is characterized by changes in species richness, floristic composition at a regional scale and in ecological guilds (decrease in dispersal by animals and in non-pioneers, understorey and endemic species). These findings have important implications for the conservation of these forests.

Geographical (latitude and longitude) and temporal factors (age after disturbance) have both strongly influenced the species distribution in the 18 sites (correlation coefficients from 0.45 to 0.63 in DCA). The environmental differentiation derived from the geographical location (i.e. rainfall and temperature) is supposed to be an important factor determining the diversity at a regional scale (Oliveira-Filho and Fontes, 2000; Scudeller et al., 2001; Legendre et al., 2005). Nevertheless, disturbance followed by ecological succession may also influence regional diversity, since species differing in environmental requirements occupy the new created habitats (Budowski, 1965; Pickett et al., 1992; Guariguata and Ostertag, 2001). Our study showed that younger forests are comprised mainly by widespread species, i.e. occurring also in other vegetation types (for example, *Hyeronima alchorneoides*, *Alchornea triplinervia*

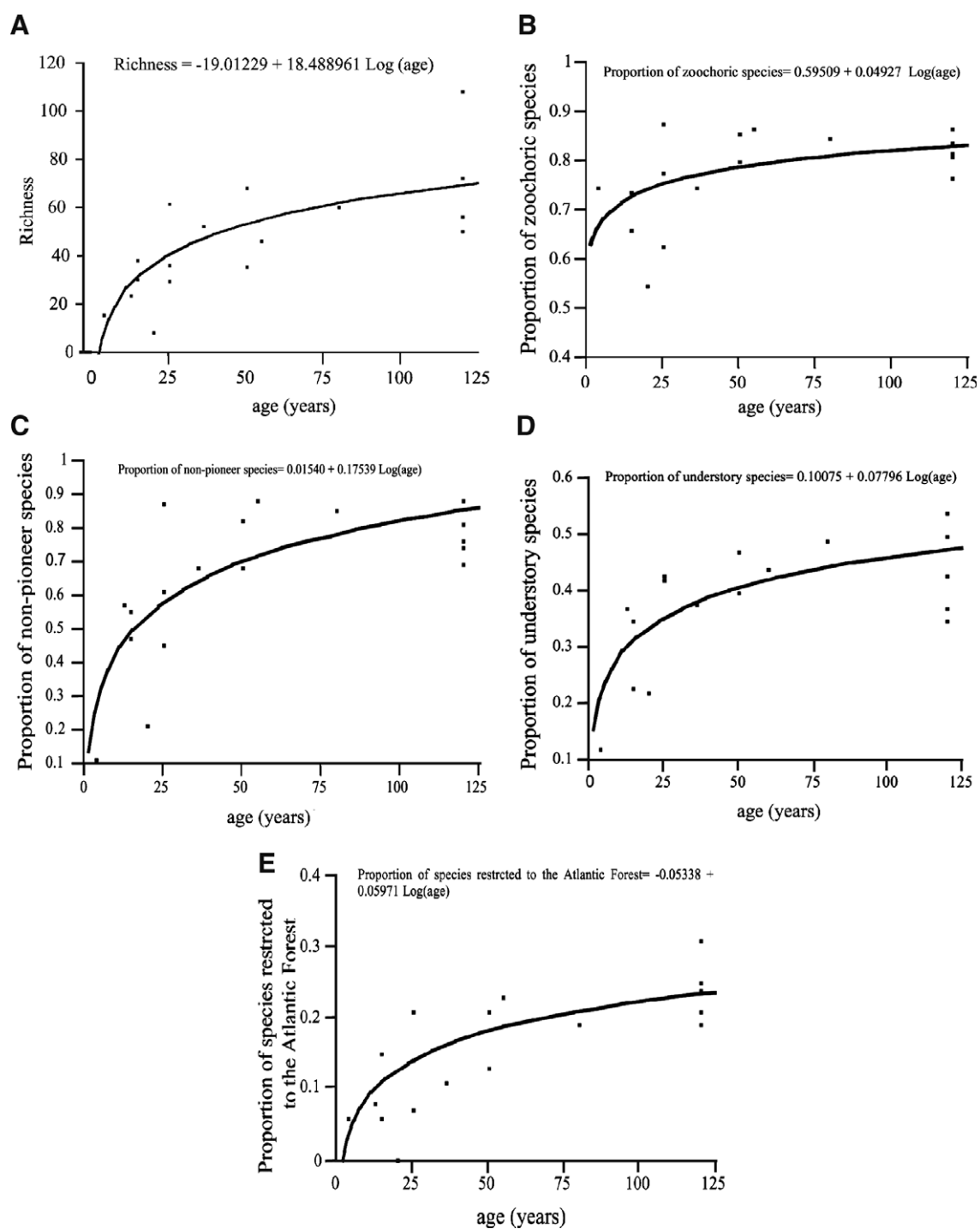


Fig. 3 – Relation between the age of the fragment (time since the last strong disturbance), species richness and the proportion of species in each one of the guilds for the 18 Southern Atlantic Forests in Brazil. (A) species richness; (B) dispersal mode; (C) successional group; (D) vertical position; (E) distribution. A: 1 missed outlier; B: 2 missed outlier; C: 1 missed outlier.

and *Guapira opposita*). As a consequence, not only geographical location, but also time since disturbance affects species distribution and β -diversity. Thus, conservation proposals must take this factor into consideration.

The positive relationship between the increase in the age of the forest and in the proportion of animal-dispersed species has been shown in previous works (Tabarelli and Peres, 2002; Nunes et al., 2003). Our model allows us to predict that

a forest needs approximately 65 years to achieve a proportion of 80% of animal-dispersed species. These findings suggest that conservation of secondary forests may, in a relatively short period of time, recover the fauna associated with the Atlantic Rain forest (although factors such as animal population availability in remnant fragments may influence this process). In addition, the increase of seed dispersers also influences all other animal guilds, leading to the recovery of

the former forest food chains (Howe and Vanderkerckhove, 1981; De Walt et al., 2003).

The increase in the proportion of non-pioneer species was already expected. Mature forests usually have a great amount of non-pioneer species (Tabarelli and Mantovani, 1999), while some pioneer species usually persist due to natural gaps (Denslow, 1987; Tabarelli and Mantovani, 2000). According to our model we predict that a Southern Atlantic Forest patch needs about 157 years to regain this character. This could be linked to the increase in the proportion of understorey species while the forest gets older. Our model predicts that the