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ORIGINAL ARTICLE – Conservation of Nature

Dynamics of Tree Population Structure After Disturbance of Araucaria Forest Remnants

Alyne Regina Ruggiero[1]
Lauri Amândio Schorn[1]
Kristiana Fiorentin dos Santos[1]
Tatiele Anete Bergamo Fenilli[1]

[1]Universidade Regional de Blumenau (FURB), Departamento de Engenharia Florestal, Blumenau, SC, Brasil.

Abstract

This study aimed at evaluating and compare the changes from 2012 to 2016 in the structure and floristic composition of a remnant Araucaria Forest. The entry and mortality rates were 2.2% year^{-1} and 6.9% year^{-1}, respectively. Among the most represented species, those with the greatest yearly increases in their numbers were *Sebastiania brasiliensis*, *Eugenia uniflora*, and *Allophylus* sp. Average mortality density was 498 ind ha^{-1}, and was particularly high for the following species: *Casearia decandra* (representing 32.3% of total mortality), *Eugenia* sp. (27.2%), *Cinnamodendron dinisii* (24.5%), and *Lithraea brasiliensis* (25.2%). The pioneer species represented 8.33% of income and 29.17% mortality, and secondary species composed 33.33% and 62.50% of income and mortality, respectively. Climax species accounted for 8.33% of income and did not contribute to mortality. The high tree mortality observed in the present study can be attributed, among others factors, to the effects of natural disturbance that occurred in the period.

Keywords: Ecological groups, importance value, income, Mixed Ombrophilous Forest, mortality.

1. INTRODUCTION AND OBJECTIVES

The accelerated fragmentation of tropical forests is one of the greatest threats to biodiversity today (Oliveira-Filho et al. 2007). Like most of the forests in the Atlantic domain, the Mixed Ombrophilous Forest has been intensely disturbed and fragmented (Higuchi et al. 2012) due to a process of land occupation that has resulted in a mosaic of vegetation remnants with different sizes, shapes, and stages of degradation (Negrini et al. 2014). In addition, natural events such as gales are becoming more and more frequent, which can alter the structure of forest remnants, especially where forests are more fragmented.

In recent decades, scientific interest in aspects of forest dynamics has been increasing (Silva et al. 2011). An understanding of tree community dynamics makes it possible to understand the role of the forest ecosystem (Gross et al. 2018) at both the species level and the whole-forest level (Figueiredo-Filho et al. 2010).

The study of floristic dynamics provides important information that can be implemented in the sustainable management of natural forests, in addition to furthering our understanding of the possible consequences of recent anthropogenic and natural changes in the tropics, such as deforestation, forest fragmentation, and global climate change (Sheil et al. 2000). Monitoring the dynamics of communities and populations of tree species in fragmented landscapes is essential because it increases our knowledge of the floristic and structural changes that occur over time (Nunes et al. 2016).

Thus, there is a considerable need to analyze the growth and changes that occur in the structure and floristic composition of Mixed Ombrophilous Forest remnants, as this information could assist in strategies aimed at the sustainable use, maintenance, and conservation of these ecosystems (Cubas et al. 2016). Given the above, the present study aimed to evaluate and compare the changes that occurred in the structure and floristic composition of a remnant of Mixed Ombrophilous Forest in Southern Brazil, from 2012 to 2016.

2. MATERIALS AND METHODS

2.1. Study area

The present study was carried out in a forest remnant located in the "Emílio Einsfeld Filho PRNH " Private Reserve of Natural Heritage (PRNH), located in the municipalities of Campo Belo do Sul and Capão Alto, Santa Catarina, Brazil. According to the Köppen classification system, the climate is classed as humid subtropical mesothermal (Cfb). The average temperature and average annual precipitation are approximately 15.4 °C and 1,735 mm, respectively (Alvares et al. 2013). The altitudinal gradient is between 650 to 900 m (ICMBio, 2008). The region of the Santa Catarina Plateau of southern Brazil, where the area object of the present study is inserted, was subjected to a natural disturbance, characterized by a strong wind in September 2015 (Weathers Park, 2022) and which caused the fall of a large number of trees.

The remnant has a total of 3,365 ha, with approximately 71.59% of Mixed Ombrophilous Forest (IBGE, 2012). Much of the vegetation in the study area has suffered anthropogenic action through selective logging in the past, mainly of high commercial value woods such as araucarias and imbuias. However, these interventions have been suspended for decades (Zeller, 2010).

The region that encompasses the municipalities of Campo Belo do Sul and Capão Alto is located in the southern plateau, which in the State of Santa Catarina is bordered to the east by Dense Ombrophylous Forest in addition to deciduous forest along the banks of the Uruguay River (Vibrans et al. 2013). The main soils that have been identified at the site are litholic neosols, cambisols, and nitisols, with more abundant in the vicinity of the Pelotas and Canoas/Caveiras rivers (EMBRAPA 2006).

2.2. Field sampling

In February 2012, Schorn et al. (2012) initiated a permanent forest inventory in the study area, which included 20 plot of 10 m × 50 m randomly selected within the area, comprising a total sample area of 10,000 m² (Figure 1). 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. All individual trees with circumference at breast height (CBH; measured at 1.30 m above the ground) greater than 15 cm were sampled, with their taxonomic identifications, CBH, and heights measured. A subsequent inventory was carried out in 2016 within the same sample plots, and new individuals satisfying the CBH > 15 cm threshold were identified and measured. Dead, standing, or fallen trees were recorded. For the surviving individuals, the variables measured in 2012 were remeasured and evaluated. Between the two survey occasions, a gale occurred in the study area, eliminating part of the upper tree layer in four sample units.

