

# Forest destructuring as revealed by the temporal dynamics of fundamental species – Case study of Santa Genebra Forest in Brazil

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## ABSTRACT

Variation in the composition of the tree population is common throughout the history of a well-preserved forest community, with this natural process maintaining the forest structure and giving rise to ecological processes necessary for the perpetuation of the ecosystem. However, fragmentation of forests can lead to the collapse of such a structure, especially when natural thinning of the dominant tree species is accompanied by other significant changes. This paper traces changes in the composition of the community of a forest of relevant ecological interest in Campinas (SP, Brazil) as that forest moves toward deterioration as indicated by a massive loss of individuals of fundamental species composing the canopy and subcanopy. The death of trees of the species traditionally forming the canopy, the result of natural processes, was probably intensified by anthropic factors, and led to a general destructuring of the community. The aim of this paper is to demonstrate that the dynamics of these fundamental species can be used as an indicator of the conservation of the ecosystem, as well as indicating the installation of a process which will lead to the collapse of the structure if adequate measures of adaptive management are not taken before the destructuring is irreversible.

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## 1. Introduction

The existence of forest fragments dating back for many years makes the Southeastern part of Brazil a natural laboratory for the evaluation of the long-term effects of fragmentation on the dynamics and integrity of forest communities. Not only is the Atlantic Forest considered to be one of the most important hotspots of the world (Mittermeier et al., 2004), but it is also the most threatened biome of Brazil, with only 7.9% preserved in fragments larger than 100 ha (Fundação SOS Mata Atlântica and INPE, 2013), which

emphasizes the importance of such fragments for the conservation of biodiversity as well as ecosystem services. Moreover, the fragmentation dates back further than that in other areas, such as the Amazon. The analysis of mature or old secondary vegetation in landscapes with a history of occupation is important, since the sampling of immature secondary vegetation may lead to biased results (Chazdon et al., 2009). The restoration of a degraded ecosystem is difficult and expensive (Rodrigues et al., 2009), so that it is especially important to be able to identify signs of the onset of forest destructuring, so that steps can be taken to restore an ecosystem while it is still resilient.

The question is whether the dynamics of a forest, which has been fragmented for several decades, has been able to maintain the general characteristics of that forest without intervention to promote the conservation of biodiversity. The maintenance of a canopy composed predominately of the trees of certain fundamental species (Walker, 1992) forms a basic cover which allows the continuation of the ecological processes necessary for the perpetuation of the

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community. The possibility of identifying if and when an anthropically disturbed ecosystem has already initiated an irreversible process of destructuring and whether it might be possible to undertake effective adaptive management measures soon enough to make reversal and the long-term sustainability of that system possible are of great interest to effective forest conservation. The present paper was designed to help identify elements indicative of this critical point.

## 2. Materials and methods

### 2.1. Study area

The municipal reserve of Santa Genebra (MRSG) has a total area of 251.77 ha and constitutes one of the major remnants of Seasonal Semideciduous Forest (a subtype of Atlantic Forest) in the state of São Paulo. It is a fragment isolated from other forests and surrounded by agricultural areas and residential neighborhoods. The local climate is of the Cwa type, defined as hot and humid, with dry winters and hot, rainy summers (Koeppen, 1948).

### 2.2. Sampling

The 1-ha area of study (200 m × 50 m) was marked off in the interior of the MRSG, 250 m from the closest borders. It was subdivided into 100 plots of 10 m × 10 m. All the trees and shrubs in each plot with a girth at breast height (GBH; 1.3 m from the ground) greater than 15 cm were registered, including species name, stem circumference at a height of 1.3 m (using either a measuring tape or a paquimeter), total height (H) (using a measuring stick), and location in the plot (using Cartesian coordinates). For specimens with two or more branches at the height of 1.3 m, the sum of the basal area of those branches was used to provide a single GBH value. Botanical samples were collected from all of the plants for laboratory identification and deposited in the UEC Herbarium (UNICAMP).

Sampling was done over a period of 20.6 years, taking place at four different times: between August 1982 and March 1985 (t1), between July 1994 and July 1995 (t2), between March and September of 1999 (t3) and between March and September of 2004 (t4). These sampling times have been referred to by the following dates: 1983 (t1), 1994 (t2), 1999 (t3) and 2004 (t4).

