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Dynamics of natural regeneration after disturbance in a remnant of Mixed Ombrophilous Forest in southern Brazil

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ABSTRACT

This study evaluated changes in the structure for remnant Mixed Ombrophilous Forest recovering from logging, which ceased over 40 years ago. Regarding the dynamics of the floristic composition of natural regeneration, 18 species remained (23.38% of the total) and 27 new species entered (35.06% of the total). The greatest increases were observed for *Allophylus edulis*, *Myrsine umbellata*, and *Miconia cinerascens*. When analyzing the dynamics of regeneration in ecological groups, it was observed that pioneer species had a similar value in both surveys (29.4% and 29.6%); secondary species decreased from 56.6% to 52.8%, and late-successional species increased from 0.2% to 6.0%. Therefore, the forest fragment studied is in a healing phase after disturbance, characterized by the increased regeneration of pioneer species as a result of sufficient light entering the interior of the forest.

Keywords: horizontal structure, ingress, mortality, succession stages.

Dinâmica da regeneração natural após distúrbio em uma remanescente de Floresta Ombrófila Mista no Sul do Brasil

RESUMO

O presente estudo teve como objetivo avaliar as alterações ocorridas, no período de 2012 a 2016, na estrutura da regeneração natural de um remanescente de Floresta Ombrófila Mista, sem intervenções há mais de 40 anos. Em relação a dinâmica da composição florística da regeneração natural, houve a saída de 18 espécies (23,38% do total) e a entrada de 27 novas espécies (35,06% do total). Os maiores acréscimos foram observados para *Allophylus edulis*, *Myrsine umbellata e Miconia cinerascens*. Analisando a dinâmica da regeneração em grupos ecológicos, observou-se que as espécies pioneiras tiveram um valor similar em ambos os levantamentos (29,4 a 29,6%). As espécies secundárias decresceram de 56,6% para 52,8%. E as espécies de sucessão tardia aumentaram de 0,2 a 6,0%. Logo, o remanescente estudado encontra-se em fase de cicatrização de distúrbio, caracterizada pelo aumento da regeneração de espécies pioneiras, uma vez que há quantidade suficiente de luminosidade incidindo no interior da floresta.

Palavras-chave: estágios de sucessão, estrutura horizontal, ingresso, mortalidade.

1. INTRODUCTION

Mixed Ombrophilous Forest (MOF), also known as Araucaria forest, is one of the main forest types of southern Brazil (Higuchi *et al.*, 2012a). Its geographical distribution occurs predominantly in the southern plateau region and is associated with places of high altitude and low average annual temperatures (Higuchi *et al.*, 2012a). This forest formation consists mainly of *Araucaria angustifolia* (Bertol.) Kuntze, in association with *Ocotea porosa* (Nees & Mart.) Barroso, *Ilex paraguariensis* A. St.-Hil., *Mimosa scabrella* Benth., *Cedrella fissilis* Vell., *Roupala brasiliensis* Klotzsch, in addition to numerous species belonging to the Myrtaceae family (Higuchi *et al.*, 2012a, 2012b, 2015; Dalla Rosa *et al.*, 2016).

However, the MOF has been intensely altered by strong deforestation because of logging, the expansion of agriculture and livestock, the homogeneous reforestation of exotic species, and the advancement of urban areas, and is thus considered one of the most threatened forest types in Brazil (Ribeiro *et al.*, 2009; Vibrans *et al.*, 2013; Souza *et al.*, 2014; Aguiar *et al.*, 2017). In fact, only 12.6% of the original MOF extension remains (Ribeiro *et al.*, 2009). A lack of knowledge regarding native MOF management has contributed to the reduction in area and low diversity of natural remnants (Hess *et al.*, 2010). Currently, in the State of Santa Catarina, only 24.4% of the original MOF remains, with forest areas distributed in fragmented remnants not exceeding 50 ha (Vibrans *et al.*, 2013). However, even with the disturbances that have occurred, the remaining fragments can be maintained through natural ecological processes, as evidenced by the natural regeneration of tree species (Santos *et al.*, 2018).

Therefore, because of the great environmental and social importance of the MOF, the conservation and restoration of its remnant fragments is a primary objective of MOF management (Higuchi *et al.*, 2012a). In this context, studies of natural regeneration are extremely important because they generate results that enable a better understanding of the behavior of tree communities (Aguiar *et al.*, 2017). With regard to this, a greater understanding of the plant succession process in areas with different disturbance histories is essential, as it can generate data that detect the need to facilitate natural regeneration actions, as well as forest management incentives that facilitate recovery of other similar areas (Larsen *et al.*, 2019). Thus, these studies can support the conservation and recovery plans of forest ecosystems by enabling the identification of limiting environmental factors and inferring the future dynamics of forests (Aguiar *et al.*, 2017; Dalla Rosa *et al.*, 2016).

