

Anais da Academia Brasileira de Ciências

ISSN: 0001-3765 aabc@abc.org.br Academia Brasileira de Ciências Brasil

COSTA, MAYKE B.; DE MENEZES, LUIS FERNANDO T.; NASCIMENTO, MARCELO T. Post-fire regeneration in seasonally dry tropical forest fragments in southeastern Brazil Anais da Academia Brasileira de Ciências, vol. 89, núm. 4, octubre-diciembre, 2017, pp. 2687-2695

Academia Brasileira de Ciências Rio de Janeiro, Brasil

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Anais da Academia Brasileira de Ciências (2017) 89(4): 2687-2695 (Annals of the Brazilian Academy of Sciences)
Printed version ISSN 0001-3765 / Online version ISSN 1678-2690 http://dx.doi.org/10.1590/0001-3765201720160728
www.scielo.br/aabc | www.fb.com/aabcjournal

Post-fire regeneration in seasonally dry tropical forest fragments in southeastern Brazil

MAYKE B. COSTA1, LUIS FERNANDO T. DE MENEZES1 and MARCELO T. NASCIMENTO2

¹Departamento de Ciências Agrárias e Biológicas, Universidade Federal do Espírito Santo, Rodovia BR 101 Norte, Km 60, Litorâneo, 29932-540 São Mateus, ES, Brazil ²Laboratório de Ciências Ambientais, Universidade Estadual do Norte Fluminense, Avenida Alberto Lamego, 2000, Parque Califórnia, 28013-620 Campos dos Goytacazes, RJ, Brazil

Manuscript received on October 28, 2016; accepted for publication on July 31, 2017

ABSTRACT

Seasonally dry tropical forest is one of the highly threatened biome. However, studies on the effect of fire on these tree communities are still scarce. In this context, a floristic and structural survey in three forest areas in the southeast of Brazil that were affected by fire between 14 and 25 years ago was performed with the objective of evaluating post-fire regeneration. In each site, five systematically placed plots (25 m x 25 m each) were established. The more recently burnt site had significantly lower values of richness and diversity than the other two sites. However, the sites did not differ in density and basal area. *Annona dolabripetala*, *Astronium concinnum*, *Joannesia princeps* and *Polyandrococos caudescens* were within the 10 most important species for the three sites. Comparing these data with adjacent mature forests, the results indicated differences both in structural and floristic aspects, suggesting that the time after fire was not sufficient for recuperation of these areas. The recovery process indicate at least 190 years for areas return to basal area values close to those observed in mature forests nearby.

Key words: Atlantic forest, fire ecology, forest succession, forest structure, post-fire recovery.

INTRODUCTION

Seasonally dry tropical forest (SDTF), which shows high diversity, high endemism, and high floristic turnover, is currently considered one of the most highly threatened biome (Banda-R et al. 2016), with fire and fragmentation having important roles in this process (Janzen 1988, Miles et al. 2006) and approximately 42% of tropical forests are classified in this category (Murphy and Lugo 1986). However, the majority of studies on ecological succession

Correspondence to: Marcelo Trindade Nascimento

E-mail: mtn@uenf.br

in tropical forests have been done in rain forests (Vieira and Scariot 2006).

Ecologically, fire is a natural phenomenon that is responsible for affecting ecosystem functioning and influencing forest composition and structure. The predictions of its impact on the vegetation are complex, since plants have different responses and diverse interactions with the environment and fauna (Libano and Felfili 2006).

In general, we can consider that the recovery process of a tropical forest after disturbance by a fire is highly dependent on seed sources provided by the surviving trees (forest islands) and by resprouting (Corlett and Primack 2011). Another important aspect is that the recovery time of the disturbed forest, is, in general, slow and depends upon the intensity of the disturbance and the surrounding vegetation. Saldarriaga and Uhl (1991) estimated that between 140 and 200 years were necessary for tracts abandoned slash-and-burn areas in humid tropical forest in the Venezuelan amazon to attain biomass similar to native forest. However, 45 years secondary seasonal forests attained values for biomass similar to surrounding native forests due to the resprouting capacity of the individuals after disturbance by fire (Oliveira-Filho et al. 2004).