### 2.3. Analysis of data

A Wilcoxon signed rank test (Wilcoxon, 1945) with correction for continuation was made to compare the number of individuals, basal area per plot ( $\text{m}^2 \text{ha}^{-1}$ ), basal area per individual ( $\text{m}^2 \text{ind}^{-1}$ ), height (m), and number of individuals (both dead and recruited individuals), with the 100  $\text{m}^2$  sub-plots used as repetitions. "Recruited" individuals are those which have reached the critical circumference of 15 cm since the previous sample.

Each individual plant was located by Cartesian coordinates and represented by a colored dot according to height. The colors corresponding to intermediate heights for trees located close together were calculated by interpolation using the Nearest Neighbor method. Linear regression models were used, with individuals as units, to verify the negative changes in number of individuals (mortality) during the periods between t1 and t2 and between t2 and t4 and correlate it with initial values of basal area of individual, height, and number of individuals per plot.

Models for the distribution of species abundance (SAD) for each year were constructed using the data about number of individuals per species in each year, with that yielding the smallest value using Akaike's information criteria considered to have the best fit (Akaike, 1974). This criterion is based on log-likelihood. To evaluate the differences in community composition over the years a Procrustean

analysis was performed, where a pair of data matrices (composition in t1 vs. t2, t2 vs. t3, etc.) was compared by a rotational-fit algorithm that minimizes the residuals of the sum of squares between the two matrices (Gower, 1971; Peres-Neto and Jackson, 2001).

For each species with at least 10 individuals, the minimum height of adults was determined on the basis of the curve of best fit of height vs. basal area (data for t1). The point at which a 1-cm increase in diameter corresponded to an increase in height of less than 10% was considered the minimum height value for an adult of the species. The minimum values were used to separate the species into two groups – canopy species/emergents and subcanopy species – Appendix A.

Before and after separating the species, a temporal analysis of changes in the number of individuals per species was made to study the dynamics of the populations during the period, using randomization tests (Manly, 2007) – Appendix B.

## 3. Results

### 3.1. Overall structural changes

During the 20.6 years of the study, a significant decrease in the number of trees and shrubs was found ( $1430\text{--}1096 \text{ ind ha}^{-1}$ ) ( $p < 0.0001$ , Wilcoxon), especially in the period from 1983 to 1994 ( $p < 0.0001$ , Wilcoxon). There was also a significant decrease in the basal area per plot ( $22.43\text{--}19.19 \text{ m}^2 \text{ ha}^{-1}$ ) ( $p = 0.0242$ , Wilcoxon). On the other hand, there was a significant increase in the basal area per individual ( $p = 0.0445$ , Wilcoxon). There was also a generalized decrease in the height of the individuals during the total period of study (Fig. 1) ( $p < 0.0001$  Wilcoxon). The median height of individuals decreased from an initial value of 7.0 to 5.5 m at the time of the final sampling.

For all of three between-sampling periods (t1–t2, t2–t3 and t3–t4), linear regression models showed a significant increase in mortality in relation to initial basal area and height of individuals. During the second two periods (t2–t3 and t3–t4) a similar significant increase in mortality was found in relation to initial values of number of individuals per subplot (Appendix C).