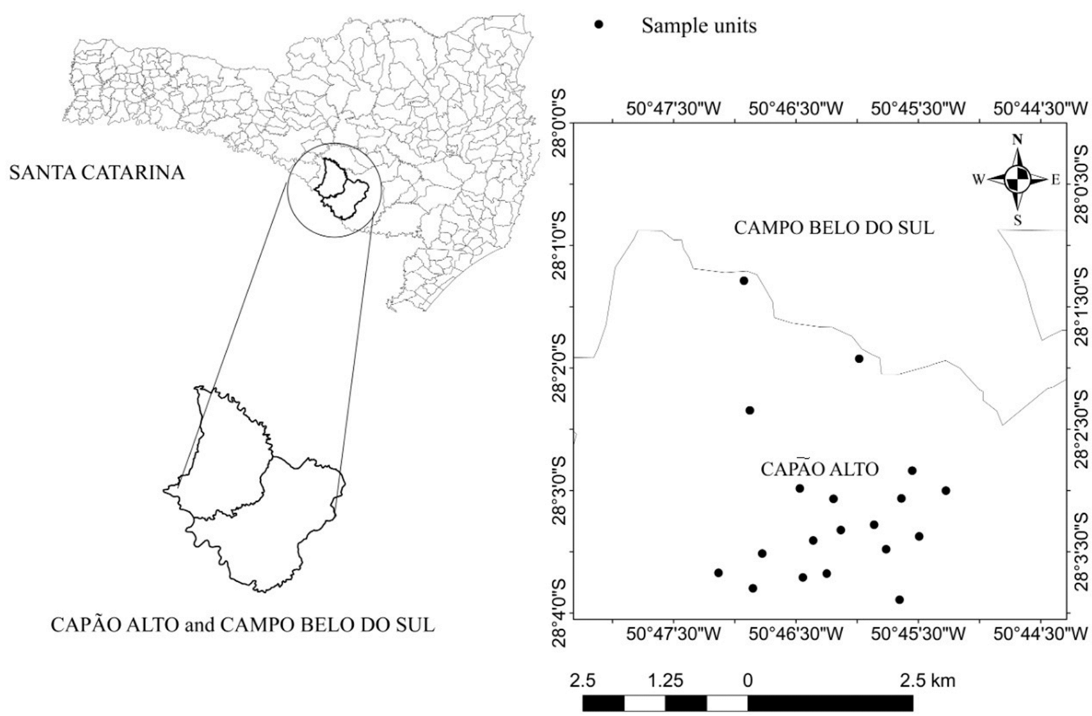


Figure 1. Geographic location of the sample units in a Araucaria Forest remnants.

2.3. Data analysis

The species found in the plots were identified by the expert opinions and specialized literature. The individuals were classified at family, genus and species level according to the APG IV system (APG IV, 2016). 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 climactic species (C). The dynamics were evaluated by changing the values of diversity and structure of species between the two periods surveyed.

The following phytosociological parameters were calculated to characterize the horizontal structure of the forest: absolute and relative density (AD and RD), absolute and relative dominance (ADo and RDo), absolute and relative frequency of occurrence (AF and RF), and relative importance values (IV), according to the methodologies outlined in Daubenmire (1968) and in Mueller-Dombois & Ellenberg (1974).

The dynamics rates (mortality, recruitment, turnover, and net changes) were calculated. The income of individuals was determined for each species using the Equation 1 taken from Schaaf et al. (2005):

$$I = I_S - D + R \tag{1}$$

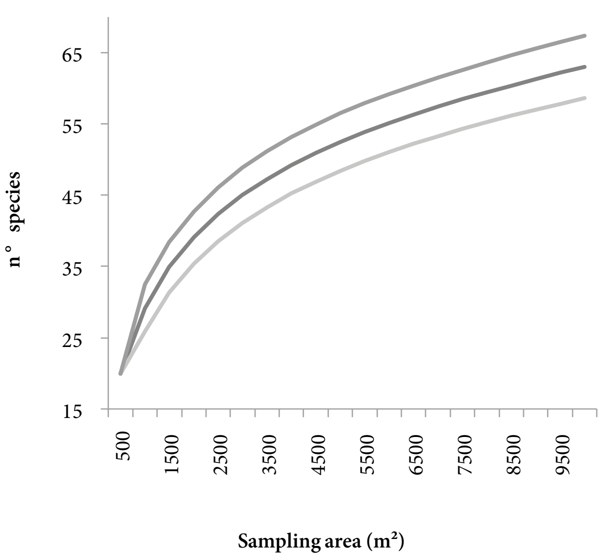
where, I = net increase or growth of the forest; I_S = sum of the increments of the trees that survived in the studied period; D = volume of trees that died during the period; R = ingrowth volume measured at the end of the period.

The species rarefaction curve was constructed using Excel. The calculations covered all species sampled in the study area. Means between the two evaluation periods were compared using t-test (alpha was set at = 0.05).

3. RESULTS AND DISCUSSION

3.1. Changes in tree species diversity

An examination of the relationship between the number of species and the sampled area showed that the number of species increased as new sample units were measured up to a plateau, characterized by the absence of new species. In 2012, the upward trajectory of the curve continued up to 2,500 m², with a greater tendency to stabilize after 5,500 m² of sampling (Figure 2). Therefore, after 5,500 m² had been sampled, with each 10% increase in sampling area, fewer than 5% of the species identified were new species (Figure 2, left). In 2016, the curve maintained the same pattern as in 2012 (Figure 2, right). Therefore, the units sampled in the area were sufficient to characterize the vegetation under study. According to Kersten and Galvão (2011), sample sufficiency is achieved when the increase of 10% in area allows a maximum increase of 5% of new species sampled.



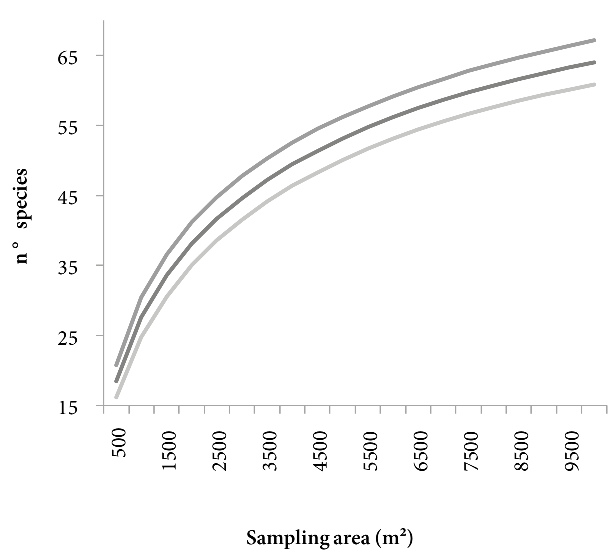


Figure 2. Rarefaction curve of species accumulation across sampling units of a Araucaria Forest remnants, in 2012 (left) and 2016 (right).

