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Original Papers

Factors influencing early natural regeneration in areas under passive restoration in Araucaria Forest, southern Brazil

Guilherme Diego Fockink[1,2,4,11], *Charline Zangalli*[1,3], *Emanoéli de Oliveira*[1,5], *Nataniele Maria Ferreira*[1,6], *Leonardo dos Santos de Jesus*[1,7], *Ana Paula Moreira Rovedder*[2,8], *Marcos Felipe Nicoletti*[1,9] & *Maria Raquel Kanieski*[1,10]

Abstract
Passive restoration is widely adopted in restoration areas previously used by pine plantations. However, little is known about which environmental factors influence the initial natural regeneration in these areas. Our objective was to relate environmental variables to the floristic-structural patterns of early natural regeneration in areas under passive restoration post-harvest of *Pinus taeda*. We related natural regeneration data with vegetation and soil variables obtained in 19 plots (100 m²). The ordering of the floristic-structural data of natural regeneration was carried out by NMDS (Non-Metric Multidimensional Scaling) analysis, and the significant variables ($p < 0.05$) were plotted *a posteriori*. The results indicate that soil conditions are adequate for natural regeneration development in the study areas. The variables pH, clay, and canopy cover showed a relationship with the floristic-structural composition of the initial natural regeneration. These findings indicated a gradient of texture and acidity and a successional gradient among the sites. In general, tree species show an association with sites containing high canopy cover and soils of greater acidity and clay content. On the other hand, pioneer-shrub species predominate in sites with low canopy cover and soils that are less clayey and acidic.
Key words: canopy cover, floristic, soil variables, successional gradient.

Resumo
A restauração passiva é amplamente utilizada para restauração de áreas anteriormente ocupadas por plantações de pinus. No entanto, pouco se sabe sobre quais fatores ambientais influenciam a regeneração natural inicial nessas áreas. Nosso objetivo foi relacionar variáveis ambientais com os padrões florístico-estruturais de regeneração natural inicial em áreas sob restauração passiva pós-colheita de *Pinus taeda*. Relacionamos dados de regeneração natural com variáveis de vegetação e solo obtidas em 19 parcelas (100 m²). A ordenação dos dados florístico-estruturais da regeneração natural foi realizada pela análise NMDS (Non-Metric Multidimensional Scaling), e as variáveis significativas ($p < 0,05$) foram plotadas *a posteriori*. Os resultados indicam que as condições do solo são adequadas para o desenvolvimento da regeneração natural nas áreas de estudo. As variáveis pH, argila e cobertura de copa apresentaram relação com a composição florístico-estrutural da regeneração natural inicial. Estes indicaram um gradiente de textura e acidez e um gradiente sucessional entre os locais. Em geral, as espécies arbóreas apresentam associação com locais onde há alta cobertura de copa e solos de maior acidez e teor de argila. Por outro lado, espécies arbustivas pioneiras predominam em locais com baixa cobertura de copa e solos menos argilosos e menos ácidos.
Palavras-chave: cobertura de copa, florística, variáveis de solo, gradiente sucessional.

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[1] Universidade do Estado de Santa Catarina, Depto. Engenharia Florestal, Lages, SC, Brasil.
[2] Universidade Federal de Santa Maria, Depto. Ciências Florestais, Santa Maria, RS, Brasil.
[3] Universidade Estadual do Centro-Oeste, Depto. Engenharia Florestal, Irati, PR, Brasil. ORCID: <https://orcid.org/0000-0002-7667-3389>.
[4] ORCID: <https://orcid.org/0000-0003-0949-1398>. [5] ORCID: <https://orcid.org/0000-0002-8587-895X>. [6] ORCID: <https://orcid.org/0000-0001-7246-9172>.
[7] ORCID: <https://orcid.org/0000-0002-6927-1314>. [8] ORCID: <https://orcid.org/0000-0002-2914-5954>. [9] ORCID: <https://orcid.org/0000-0003-4732-0119>.
[10] ORCID: <https://orcid.org/0000-0003-1078-5641>.
[11] Author for correspondence: guilhermefockink@gmail.com