In this light, this study evaluated the changes that occurred from 2012 to 2016 in the structure of the natural regeneration of a remnant of Mixed Ombrophilous Forest that has remained without intervention for more than 40 years, in the state of Santa Catarina, Brazil.

2. MATERIAL AND METHODS

2.1. Characterization of the study area

The studied forest remnant is located in Fazenda Guamirim Gateados and is part of the "Emílio Einsfeld Filho" Private Reserve of Natural Heritage (PNHR), located in the municipalities of Campo Belo do Sul and Capão Alto, Santa Catarina, Brazil. The experimental area has a total of 3,365 ha, with approximately 72% forest cover, characterized by several succession stages of Mixed Ombrophilous Forest. Sampling was conducted within a radius of up to 500 m from the coordinate point 28°02'55.00" S and 50°45' 59.56" W.

Much of the vegetation in the study area has been subjected to selective logging, which targeted high commercial value woods (Zeller, 2010). According to the Köppen climate classification, the climate of the region is characterized as humid subtropical mesothermal (Cfb), with cool summers, no defined dry season, and frequent severe frosts. The average annual temperature is approximately 15.8°C, varying from 11.4°C in the coldest month to 20.3°C in the hottest month. The average annual precipitation is 1,742 mm (Alvares *et al.*, 2013). The region that encompasses the municipality of Campo Belo do Sul is located in the southern plateau, which in the State of Santa Catarina is bordered to the east by dense ombrophilous forest in addition to deciduous forest along the banks of the Uruguay River (Vibrans *et al.*, 2013).

2.2. Data collection

In February 2012, 20 permanent circular plots were established in a random design in the experimental area. Each plot was 5 m in diameter, and the total sample area was 392.5 m² (Figure 1). In 2016, the same sample units were remeasured. Between the two survey occasions, a gale occurred in the study area, eliminating part of the upper tree layer in four sample units. The collected data corresponded to the number, height, and identification of the regenerating individuals in the sample units. Individuals with a minimum height of 0.50 m and a diameter breast height of less than 15 cm were considered to be regenerating.