Thus, understanding the recovery process of the structure and composition of the plant community and which variables control this process is a central question in tropical plant ecology. The complex interaction of the biotic and abiotic components and the limiting factors in secondary succession should be understood to aid in the management and priorization of decisions on the future necessities for conservation in this region (Powers et al. 2009), however, the principle mechanisms of succession and regeneration in these SDTF are still unexplored (Quesada et al. 2009).

The aim of this study was to determine the floristic and structural characteristics of forest fragments that were disturbed by fire between 14 and 25 years ago. Our specific questions were: (i) What is the response of species richness and diversity during the successional process after fire?;

(ii) Is there a characteristic group of tree species in post-fire succession related to SDTF?

MATERIALS AND METHODS

STUDY AREA

The study was carried out in three forest areas that were burned, 14 years ago (Sooretama Biological Reserve, SO, 18° 33' to 19° 05' S; 39° 55' to 40° 15' O) and 25 years ago (Córrego do Veado Biological Reserve, CV, 18° 16' to 18° 25' S; 40° 06' to 40° 12' O and Córrego Grande Biological Reserve, CG, 18° 12' to 18° 18' S; 39° 45' to 39° 50' O). All areas are located within conservation units in the northern part of the State of Espírito Santo, Brazil, and after the fire they have not been disturbed (Table I). The main forest type in this region is the Seasonally dry tropical forest (SDTF) or Seasonal Semideciduous forest in the Brazilian classification (IBGE 2012). According to the Köppen classification system (Köppen 1946), the climate of the region is type Awi (tropical wetdry isothermal). The mean annual rainfall is 1202 mm, with the driest months between June and August. The mean annual temperature is 23.3°C, the monthly mean ranging from 14.8°C to 34.2°C (Jesus et al. 2010). The predominant soil type in the region is Dystrophic Red-Yellow Latossol, but there also is significant proportion of Dystropic and Eutrophic Red-Yellow Argisoils (EMBRAPA 1978).

TABLE I

General information on the size of the studied forest fragments, size of area affected by the fire, date of fire, mean altitude, temperature (T) and mean annual precipitation (P) in the three forest fragments, Biological Reserve Sooretama (SO), Biological Reserve Córrego de Veado (CV) and Biological Reserve Córrego Grande (CGO), State of Espírito Santo, Brazil.

Site	Fragment Size (ha)	Burned area (ha)	Date of fire	Altitude (m)	T (°C)	P (mm)
SO	27858	2500	8/1998	113	25.8	1212
CV	2392	1913	10/1987	106	24.1	1068
CG	1485	445	12/1987	55	27.0	1300

The fires in these three areas occurred in the dry season, during "El-Nino" events (ENSO) and were crown fires (high intensity) with high tree mortality post-fire.

SAMPLING AND DATA ANALYSIS

In June 2012 five plots (25 m x 25 m each) were systematically installed in each of the three study areas. All plots were in plateau areas that had suffered crown fires and were located at least a 50 m from the forest edge and did not include valleys or watercourses. The distance between plots ranged from 0.8 to 2.5 km in function of the shape and size of each forest area. The distance between the plots and the forest edge varied from 50 to 750 m depending of the study area.

In each plot the diameter and height of all individuals with a DBH \geq 5 cm were measured. Standing dead trees and the number of lianas on trees that had roots within the plot were also assessed to aid in the evaluation of the degree of disturbance in the fragments. The families were classified according to the APG IV system (APG IV 2016). Voucher specimens were incorporated at the herbarium SAMES of the Universidade Federal do Espírito Santo (UFES).

The species were classified into the ecological groups according to their successional status as pioneers, early secondary and late secondary (Gandolfi et al. 1995) based on our field experience and literature (Paula and Soares 2011). They were also grouped by dispersal syndrome. The dispersal syndrome was based on fruit/seed type, using the morphological criteria described by Van Der Pijl (1982): zoochoric and abiotic (anemochoric and autochoric).

Differences in forest structure among the sites were evaluated using number of individuals (N), number of bifurcated individuals (Birf) and number of standing dead trees (Stdead), total basal area (BA) and individual basal area (IBA), relative

density (RD), relative dominance (RDo) and cover value (CV= RD+RDo) (Kent and Coker 1992).

The Shannon-Weiner diversity index (H') was calculated for each site along with comparisons of species richness and diversity using rarefaction curves based on the number of individuals sampled in each plot. All calculations were done using EcoSim 7 (Gotelli and Entsminger 2001).