Introduction

Recent estimates indicate that the Brazilian Atlantic Forest, which is one of the hottest global biodiversity hotspots, has 7.2 million hectares of degraded riparian areas (Rezende *et al*. 2018). According to the same authors, restoration of these areas is crucial for mitigating climate change, boosting sustainable development, and preventing processes of extinction. Among the phytoecological units of the Atlantic Forest, Mixed Ombrophilous Forest (Araucaria Forest), characteristic of the highest regions of southern Brazil (IBGE 2012) is one of the least addressed forest ecoregions in ecological restoration studies (Londe *et al*. 2020), while at the same time being highly fragmented and threatened (Kersten *et al*. 2015). In this region, many riparian areas were occupied in the past by pine and eucalyptus plantations; however, there is current demand for the environmental adequacy of these areas that are protected by Brazilian environmental legislation - Law 12621/2012 (Brasil 2012). Thus, forest restoration techniques are necessary to comply with legislation and reestablish native vegetation and associated ecosystem services.

Passive restoration, a technique where the sites are fenced to avoid stressors, and where natural regeneration occurs without human intervention (Morrison & Lindell 2011), is largely used for the restoration of areas previously occupied by pine plantations (Salami *et al*. 2015, 2018; Oliveira *et al*. 2021). This technique shows high resilience and potential for perpetuation of the restoration process in this region (Fockink *et al*. 2022). However, little is known about how environmental factors and changes promoted by forestry affect the initial natural regeneration of vegetation.

The distribution of species in their natural habitats occurs due to complex interactions between several ecological, biotic, abiotic, deterministic, and stochastic factors (Aguiar *et al*. 2021). In Araucaria Forest, studies have highlighted that variations in floristic composition, structure, and forest dynamics occur as a function of edaphic and climatic factors and the history of anthropogenic degradation of the environment (Higuchi *et al*. 2012; Kersten *et al*. 2015). Variations on the local scale of physiochemical soil and canopy structure variables, for example, are correlated with the distribution, composition, and structure of the tree community and natural regeneration in fragments of Araucaria Forest (Higuchi *et al*. 2015; Cordeiro *et al*. 2020). Soil physicochemical variables are sensitive to changes in the environment and capable of inferring about the recovery (Mendes *et al*. 2019) and functionality of the ecosystem, especially when related to vegetation variables (Rocha *et al*. 2015). Despite their relevance, these variables are little used in forest restoration projects; less than 50% of restoration studies carried out in the Atlantic Forest consider soil quality indicators (Mendes *et al*. 2019).

Thus, understanding the relationship between soil and vegetation variables and the floristic and structural patterns of natural regeneration is essential to support conservation and restoration strategies (Ansolin *et al*. 2016), providing information about the occurrence of species and the organization of plant communities (Higuchi *et al*. 2012), as well as possible limitations caused by the previous use of these sites by pine plantations (Salami *et al*. 2018).

Our objective in the current study was to relate soil and vegetation variables to the floristic-structural patterns of early natural regeneration in areas under passive restoration post-harvest of *Pinus taeda* L., located in the Araucaria Forest domain. We seek to understand which soil and vegetation factors are related to early natural regeneration and whether soil conditions are adequate for reestablishing vegetation at these sites. In the current study, we look to answer the following questions: (1) Do the soils of areas under passive restoration post-harvest of pine have the necessary conditions for the reestablishment of native vegetation? (2) What soil and vegetation variables are related to the floristic-structural patterns of natural regeneration in these areas?