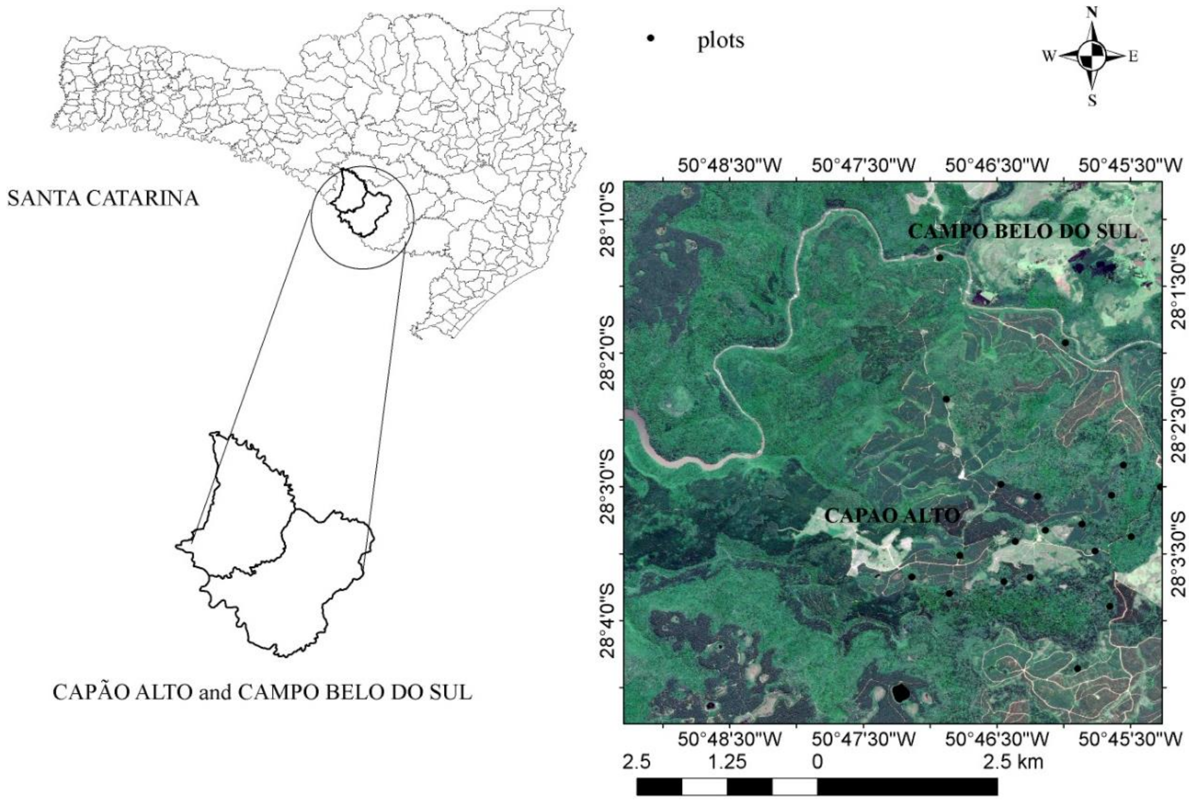

Figure 1. Geographic location of the plots in a remnant of Mixed Ombrophilous Forest in Santa Catarina, Brazil.

2.3. Data analysis

Using data collected in the permanent plots from 2012 and 2016, the floristic and phytosociological parameters of natural regeneration were estimated. For this, the species found in the plots were identified by visual analysis in the field or in the expert opinions and specialized literature. For the ecological classification of species, in addition to observations in the field, the methodology described by Vibrans *et al.* (2013) was followed. This system considers the following categories: pioneer species (P), secondary species (SE), and late-successional species (LS).

The dynamics of regeneration were evaluated by changing the values of diversity and structure of species between the two periods surveyed. The parameters used to estimate the regeneration structure were density and frequency, based on Mueller-Dombois and Ellenberg

(1974), and the category of size and value of the regeneration based on Finol (1971). Species diversity was calculated using the Shannon's Diversity Index (H′), Simpson's diversity index (D), and Pielou's equability index (J′) (Brower and Zar, 1984). All analyses were done by the PAST® statistical software, Version 2.17c, according to the methodology described by Felfili and Rezende (2003) and Magurran (2004).

The regeneration-size category parameter (absolute and relative) refers to the distribution of regenerating individuals in height classes by determining the phytosociological values of natural regeneration. The regeneration value, in absolute and relative terms, in turn expresses the importance of species in the community by averaging their relative density, frequency, and size category. The calculations covered all species sampled in the study area. Changes in species density were analyzed using the paired t-test (alpha was set at = 0.05).

3. RESULTS AND DISCUSSION

3.1. Floristic composition

In general, in both surveys, 77 species were found, represented by 51 genera and 32 botanical families. Specifically, in 2012 and 2016, 50 (12,382 ind ha^{-1}) and 59 species (12,313 ind ha^{-1}) were found, respectively, of which 18 were exclusive to the first survey and 28 were exclusive to the second (Table 1). The species richness found in this study was similar to that found by Aguiar *et al.* (2017) in an MOF experiment in Lages, SC, Brazil, and by Santos *et al.* (2015) in a fragment with the same forest typology also in Lages, SC, Brazil.

The family with the greatest richness was Myrtaceae, followed by Lauraceae. Emphasizing the ecological importance of the Myrtaceae family, it has also been classified as highly representative of MOFs by several authors (Vibrans *et al.*, 2011; Meyer *et al.*, 2013; Higuchi *et al.*, 2015; Santos *et al.*, 2015, 2018; Dalla Rosa *et al.*, 2016; Silva et al., 2017; Santana *et al.*, 2018; Vefago *et al.*, 2019), occurring in areas of different altitudes (Dalla Rosa *et al.*, 2016).

Table 1. Floristic and structural descriptors evaluated for natural regeneration in 2012 and 2016 in a remnant of Mixed Ombrophilous Forest in Santa Catarina, Brazil.

Descriptors evaluated	2012	2016
Number of species	50	59
Number of genres	43	37
Number of families	29	24
Shannon's diversity index (H′)	3.15	3.26
Pielou's equability index (J′)	0.81	0.79
Simpson's diversity index (D)	0.94	0.94
Number of individuals per hectare	12,382	12,313

The H′ and J′ values were 3.15 and 0.81 in 2012 and 3.26 and 0.79 in 2016, respectively. The estimated value for D was 0.94 for both surveys (Table 1). The H′ value was similar to that found in an experiment by Aguiar *et al.* (2017) in an MOF in Lages, SC, Brazil (3.34) and by Santos *et al.* (2018), also in an MOF in Lages, SC (3.42). Higher values were found by Dalla Rosa *et al.* (2016) in a remnant of the same forest typology in Urubici, SC, Brazil (2.51). In contrast, lower values were found by Santos *et al.* (2015) in an MOF fragment in Lages, SC, Brazil. According to Nascimento *et al.* (2001), diversity values close to 3.00 characterize a medium diversity, which is expected in secondary succession stage MOF forests that have suffered anthropic influences.

