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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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A B S T R A C T

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 ($0.26 \leqslant r^2 \leqslant 0.63$; $P < 0.05$) 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.

1. Introduction

The Atlantic Rain Forest once covered almost all of the Brazilian coastal zones of the approximately 1,350,000 km^2 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 lead to high levels of fragmentation and subsequent species extinctions (Morellato 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 liasions, 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 km^2 (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 sucessional 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 preserved 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 sucessional 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. widespread)? (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).