Floristic similarity was calculated using Morisita's index based on species abundance (Brower and Zar 1984). A dendogram was generated by cluster analysis using UPGMA and an Analysis of Similarities (ANOSIM), using the software PAST v. 2.17c (Hammer et al. 2001), was run to test statistically whether there is a significant difference between two or more groups of sampling units.

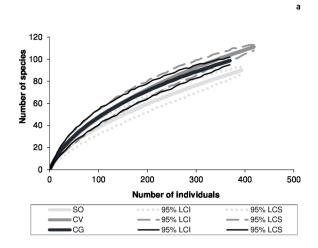
The structural characteristics of the vegetation (density, basal area, volume, number of bifurcated individuals and number of standing dead trees), ecological groups and dispersal syndrome in the study area were compared using Analysis of Variance (ANOVA) after testing for normality of variance. When statistical differences were found between the means the Tukey's test was performed as a post hoc test (Brower and Zar 1984). These analyses were done using the software PAST v. 2.17c (Hammer et al. 2001).

The areas studied by Paula and Soares (2011) in the Biological Reserve Sooretama and by Jesus and Rolim (2005) in the Natural Reserve of Vale do Rio Doce near Linhares (ES), an adjacent area to the Biological Reserve Sooretama were used as reference since they are mature forests.

RESULTS

IMPACT AND RECOVERY OF FLORISTIC COMPOSITION

A total of 1248 individuals, distributed in 226 morphospecies, 137 genera and 49 families were found in the three study areas. It was possible to



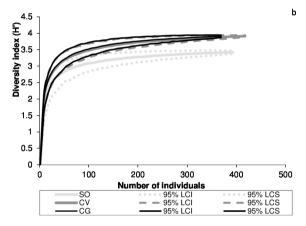


Figure 1 - Species rarefaction curves for richness (a) and for diversity H' (b) of tree species sampled in the forest fragments Sooretama (SO, 14 years after fire), Córrego do Veado (CV, 25 years after fire) and Córrego Grande (CG, 25 years after fire), ES, Brazil. Dotted lines are the upper and lower confidence intervals (95%).

identify 200 (88.5%) to species, 23 (10.2%) only to genus and 3 (1.3%) only to family. In general, Fabaceae was the family with the largest number of species in all of the study plots, however CG was the area with the least number of species in this family.

In relation to richness of tree species, CV had the highest number of species (113) of which 56 (49.5%) were exclusive to this site. CG had 102 species with 63 (61.8%) being exclusive to this site and SO, the site with the lowest richness, had 94 species of which only 37 (39.4%) were exclusive.

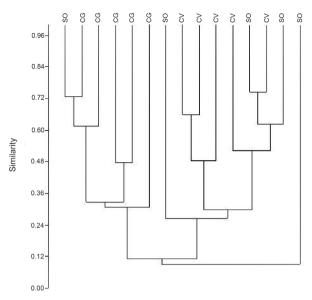


Figure 2 - Dendrogram of floristic similarity using Morisita's Index for plots of the burnt forest fragments (Cophenetic correlation= 0.87). (Sooretama, SO, 14-yrs after fire, Córrego do Veado, CV, 25-yrs after fire and Córrego Grande, CG, 25-yrs after fire).

The two sites with a longer post-fire history, CV and CG, did not significantly differ in either species richness or species diversity. The site with the more recent fire, SO, had significantly lower values than the other two sites (Fig. 1).

The floristic similarity varied among the areas, with a larger floristic difference between CG and the other two sites (CV and SO). The dendrogram showed that CG formed a group, isolated and significantly different (ANOSIM, $R=0.53~p \le 0.001$) from those CV and most SO groups (Fig. 2). No strong relationship was observed between time after fire and floristic similarity in these sites. Tree similarities among burnt forest fragments and the mature forest were very low and varied from 2.5% (SO vs mature) to 8.4% (CG vs mature).

Overall, 11.4% of the species were pioneers, 41.3% were early secondary and 47.3% were late secondary species, quite distinct from the values observed in mature forests (Fig. 3). In all three areas, a low percentage of pioneer species was observed, with values always lower than 20%.