Regarding J′, Dalla Rosa *et al.* (2016), Santos *et al.* (2015), Aguiar *et al.* (2017) and Santos *et al.* (2018) found values close to that of this study: 0.75, 0.76, 0.82 and 0.83, respectively. This indicates high ecological dominance. According to Brower and Zar (1984), the Simpson diversity index (D) measures the probability that two individuals, selected at random from the same sample, belonging to the same species. That is, the higher the D value, the greater the diversity and the lesser the dominance of species (Klauberg *et al.*, 2010).

The quantitative data of the floristic descriptors evaluated (Table 1) revealed little change between the two surveys. It is observed that the diversity values found in this study reflect the pattern already verified in other studies in the same formation and confirm that the MOF in Santa Catarina is, in general, undergoing regeneration after decades of selective exploration. However, in this study, the observed changes were small, which indicates the existence of disturbances such as gusts and tree falls in the area, which can increase environmental filters and facilitate the entry of pioneer species.

3.2. Phytosociological parameters of natural regeneration

In the 2012 survey, the species *Eugenia* sp., *Allophylus edulis* (A.St.-Hil., Cambess. & A. Juss.) Radlk., *Casearia decandra* Jacq., *Matayba elaeagnoides* Radlk., and *Myrsine umbelata* Mart. were the most important in terms of density, which together accounted for 46.7% of the total stems (Table 2). These species were also the most representative in terms of frequency. In 2016, these same species remained the most important; however, there was a change in their order: *Allophylus edulis*, *Myrsine umbellata*, *Casearia decandra*, *Matayba elaeagnoides* and *Eugenia* sp. The mentioned species added up to 43.4% of the total density (Table 2). According to Higuchi *et al.* (2015), the variation of the most abundant species can be explained due to their different life strategies and respective capacities to develop in the forest understory. Some species may produce more propagules; however, they are inefficient competitors. Other species may produce few propagules, but with good competitive capacity.

Approximately half of the species (51.67%) were found in only 5% of the sample units, demonstrating the great diversity of species present in the regeneration of this forest type. In a study by Vefago *et al.* (2019), *Allophylus edulis* and *Matayba elaeagnoides* were also among the most representative species. *Araucaria angustifolia* (Bertol.) Kuntze, despite being considered the species that most characterizes MOF, went from 7th to 13th rank between the 2012 and 2016 survey; that is, it represented 4.3% of the density in 2012 (535.0 ind ha^{-1}), and only 2.7% in 2016 (331.2 ind ha^{-1}). However, despite the decrease in density in the plots, the species were more concentrated spatially in 2012 (FR: 3.2%) than in 2016 (FR: 4.1%). Other studies have also shown that this species had low representativeness (Dalla Rosa *et al.*, 2016; Vefago *et al.*, 2019). According to Dalla Rosa *et al.* (2016), *A. angustifolia* has a limited number of regenerating individuals in the understory of the MOF and this limitation is even more extreme at high altitudes (>1,500 m).

3.3. Dynamics of floristic composition of natural regeneration

There were considerable changes in the floristic composition of natural regeneration between the two surveys (Table 3). For example, 18 species remained (23.38% of the total) and 27 new species entered (35.06% of the total). From this, we can see the dynamism that occurred in natural regeneration, which shows that the occurrence of species in the regenerative stratum will not guarantee their presence in the tree stratum in the future.

Table 2. Phytosociological parameters of 20 species of greatest of values relative natural regeneration in 2012 and 2016 in a remnant of Mixed Ombrophilous Forest in Santa Catarina, Brazil.