forests studied here need about 167 years to reach the levels expected for mature forests. During the development of a plant community following a secondary succession there is an increase in the amount of species with larger individuals, which in turn leads to stratification (Guariguata and Ostertag, 2001) and structural complexity. In this context, Rubiaceae and Myrtaceae, two very common families in the understorey of South American rain forests (Melo and Mantovani, 1994; Silva, 1994; Guilherme et al., 2004) contribute to forest enrichment.

The increase in the age of the fragment was also followed by an increase in the proportion of species restricted to the Atlantic Forest. Previous studies have shown that the proportion of endemic species increases with an increase in time after disturbance (Endress, 2002; De Walt et al., 2003). In mature Atlantic Forest the proportion of endemic species is around 40% (Mori et al., 1981; Guedes-Bruni and Morim de Lima, 1994; Thomas et al., 1998). The data in the regression suggest that Southern Atlantic Forests need much more time (almost two thousand years) after a disturbance to reach these 40% of endemics that occur in mature forests. While part of these endemic species have locally restricted distribution (Scudeller et al., 2001), several are rare species (i.e. with one or less than one individual per hectare). Rare species represent 30–40% of the tree species richness in tropical forests (Lepsch-Cunha et al., 2001). Due to problems caused by endogamy, these species need a large area in order to sustain their populations (Kageyama and Gandara, 1993) and are the most susceptible to extinction after fragmentation (Zhu et al., 2004). Thus our results indicate that late successional forests are important for conservation of rare or endemic species.

From the data showed in this article we can conclude that disturbance and the subsequent secondary succession of the Atlantic Forest lead to changes in species composition and in the ecological guilds in plant communities. Even considering that secondary succession confers some resilience to tropical forests (Ruiz-Jaén and Aide, 2005) the recuperation is not performed at a constant rate. Despite the fact that ecological characters are strongly related to each other (high r_s values), guilds from plant communities are recomposed at different speeds. The first character to be recomposed is the number of species that have their fruits or seeds dispersed by animals, followed by number of non-pioneer species, then the understorey species and at last the proportion of species that are endemic to the Atlantic Forest. In addition, the dataset used in this study covered the past two centuries, when one can assume that the Atlantic Forest was more extensive. Thus it is possible that these succession times will be much slower

(and presumably incomplete) in the future due to the severe depletion of rain forest vegetation. These results show that all of these factors might be considered when devising strategies for the conservation of the Brazilian Atlantic Forest.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.biocon.2008.04.013.

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