Key factors affecting succession in upper montane forest areas of "Planalto Sul Catarinense" Region, Brazil

Factores determinantes de la sucesión de la vegetación en las zonas de alta montaña de la región "Planalto Sul Catarinense", Brasil

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SUMMARY

The understanding of the succession process is a fundamental condition in defining strategies for the conservation and sustainable use of forest ecosystems. Therefore, we aimed at testing which ecological factors affect short-term successional changes in the upper-montane forests of the "Planalto Sul Catarinense" Region, Brazil. We evaluated the influence of propagules source, soil seed bank, edaphic and topographic variables, nucleating elements and natural regeneration floristic-structural composition on demographic rates of tree-shrub regenerating component in three disturbed open vegetation areas at São Joaquim National Park. We inventoried the regenerative component in 2014, 2015 and 2016, within one 20x100 m transect in each area. Afterwards, demographic rates were determined for each period. The influence of explicative variables on demographic rates of the regenerating component was tested through the Generalized Least Square (GLS) model. We found an increment in both individuals and richness over time. When analyzing the influence of the explanatory variables on the speed of the successional process, we observed that only the floristic-structural composition of the natural regeneration was determinant. We conclude that the speed of the represented succession is, to a large extent, a feature related to the phase of the successional trajectory in which the vegetation is found.

Key words: vegetation dynamics, natural regeneration, resilience.

RESUMEN

Se busca evaluar los factores ecológicos que afectan los cambios sucesionales en los bosques de la alta montaña de la región "Planalto Sul Catarinense", Brasil. Se analizó la influencia de la fuente de propágulos, banco de semillas del suelo, variables edáficas y topográficas, elementos nucleadores y composición florístico-estructural de la regeneración natural en las tasas demográficas del componente de regeneración de árboles y arbustos en tres áreas de vegetación abierta perturbada en el Parque Nacional Nacional de São Joaquim. Se inventarió el componente regenerativo en 2014, 2015 y 2016, dentro de un transecto de 20x100 m en cada área. Entonces, se determinó las tasas demográficas para cada período. La influencia de las variables explicativas en las tasas demográficas del componente de regeneración se evaluó mediante el modelo de mínimos cuadrados generalizados (GLS). Se encontró un incremento tanto en los individuos como en la riqueza a lo largo del tiempo. Al analizar la influencia de las variables explicativas sobre la velocidad del proceso sucesorio, se observó que solo la composición florístico-estructural de la regeneración natural fue determinante. Por lo tanto, se puede inferir que la velocidad de sucesión representa una característica inherente a la fase sucesional de la vegetación. Se concluye que el proceso de sucesión se desarrolló de forma diferente entre áreas, con el pastizal presentando un proceso de invasión leñosa.

Palabras clave: dinámica de la vegetación, regeneración natural, resiliencia.

INTRODUCTION

Natural vegetation development – *i.e.*, the arrival of new species and changes in the composition, structure and size of populations – is affected by disturbances of variable intensity, frequency and duration (Chazdon 2003, Chazdon 2012, Meiners *et al.* 2015). Thus, studies on the process of vegetation dynamics after disturbances are necessary, since they are essential for understanding the regeneration potential of plant communities (Chazdon *et al.* 2007) and for determining the influence of anthropic disturbances on ecosystems (Meiners *et al.* 2015).

The process of vegetation succession, expressed by the floristic and structural changes over time, was one of the major themes of ecological debates in the last century, beginning with the pioneering works of Clements (1916) and Gleason (1926). While Clements understood the vegetation as a single organism and the succession as a deterministic process towards a climax, fundamentally determined by the climate, Gleason saw the vegetation as an element formed from an independent set of species, whose changes along time occurred in a less deterministic way, being influenced by several factors, besides the climate. Some decades later, Connel and Slatyer (1977) suggested an alternative view over the succession mechanisms, showing the possibility of different models, namely facilitation, tolerance and inhibition. According to these authors, the facilitation model involves the colonization of pioneer species, which changes the environment, allowing the arrival of late species. In the tolerance model, the area is colonized at the same time by the initial and late species. In the inhibition model, colonizers prevent other species, thus hindering forest succession.

Today, the consensus is that forest succession is a highly complex process, related to the natural regeneration capacity of the tree component and the disturbance regime (Chazdon *et al.* 2007), affected by a series of stochastic and deterministic environmental factors (Meiners *et al.* 2015). Several studies have shown (*e.g.* Martins *et al.* 2015) that succession is highly heterogeneous in space, varying according to the disturbance history (regime and recovery time) and environmental factors (*e.g.* soil, nucleating elements – safe sites for plants – competition, rain, seed bank and sprouting). Similarly, the speed of succession, which is related to the resilience of vegetation, may be variable, occurring slowly in degraded sites (Chazdon 2012). In extreme situations, specific groups of plants or taxons can inhibit this process, as shown by the inhibition model of Connel and Slatyer (1977). In the subtropical part of the Brazilian Atlantic Forest, many studies have been conducted in forests ranging from late-successional areas (*e.g.* Schorn and Galvão 2009) to early-successional ones (Marcílio-Silva *et al.* 2016). In the higher parts of the Brazilian southern plateau, where a mosaic of grasslands and forests forms the natural vegetation, studies have shown that nucleating elements (Carlucci *et al.* 2011a, Dallabrida *et al.* 2017) and the proximity of the propagules source (Carlucci *et al.* 2011b) play important roles as succession catalyzers. Besides, it is noteworthy that in this region, there is a process of replacement of the grassland areas by shrub-like vegetation, linked to changes in both the disturbance regime and climate (Müller *et al.* 2012, Sühs *et al.* 2020).