3.2. Horizontal structural dynamics

In 2012, mean tree density across sampling plots was 1,810 ind ha^{-1}, with trees belonging to 62 species, 51 genera, and 27 families. In 2016, a mean density of 1,471 ind ha^{-1} was measured, composed of 63 species, 48 genera, and 28 families. Therefore, there was an 11.98% decrease in the number of ind ha^{-1} between survey years. Changes in forest density between the two surveys were significant (alpha was set at = 0.05). This decrease in density and other values of the forest structure, described below, may be, among others factors, due to the strong winds that occurred in this region of the State of Santa Catarina in September 2015, which caused damage to forests and the fall of a large number of individual trees, many of which were large. In the study area, the formation of large clearings was observed, which included sample plots, at the time of the survey carried out in 2016. Santos et al. (2015), analyzing the influence of the passage of a hurricane in Mixed Ombrophilous Forest at the National Park of Aparados da Serra, southern of Brazil, also observed that there were changes in the structure of the tree community.

The family with the highest species richness was Myrtaceae, in both surveys. Several studies have pointed out that this family is the most diverse tree species in Mixed Ombrophilous Forests (Higuchi et al. 2012, Higuchi et al. 2013, Silva et al. 2012, Negrini et al. 2014, Souza et al. 2014, Marcon et al. 2014, Ansolin et al. 2016, Cubas et al. 2016, Silva et al. 2017, Gonçalves et al. 2018, Stedille et al. 2018).

The most representative species in 2012 were *Casearia decandra*, *Eugenia* sp., and *Cinnamodendron dinisii*. In 2016, these same species stood out again, although they contributed less to the relative density, that is, they represented 28.0% of the relative density in 2012 and 23.8% in 2016 (Table 1). According to Figueiredo-Filho et al. (2010), the number of trees, species, genera, and families present in Mixed Ombrophilous Forests is quite variable; this may be due to different environmental conditions, successional stages and other factors.

Table 1. Phytosociological estimators of 30 species of greatest of importance values in 2012 and 2016 in a Araucaria Forest remnants.

Species	AD (n ha^{-1})		RD (%)		ADo (n ha^{-1})		RDo (%)		AF (%)		RF (%)		IV (%)	
	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016
Allophylus sp.	54	43	2.98	2.70	0.40	0.22	0.86	0.50	65	45	3.26	2.44	2.36	1.92
Araucaria angustifolia (Bertol.) Kuntze	101	87	5.57	5.45	7.30	7.55	15.52	16.94	85	90	4.26	4.88	8.45	9.18
Calyptranthes concinna DC.	83	68	4.58	4.26	1.11	1.11	2.36	2.48	70	60	3.51	3.25	3.48	3.39
Campomanesia guaviroba (DC.) Kiaersk.	9	9	0.50	0.56	0.07	0.08	0.15	0.19	20	20	1.00	1.08	0.55	0.61
Cariniana estrellensis (Raddi) Kuntze	6	14	0.33	0.88	0.77	0.84	1.63	1.89	15	15	0.75	0.81	0.91	1.21
Casearia decandra Jacq.	189	132	10.43	8.28	0.89	0.67	1.89	1.51	100	95	5.01	5.15	5.78	5.34
Casearia obliqua Spreng.	31	23	1.71	1.44	0.22	0.19	0.46	0.42	35	30	1.75	1.63	1.31	1.19
Cinnamodendron dinisii Schwacke	147	119	8.11	7.46	2.25	1.97	4.79	4.42	85	80	4.26	4.34	5.72	5.96
Dicksonia sellowiana Hook.	30	25	1.66	1.57	0.82	0.91	1.74	2.04	30	40	1.50	2.17	1.63	1.77
Drimys brasiliensis Miers	12	11	0.66	0.69	0.06	0.06	0.13	0.12	25	20	1.25	1.08	0.68	0.56
Eugenia uniflora L.	64	65	3.53	4.08	0.66	0.75	1.41	1.68	55	50	2.76	2.71	2.57	2.92
Eugenia sp.	172	129	9.49	8.09	1.78	1.59	3.79	3.57	80	80	4.01	4.34	5.76	5.82
Lithraea brasiliensis Marchand	107	84	5.91	5.27	4.75	4.07	10.11	9.14	90	80	4.51	4.34	6.84	5.95
Luehea divaricata Mart. et Zucc.	27	31	1.49	1.94	0.68	0.69	1.46	1.55	60	55	3.01	2.98	1.98	2.10
Matayba elaeagnoides Radlk.	42	27	2.32	1.69	1.68	1.31	3.58	2.94	40	30	2.01	1.63	2.63	2.04
Myrceugenia sp.	16	13	0.88	0.82	0.31	0.27	0.66	0.60	25	25	1.25	1.36	0.93	0.90
Myrsine umbellata Mart.	61	45	3.37	2.82	1.36	1.11	2.89	2.49	80	80	4.01	4.34	3.42	3.13
Nectandra megapotamica (Spreng) Mez	19	14	1.05	0.88	0.79	0.50	1.68	1.13	25	15	1.25	0.81	1.33	0.95
Ocotea pulchella (Nees) Mez	65	50	3.59	3.13	3.23	3.30	6.87	7.42	80	75	4.01	4.07	4.82	4.88

Table 1. Continued...

Species	AD (n ha^{-1})		RD (%)		ADo (n ha^{-1})		RDo (%)		AF (%)		RF (%)		IV (%)	
	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016	2012	2016
Pera glabrata (Schott) Poepp. ex Baill.	22	12	1.21	0.75	0.56	0.41	1.18	0.91	60	35	3.01	1.90	1.80	1.06
Podocarpus lambertii Klotzsch ex Endl.	21	11	1.16	0.69	0.85	0.87	1.81	1.95	45	35	2.26	1.90	1.74	1.38
Prunus myrtifolia (L.) Urb.	13	11	0.72	0.69	1.09	0.95	2.32	2.13	45	30	2.26	1.63	1.77	1.37
Roupala montana Aubl.	21	19	1.16	1.19	0.92	0.99	1.95	2.21	30	30	1.50	1.63	1.54	1.64
Sebastiania brasiliensis Spreng.	94	95	5.19	5.96	0.50	0.51	1.07	1.14	50	40	2.51	2.17	2.92	3.22
Sebastiania commersoniana (Baill.) L.B. Sm. et Downs	40	47	2.21	2.95	0.80	0.96	1.71	2.17	55	60	2.76	3.25	2.22	2.78
Styrax leprosus Hook. & Arn.	85	53	4.69	3.32	3.21	2.38	6.82	5.33	70	45	3.51	2.44	5.01	3.60
Vernonanthura discolor (Spreng.) H.Rob.	21	17	1.16	1.07	2.12	1.94	4.50	4.35	45	35	2.26	1.90	2.64	2.31
Xylosma ciliatifolia (Clos) Eichler	11	7	0.61	0.44	0.24	0.21	0.52	0.48	25	15	1.25	0.81	0.79	0.52
Zanthoxylum kleinii (R.S.Cowan) P.G.Waterman	39	36	2.15	2.26	2.28	1.73	4.84	3.88	70	60	3.51	3.25	3.50	3.05
Zanthoxylum rhoifolium Lam.	26	11	1.43	0.69	0.20	0.14	0.44	0.32	35	30	1.75	1.63	1.21	0.84

AD: absolute density; RD: relative density; ADo: absolute dominance; RDo: relative dominance; AF: absolute frequency; RF: relative frequency; IV: importance value.