### 3.2. Changes in species composition

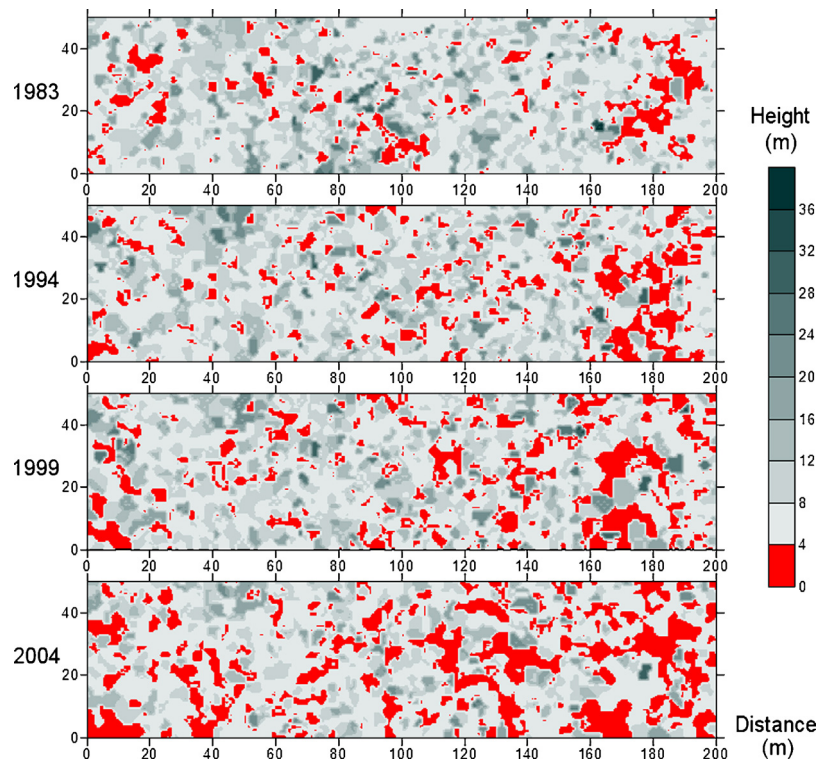
Based on the Akaike criterion, the adjustment of the theoretical models of the distribution of abundance was the same for all of the sampling periods (Mandelbrot). Moreover, the dominant species were the same over time: *Trichilia claussoni*, *Aspidosperma polyneuron*, *Psychotria vauthieri* and *Astronium graveolens*.

A Manova test showed that the composition at different periods represented different populations, i.e. there was a significant difference in the composition of the four periods ( $p < 0.001$ ). This was confirmed by a test of homogeneity of variance ( $p < 0.001$ ). The ad-hoc Tukey test showed which specific periods revealed significant differences. Fig. 2 shows that it was the changes between t4, t3, and t2 and the initial sampling time (t1) which were statistically different, as well as those between t2 and t4.

The results of Procrustes rotation (t1 vs. t2, t1–t3, t1–t4, t2–t3, t2–t4, t3–t4) supplement the results above and reinforce the idea of a progressive change in species composition (Appendix D).

The consideration of the age of the individuals trees (juvenile and adult) made it possible to separate the trees into two strata (subcanopy and canopy/emergent species), each composed of typical species (Appendix A – Fig. 3).

The number of juvenile individuals of canopy species remained relatively constant from the initial to final sampling period ( $p = 0.6255$ , Wilcoxon). On the other hand, there was a significant decrease in the number of adult trees, decreasing from 290 to 176



**Fig. 1.** Height of vegetation. Representation of aerial view of the area under study and the height (m) interpolated from the individuals with GBH  $\geq 15$  cm. Municipal Reserve of Santa Genebra, Campinas, SP.

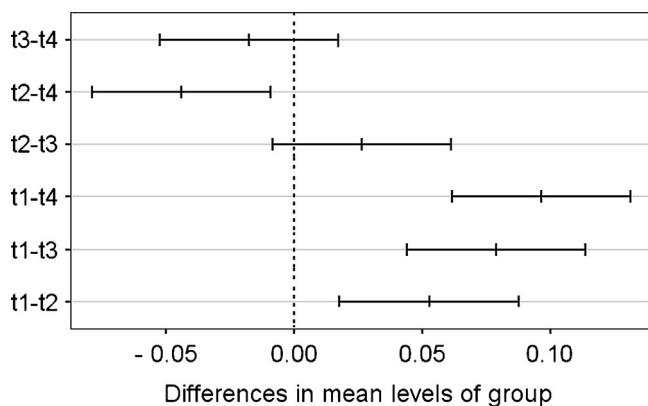
individuals from the first to the final period ( $p < 0.0001$ , *Wilcoxon*) (Appendix E – Fig. 4a). Nineteen of the 100 plots no longer had adult individuals of the canopy species. The height of the adults of the canopy species showed a significant reduction ( $p < 0.0001$ , *Wilcoxon*), with the median height decreasing from 12.5 to 12.0 m (Fig. 4b). The basal area per plot of the adults of the canopy species was reduced from 10.12 to 8.99 m<sup>2</sup> ha<sup>-1</sup> ( $p = 0.0324$ , *Wilcoxon*) (Fig. 4c). On the other hand, the basal area per adult individual of the trees of this stratum showed no significant changes, varying from 0.035 to 0.045 m<sup>2</sup> ind<sup>-1</sup> ( $p = 0.0611$ , *Wilcoxon*) (Fig. 4d).