Considering that understanding forest succession is critical to assess the human impacts on natural environments, we aimed at testing which factors influence short-term successional changes in high montane areas in the Southern Plateau of Santa Catarina, Brazil. To this end, we tested the influence of biotic and abiotic variables in three areas that have undergone past anthropogenic impacts relative to i) the propagules source, ii) the soil seed bank, iii) the floristic-structural composition of the regenerating component of the area, iv) environmental variables and v) nucleating elements, on the rates of dynamics of arbustive-arboreal regeneration. The selected areas have been protected for approximately ten years and are currently part of the São Joaquim National Park. Two areas were originated from past deforestations of the high montane forest, and one has been a grassland since remote times (see Belhling 2002), although it was impacted by cattle raising for decades. We aimed at answering if those biotic and abiotic variables mentioned above affect the speed of vegetative succession. Due to the long history of degradation in this region, we expect that the seed bank will be represented mostly by ruderal herbaceous species, such that the succession will be positively influenced by the proximity of the propagules sources, by better soils quality, by the presence of nucleating elements and by the characteristics of the regenerating vegetation.

METHODS

We inventoried three open vegetation areas (Area 1: 28°05'41.5"S, 49°30'14.71"W, altitude of 1,628 m; Area 2: 28°04'46.87"S, 49°30'51.29"W, altitude of 1,356 m; Area 3: 28°09'49.19"S, 49°36'47.56"W, altitude of 1,660 m), next to forest remnants, at the National Park of São Joaquim, in the municipality of Urubici, Santa Catarina, Brazil (figure 1). Areas 1 and 2, originally covered by forests, were deforested around the 60s (area 1) and 80s (area 2) and were kept as pastures until being protected (since 2007 for area 1 and since 2008 for area 2) (Dallabrida *et al.* 2017). According to the same authors, area 3 was a grassland used for cattle raising since the XIX century and protected since 2008. Therefore, these areas have a long disturbance history and currently are undergoing a post-disturbance recovery process. According to the Brazilian vegetation classification system (IBGE, 2012), the grassland site (Area 3) is classified as "estepes/campos de altitude", which is a relictual vegetation, existent throughout the quaternary, preceding the human presence in the region (Behling 2002).

The natural vegetation is formed by a mosaic of grasslands and upper-montane Araucaria forests. The climate in the region, according to Köppen's classification (Kottek *et al.* 2006), is Cfb, with annual average temperature of 12.7 °C and annual average rainfall of 1,753 mm (Dallabrida *et al.* 2017).

According to the Brazilian System of Soil Classification (Santos *et al.* 2013), the soils of the areas are "Neossolos Litólicos" (Leptsols), "Cambissolos Húmicos" (Cambisols), "Nitossolos Brunos Distroférricos" (Nitisols) and "Organossolos Fólicos Sápricos" (Histosols). Leptsols are found at the highest and most steeping parts; Cambisols are predominant in lower slopes. In area 2, deeper soils,
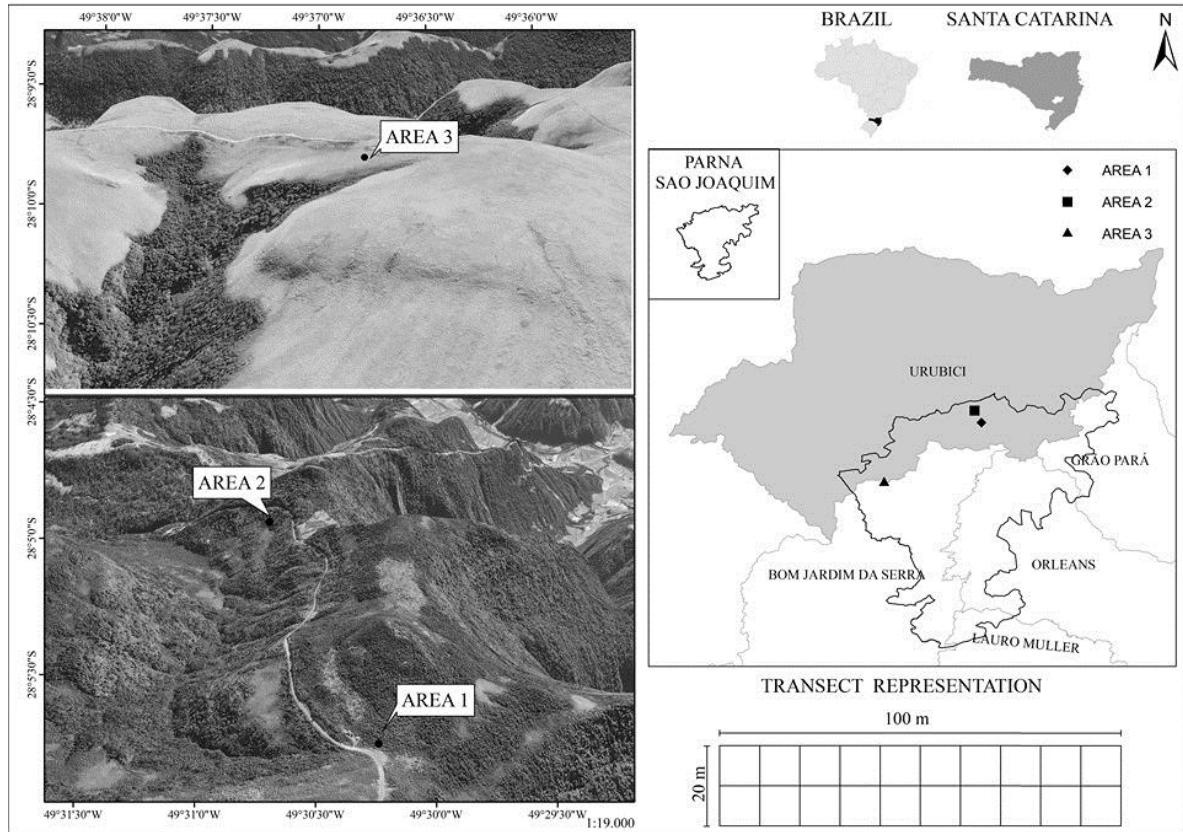
Figure 1. Location of study sites and sampling transect representation in Upper Montane Araucaria Forests, in the municipality of Urubici, Santa Catarina.