Material and Methods

Characterization of the study area

This study was conducted in riparian forests previously occupied by *P. taeda* stands, located in the municipality of Ponte Alta do Norte, Santa Catarina state, southern Brazil (27º09’30”S, 50º27’52”W) (Fig. 1). These areas are in the process of restoration after harvest of 374.59 ha of pine plantation. The stands of pine were harvested from these areas to meet the requirements provided for in the Brazilian environmental legislation, aiming at the restoration of native vegetation.

The altitude of the study areas varies between 991 m and 1,125 m, with an average altitude of 1,069 m at sea level. The vegetation in the region is

Mixed Ombrophilous Forest (IBGE 2012), known as Araucaria Forest. The climate is Cfb - humid subtropical, with an average annual temperature of 15.6 °C and an average annual rainfall of 1,747 mm (Alvares *et al*. 2013). The predominant soils are Haplic Cambisols, Humic Cambisols, Litholic Neosols, and Bruno Nitisols (Potter *et al*. 2004).

The removal of pine plantations from these areas was carried out in the period between 2015 and 2016, being the first cutting cycle after the implantation of the stands. The harvest was carried out mechanically and manually, according to the slope of the land in each area. The harvested wood was removed from the areas, leaving only the crop residues. Since then, the areas have been isolated for the natural regeneration process (passive restoration) to take place, with continuous monitoring of *P. taeda* regeneration and removal of regenerating individuals by cutting. We assessed these areas during the years 2019 and 2020, when the areas had been in the natural restoration process for between three to five years.

Data collection

We carried out the collection of soil samples in 19 permanent plots of 25 m × 4 m (100 m^2) in the areas under restoration. We collected 19-soil samples at a depth of 0–20 cm, each composed of 15 subsamples collected randomly within the each plot (SBCS 2016). The soil was taken to the laboratory for chemical analysis. The following variables were determined: pH in water, aluminum (Al), calcium (Ca), magnesium (Mg), potassium (K), phosphorus (P), soil organic matter (SOM), base saturation (V), effective cation exchange capacity (effective CEC), cation exchange capacity at pH 7 (CEC at pH 7), aluminum saturation (m), and clay content (SBCS 2016).

We evaluated the soil penetration resistance (PR) using a digital electronic penetrometer. In each plot, we took six equidistant readings at a depth of 0–20 cm. We collected three soil samples in each plot, to determine the condition of soil moisture at the time of evaluation by the gravimetric method, as proposed by Teixeira *et al*. (2017). We fitted a linear regression to standardize the PR readings for the same soil moisture content. Subsequently, we determined the average PR (average penetration resistance along the 0–20 cm depth).

We obtained the floristic composition and abundance of tree/shrub natural regeneration and vegetation variables of canopy cover (CC) and herbaceous cover (HC) from a study carried out by Fockink *et al.* (2022) for the same sample plots where we performed the soil sampling. The natural regeneration included all tree/shrub individuals with a height > 50 cm and circumference at breast height - CBH ≤ 15 cm. The CC and HC were obtained by the line intersection method. The CC considered all the native tree/shrub