The basal area was 46.99 m² ha^{-1} in 2012 and 44.58 m² ha^{-1} in 2016, with significant changes in the period between measurements (alpha was set at = 0.05). The decrease in the basal area between the years of study was 2.41%, which indicates higher mortality in relation to the hospitalization rate. According to Chazdon et al. (2007), the basal area of secondary forests is more affected by the diameter of the trees and growth rates in height than by net changes in density due to the recruitment and mortality of the trees.

Regarding the dominant species, *Araucaria augustifolia*, *Lithraea brasiliensis*, *Ocotea pulchella*, *Styrax leprosus,* and *Ilex theezans*, represented 44.33% and 43.69% of all tree species in 2012 and 2016, respectively. Of the species mentioned, only *A. angustifolia* and *O. pulchella* showed increases in basal area from 2012 to 2016, while the others showed decreases. *Araucaria augustifolia* was the most dominant species in the stratum, in addition to being the only species that represented more than 15% of the basal area in both surveys. Individuals of *A. angustifolia* were not present in greater numbers than other species; however, they constituted the largest diameters. *Araucaria angustifolia* was also shown to be dominant in Mixed Ombrophilous Forests in studies by Figueiredo-Filho et al. (2010), Higuchi et al. (2013), Sawczuk et al. (2014), Cubas et al. (2016), and Salami et al. (2017).

The species that increased their dominance the most between study years were: *Araucaria angustifolia* (1.42%), *Ocotea pulchella* (0.55%), *Sebastiania commersoniana* (0.46%), *Dicksonia sellowiana* (0.30%), and *Eugenia uniflora* (0,27%) (Table 2). In contrast, the species whose dominance decreased the most between years were: *Styrax leprosus* (-1.49%), *Lithraea brasiliensis* (-0.97%), *Zanthoxylum kleinii* (-0.96%), *Matayba elaeagnoides* (-0.64%), and *Nectandra megapotamica* (-0.55%). Considering that the main causes of these alterations are related to the natural event that occurred in the area, it is not possible to define with the available data, if there are species that are more affected or benefited in relation to dominance, resulting from the same event.

In 2012 and 2016, 27% and 21% of the species presented frequency of occurrence values equal to or greater than 50%, meaning that these species were present in ≥ 50% of plots, indicating that few of them, in isolation, determine significantly, in terms of density, the physiognomy of 2012 and 2016 of the forest.

Among the most frequently-occurring species in 2012, the following stand out: *Casearia decandra*, *Lithraea brasiliensis*, *Araucaria angustifolia*, *Cinnamodendron dinisii* and *Eugenia* sp., which were present in 100%, 90%, 85%, 85%, and 80% of the sample units, respectively. The same species were more frequent in 2016, with frequency values between 95% and 80% and few changes in the period.

A total of 50% of species in 2012 and 57% in 2016 presented frequency of occurrences between 5% and 20%. However, it was observed that they were mainly species whose individuals were in the initial stages of establishment and had smaller diameters. According Vibrans et al. (2011), *Araucaria angustifolia* can be considered generalist, with a wide range of environmental conditions. In a study by Formento et al. (2004), in a remnant of Mixed Ombrophilous Forest in Campo Belo do Sul, Brazil, the authors also observed that *Lithraea brasiliensis* was present in 69 and 94% of the plots in 1992 and 2003, respectively, while *A. angustifolia* occurred in 63% of the plots in 2003. The values found for frequency, in this study and in others, show that species with high values for this variable, in general, also present high density. Another important finding of this study is that the changes observed in the frequency of species between 2012 and 2016, in general, were numerically small, while for the forest average there were changes considered significant in this period (alpha was set at = 0.05) (Table 1).

The species with the greatest importance values (IV) were, in descending order, *Araucaria augustifolia*, *Lithraea brasiliensis*, *Casearia decandra*, *Eugenia* sp., and *Cinnamodendron dinisii* in 2012, which together represented 32.55% of the total importance value. In 2016, these same species also represented the highest IV, representing 32.25% of the total and the order of their importance values underwent little change. The high dominance of *A. angustifolia* was responsible for the high relative importance in the rest of the study. *Araucaria angustifolia* and *L. brasiliensis* are frequently observed as common species in fragments of Mixed Rainforest (Ferreira et al. 2016). *Araucaria angustifolia* was also recorded as having the highest VI in the studies by Schaaf et al. (2005), Sawczuk et al. (2014), Higuchi et al. (2016) and Cubas et al. (2016). However, Formento et al. (2004) found that *L. brasiliensis* was the most important species in an area of Mixed Ombrophilous Forest with 20 years in regeneration after the interruption of selective logging of *A. angustifolia*.

Approximately 58.8% of the species showed a decrease in IV between study years, while in 36.8% experienced increased importance and 4.4% remained stable. The species that showed the highest increases in IV were *Araucaria angustifolia* (0.73%), *Sebastiania commersoniana* (0.56%), *Myrcine* sp. (0.45%), *Eugenia uniflora* (0.35%), and *Cariniana estrellensis* (0.30%). Formento et al. (2004), evaluating the dynamics of a remnant of Mixed Ombrophilous Forest in 1992 and 2003, also observed that *Ocotea pulchella*, *S. commersoniana* and *A. angustifolia* increased their participation in the composition and structure of the forest.