Localización de los sitios de estudio y representación de los transectos de muestreo en los Bosques de Araucarias de Alta Montaña, en el municipio de Urubici, Santa Catarina.

such as Nitisols, are frequent in the locations with better natural drainage, and Leptsols with a dark superficial horizon, at those parts close to a watercourse. In area 3, Histosols occur with a black H horizon. The soils of areas 1 and 2 are originated from basalt, and the ones of area 3 from rhyodacite, both from "Serra Geral" formation. Terrain varies from soft wavy to strongly wavy.

The tree-shrub species was surveyed by Dallabrida *et al.* (2017) in 2014 and, later, in 2015 (Dallabrida *et al.* 2019). Three 20 x 100 m transects subdivided in 10x10 m plots were used, totaling 2,000 m^2 in each area. These transects were perpendicularly allocated to the fragments edge, with their extension covering the open vegetation area. In 2016, we sampled and tagged all tree-shrub individuals over 1 m high and under 5 cm of diameter at breast height (dbh) to determine the demographic rates. The same inclusion level was standardized for all the other years (2014 and 2015) (Dallabrida *et al.* 2017, 2019). Subsequently, the surviving and dead individuals were counted, and those which reached 1 m high were recruited. The recruited individuals were identified by specialists and the species classified in families according to the system APG IV (2016).

The rates of recruitment, mortality and abundance net change for the 2014-2015 and 2015-2016 periods were determined and summarized by their average values considering the two periods. Recruitment and mortality rates were obtained by the algebraic models described by Sheil and May (1996): M = (1 - ((No - m)/ No)$^{1/t}$) × 100, R = (1 - (1 - r/Nt)$^{1/t}$) × 100. Where: M = annual mortality rate (% year^{-1}), R = annual recruitment rate (% year^{-1}), No = initial number of individuals, t= time interval between the inventories, Nt = final number of individuals after t, m = number of dead individuals, r = number of recruited individuals. The rates of abundance net change (Chn) were determined by the equation described by Korning and Balslev (1994): Chn = [(Nt/No)$^{1/t}$ -1] x100.

We also determined the rate of floristic-structural (community species composition and abundance) changes over time, according to Collins *et al.* (2000), though adapted to our data, with a smaller number of time intervals, thus with no testing of slopes significance. For each plot, we determined the slope coefficient of the straight line connecting two points, which represented the temporal floristic-structural similarity for 2014-2015 and 2014-2016. The positi-

ve values of the slope coefficient show a trend of increasing dissimilarities over time, negative values indicate a tendency of increasing similarities over time, and the slope coefficient equal to zero shows a no changing pattern.

Demographic and floristic-structural change rates were ordered by a Principal Component Analysis (PCA) to identify the main dynamics pattern synthesized by the PCA axis 1, which explained most of the total inertia. The PCA axis 1 significance was verified by the Scree Plot analysis.

To determine which ecological factors affect PCA axis 1, we considered the following variables: i) the propagules source, ii) the quality of the seed bank, iii) the floristic-structural composition of the regenerating component, iv) the soil variables and v) the presence of nucleating elements.

i) The quality of the propagules source was summarized by a synthetic variable related to the floristic-structural composition of the adjacent forest fragment and the distance from each plot to the fragment edge. The tree communities data (trees over 5 cm of diameter at breast height) obtained from Duarte *et al.* (2018) were ordered by a Principal Coordinates Analysis (PCoA). We assumed that the ordination of the community data from adjacent forest fragments would summarize the quality of vegetation as a potential propagules source. The quality of the propagule source was considered as the sum of the centroid value of each fragment and the distance of each plot of the regenerative component to the forest fragment edge.

ii) Based on Duarte *et al.* (non-published data), as the quality of the seed bank, we considered the floristic-structure composition (community species composition and abundance) of the emerging seedlings from the seed bank of each plot (Brown 1992). After a PCoA ordination, the scores of each plot along the PCoA axes 1 and 2 were used as explanatory variables for the dynamics patterns (Dynamics PCA axis 1). Still, to verify which seed bank species were related to axes 1 and 2 of PCoA, we applied a Multivariate Generalized Linear Model, according to Wang *et al.* (2012), with the negative binomial distribution.

iii) As the structural-floristic composition of the regenerating component, we used the data (community species composition and abundance) obtained by Dallabrida *et al.* (2017), which were subjected to the same analytical approach described in the previous item (ii);

iv) Soil (physico-chemical properties and compaction) and topographic (altitude, maximum elevation gap and average declivity) variables, obtained for the same plots by Dallabrida *et al.* (2017), were ordered by the Principal Components Analysis (PCA). The plots scores along PCA axes 1 and 2 were extracted to be used as explanatory variables for the dynamics pattern (Dynamics PCA axis 1);

v) Nucleating elements of each plot were considered as the sum of the counting of rocks, dead tree ferns, fallen trunks and adult tree individuals (dbh ≥ 5 cm) (Dallabrida *et al.* 2017).