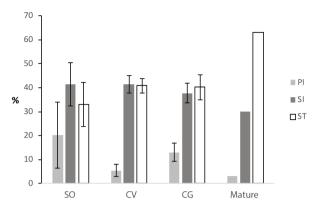


Figure 3 - Distribution of the percentage of species in ecological groups in the burnt forest fragments Sooretama (SO, 14-yrs after fire), Córrego do Veado (CV, 25-yrs after fire), Córrego Grande (CG, 25-yrs after fire) and an adjacent mature forest (Paula and Soares 2011), State of Espírito Santo, Brazil. PI – pioneers, SI – early secondary and ST – late secondary.

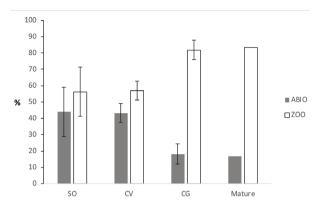


Figure 4 - Classification of the percentage of species by dispersal syndromes (abiotic and zoocoric) in the burnt forest fragments Sooretama (SO, 14-yrs after fire), Córrego do Veado (CV, 25-yrs after fire) and Córrego Grande (CG, 25-yrs after fire) and an adjacent mature forest (Paula and Soares 2011), ES, Brazil.

TABLE II

Structural parameters of the tree communities analyzed in the three forest fragments Sooretama (SO, 14 years after fire), Córrego do Veado (CV, 25 years after fire), Córrego Grande (CG, 25 years after fire) and in a mature forest (MF), State of Espírito Santo, Brazil. D = density/ha, BA = basal area (m^2/ha), Vol = volume (m^3/ha), %Bifur = percent of bifurcated individuals and % Stdead = percent of standing dead individuals. The values in the same column followed by different letters are statistically different ($p \le 0.05$).

Site	D	BA	Vol	% Bifur	% Stdead
SO	$1354 \pm 222a$	$3.84 \pm 0.25a$	$44.84 \pm 3.86a$	$7.3 \pm 2.16a$	$11.34 \pm 3.5a$
CV	$1379\pm188a$	$5.70 \pm 0.59a$	$79.22 \pm 2.38a$	$13.9 \pm 6.12ab$	$4.18\pm2.3b$
CG	$1261 \pm 322a$	$6.06 \pm 0.24 a$	$83.53 \pm 4.79a$	$20.8 \pm 6.46b$	$5.84 \pm 2.6b$
MF	1519^{1}	47.15 ¹	-	9.69^{2}	5.59^{2}

¹ Paula and Soares 2011, ² Jesus and Rolim 2005.

The predominant dispersal syndrome of the species in all the sites was zoochoric, 68.2%, compared to abiotic dispersal, 31.8%. Among sties, CG had the highest percentage of zoochoric species (83%), a value that was close to that observed in mature forests (Fig. 4).

RECOVERY OF FOREST STRUCTURE AFTER FIRE

The three burnt forest fragments had, in general, distinct structural values when compared to mature forest (Table II). The values of tree density and total basal area in the burnt forest fragments were much lower than the value found for mature forest, even for the fragments of 25 years after fire. The tree

diameter distribution in the burnt forest fragments (SO, CV and CG) indicated a higher density of individuals in classes with smaller DBH (5-10 cm and 10-15 cm), with few trees having a DBH higher than 25 cm (Fig. 5), with no differences among fragments (Kolmogorov-Smirnov test, p> 0.05). Considering the mature forest, about 12% of trees were higher than 25 cm DBH, however, in the burnt forest fragments only 1.7% (SO), 4.2% (CV) and 6.2% (CG) of trees were large trees (DBH > 25 cm). Among the burnt forest fragments, the main difference was in the number of standing dead trees that was higher at SO (Table II).

Approximately 83% of the live trees sampled had lianas. In the burnt forest fragments, the

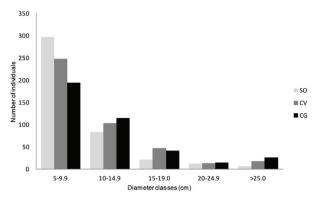


Figure 5 - Distribution of the number of individuals with DBH ≥ 5 cm per diameter classes in the burnt forest fragments Sooretama (SO, 14-yrs after fire, n= 1354 ind.ha⁻¹), Córrego do Veado (CV, 25-yrs after fire, n= 1379 ind.ha⁻¹) and Córrego Grande (CG, 25-yrs after fire, n= 1261 ind.ha⁻¹), ES, Brazil.