For the subcanopy species, however, no significant difference in number of juvenile individuals was found ( $p = 0.3516$ , *Wilcoxon*). The number of adults of this stratum, however, decreased significantly in number from 436 to 134 individuals from the initial to the final sampling ( $p < 0.0001$ , *Wilcoxon*) (Appendix E – Fig.

5a). The height of this stratum underwent a significant reduction ( $p < 0.0001$ , *Wilcoxon*), with the median height of the adults decreasing from 7.0 to 6.5 m (Fig. 5b). The basal area of the adults per plot for this stratum also decreased, from 3.31 to 1.42 m<sup>2</sup> ha<sup>-1</sup> ( $p < 0.0001$ , *Wilcoxon*) (Fig. 5c), although the basal area per individual adult of this stratum increased from 0.008 to 0.011 m<sup>2</sup> ind<sup>-1</sup> ( $p = 0.0028$ , *Wilcoxon*) (Fig. 5d).

A total of 132 species of trees/shrubs was registered during all of the samplings, with 85 present at all times. At t1 (1983) 101 species were registered. By t4 (2004), 14 of those species were no longer present, but 26 new species had entered the community, for a total of 113 species at that time. Thirteen of the species with the greatest number of individuals (71% of the individuals sampled at t1) underwent a great reduction in absolute number of individuals (Appendix F – Table 6), a trend especially true for most important canopy and subcanopy species. The dominant canopy species, *A. polyneuron*, underwent a great reduction in the number of both juvenile and adult individuals; *A. graveolens*, on the other hand, underwent a reduction only in adult individuals, with the number of juvenile individuals actually increasing (Appendix F – Table 7). For the subcanopy species, *T. claussoni*, the most abundant, underwent a great reduction in number of adult individuals, although the number of juvenile individuals remained stable, whereas *P. vauthieri* (second most numerous) underwent a reduction in number of both adult and juvenile individuals (Appendix F – Table 8).

In addition to the decrease of 42.5% in number of individuals of *A. polyneuron* during the 10.6-years of the study, there had already been a significant decrease of 24% after the second sampling (period t1–t2), indicating the onset of the decline of this population. These changes paralleled those of the floristic composition as a whole. Although it was not possible to establish a specific turning point in the dynamics of the community, the changes observed were emerging by the second sampling, at which time the make-up seemed to have already reached a critical point in the development of the ecosystem.



**Fig. 2.** Changes in the forest. Ad-hoc Tukey test comparing changes for the various periods of sampling (95% family-wise confidence level). Municipal Reserve of Santa Genebra, Campinas, SP.

#### 4. Discussion

During the period studied, a massive loss in structuring of the community was observed, including the death of adult individuals of both the canopy and the subcanopy, the latter probably due to the death of the former. The overall consequence was the establishment of a less dense forest coverage with smaller trees, leaving the forest susceptible to takeover by lianas. The deaths of adult individuals of the canopy and subcanopy were not compensated for by an increase in number of juvenile individuals; moreover, the growth of those juvenile individuals which were present may have been limited by the abundance of lianas, thus compromising the continuity of the dynamics of the forest.

The generalized decrease in number of individuals during the period, as well as the increase in general basal area and number of dead trees, may indicate the process of competitive thinning, which affects adult trees. The decrease in density observed, however, was not accompanied by an increase in nor stabilization of the basal area. Along with the decrease in height, the decrease in basal area indicated a trajectory of disturbance, resulting in a final situation where the forest structure is shown to be discontinuous. The values of basal area found at t1 (22.43 m<sup>2</sup> ha<sup>-1</sup>) and t4 (19.19 m<sup>2</sup> ha<sup>-1</sup>) are well below those found in the literature for fragments of the same type of vegetation in the state of São Paulo (31–42 m<sup>2</sup> ha<sup>-1</sup> with the same criteria of sampling) (Durigan et al., 2000; Fonseca and Rodrigues, 2000; Ivanauskas et al., 1999).