We fitted a linear model by the Generalized Least Square (GLS) method to analyze the influence of the explanatory variables (i, ii, iii, iv, and v) on the dynamics pattern of the regenerative component (Dynamics PCA axis 1). The Dynamics PCA axis 1, which is the one that most explains the total inertia of demographic variables, can be considered as a synthetic variable that summarizes the main gradient of vegetative changes regarding the evaluated plots. This approach allowed to incorporate the heterogeneity of the evaluated variables, such as the spatial variations associated with different areas. Because of presenting a few individuals and empty plots, which would represent a bias in the analysis, area 3 was not included here. The residuals heterogeneity was incorporated into the model by an exponential function of the covariate variance. Significant explanatory variables were selected by the stepwise procedure based on the information criteria of Akaike (AIC) (Venables and Ripley 2002). The final model was validated through the residual analysis. All analyses were performed with R (R Core Team 2019), along with MASS (Venables and Ripley 2002), nlme (Pinheiro *et al.* 2016), vegan (Oksanen *et al.* 2016), mvabund (Wang *et al.* 2012) and codyn (Hallett *et al.*2020) packages. All data used in the analyses are available in Duarte *et al.* (2021).

RESULTS

Structural-floristic composition, dynamics and speed of the succession process. We sampled 761 individuals, distributed in 34 species, 23 genera and 16 families in 2014; 996 individuals, distributed in 35 species, 24 genera and 17 families in 2015; 1,160 individuals, distributed in 38 species, 25 genera and 18 families in 2016 (table 1). The richest families were Myrtaceae, followed by Asteraceae, Lauraceae and Solanaceae. The most expressive genera were *Myrceugenia*, *Baccharis* and *Solanum*. The most abundant species were *Baccharis uncinella* DC. in area 1, *Campovassouria cruciata* (Vell.) in area 2 and *Baccharis lymanii* G.M.Barroso ex G.Heiden in area 3.

In the Principal Components Analysis (PCA) of vegetation dynamics rates, axes 1 and 2 explained 89.45 % of the total inertia, and both were significant according to the Scree Plot analysis (figure 2A). The most correlated variables with axis 1 (figure 2B) – the most explanatory one (60.34 %) – were the recruitment (0.61), the net change in the number of individuals (0.54) and the structural-floristic change (0.54). While on the left are the most stable plots, predominantly in area 1, on the right side are the more dynamic plots, mostly in area 2. Thus, from left to right of axis 1, there is a gradient of succession speed.

Table 1. Sampled species in upper montane Araucaria Forest areas, in "Planalto Sul Catarinense" Region, Santa Catarina. N1 = number of individuals in 2014, N2 = number of individuals in 2015 and N3 = number of individuals in 2016. H = registration number at the Lages Herbarium, Santa Catarina State University (LUSC).

Especies muestreadas en áreas de Bosque de Araucarias de alta montaña, en la región "Planalto Sul Catarinense", Santa Catarina. N1 = número de individuos en 2014; N2 = número de individuos en 2015 y N3 = número de individuos en 2016. H = número de registro en el Herbario Lages, de la Universidad del Estado de Santa Catarina (LUSC).

Family/ Species	Area 1			Area 2			Area 3			H
	N1	N2	N3	N1	N2	N3	N1	N2	N3	
Anacardiaceae										
Schinus polygama (Cav.) Cabrera	2	2	2							8,763
Aquifoliaceae										
Ilex microdonta Reissek		1	2							8,764
Araucariaceae										
Araucaria angustifolia (Bertol.) Kuntze	2	2	2			1				8,765
Asteraceae										
Baccharis lymanii G.M.Barroso ex G.Heiden									48	-
Baccharis microdonta DC.	9	9	9	7	20	32				8,771
Baccharis uncinella DC.	138	154	165	149	161	165	2	2	5	8,768
Campovassouria bupleurifolia (DC.) R.M. King *et* H. Rob.	1	1	2							-
Campovassouria cruciata (Vell.) R.M.King *et* H.Rob.	4	3	4	70	150	184				8,772
Senecio brasiliensis (Spreng.) Less.			2	49	68	20				8,766
Symphyopappus itatiayensis (Hieron.) R.M.King *et* H.Rob.	17	16	13							8,773
Vernonanthura montevidensis (Spreng.) H.Rob.	3	3	3	9	9	9				8,770
Berberidaceae										
Berberis laurina Billb.	10	17	28	18	21	24				8,774
Celastraceae										
Maytenus boaria Molina	3	4	6							8,775
Clethraceae										
Clethra uleana Sleumer						1				8,776
Escalloniaceae										
Escallonia bifida Link *et* Otto				2	2	2				8,779
Euphorbiaceae										
Croton cf. *patrum* L.B.Sm. *et* Downs				14	10	8				8,762
Fabaceae										
Mimosa pilulifera Benth.				1	1	1				8,780
Mimosa scabrella Benth.				8	7	5				-
Lauraceae										
Cinnamomum amoenum (Nees *et* Mart.) Kosterm.				3	6	6				8,781
Ocotea pulchella (Nees *et* Mart.) Mez	5	6	7							8,782
Persea willdenovii Kosterm.	3	5	5							8,783
Melastomataceae										
Leandra sp.				1	1	1				8,785