SPECIES	AD (n ha^{-1})		RD (%)		AF (%)		RF (%)		ASC		RSC (%)		ANR		RNR (%)	
	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016
Allophylus edulis (A.St.-Hil., Cambess. & A. Juss.) Radlk.	1248.4	1707.0	10.1	13.9	65.0	65.0	5.9	7.6	22.5	29.1	10.3	15.0	445.3	600.4	8.7	12.1
Annona emarginata (Schltdl.) H.Rainer	382.2	484.1	3.1	3.9	40.0	25.0	3.6	2.9	7.2	8.6	3.3	4.4	143.1	172.6	3.3	3.8
Araucaria angustifolia (Bertol) Kuntze	535.0	331.2	4.3	2.7	35.0	35.0	3.2	4.1	9.4	5.9	4.3	3.0	193.2	124.0	3.9	3.3
Brunfelsia pilosa Plowman	51.0	229.3	0.4	1.9	10.0	20.0	0.9	2.3	1.1	4.1	0.5	2.1	20.7	84.5	0.6	2.1
Campomanesia guaviroba (DC.) Kiaersk.	25.5	101.9	0.2	0.8	5.0	10.0	0.5	1.2	0.4	1.4	0.2	0.7	10.3	37.8	0.3	0.9
Casearia decandra Jacq.	1095.5	917.2	8.8	7.4	80.0	45.0	7.2	5.3	20.6	15.8	9.4	8.1	398.7	326.0	8.5	6.9
Casearia obliqua Spreng.	51.0	25.5	0.4	0.2	10.0	5.0	0.9	0.6	1.1	0.1	0.5	0.0	20.7	10.2	0.6	0.3
Cinnamodendron dinisii Schwacke	229.3	382.2	1.9	3.1	30.0	35.0	2.7	4.1	3.8	6.4	1.7	3.3	87.7	141.2	2.1	3.5
Cupania vernalis Cambess.	458.6	76.4	3.7	0.6	40.0	10.0	3.6	1.2	7.3	1.4	3.3	0.7	168.6	29.3	3.5	0.8
Eugenia sp.	1579.6	738.9	12.8	6.0	90.0	40.0	8.1	4.7	28.2	12.4	12.9	6.4	565.9	263.7	11.2	5.7
Eugenia uniflora L.	203.8	305.7	1.6	2.5	30.0	30.0	2.7	3.5	4.1	4.6	1.9	2.4	79.3	113.4	2.1	2.8
Luehea divaricata Mart. & Zucc.	25.5	76.4	0.2	0.6	5.0	15.0	0.5	1.8	0.5	0.6	0.2	0.3	10.3	30.7	0.3	0.9
Matayba elaeagnoides Radlk.	993.6	789.8	8.0	6.4	70.0	60.0	6.3	7.0	16.1	10.2	7.4	5.2	359.9	286.7	7.2	6.2
Miconia cinerascens Miq.	101.9	509.6	0.8	4.1	15.0	10.0	1.4	1.2	2.0	6.6	0.9	3.4	39.6	175.4	1.0	2.9
Myrsine umbellata Mart.	866.2	1197.5	7.0	9.7	55.0	55.0	5.0	6.4	15.5	19.2	7.1	9.9	312.2	423.9	6.3	8.7
Podocarpus lambertii Klotzsch ex Endl.	178.3	101.9	1.4	0.8	15.0	10.0	1.4	1.2	2.3	1.5	1.0	0.8	65.2	37.8	1.3	0.9
Roupala montana Aubl.	152.9	51.0	1.2	0.4	25.0	10.0	2.3	1.2	2.3	0.6	1.1	0.3	60.1	20.5	1.5	0.6
Rudgea parquioides (Cham.) Müll.Arg.	433.1	356.7	3.5	2.9	50.0	30.0	4.5	3.5	7.9	6.3	3.6	3.2	163.7	131.0	3.9	3.2
Sebastiana brasiliensis Spreng.	687.9	687.9	5.6	5.6	45.0	25.0	4.1	2.9	13.9	11.3	6.4	5.8	248.9	241.4	5.3	4.8
Styrax leprosus Hook. & Arn.	433.1	254.8	3.5	2.1	50.0	25.0	4.5	2.9	7.2	4.5	3.3	2.3	163.4	94.8	3.8	2.4

AD: absolute density; RD: relative density; AF: absolute frequency; RF: relative frequency; ASC: absolute size class; RSC: relative size class; ANR: absolute natural regeneration; RNR: relative natural regeneration.

Table 3. Dynamics of the structure of the regenerative stratum in a remnant of Mixed Ombrophilous Forest in Santa Catarina, Brazil.