TABLE III

Number of lianas on tree regeneration in the three forest fragments Sooretama (SO, 14 years after fire), Córrego do Veado (CV, 25 years after fire) and Córrego Grande (CG, 25 years after fire), State of Espírito Santo, Brazil. Absent= without any liana/stem, Low= 1 to 5 lianas/stem, Medium = 6 to 10 lianas/stem, High= More than 10 lianas/

	Stem.		
Presence of lianas	SO(%)	CV(%)	CG(%)
Absent	9	16.6	24.4
Low	43.3	39	45.5
Medium	10.6	10	12
High	37.1	34.4	18.1

predominant category was low infestation. However, SO had the highest percentage of individuals with lianas and the lowest without (Table III).

The ten species with the highest cover values differed among the burnt forest fragments. However, Annona dolabripetala (Annonaceae), Astronium concinnum (Anacardiaceae), Joannesia princeps (Euphorbiaceae) and Polyandrococos caudescens (Arecaceae) were always at the top of the list in these fragments. Although they were not within the ten most important species in mature forest (Table IV) with only Eriotheca macrophylla (Malvaceae) occurring in both list.

DISCUSSION

As expected, the lower species richness and diversity was found in the site SO (14-yrs after fire) which showed a higher percentage of pioneer species in comparison to the other two sites (25-yrs after fire). However, species richness found at SO (94 species/0.31 ha, DBH \geq 5 cm) can be considered high when compared to a burnt forest site in the same region that was sampled 10 years after a fire (33 species/0.24 ha, DBH \geq 5 cm) (Rolim and Jesus 2002). The large difference in species richness between the two sites after fire appears to be related to the fact that the site SO is located in a much larger forest fragment (\sim 28.000 ha vs 2400 ha) and it is within a forest dominated landscape.

Guariguata and Dupuy (1997) observed that recovery of species richness is slow in a disturbed tropical forest (~80-yrs) and is dependent on the type and intensity of the disturbance. However, based on the results of the present study (mean of 103 species/0.31 ha and 226 species/0.93 ha) a higher increase in species richness than expected was observed, since 265 tree species were reported in a hectare in an adjacent mature forest (Paula and Soares 2011). This relatively fast recovery in species composition might be related to the resprouting ability of some tree species. In this study, 14% of the individuals sampled were bifurcated, probably due to resprouting after the fire, a common strategy of many tree species and considered a fundamental process in the rapid recovery of degraded areas (Rodrigues et al. 2004).

The percentages of pioneer species in the study sites (< 20%) can be considered low and much different than the results found by S.G. Rolim (unpublished data) for two disturbed forests nearby our sites, one area with six years after a clear cut (91% pioneers) and another area with 22 years after a clear cut (67% pioneers). This difference in the number of pioneers seems to be related to the destruction of the soil seed bank by the fire.

TABLE IV

List of the 10 most important species in cover values in the three forest fragments Sooretama (SO, 14 years after fire),
Córrego do Veado (CV, 25 years after fire), Córrego Grande (CG, 25 years after fire) and a mature forest (MF), State of
Espírito Santo, Brazil. MF data from Paula and Soares (2011).