Continue

Table 1. Continued

Myrtaceae										
Myrceugenia cf. *mesomischa* (Burret) D.Legrand *et* Kausel	1	2								8,791
Myrceugenia euosma (O.Berg) D.Legrand	12	17	20	12	15	15				8,786
Myrceugenia glaucescens (Cambess.) D.Legrand *et* Kausel	6	12	24	4	6	10				8,794
Myrceugenia miersiana (Gardner) D.Legrand *et* Kausel	1	3	7							8,787
Myrceugenia myrcioides (Cambess.) O.Berg	6	6	7							8,789
Myrceugenia oxysepala (Burret) D.Legrand *et* Kausel	1	2	6	3	4	4				8,790
Myrceugenia pilotantha (Kiaersk.) Landrum	2	4	4							8,788
Myrceugenia regnelliana (O.Berg) D.Legrand *et* Kausel	11	20	25	3	6	7				8,792
Siphoneugena reitzii D.Legrand	2	5	7	1	1	1		1	1	8,793
Primulaceae										
Myrsine coriacea (Sw.) R.Br. ex Roem. *et* Schult.	1	2	2	3	4	8				8,795
Scrophulariaceae										
Buddleja reitzii E. M. Norman *et* L. B. Sm.				2	2	2				8,777
Solanaceae										
Solanum cassioides L.B.Sm. *et* Downs	48	60	92							8,798
Solanum paranense Dusén	60	72	70	16	32	34				8,796
Solanum pseudocapsicum L.				2	1		1			8,797
Symplocaceae										
Symplocos pentandra (Mattos) Occhioni ex Aranha	4	4	4							8,799
Winteraceae										
Drimys angustifolia Miers	29	33	38	3	3	5				8,800
Total	380	464	560	379	529	546	2	3	54	

Which factor determines the velocity of vegetative succession?. The ordinations of the explanatory variables on the dynamics of the regenerative component showed that: i) the adjacent forest fragments have structural-floristic differences (figure 3A); ii) the areas have high environmental heterogeneity, with clear gradients of fertility (axis 1 of environmental PCA - figure 3B) and soil compaction (axis 2 of environmental PCA – figure 3B); and iii) both the seed bank (figure 3C) and the regenerative component (figure 3D) have high structural-floristic variation.

In the floristic-structural composition of the seed bank (table 2), *Galium humile* Cham. *et* Schltdl was associated to positive values of PCoA axis 1 (where most of the plots of area 1 are located); *Juncus capillaceus* Lam., associated to negative values of PCoA axis 1 (plots of area 2, predominantly) and *Digitaria* cf. *horizontalis* Willd., associated to positive values PCoA axis 2. For the regenerative component, *S. brasiliensis* predominated at the plots with positive values in PCoA axis 1 (plots of area 2), *Solanum cassioides* L.B.Sm. *et* Downs was associated with negative values of PCoA axis 1 (plots of area 1); *B. uncinella,* associated with positive values of PCoA axis 2 (plots of area 1 predominantly) and *C. cruciata* with negative values of PCoA axis 2 (plots of both areas, but where most of the plots of area 2 are located). Therefore, *G. humile* in the seed bank and *S. cassioides, Drimys angustifolia* Miers, *Symphyopappus itatiayensis* (Hieron.) R.M.King *et* H.Rob and *Solanum paranense* Dusén in the natural regeneration characterized area 1. *J. capillaceus* in the seed bank and *S. brasiliensis* in the natural regeneration marked area 2.

Only the floristic-structural composition of natural regeneration influenced the speed of the successional process (PCoA regenerative axis 1: $P = 0.0015$, PCoA regenerative axis 2: $P = 0.0180$) (figures 4A, B; table 3). The final model is well adjusted, being suitable for interpretation (figures 4C, D, E, F). The residuals were normally distributed and did not have any trend, showing that the spatial heterogeneity among the areas was well captured by the model (GLS).

The succession speed presented a positive correlation with axis 1 of PCoA of the natural regeneration (figure 4A) and a negative correlation with axis 2 of the same ordination (figure 4B). Thus, considering the species distribution along the axis of the natural regeneration PCoA (table 2), we can infer that while a faster succession occurred in the sites with higher abundance of *S. brasiliensis* and *C. cruciate*, a slower one took place in the areas with superior presence of *S. cassioides, D. angustifolia, S. itatiayensis, S. paranense* and *B. uncinella*.
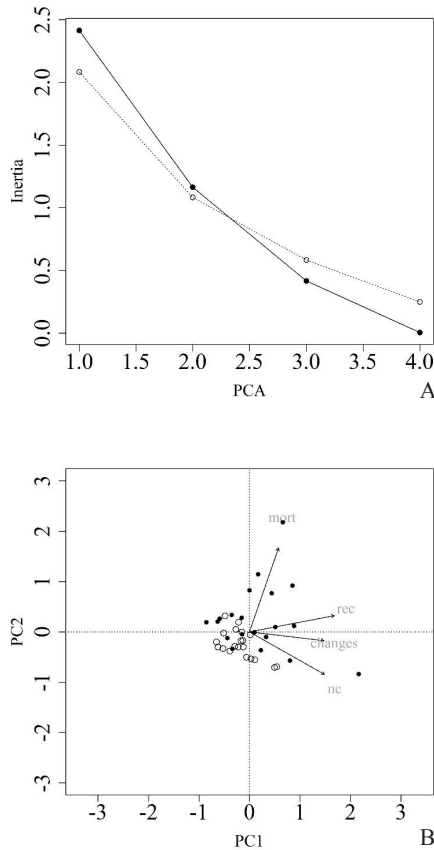
Figure 2. Scree plot (A) (dotted line representing random values determined by the broken stick distribution, continuous line representing values of inertia observed for each ordination axis) and ordination (B) (Empty circles: Area 1, Filled circles: Area 2) of the demographic rates (mort = mortality rate, rec = recruitment rate, nc = number of individuals net change) and floristic-structural change rate (changes) from Principal Component Analysis (PCA), in Upper Montane Araucaria Forest areas, in "Planalto Sul Catarinense" Region, in Brazil.