SPECIES	RD (%)		RF (%)		RSC (%)		RNR (%)		CHANGES
	2012	2016	2012	2016	2012	2016	2012	2016	RNR (%)
Allophylus edulis (A.St.-Hil., Cambess. & A. Juss.) Radlk.	10.1	13.9	5.9	7.6	10.2	15.0	8.7	12.1	3.4
Allophylus guaraniticus (A. St.-Hil.) Radlk.		5.2		4.7		5.6		5.2	
Annona emarginata (Schltdl.) H.Rainer	3.1	3.9	3.6	2.9	3.3	4.4	3.3	3.8	0.5
Araucaria angustifólia (Bertol) Kuntze	4.3	2.7	3.2	4.1	4.3	3.0	3.9	3.3	-0.6
Baccharis dentata (Vell.) G.Barroso		0.6		0.6		0.5		0.6	
Bernardia pulchella (Baill.) Müll.Arg	0.2	0.4	0.5	0.6	0.2	0.5	0.3	0.5	0.2
Brunfelsia cuneifólia J.A.Schmidt		0.6		1.2		0.7		0.8	
Brunfelsia pilosa Plowman	0.4	1.9	0.9	2.3	0.5	2.1	0.6	2.1	1.5
Calyptranthes concinna DC.	2.1		3.2		2.1		2.4		
Campomanesia guaviroba (DC.) Kiaersk.	0.2	0.8	0.5	1.2	0.2	0.7	0.3	0.9	0.6
Capsicum sp.	0.2		0.5		0.2		0.3		
Casearia decandra Jacq.	8.8	7.4	7.2	5.3	9.4	8.1	8.5	6.9	-1.6
Casearia obliqua Spreng.	0.4	0.2	0.9	0.6	0.5	0.0	0.6	0.3	-0.3
Cinnamodendron dinisii Schwacke	1.9	3.1	2.7	4.1	1.7	3.3	2.1	3.5	1.4
Cinnamomum amoenum (Nees & Mart.) Kosterm.		0.2		0.6		0.2		0.3	
Citronella gongonha (Mart.) R.A.Howard	0.2		0.5		0.2		0.3		
Cupania vernalis Cambess.	3.7	0.6	3.6	1.2	3.3	0.7	3.5	0.8	-2.7
Dalbergia frutescens (Vell.) Britton	0.4		0.5		0.4		0.4		
Daphnopsis racemosa Griseb.	0.2	0.2	0.5	0.6	0.2	0.2	0.3	0.3	0.0
Drimys brasiliensis Miers	0.2	0.2	0.5	0.6	0.2	0.2	0.3	0.3	0.0
Eugenia pyriformis Cambess.	0.2		0.5		0.2		0.3		
Eugenia rostrifolia D.Legrand	2.3	0.2	2.7	0.6	2.3	0.2	2.4	0.3	-2.1
Eugenia uniflora L.	1.6	2.5	2.7	3.5	1.9	2.4	2.1	2.8	0.7
Eugenia sp.	12.8	6.0	8.1	4.7	12.8	6.4	11.2	5.7	-5.5
Ilex theezans Mart. ex Reissek	1.2		1.8		1.3		1.4		

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Lamanonia ternata Vell.	0.2		0.5		0.2		0.3		
Leandra regnellii (Triana) Cogn.		0.2		0.6		0.2		0.3	
Ligustrum lucidum W.T.Aiton		0.2		0.6		0.2		0.3	
Lonchocarpus campestris Mart. ex Benth	0.4		0.5		0.4		0.4		
Lonchocarpus latifolius (Willd.) DC.		0.4		0.6		0.5		0.5	
Luehea divaricata Mart. & Zucc.	0.2	0.6	0.5	1.8	0.2	0.3	0.3	0.9	0.6
Matayba elaeagnoides Radlk.	8.0	6.4	6.3	7.0	7.4	5.2	7.2	6.2	-1.0
Maytenus aquifolia Mart.	0.2		0.5		0.2		0.3		
Miconia cinerascens Miq.	0.8	4.1	1.4	1.2	0.9	3.4	1.0	2.9	1.9
Mimosa scabrella Benth.	0.2		0.5		0.2		0.3		
Myrceugenia mesomischa (Burret) D. Legrand et Kausel		0.2		0.6		0.2		0.3	
Myrceugenia sp.	0.4		0.9		0.4		0.6		
Myrcia glabra (O.Berg) D. Legrand		0.2		0.6		0.2		0.3	
Myrcia hartwegiana (O.Berg) Kiaersk.		0.2		0.6		0.2		0.3	
Myrcianthes pungens (O.Berg) D.Legrand	0.4		0.9		0.5		0.6		
Myrocarpus frondosus Allemão	1.2		0.9		1.4		1.2		
Myrsine lorentziana (Mez) Arechav.		0.4		0.6		0.5		0.5	
Myrsine sp.	0.2		0.5		0.2		0.3		
Myrsine umbellata Mart.	7.0	9.9	5.0	7.0	7.1	10.1	6.3	9.0	2.7
Nectandra lanceolata Nees	0.2	0.4	0.5	0.6	0.2	0.5	0.3	0.5	0.2
Nectandra megapotamica (Spreng.) Mez	2.7	1.2	2.3	2.3	2.0	1.4	2.3	1.7	-0.6
Ocotea puberula (Rich.) Nees.	1.2	0.2	2.3	0.6	0.7	0.2	1.4	0.3	-1.1
Ocotea pulchella (Nees) Mez	4.3	0.2	4.5	0.6	4.4	0.2	4.4	0.3	-4.1
Ocotea pulchra Vattimo-Gil		0.8		1.8		0.9		1.2	
Ocotea sp.		0.4		1.2		0.5		0.7	
Pavonia sepium A.St.-Hil.		1.2		1.2		1.2		1.2	
Pera glabrata (Schott) Poepp. ex Baill.	0.2		0.5		0.2		0.3		
Pimenta pseudocaryophyllus (Gomes) Landrum		0.4		0.6		0.5		0.5	