In contrast, the species that showed the greatest decreases in IV were *Styrax leprosus* (-1.41%), *Lithraea brasiliensis* (-0.89%), *Pera glabrata* (-0.74%), *Matayba elaeagnoides* (-0.59%), and *Zanthoxylum kleinii* (-0.45%). Considering the average values of IV of the forest, the changes observed between 2012 and 2016 were significant (alpha was set at = 0.05) (Table 1). Sawczuk et. al. (2014), which studied changes in the horizontal structure of a Mixed Ombrophilous Forest in the Center South of Paraná, Brazil from 2002 to 2008, also observed that the species with the greatest increase in IV was *Araucaria angustifolia* (1.50%). The same study found that *S. leprosus* (-1.00%) was the species with the second largest IV loss and that *Ilex paraguariensis* experienced the greatest IV loss. This and other studies reaffirm the outstanding dynamics of *A. angustifolia* in regeneration remnants of the Mixed Ombrophilous Forest, where it tends to increase its importance in the forest structure.

Analyzing the ecological group dynamics revealed that secondary species experienced an IV decrease of 6.4% and pioneer species suffered a 0.2% loss in IV (Figure 3). Climax and unidentified species showed an IV increases of 0.3% and 0.4%, respectively. Finally, dead individuals underwent an IV increase of 6.0%, which can be attributed to the fall of large trees on the site, thus demonstrating the effects of natural disturbance that occurred in the area to the point of increasing mortality. According to Chazdon et al. (2007, 2016), the changes generated by a disturbance interfere with the forest microclimates, which favors the initiation of successional processes. Some factors, such as previous land use, the degree of proximity to primary forests, and the abundance of fauna, can contribute to variations in successional trajectory.

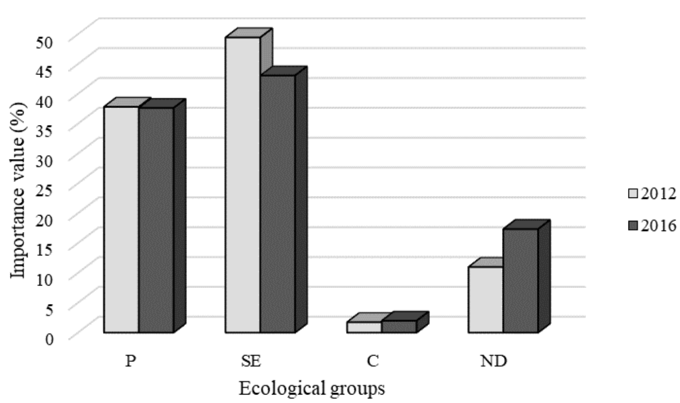


Figure 3. Value of importance by ecological group evaluated for the tree component in 2012 and 2016 of a Araucaria Forest remnants.
P - pioneers; SE - secondary; C - climax; ND - species with undefined ecological groups.

Therefore, these results indicate that the forest remnant studied is still in the process of succession, since pioneer and secondary species presented the greatest decreases in relation to their importance values in the assessed plots. Such observations reveal the need for more detailed and long-term dynamic studies.

3.3. Tree layer dynamics

In the period from 2012 to 2016, the entry and mortality rates were 2.2% year^{-1} and 6.9% year^{-1}, respectively, which represents a negative net change of 4.7%. Therefore, the results of the present study indicate that mortality was above normal and income was, on average, as expected for this forest typology.

A study by Figueiredo-Filho et al. (2010), which evaluated the dynamics of a Mixed Ombrophilous Forest, found that there was an increase in the basal area when average entry rate was close to 3% year^{-1} and mortality rate was between 1 and 2% year^{-1}. According to Salami et al. (2017), variations in dynamics rates among different areas on a regional scale reflect differences in successional stages, environmental variables, and disturbance history.

During the study period, approximately 159 incoming individuals were registered per hectare, or 39.75 ind year^{-1} (Table 2). Among the most representative species, those with the greatest increase in the number of incoming individuals were *Sebastiania brasiliensis* (18%), *Eugenia uniflora* (15%), and *Allophylus* sp. (11%).

The average mortality found across all plots was 498 ind ha^{-1} (124.5 ind year^{-1}), with *Casearia decandra*, *Eugenia* sp., *Cinnamodendron dinisii,* and *Lithraea brasiliensis* presenting particularly high mortality values representing 32.3%, 27.2%, 24.5%, and 25.2% of the total mortality, respectively. According to Luo & Chen (2011), tree mortality increases due to aging and reactions to small disturbances. The same authors mention that asymmetric competition is a dominant cause of tree mortality in forests.

In a study by Mognon et al. (2012), which evaluated a remnant of Mixed Ombrophilous Forest in southern Paraná, Brazil, found similar a value for income (1.97% year^{-1}) and a lower mortality measure (1.80% year^{-1}). In a study by Figueiredo-Filho et al. 2010, which evaluated the dynamics in a Mixed Ombrophilous Forest in the Irati National Forest, Paraná, Brazil, it was observed that tree mortality was slightly higher than inflow, although this did not affect the net growth of the average basal area per hectare. Therefore, Mixed Ombrophilous Forests vary greatly in income, growth, and mortality (Cubas et al. 2016).

The average ratio between income and mortality was 0.32, meaning that mortality was greater than income in the analyzed period. This result demonstrates that, although there is an imbalance between the two parameters, there is a tendency for this relationship to approach 1.0 as the forest develops to more advanced successional stages.

In the present study, 35.3% of species experienced both income and mortality from 2012 to 2016, and ratios ranging from 0.07 to 3.33 were observed. Among the other species, 17.65% (12 species) showed only income, and 35.3% (24 species) suffered only mortality. The species that showed the highest dynamism (those providing the highest income: mortality ratios) were *Sebastiania brasiliensis* and *Luehea divaricata*. According to Chazdon et al. (2007, 2016), dynamics studies provide information on the real rates of change in vegetation and the factors that influence this at local, landscape, and regional scales.

In terms of ecological groups, pioneer species comprised 8.33% of all income and 29.17% of total mortality. Secondary species represented 33.33% and 62.50% of total income and mortality, respectively. Meanwhile, climax species constituted 8.33% of income and did not experience mortality. Therefore, the rates of change in tree communities after major disturbances are determined by a complex set of interactions between local factors, landscape structure, regional species groups, and species life histories (Chazdon et al. 2007, 2016). And despite disturbances do not result in structural deterioration, they have the potential to slow the succession process in the area under study (Dallabrida et al. 2017).