Scree plot (A) (la línea de puntos representa los valores aleatorios estimados con la distribución de "vara rota", la línea continua representa los valores de inercia observados para cada eje de ordenación) y ordenación (B) (Círculos vacíos: área 1, círculos llenos: área 2) de las tasas demográficas (tx_mort = tasa de mortalidad; tx_rec = tasa de reclutamiento; tx_ml = cambio neto del número de individuos y tasa de cambio florístico-estructural por un Análisis de Componentes Principales (PCA), en áreas de Bosque de Araucarias de Alta Montaña, en "Planalto Sul Catarinense", en Brasil.

DISCUSSION

After being protected from anthropogenic impacts for about one decade, the evaluated open vegetation areas showed an increase in the number of tree-shrub individuals, thus characterizing an encroachment process. There was also a small increase in species richness from 34 to 38 species. These results support the idea that the structural (abundance) recovery of vegetation occurs at a faster pace than do the changes in the floristic composition and richness. Likewise, as suggested by Chazdon (2003), the low floristic change can be partially explained by the long degradation history. It is noteworthy that our findings have to be interpreted in light of the current study temporal scale (2014-2016), which evaluated short-term changes in areas that have been protected for about a decade.

Shrubs rapidly encroached the natural grassland of area 3. Woody encroachment is a major threat to high-altitude natural grassland areas in southern Brazil, being a process regulated by site conditions and climatic changes (Müller *et al.* 2012, Sühs *et al.* 2020). In turn, forest succession is an expected process for past deforested areas (Rocha *et al.* 2016), and taking into account the limiting environmental conditions in the studied regions (*e.g.* frosts), the group of pioneer species has an important role in facilitating the succession process (Duarte *et al.* 2018). We also observed variations in the speed of the vegetational succession process. Thus, as noted for forests in advanced successional stages (*e.g.* Machado and Oliveira-Filho 2010), the initial recovery process also shows a high spatial heterogeneity, suggesting the complexity of this process.

Similar to the dynamics patterns, the plots also had variations related to biotic and abiotic factors, which were previously discussed in detail by Dallabrida *et al.* (2017) and Duarte *et al.* (2018). Despite the high environmental heterogeneity, only the floristic-structural properties of the regenerating component influenced the speed of succession. While faster changes were observed for the plots with the presence of Asteraceae *S. brasiliensis* and *C. cruciata*, slower dynamics was associated to the presence of *S. cassioides, D. angustifolia, S. itatiayensis, S. paranense* and *B. uncinella*. The ruderals *S. brasiliensis* and *C. cruciate* were already reported in degraded areas (Silveira and Maranho 2012), presenting a relatively shorter lifespan. In this sense, we can infer that for our studied areas the speed of the post-disturbance recovery represented a vegetation property inherent to the successional stage in which it is found. The lack of influence of the seed bank in our study reinforces what other studies (Vieira and Overbeck 2020, Silva and Overbeck 2020) have already evaluated for the region regarding this vegetative component quality.