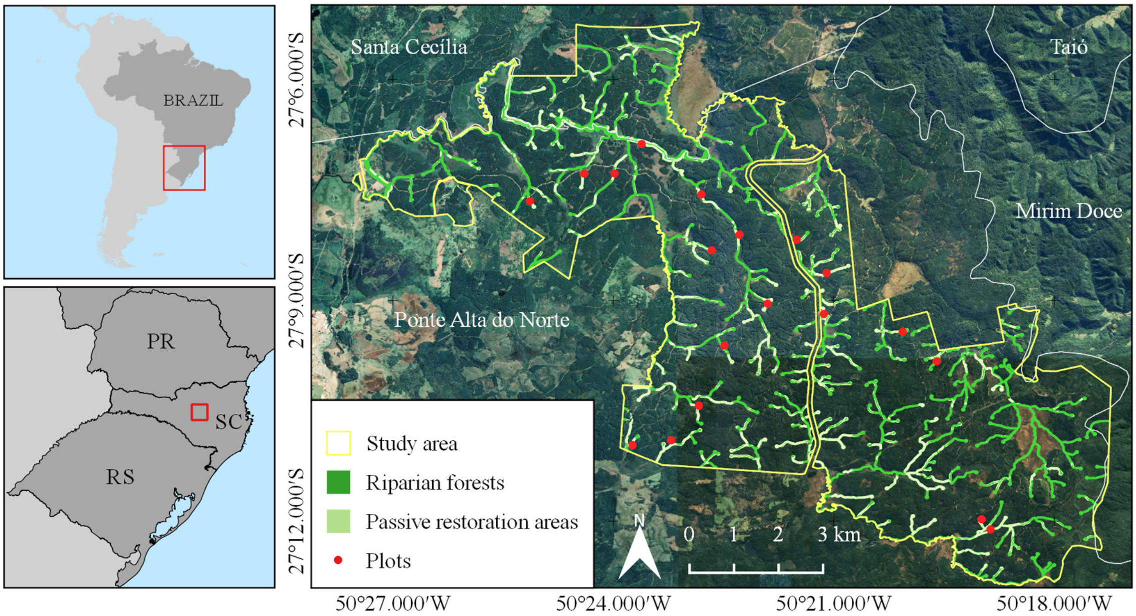

Figure 1 – Location of the study area, Ponte Alta do Norte, Santa Catarina, southern Brazil.

vegetation and the HC all the native herbaceous vegetation projected over the central line in each plot. Subsequently, the values were converted into percentages.

Data analysis

We submitted the soil attributes and variables of the vegetation to descriptive statistics. In addition, we compared the soil chemical variables with the values found by the Soil Map of the state of Santa Catarina (Potter *et al*. 2004) for Haplic Cambisols, Bruno Nitosols, and Litholic Neosols occurring in the Ponte Alta do Norte region and predominant in the area of study. We compared the PR with the values obtained in the literature. The vegetation and edaphic variables were used in the multivariate analysis NMDS (Non-Metric multidimensional scaling) (Minchin 1987).

We correlated the floristic-structural composition data of natural regeneration with soil and vegetation variables by means of multivariate analysis NMDS, with four dimensions. For this, we created a matrix with species abundance data per plot, based on Bray-Curtis dissimilarity. We removed species with fewer than five individuals from the analysis, as rare species make it difficult to interpret the data and add little relevant information. We verified the suitability of the ordering by the stress value, and adjusted the edaphic and vegetation variables *a posteriori*, using the *envfit* function with 1,000 permutations. Subsequently, we tested the multicollinearity level of the variables by the variance inflation factor (VIF) using the *vifstep* function. Variables that showed high multicollinearity (VIF greater than 10) were excluded from the analysis. In the ordering we plotted the significant variables ($p < 0.05$) most relevant to the floristic-structural composition of natural regeneration in vectors. Statistical analyses were performed using R Studio software (R Development Core Team 2020), using *vegan* (Oksanen *et al*. 2019) and *usdm* (Naimi 2017) packages for NMDS.

Results

The soils in the areas under restoration present high acidity, high levels of SOM and exchangeable Al, and low levels of nutrients such as Ca, P, and K. The high levels of exchangeable Al and the low presence of these nutrients contribute to the high aluminum saturation and low base saturation observed. The high levels of SOM contribute to the high CEC at pH7 and effective CEC. The clay content characterizes the soils as having a medium texture. The PR presents values below the critical limit, indicating low soil compaction (Tab. 1). There is high variation, mainly in relation to the Mg and Ca content, base saturation (V), clay content, and PR in these soils, while the pH in water, exchangeable aluminum, Al saturation (m), and CEC at pH7 show low coefficients of variation (Tab. 1), indicating more homogeneous soil conditions in terms of acidity and aluminum content.