Given the above, any comparison between remnants requires more information about past human interventions in each studied remnant, and many other factors that may influence the differences detected such as succession stage, area sampled, site, limit of inclusion, among others (Figueiredo-Filho et al. 2010). However, the succession of tropical forests is driven by many factors; the more we understand how they operate in these locations, the more accurately we can predict how this process operates on large scales (Chazdon et al. 2007, 2016).

Table 2. Density, income, mortality and changes in the period between 2012 and 2016 of a Araucaria Forest remnants.

Species	Density		Ingress (I)		Mortality (M)		Change	I/M	EG
	2012	2016	n° ha^{-1}	%	n° ha^{-1}	%	%		
Aleurites moluccana (L.) Willd.	4	4							ND
Allophylus sp.	54	43	11	20	22	41	-20	0.50	ND
Annona emarginata (Schltdl.) H.Rainer	8	5			3	38	-38		P
Araucaria angustifolia (Bertol.) Kuntze	101	87	4	4	18	18	-14	0.22	P
Banara tomentosa Clos	1	3	2	200			200		SE
Bernardia pulchella (Baill.) Müll. Arg.	5	2			3	60	-60		SE
Calyptranthes concinna DC.	83	68	5	6	20	24	-18	0.25	SE
Campomanesia guaviroba (DC.) Kiaersk.	9	9	1	11	1	11		1.00	SE
Cariniana estrellensis (Raddi) Kuntze	6	14	8	133			133		SE
Casearia decandra Jacq.	189	132	4	2	61	32	-30	0.07	SE
Casearia obliqua Spreng.	31	23			8	26	-26		SE
Cinnamodendron dinisii Schwacke	147	119	8	5	36	25	-19	0.22	P
Citronella gongonha (Mart.) R.A.Howard	1	0			1	100	-100		SE
Cordia americana (L.) Gottshling & J.E.Mill.	0	2	2						C
Cupania vernalis Cambess.	7	4			3	43	-43		P
Dalbergia frutescens (Vell.) Britton	4	4							SE
Dicksonia sellowiana Hook.	30	25	4	13	9	30	-17	0.44	C
Drimys brasiliensis Miers	12	11			1	8	-8		SE
Eugenia pyriformis Cambess.	4	2			2	50	-50		SE
Eugenia rostrifolia D.Legrand	4	0			4	100	-100		SE
Eugenia uniflora L.	64	65	15	23	14	22	2	1.07	P
Eugenia sp.	172	129	4	2	47	27	-25	0.09	ND
Helietta apiculata Benth.	3	0			3	100	-100		SE
Ilex theezans Mart. ex Reissek	66	59	2	3	9	14	-11	0.22	SE
Jacaranda micranta Cham.	9	8			1	11	-11		SE
Lamanonia ternata Vell.	4	3			1	25	-25		SE
Lithraea brasiliensis Marchand	107	84	4	4	27	25	-22	0.15	P
Lonchocarpus campestris Mart. ex Benth.	1	1							SE
Luehea divaricata Mart. et Zucc	27	31	6	22	2	7	15	3.00	SE
Matayba elaeagnoides Radlk.	42	27			15	36	-36		SE
Maytenus ilicifolia Mart. ex Reissek	0	2	2						SE
Moquiniastrum polymorphum (Less.) G. Sancho	3	2			1	33	-33		P
Myrceugenia sp.	16	13	2	13	5	31	-19	0.44	ND
Myrcia guianensis (Aubl.) DC.	1	1							C
Myrcia laruotteana Cambess.	4	9	5	125			125		SE
Myrcianthes pungens (O.Berg) D. Legrand	3	3							SE
Myrciaria sp.	14	6			8	57	-57		ND
Myrcine sp.	0	5	5						ND
Myrocarpus frondosus Allemão	1	1							SE
Myrsine umbellata Mart.	61	45	4	7	20	33	-26	0.20	SE
Nectandra megapotamica (Spreng) Mez	19	14			5	26	-26		P
US -1	1	3	2	200			200		ND
US - 2	1	5	4	400			400		ND

Table 2. Continued...

Species	Density		Ingress (I)		Mortality (M)		Change	I/M	EG
	2012	2016	n° ha^{-1}	%	n° ha^{-1}	%	%		
US - 3	1	2	1	100			100		ND
US - 4	2	2	2	100	2	100		1.00	ND
US - 5	0	2	2						ND
US - 6	0	2	2						ND
Ocotea pulchella (Nees) Mez	65	50	2	3	17	26	-23	0.12	P
Ocotea sp.	3	2			1	33	-33		ND
Parapiptadenia rigida (Benth.) Brenan	4	4							SE
Pera glabrata (Schott) Poepp. ex Baill	22	12	1	5	11	50	-46	0.09	SE
Piptocarpha angustifolia Dusén ex Malme	1	0			1	100	-100		P
Podocarpus lambertii Klotzsch ex Endl.	21	11			10	48	-48		SE
Prunus myrtifolia (L.) Urb.	13	11	1	8	3	23	-15	0.33	SE
Quillaja brasiliensis (A.St.-Hil. & Tul.) Mart.	1	0			1	100	-100		P
Roupala montana Aubl.	21	19	1	5	3	14	-10	0.33	SE
Sapium glandulosum (L.) Morong	6	3			3	50	-50		P
Sebastiania brasiliensis Spreng.	94	95	18	19	17	18	1	1.06	P
Sebastiania commersoniana (Baill.) L.B. Sm. et Downs	40	47	10	25	3	8	18	3.33	P
Seguieria aculeata Jacq.	6	4			2	33	-33		SE
Solanum paniculatum L.	0	2	2						P
Solanum sanctaecatharinae Dunal	1	1							P
Strychnos brasiliensis (Spreng.) Mart.	8	5			3	38	-38		SE
Styrax leprosus Hook. & Arn.	85	53			32	38	-38		SE
Vernonanthura discolor (Spreng.) H.Rob.	21	17	1	5	5	24	-19	0.20	SE
Xylosma ciliatifolia (Clos) Eichler	11	7			4	36	-36		SE
Zanthoxylum kleinii (R.S.Cowan) P.G.Waterman	39	36	10	26	13	33	-8	0.77	SE
Zanthoxylum rhoifolium Lam.	26	11	2	8	17	65	-58	0.12	SE
TOTAL	1,810	1,471	159		498			0.32	

I/M: relationship between income and mortality; EG: ecological group. US: species of unidentified; P: pioneers; SE: secondary; C: climax; ND: species with undefined ecological groups.