Continue...

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Piptocarpha angustifolia Dusén ex Malme	0.2	0.2	0.5	0.6	0.2	0.2	0.3	0.3	0.0
Podocarpus lambertii Klotzsch ex Endl.	1.4	0.8	1.4	1.2	1.0	0.8	1.3	0.9	-0.4
Prunus myrtifolia (L.) Urb.	0.8		1.8		0.9		1.2		
US – 1		0.6		1.2		0.7		0.8	
US – 2		0.8		1.2		0.9		1.0	
US – 3		0.4		0.6		0.5		0.5	
US – 4		0.2		0.6		0.2		0.3	
US – 5		0.2		0.6		0.2		0.3	
US – 6		0.6		0.6		0.7		0.6	
US – 7		0.2		0.6		0.2		0.3	
US – 8		0.4		0.6		0.3		0.4	
US – 9	0.2	0.2	0.5	0.6	0.2	0.2	0.3	0.3	0.0
Roupala montana Aubl.	1.2	0.4	2.3	1.2	1.1	0.3	1.5	0.6	-0.9
Rudgea parquioides (Cham.) Müll.Arg	3.5	2.9	4.5	3.5	3.6	3.2	3.9	3.2	-0.7
Schaefferia argentinensis Speg.		0.2		0.6		0.2		0.3	
Sebastiania brasiliensis Spreng.	5.6	5.6	4.1	2.9	6.3	5.8	5.3	4.8	-0.5
Sebastiania commersoniana (Baill.) L.B. Sm. & Downs		4.2		1.2		0.7		2.0	
Seguieria aculeata Jacq.	0.2		0.5		0.2		0.3		
Strychnos brasiliensis (Spreng.) Mart.	0.2	0.2	0.5	0.6	0.2	0.2	0.3	0.3	0.0
Styrax leprosus Hook. & Arn.	3.5	2.1	4.5	2.9	3.3	2.3	3.8	2.4	-1.4
Trichilia elegans A. Juss.		0.2		0.6		0.2		0.3	
Xylosma ciliatifolia (Clos) Eichler	0.4		0.9		0.4		0.6		
Zanthoxylum kleinii (R.S.Cowan) P.G.Waterman	0.2	0.6	0.5	1.2	0.2	0.7	0.3	0.8	0.5
Zanthoxylum rhoifolium Lam.		0.2		0.6		0.2		0.3	

RD: relative density; RF: relative frequency; RSC: relative size class; RNR: relative natural regeneration; US: unidentified species.

The greatest increases were observed for *Allophylus edulis* (+3.4%), *Myrsine umbellata* (+2.7%), and *Miconia cinerascens* Miq. (+1.9%), of which only *M. cinerascens* was classified as a pioneer, while the others were classified as secondary species. This fact indicates that this remnant forest is in a reestablishment phase after disturbance, since there is sufficient light shining into the forest to initiate the development/ recruitment of both pioneer and secondary species. Regarding the decreases, the species *Eugenia* sp., *Ocotea pulchella* (Nees & Mart.) Mez, and *Cupania vernalis* Cambess. stood out (–5.5%, –4.1%, and –2.7%) and the latter two were classified as pioneers. A study by Gross *et al.* (2018) reported that the dynamics of the Araucaria forest varied mainly in terms of tree mortality and rates of basal area loss.

3.4. Dynamics of the regeneration of ecological groups

Analyzing the dynamics of regeneration in ecological groups, it was observed that the pioneer species had similar values in both surveys (29.4% and 29.6%, respectively) (Figure 2). In contrast, secondary species decreased from 56.6% to 52.8%, while late-successional species increased from 0.2% to 6.0% between the first and the second survey, respectively. Meyer *et al.* (2013), when evaluating the natural regeneration of the MOF in Santa Catarina, Brazil, observed that the secondary, pioneer, and late-successional species corresponded to 54.37%, 29.66% and 15.97% of the total, respectively, which partially reflects the history of use of this forest.