The high values of HC and intermediate values of CC (Tab. 1) characterize the vegetation in the areas under restoration as typical of the initial stages of the ecological succession of Araucaria Forest, where the herbaceous-arbustive component predominates, with some pioneer trees. The natural regeneration in the studied areas presented 1,409 individuals of 107 tree and shrub species, belonging to 50 genera and 28 botanical families. Among these species, seven were identified at the family level, four at the genus level, and ten were classified as morphospecies. *Grazielia intermedia* (DC.) R.M. King & H. Rob., *Solanum variabile* Mart., *Grazielia serrata* (Spreng.) R.M.King & H.Rob., and *Baccharis uncinella* DC. were the most abundant species (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.26155345.v1>). Only 44 species included more than five regenerate individuals and were considered in the NMDS analysis.

The NMDS analysis shows a stress of 8.42%, indicating that the ordering is adequate for interpretation. The first two axes of the NMDS explained 30.01% and 26.41% of the total inertia of the data (Fig. 2). The variables: pH (0.008, $p < 0.01$), clay (0.026, $p < 0.05$), and CC (0.047, $p < 0.05$) explain the variation data significantly (Tab. S2, available on supplementary material <https://doi.org/10.6084/m9.figshare.26155345.v1>). The soil variables synthesize a gradient of texture and acidity along the first axis, while the CC synthesizes a successional gradient.

The highest positive score with the first axis was pH. Clay and CC presented high negative scores with this axis. On the second axis, both variables had low scores. pH showed negative scores, while clay and CC had positive scores with this axis. *Austroeupatorium laetevirens* (Hook. & Arn.) R.M.King & H.Rob. (Austlaet), *G. serrata* (Grazserr) and *Baccharis microdonta* DC. (Baccmicr) showed a higher positive score with

Table 1 – Average, minimum and maximum values, standard deviation (SD), coefficient of variation (CV) of soil and vegetation variables in areas under passive post-harvest of *Pinus taeda*, southern Brazil.

Variables	Average	SD	Minimum	Maximum	CV
pH in water	4.33	0.21	4.04	4.70	4.85
Al (cmol$_C$ dm^{-3})	4.88	0.84	3.30	6.50	17.21
Ca (cmol$_C$ dm^{-3})	0.95	0.41	0.45	1.94	43.16
Mg (cmol$_C$ dm^{-3})	0.72	1.32	0.07	4.47	183.33
CEC at pH7 (cmol$_C$ dm^{-3})	30.18	5.93	19.31	40.51	19.65
Effective CEC (cmol$_C$ dm^{-3})	6.67	1.90	4.76	12.06	28.49
K (mg dm^{-3})	50.53	13.67	22.00	71.00	27.05
V (%)	5.96	3.99	1.87	14.00	66.95
SOM (%)	8.88	2.11	5.70	13.20	23.76
Clay (%)	22.47	8.68	9.00	41.00	38.63
P (mg dm^{-3})	5.83	1.46	3.20	9.10	25.04
m (%)	74.90	12.49	51.04	90.82	16.68
PR (MPa)	1.13	0.50	0.36	2.36	44.25
CC (%)	67.00	24.40	16.80	100.00	36.42
HC (%)	97.00	8.30	61.70	100.00	8.56

Al = exchangeable aluminum; Ca = calcium; Mg = magnesium; CEC at pH7 = cation exchange capacity at pH 7; effective CEC = effective cation exchange capacity; K = potassium; V = base saturation; SOM = soil organic matter; Clay = clay content; P = phosphorus; m = aluminum saturation; PR = soil penetration resistance; CC = canopy cover; HC = herbaceous cover.