Species	SO	CV	CG	MF
Annona dolabripetala Raddi	14.02	4.66	13.27	-
Astrocaryum aculeatissimum Schott (Burret)	-	-	4.01	-
Astronium concinnum Schott	13.01	10.98	-	-
Astronium graveolens Jacq.	3.06	-	-	-
Bixa arborea Huber	3.68	-	-	-
Brasiliocroton mamoninha P.E. Berry & Cordeiro	4.96	2.80	-	-
Cecropia hololeuca Miq.	6.10	-	-	-
Cordia trichotoma (Vell.) Arráb. ex Steud.	3.16	-	-	-
Coussapoa curranii S.F.Blake	-	-	-	5.14
Cupania cf. racemosa (Vell.) Radlk.	-	-	2.70	-
Deguelia costata (Benth.) A.M.G. Azevedo & R.A. Camargo	-	5.94	-	-
Dialium guianense (Aubl.) Sandwith	-	-	-	5.35
Eriotheca macrophylla (K. Schum.) A. Robyns	-	-	2.19	11.41
Eugenia ubensis Cambess.	-	-	-	3.87
Ficus gomelleira Kunth	-	-	-	8.33
Goniorrhachis marginata Taub.	-	5.11	-	-
Guatteria sellowiana Schltdl.	-	-	2.33	-
Guazuma crinita Mart.	-	3.42	-	-
Hydrogaster trinervis Kuhlm.	-	-	-	5.80
Inga subnuda Salzm. ex Benth.	-	-	4.33	-
Joannesia princeps Vell.	4.75	7.32	-	-
Luehea divaricata Mart. & Zucc.	3.74	-	-	-
Machaerium fulvovenosum H.C.Lima	-	4.98	-	-
Melanoxylon brauna Schott	-	2.83	-	-
Pogonophora schomburgkiana Miers ex Benth.	-	-	3.33	-
Allagoptera caudescens (Mart.) Kuntze	5.15	6.88	-	-
Protium heptaphyllum (Aubl.) Marchand	-	-	5.46	-
Pterocarpus rohrii Vahl	-	-	-	3.93
Rinorea bahiensis (Moric.) Kuntze	-	-	-	15.30
Sterculia speciosa K.Schum.	-	-	-	6.87
Tapirira guianensis Aubl.	-	-	13.70	-
Terminalia kuhlmannii Alwan & Stace	-	-	-	3.67
Thyrsodium spruceanum Benth.	-	_	3.96	_

Van Nieuwstadt et al. (2001) found that a severe fire could reduce by 85% the viability of seeds in the soil seed bank. Local residents reported that in our burnt sites fire was intense and lasted several days. Thus, it appears that this event destroyed the soil seed bank, eliminating seeds of pioneer species that in general have dormancy and use a "waiting" strategy for the opening of a canopy gap and a large increase in light intensity to stimulate germination (Dalling et al. 1997).

Saldarriga et al. (1988), using the equation ln $Y= 1.75 + 0.34 \ln (X)$ where Y is the mean basal area (m².ha⁻¹) and X is age (years), estimated that approximately 190 years would be necessary for abandoned agricultural areas to attain a value of basal area similar to mature forests (35 m².ha⁻¹). This premise is corroborated by the data in the present study. Applying the formula proposed by Saldarriga et al. (1988) and considering that CG and CV were disturbed 25 years ago, the expected result would be a basal area of 5.9 m²/ha and the results found for CV and CG were 5.7 and 6.1 m²/ ha, respectively. Thus, it is interesting to note that although this formula is based on data collected in Amazonian forests of the upper Rio Negro, in Colombia and Venezuela, it appears to be adequate for applying in the seasonal semideciduous forest in the north of the State of Espírito Santo. So, the recovery of disturbed areas to values close to those observed in mature forests (30 m²ha⁻¹, Rolim and Jesus (2002) and 47.15 m²ha⁻¹, Paula and Soares (2011) would take 190 to 300 years after fire.

The low bifurcation/resprouting rate observed in this study and the small number of remnant trees (DBH > 30 cm), suggest that most tree species in this forest type does not have fire tolerance. The most important post-fire species were different, as would be expected, from the main species that occur in mature forests. Among the species with the highest cover values in the mature forest are *Rinorea bahiensis* (Violaceae), *Hidrogaster trinervis* (Malvaceae), *Senefeldera multiflora*

(Euphorbiaceae), *Dialium guianensis* (Fabaceae) and *Terminalia kuhlmannii* (Combretaceae) (Jesus and Rolim 2005, Paula and Soares 2011) and none of these were reported as an important species in the three sites studied. Thus, 25 years after the fire the natural regeneration process indicates that the occurrence of resprouting and survival post-fire of individuals in the study areas appears to have favored another group of species and not those species that occur with the highest cover values in the mature forest.

ACKNOWLEDGMENTS

We gratefully acknowledge the Instituto Chico Mendes (ICMBIO) in ensuring access to sites and its local staff of the Rebio Sooretema, Rebio Córrego do Veado and Rebio Córrego Grande for logistic support. Geovane Siqueira provided invaluable assistance in plant identification. We also thank Luciana Thomas and John Hay for comments that improved the early version of the manuscript. Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) provided a productivity grant to Marcelo Trindade Nascimento and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) provided the master scholarship of Mayke Blank Costa.

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