In general, pioneer species showed the highest rates of positive change (189.8%), while secondary species showed the highest rates of negative change (–573.25%) (Figure 3). In this case, it becomes evident that the availability of light in the interior of the forest is caused by the fall of individuals from the tree layer due to the actions of climatic events, which is reflected in the increase of pioneer individuals, also resulting in the mortality of secondary species in natural regeneration. In this sense, the changes observed in the floristic composition and distribution of ecological groups can be attributed to disturbances that occur in the forest.

Chazdon (2016) mentioned that disturbances in natural forests can be caused by either natural or anthropogenic activities. Considering that selective logging ceased more than 40 years ago in the study area, natural disturbances, such as gales and the fall of mature trees, are undoubtedly causing the regeneration gaps. This, consequently, provides opportunities for changes in the distribution of ecological groups in the forest, especially with the increased representativeness of pioneer species that are extremely important for the forest succession, creating conditions for the species of more advanced successional stages to establish themselves. Thus, the colonization of clearings by pioneer species detected in this study shows the occurrence of forest reestablishment after disturbances (Narvaes *et al.*, 2005).

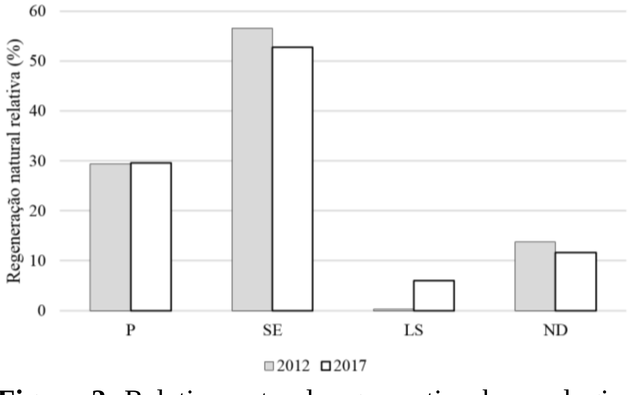

Figure 2. Relative natural regeneration by ecological groups in a remnant of Mixed Ombrophilous Forest in Santa Catarina, Brazil. P: Pioneers species; SE: Secondary species; LS: late-successional species; ND: Ecological group not defined.

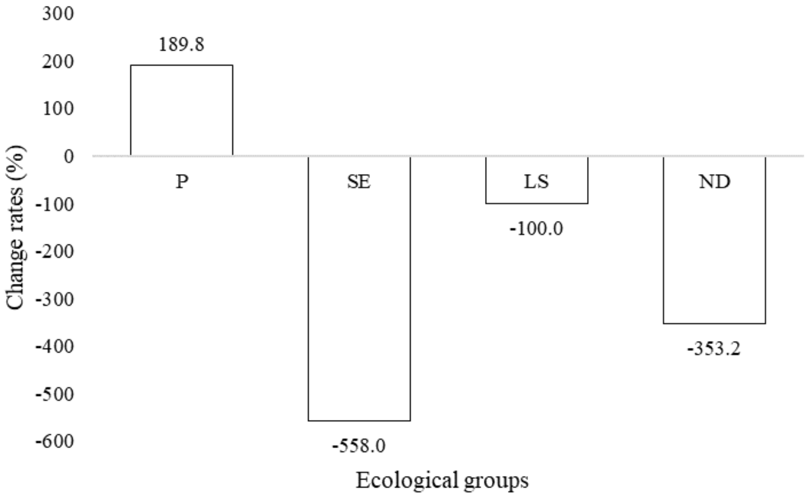

Figure 3. Average rates of change in the regenerative stratum by ecological groups in a remnant of Mixed Ombrophilous Forest in Santa Catarina, Brazil.
P: Pioneers species; SE: Secondary species; LS: late-successional species; ND: Ecological group not defined.

The changes that occurred in this fragment of MOF in the period of four years between the two vegetation censuses show that there was an increase in pioneer species and decreases in secondary and late-successional species. Therefore, the results show that the dynamics of natural regeneration of the forest may not follow the path theoretically expected in such a short period of time, as internal and external disturbances can affect the succession processes.

4. CONCLUSIONS

Considerable changes occurred in the structure and floristic composition dynamics of natural regeneration between the two data surveys.

Pioneer species had the highest rates of positive change, while secondary species had the highest rates of negative change.

This studied remnant forest fragment is in the healing phase after disturbance, since there is a sufficient amount of light falling inside the forest.

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