The spatial heterogeneity of the forest succession pattern that we found supports the idea that this complex process (Chazdon 2003, Chazdon 2012, Meiners *et al.* 2015) mostly expresses the point in time that the vegetation lies along the succession trajectory (Rocha *et al.* 2016). Rocha
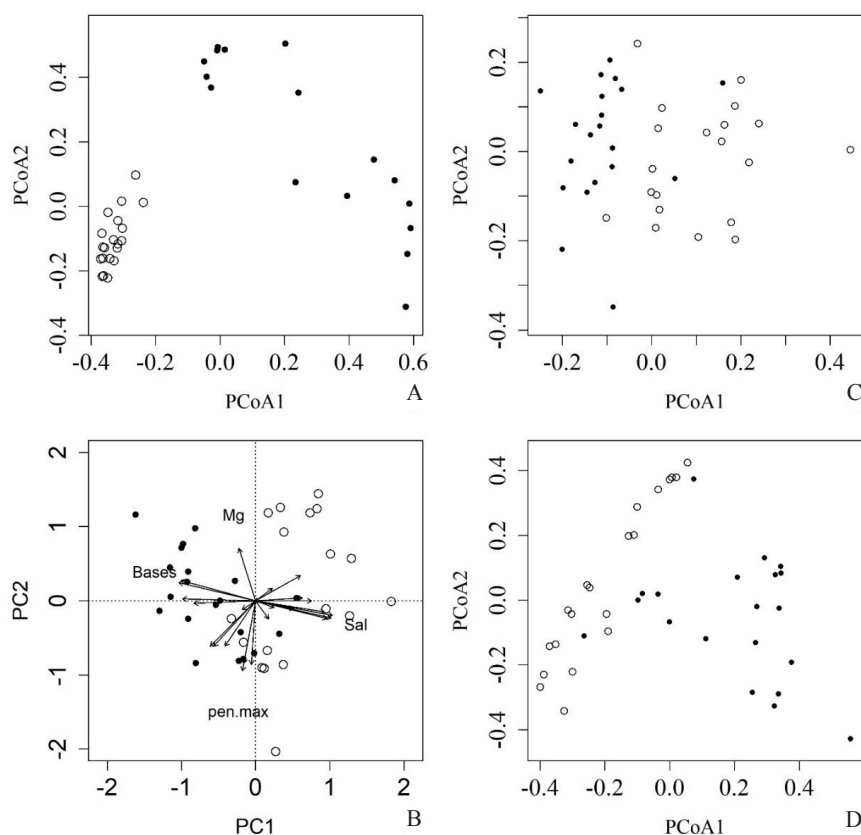
Figure 3. Ordination (Empty circles: Area 1, Filled circles: Area 2) of potentially influential variables on the speed of vegetational succession process in Upper Montane Forests in "Planalto Sul Catarinense" Region, Brazil. (A = PCoA of adult component floristic-structural composition; B = PCA of the environmental variables, showing those variables with more significant positive and negative correlation on axes 1 and 2 (Sum of Bases, Sal = Aluminum saturation, Mg = magnesium and pen.max = soil compaction); C = PCoA of seed bank floristic-structural composition and D = PCoA of regenerative component floristic-structural composition of 2014 first inventory).

Ordenación de las variables potencialmente influyentes sobre la velocidad del proceso de sucesión vegetacional en los Bosques de Alta Montaña, en "Planalto Sul Catarinense", Brasil (A = PCoA de la composición florística y estructural del componente adulto; B = PCA de las variables ambientales de la composición florística y estructural del componente regenerativo del primer inventario en 2014; C = PCoA de la composición florístico-estructural del banco de semillas e D = PCoA de la composición florística y estructural del componente regenerativo del primer inventario en 2014).

et al. (2016), studying abandoned pastures in the Amazon, observed that the historical use before the abandonment is a determinant factor in the natural regeneration process. Likewise, in subtropical high altitude areas of southern Brazil, the use history and the disturbance regime have been reported as critical factors for natural regeneration (Sühs *et al.* 2018). It is also noteworthy that, while the influence of nucleating elements, such as nurse plants, has not been reported as significant in this study, it has often been reported as highly important acting as facilitating elements in the initial succession process in southern Brazilian high-altitude areas (Carlucci *et al.* 2011b, Korndörfer *et al.* 2015, Marcílio-Silva *et al.* 2015).

CONCLUSIONS

About 10 years after protecting the areas, the short-term succession process presented a high degree of spatial heterogeneity, with recruitment exceeding mortality. Overall, our findings have partially confirmed the initial hypotheses. As we expected, the seed bank did not influence natural regeneration dynamics. Besides, the regeneration taxonomical identity was the only factor that affected the speed of succession, being faster in plots where *S. brasiliensis* and *C. cruciata*, which are ruderal species with a short lifespan, were abundant. Thus, we can infer that the speed of succession represented is, to a large extent, a feature related to the phase of the successional trajectory in which the vegetation is found.

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Table 2. Species with significant associations with axes 1 and 2 of the Principal Coordinate Analysis (PCoA), according to the Generalized Linear Multivariate Model, with the negative binomial distribution, for the seed bank and regenerative component in Upper Montane Araucaria Forest, in "Planalto Sul Catarinense" Region, Brazil.

Especies con asociaciones significativas con los ejes 1 y 2 del Análisis de Coordenadas Principales (PCoA), según el Modelo Multivariado Lineal Generalizado, con la distribución binomial negativa, para el banco de semillas y para la regeneración natural en el Bosque de Araucarias de Alta Montaña, en "Planalto Sul Catarinense", Brasil.

Seed bank species	Coefficients	P
AXIS 1 PCoA [figure 3C]		
Austroeupatorium inulaefolium (Kunth) R.M.King *et* H.Rob.	7.62	*
Baccharis vulneraria Baker	6.56	*
Dichanthelium sabulorum (Lam.) Gould *et* C.A. Clark	5.02	*
Galium humile Cham. *et* Schltdl.	8.04	**
Holcus lanatus L.	3.28	*
Juncus capillaceus Lam.	-3.69	*
AXIS 2 PCoA [figure 3C]		
Digitaria cf. *horizontalis* Willd.	8.28	*
Juncus capillaceus Lam.	2.85	*
Regenerative component species	Coefficients	P
AXIS 1 PCoA [figure 3D]		
Campovassouria cruciata (Vell.) R.M.King *et* H.Rob.	3.58	***
Drimys angustifolia Miers	-9.45	***
Senecio brasiliensis (Spreng.) Less.	12.86	***
Solanum cassioides L.B.Sm. *et* Downs	-10.43	***
Solanum paranense Dusén	-4.78	***
Symphyopappus itatiayensis (Hieron.) R.M.King *et* H.Rob.	-7.40	**
AXIS 2 PCoA [figure 3D]		
Baccharis uncinella DC.	2.24	***
Campovassouria cruciata (Vell.) R.M.King *et* H.Rob.	-2.59	**

*** = $P < 0.001$, ** = $P < 0.01$, * = $P < 0.05$

Table 3. Generalized Least Square (GLS) model coefficients, with the structure of the heterogeneity of the residue incorporated to the model by an exponential function of the covariate variance, for Upper Montane Araucaria Forest areas, in "Planalto Sul Catarinense" Region, Brazil.