4. CONCLUSIONS

The density and basal area of the forest decreased during the study period due to the influence of the higher mortality rate in relation to the entry rate, which was caused, among others factors, by strong gales that occurred in the study area.

The most important species in the forest structure did not show significant changes in structural values between the two occasions of the study.

Araucaria augustifolia was the most dominant and 'important' species across the studied period, which suggests that the species plays a role in the resilience of the forest after selective exploitation in past decades.

Secondary species showed the greatest changes in the study period, characterized by mortality and inflows.

The tree mortality rate observed in the present study was above the standards normally found, a fact that can be attributed to competition, the biological cycle of the species and the effects of natural disturbance that occurred in the period.

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CORRESPONDENCE TO

Kristiana Fiorentin dos Santos

Rua São Paulo, 3250, 89012-900, Blumenau, SC, Brasil

E-mail: kristianafiorentin@gmail.com

AUTHORS' CONTRIBUTIONS

Alyne Regina Ruggiero: data curation-equal, formal analysis-equal, investigation-equal, software-equal, validation-equal, visualization-equal, writing – original draft-equal.

Lauri Amândio Schorn: conceptualization-equal, data curation-equal, formal analysis-equal, funding acquisition-equal, investigation-equal, methodology-equal, project administration-equal, resources-equal, software-equal, supervision-equal, validation-equal, visualization-equal, writing – review & editing-equal.

Kristiana Fiorentin dos Santos: data curation-equal, formal analysis-equal, validation-equal, visualization-equal, writing – review & editing-equal.

Tatiele Anete Bergamo Fenilli: funding acquisition-equal, methodology-equal, project administration-equal, resources-equal, supervision-equal, validation-equal, visualization-equal.

REFERENCES

Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 2013; 22(6):711-728.

Ansolin RD, Silva AC, Higuchi P, Küster LC, Ferreira TS, Buzzi Júnior F et al. Heterogeneidade ambiental e variação florístico-estrutural em um fragmento de floresta com araucária na Coxilha Rica – SC. Ciência Florestal 2016; 6(4):1201-1210.

APG IV - An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants. Botanical Journal of the Linnean Society 2016; 181:1-20.

Brower JE, Zar JH. Field and laboratory methods for general ecology. Dubuque: W. M. C. Brow; 1984.

Chazdon RL, Letcher SG, Breugel M van, Martínez-Ramos M, Bongers F, Finegan B. Rates of change in tree communities of secondary Neotropical forests following major disturbances. Philosophical Transactions of the Royal Society B: Biological Sciences 2007; 362:273-289.

Chazdon RL. Renascimento de florestas: regeneração na era do desmatamento. São Paulo: Oficina de Textos; 2016.

Cubas R, Watzlawick LF, Figueiredo-Filho A. Incremento, ingresso, mortalidade em um remanescente de floresta ombrófila mista em Três Barras – SC. Ciência Florestal 2016; 26(3):889-900.

Dallabrida JP, Cruz AP, Souza CC, Silva MAF, Soboleski VF, Loebens R, Buzzi Junior F, Silva AC, Higuchi, P. Tree component demography in an upper montane Mixed Ombrophilous Forest under chronic anthropogenic disturbances. Revista Árvore 2017; 41(3):e410312.

Daubenmire R. Plant communities: A textbook of plant synecology. New York: Harper & Row; 1968.

Empresa Brasileira de Pesquisa Agropecuária. Sistema brasileiro de classificação de solos. Rio de Janeiro: EMBRAPA-SP; 2006.

Felfili JM, Rezende RP. Conceitos e métodos em fitossociologia. Brasília: Departamento de Engenharia Florestal, Universidade de Brasília; 2003.

Ferreira TS, Marcon AK, Salami B, Rech CCC, Mendes AR, Carvalho AF et al. Composição florístico-estrutural ao longo de um gradiente de borda em fragmento de floresta ombrófila mista alto-montana em Santa Catarina. Ciência Florestal 2016; 26(1):123-134.

Figueiredo-Filho A, Dias NA, Stepka TF, Sawczuk AR. Crescimento, mortalidade, ingresso e distribuição diamétrica em floresta ombrófila mista. Floresta 2010; 40(4):763-776.

Formento S, Schorn LA, Ramos RAB. Dinâmica estrutural arbórea de uma Floresta Ombrófila Mista em Campo Belo do Sul, SC. Revista Cerne 2004; 10(2):196-212.

Gonçalves DA, Silva AC, Higuchi P, Gross A, Rodrigues Junior LC, Walter FF et al. Heterogeneity of a tree species community in an alluvial area of Santa Catarina, Brazil. Floresta e Ambiente 2018; 25(2):00096514.

Gross A, Silva AC, Cruz AP, Kilka RV, Nunes AS, Duarte E et al. Fragmentation as a key driver of tree community dynamics in mixed subtropical evergreen forests in Southern Brazil. Forest Ecology and Management 2018; 411:20-26.

Higuchi P, Silva AC, Ferreira TS, Souza ST, Gomes JP, Silva KM et al. Influência de variáveis ambientais sobre o padrão estrutural e florístico do componente arbóreo, em um fragmento de Floresta Ombrófila Mista Montana em Lages, SC. Ciência Florestal 2012; 22(1):79-90.

Higuchi P, Silva AC, Almeida JA, Bortoluzzi RLC, Mantovani A, Ferreira TS et al. Florística e estrutura do componente arbóreo e análise ambiental de um fragmento de Floresta Ombrófila Mista Alto-Montana no município de Painel, SC. Ciência Florestal 2013; 23(1):153-164.

Higuchi P, Silva AC, Ferreira TS, Souza ST, Gomes JP, Silva KM et al. Florística e estrutura do componente arbóreo e relação com variáveis ambientais em um remanescente florestal em Campos Novos – SC. Ciência Florestal 2016; 26(1):35-46.

Higuchi P, Silva AC, Ferreira TS, Souza ST, Gomes JP, Silva KM et al. Influência de variáveis ambientais sobre o padrão estrutural e florístico do componente arbóreo, em um fragmento de Floresta Ombrófila Mista Montana em Lages, SC. Ciência Florestal 2018; 22(1):79-90.

Instituto Brasileiro de Geografia e Estatística. Manual técnico da vegetação brasileira. Rio de Janeiro: Fundação Instituto Brasileiro de Geografia e Estatística; 2012p.