The decrease in height of the vegetation in the subplots was the consequence of the high mortality of the larger individuals, as well as the breaking off of the tops of the taller individuals seen in the field. This led to an increase in areas with shorter trees (less than 4 m). At t1, such clearings were quite limited in number, but the ongoing death of taller individuals led to their expansion. The death of larger individuals is characteristic of disturbed vegetation, with the reduced number of taller trees being more susceptible to wind damage (Coomes and Allen, 2007; Williams-Linera, 1990). Such modifications may also indicate the synchronous senescence of the larger individuals. A decrease in density, median height, and basal area per plot area was observed for adult trees of both the canopy and subcanopy. The absence of regeneration to compensate for the loss of these individuals and the decrease in basal area led to a loss in competitiveness of the trees/shrubs, leaving large areas occupied mainly by the exuberant populations of lianas observed in the field, typical of disturbed areas (Rozza et al., 2007). Occupation by these lianas, on the other hand, restricts even more the emergence of regeneration, so the forest is unable to restructure itself (Cochrane and Schulze, 1999; Schnitzer et al., 2000). The lack of an increase in the number of juvenile trees is discouraging, since it suggests that there is no immediate compensation for the mature individuals lost. In conjunction with the increase in lianas, this suggests that reversion of the structure lost is highly unlikely at any time soon.

During the whole period of the study, the relative dominance of *A. polyneuron* was maintained for the canopy trees, suggesting that it is fundamental in the structure of the vegetation (Walker, 1992) (Appendix G – Fig. 6). The decrease in this population may have contributed to the overall changes in the structure and general composition, giving rise to the opening of large clearings and reoccupation by populations of other guilds, especially pioneer trees and lianas (Appendix G – Figs. 7 and 8).

In the subcanopy, the most relevant change was the relative loss of individuals of *P. vauthieri*, a species which prefers shade. It may have been harmed by the change in environmental conditions resulting from the decreased density of the canopy, i.e. more open conditions. This reinforces the importance of the change in the population of *A. polyneuron* on the other populations and, therefore, on the community as a whole, since, along with other canopy species,

it serves as an edifier of the physical ecosystem (Jones et al., 1997). The canopy species control the availability of light for the species of the other strata (Gandolfi et al., 2009), and the thinning of this stratum modifies the microclimate by influencing the availability of water (Caldwell et al., 1998; Lee et al., 2005), since the deeper roots of these species pump the water from the subsoil and make it available on more superficial horizons.

The acceleration in the rate of turnover observed in other tropical forests in South America has accompanied the elevation in values of the concentration of CO<sub>2</sub> and atmospheric temperature of the past few decades (Lewis et al., 2004; Phillips et al., 2008). In the MRSG the dynamics has not resulted in a renovation of the forest, but rather have led to the onset of a process which will presumably terminate in the collapse of that forest, including high mortality and the expansion of clearings. The relation of the disturbance of forests to environmental changes, especially changes in climate, has been predicted and described for various kinds of forests (forest dieback) (Lenton et al., 2008; van Mantgem et al., 2009).

It is possible that internal changes in course for the vegetation of the MRSG may accentuate the structural deterioration observed, culminating in the transition of the forest from one stable state (conserved forest) to another (e.g. capoeira – scrub dominated by lianas) the forest to a transition from one stable state. Such a “catastrophic regime shift” (Scheffer and Carpenter, 2003; Guttal and Jayaprakash, 2008) results in the development of a type of vegetation characterized by dramatically different properties.

This study has shown that in 20 years the vegetation of the forest fragment studied has undergone such great modification in structure and species composition that it is highly unlikely that the forest will be able to return to its former state. Indeed, there seems to be a strong tendency toward a catastrophic regime shift. The conservation of a forest depends directly on the maintenance of its structure, yet this is not occurring naturally here. Although large populational fluctuations may have relatively little effect in the long run for extensive forests, for a fragment such as that studied here, the consequences may be much more serious, especially in an area with a long history of occupation. It seems that once destructuring sets in, the process will not be reverted naturally. The identification of the point where destructuring begins may make it possible to adopt adequate measures in time to override the elements which restrict the regeneration of tree populations, making reversion of the process of destructuring possible and permitting the continuity of the dynamics of a healthy forest.

#### 5. Conclusion

This study has shown that this forest fragment, isolated for decades, is suffering increasing in disturbance and destructuring of the forest community, the result of natural processes, as well as the fragmentation itself. This destructuring is reflected in the massive loss of individuals of the major species constituting the canopy and subcanopy, groups which should be capable of promoting the sustainability of the forest ecosystem.

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#### Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/>

[j.ecolind.2013.09.011](#). These data include Google maps of the most important areas and the supplementary data described in this article.

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