Coeficientes del modelo de mínimos cuadrados generalizados (GLS), con la estructura de la heterogeneidad del residuo incorporado al modelo por una función exponencial de la varianza covariable, para las áreas del Bosque de Araucarias de Alta Montaña, en "Planalto Sul Catarinense", Brasil.

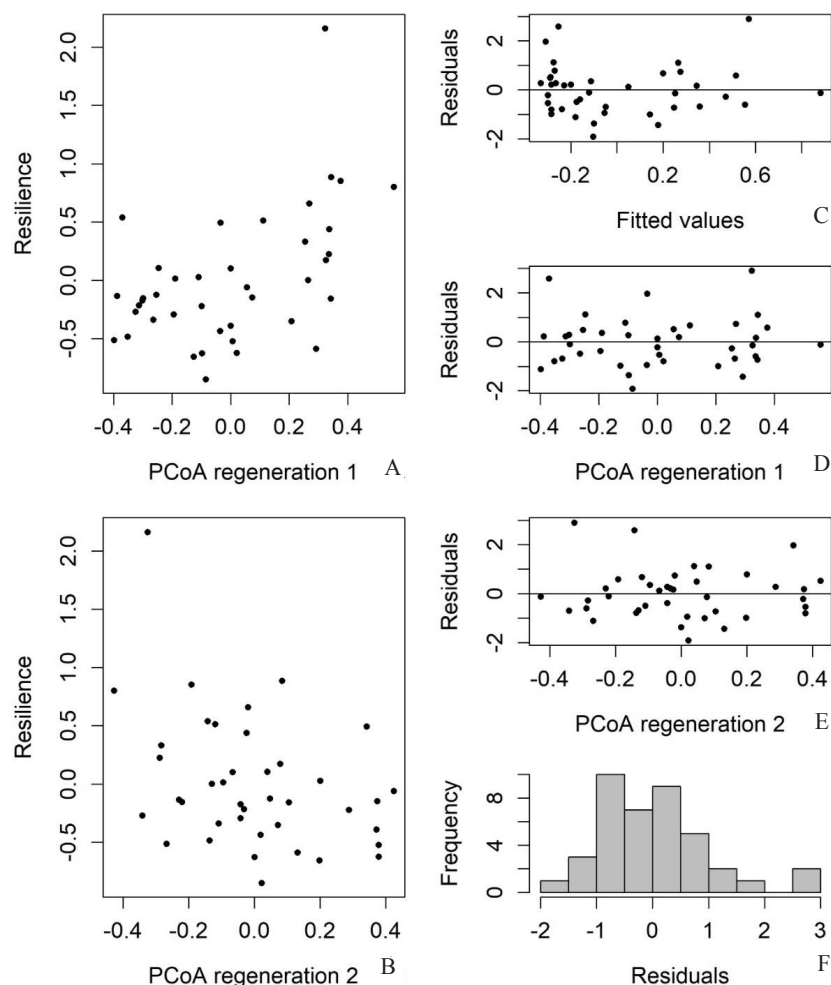|	Dynamics pattern (PCA 1 dynamics rates)	Standard error	P
Intercept	-0.004103	0.0721428	ns
PCoA regenerative axis 1	0.9779525	0.2851941	**
PCoA regenerative axis 2	-0.7969438	0.321964	**

** = $P < 0.01$, ns = non-significative.

Figure 4. Significant explanatory variables on the successional process speed [A = Resilience (PCA axis of the regenerative component dynamics rates) x PCoA axis 1 of the 2014 regenerative component floristic-structural composition; B = Resilience (PCA axis 1 of the regenerative component dynamics rates) x PCoA axis 2 of the 2014 regenerative component floristic-structural composition) and residual analysis of the adjusted model (C = Residual x adjusted values , D = Residual x PCoA axis 1 of the 2014 regenerative component floristic-structural composition; E = Residual x PCoA axis 2 of the 2014 regenerative component floristic-structural composition; F = Residual frequency], in Upper Montane Araucaria Forest areas, in "Planalto Sul Catarinense" Region, Brazil.

Variables explicativas significativas sobre la velocidad del proceso de sucesión [A = Resiliencia (eje 1 del PCA de las tasas de dinámica de de la regeneración natural) x eje 1 de la PCoA del composición florístico-estructural del componente regenerativo del primer inventario, 2014; B = Resiliencia (eje 1 del PCA de las tasas dinámicas de de la regeneración natural) x eje 2 del PCoA de la composición florístico-estructural de la regeneración natural del primer inventario, 2014) y análisis de residuos del modelo ajustado (C = Residuos x valores ajustados, D = Residuos x eje 1 del PCA de la composición florístico-estructural de la regeneración natural del primer inventario, 2014; E = Residuos x eje 2 del PCoA de la composición florístico-estructural de la regeneración natural del primer inventario, 2014; F = distribución de frecuencia de los residuos], en áreas del Bosque de Araucarias de Alta Montaña, en "Planalto Sul Catarinense", Brasil.

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