Instituto Chico Mendes de Conservação da Biodiversidade. Plano de Manejo Estação Ecológica Raso da Catarina. Brasília: Ministério do Meio Ambiente; 2008.

Kersten RA, Galvão F. Suficiência amostral em inventários florísticos e fitossociológicos. In: Felfili JM, Eisenloh PV, Melo MMRF. Fitossociologia no Brasil: métodos e estudos de casos. Viçosa: Editora UFV; 2011.

Luo Y, Chen Y. Competition, species interaction and ageing control tree mortality in boreal forests. Journal of Ecology 2011; 99:1470-1480.

Magurran AE. Measuring biological diversity. Blackwell. Oxford: Science; 2004.

Marcon AK, Silva AC, Higuchi P, Ferreira TS, Missio FF, Salami B et al. Variação florístico-estrutural em resposta à heterogeneidade ambiental em uma floresta nebular em Urubici, Planalto Catarinense. Scientia Forestalis 2014; 42(103):439-450.

Mognon F, Dallagnol F, Sanquetta C, Corte AP, Maas G. Uma década de dinâmica florística e fitossociológica em floresta ombrófila mista montana no Sul do Paraná. Revista de Estudos Ambientais 2012; 14(1):43-59.

Mueller-Dombois D, Ellenberg D. Aims and methods of vegetation ecology. New York: Wiley; 1974.

Negrini M, Higuchi P, Silva AC, Spiazzi FR, Buzzi Junior F, Vefago MB. Heterogeneidade florístico-estrutural do componente arbóreo em um sistema de fragmentos florestais no Planalto Sul Catarinense. Revista Árvore 2014; 38(5):779-786.

Nunes MH, Higuchi P, Silva AC, Van Den Berg E, Santos MCN. Dinâmica de populações de espécies arbóreas em fragmentos de floresta aluvial no sul de Minas Gerais, Brasil. Floresta 2016; 46(1):57-66.

Oliveira-Filho AT, Carvalho WAC, Machado ELM, Higuchi P, Appolinário V, Castro GC et al. Dinâmica da comunidade e populações arbóreas da borda e interior de um remanescente florestal na Serra da Mantiqueira, Minas Gerais, em um intervalo de cinco anos (1999-2004). Revista Brasileira de Botânica 2007; 30(1):149-161.

Salami B, Higuchi P, Silva AC, Ferreira TS, Marcon AK, Buzzi Júnior F et al. Dinâmica de populações de espécies arbóreas em um fragmento de floresta ombrófila mista montana em Lages, Santa Catarina. Ciência Florestal 2017; 27(1):105-116.

Santos R, Elias GA, Sartor HB, Padilha PT, Souza JC, Citadini-Zanette V. O Furacão Catarina e a floresta ombrófila mista no Parque Nacional de Aparados da Serra, sul do Brasil. Geosul 2015; 30(60):109-124.

Sawczuk AR, Figueiredo-Filho A, Dias NA, Watzlawick LF, Stepka TF. Alterações na estrutura horizontal, no período de 2002-2008, em floresta ombrófila mista no centro-sul do Estado do Paraná. Ciência Florestal 2014; 24(1):149-160.

Schaaf LB, Figueiredo-Filho A, Sanquetta CR, Galvão F. Incremento diamétrico e em área basal no período de 1979-2000 de espécies arbóreas de uma Floresta Ombrófila Mista localizada no sul do Paraná. Revista Floresta 2005; 35:271-290.

Schorn LA, Ruggiero AR, Bartolomeu PE, Heidemann A. Relatório Fitossociológico da RPPN Emílio Einsfield Filho - Campo Belo do Sul (SC). Blumenau: FURB; 2012.

Sheil D, Jennings S, Savill P. Long-term permanent plot observations of vegetation dynamics in Bundongo, a Ugandan rain forest. Journal of Tropical Ecology 2000; 16(6):675-800.

Silva AC, Higuchi P, Berg E van den, Nunes MH, Santos MCN. Variação espaço-temporal da dinâmica da comunidade arbórea em fragmentos de floresta aluvial em Minas Gerais. Cerne 2011; 17(4):465-471.

Silva AC, Higuchi P, Aguiar MD, Negrini M, Fert Neto J, Hess AF. Relações florísticas e fitossociologia de uma Floresta Ombrófila Mista Montana secundária em Lages, Santa Catarina. Ciência Florestal 2012; 22(1):193-206.

Silva JO, Silva AC, Higuchi P, Mafra AL, Gonçalves DA, Buzzi Júnior F et al. Floristic composition and phytogeography contextualization of the natural regeneration of an alluvial forest located in the "Planalto Sul Catarinense" Region, SC, Brazil. Revista Árvore 2017; 41(2):e410203.

Souza K, Faxina TC, Silva JO, Dias RAR, Silva AC, Higuchi P. Análise fitossociológica de trilha ecológica em Floresta Ombrófila Mista. Revista de Ciências Agroveterinárias 2014; 13(3):266-274.

Stedille LIB, Gomes JP, Costa NCF, Ferreira PI, Higuchi P, Mantovani A. Vegetative and environmental components in a secondary riparian forest in the Southern Plateau of Santa Catarina, Brazil. Floresta e Ambiente 2018; 25(4):e20160473.

Vibrans AC, Sevegnani L, Uhlmann A, Schorn LA, Sobral MG, Gasper AL et al. Structure of mixed ombrophyllous forests with Araucaria angustifolia (Araucariaceae) under external stress in Southern Brazil. Revista de Biologia Tropical 2011; 59(3):1371-1387.

Vibrans AC, Mcroberts R, Lingner DV, Nicoletti AL, Moser P. 2013. Extensão original e remanescentes da Floresta Ombrófila Mista em Santa Catatina. In: Vibrans AC, Sevegnani L, Gasper AL, Lingner DV. Inventário Florístico Florestal de Santa Catarina: Floresta Ombrófila Mista. Blumenau: Edifurb; 2013.

Weather Park. Histórico de condições meteorológicas no outono de 2015 em Santa Catarina. [cited 2022 abr. 19]. Available from: pt.weatherspark.com/h/s/5147/2015/2/Histórico-das-condições-meteorológicas-no-outono-de-2015-em-Santa-Catarina-México#Figures-WindSpeed.

Zeller RH. Plano de Manejo: Reserva Particular do Patrimônio Natural Emílio Einsfeld Filho, Santa Catarina. Campo Belo do Sul: Florestal Gateados; 2010.