the first axis. These species are associated with sites with low canopy cover and soils with low acidity and low clay content, and they represent the initial stage of colonization in open areas. On the opposite side, *Annona rugulosa* (Schltdl.) H. Rainer (Annorugu), *Pavonia commutata* Garcke (Pavocomm), *Myrceugenia oxysepala* (Burret) D.Legrand & Kausel (Myrcoxys), and *Eugenia pyriformis* L. (Eugepyri) showed the highest negative scores, occurring preferentially in sites with higher canopy cover and mostly clay and acid soils. The second axis covers the amplitude of the gradient. *Blepharocalyx salicifoilius* (Kunth) O. Berg (Blepsali), *Berberis laurina* Billb. (Berblaur), and *Myrceugenia euosma* (O.Berg) D. Legrand (Myrceuos) showed positive scores with the second axis, occurring in plots with high canopy cover and more acid and clayey soils. *Inga lenticifolia* Benth. (Ingalent) and *Solanum pabstii* L.B.Sm. & Downs (Solapabs) showed negative scores predominately in plots with low canopy cover and less clayey and acid soils (Tab. S3, available on supplementary material <https://doi.org/10.6084/m9.figshare.26155345.v1>).

Discussion

Our results reveal that the soil conditions are suitable for establishing vegetation, and the floristic-structural patterns of initial natural regeneration are determined by soil and vegetation factors. Variations in texture and acidity of the soil and canopy cover act as environmental filters for the regeneration of tree and shrub species in areas under passive restoration post-harvest of *P. taeda*. These results allow us to better understand the initial colonization process in these areas and explore the soil-vegetation relationship of species that are still little studied in terms of their edaphic requirements, such as pioneer shrub species.

In general, the chemical attributes of the soil presented values similar to those verified for Haplic Cambisols, Humic Cambisols, Bruno Nitosols, and Litholic Neosols occurring in the region of study, by the Soil Map of the state of Santa Catarina (Potter *et al*. 2004). The authors emphasize that these soils, under natural conditions, are strongly acidic (pH in water < 5.0), with high levels of SOM (above 6%), high aluminum saturation, high CEC in the superficial layers, low base saturation, and high clay content (> 50%), characterized by low natural fertility.

Low pH values were also observed in other studies for Cambisols and Neosols at altitudes above 1,000 m in the Araucaria Forest region in southern Brazil (Higuchi *et al*. 2012, 2013; Ansolin *et al*. 2016). The high SOM content that we observed is similar to that verified by Higuchi *et al*. (2012) in Araucaria Forest in southern Brazil, at an altitude of approximately 1,000 m (SOM = 8.11 ± 2.16%). At high altitudes, the conditions of low temperatures and high moisture decrease the rate of biomass decomposition, causing greater accumulation of organic matter in the soils (Kelling *et al*. 2019), as is the case in the studied areas. Although these soils are naturally acidic, the high soil acidity observed in post-harvest areas of *Pinus* sp. may also be due to changes in the quantity and quality of SOM deposited by forest plantations, directly influencing the chemical conditions of the soil (Salami *et al*. 2018). The presence of pine harvest residues left after the removal of individuals, may also have contributed to the high levels of SOM verified and, consequently, to the high acidity and exchangeable Al content.

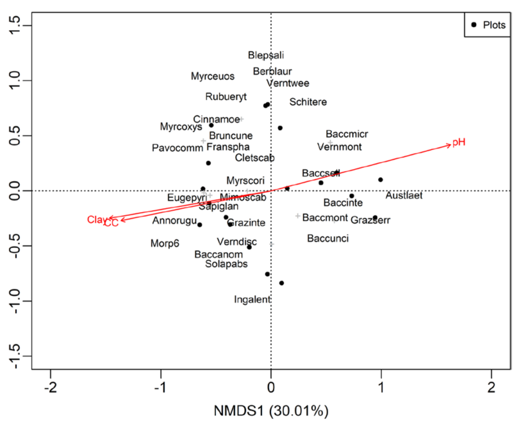

Figure 2 – Non-Metric Multidimensional Scaling (NMDS) analysis with distribution of plots (black points) and floristic composition of natural regeneration as a function of significant soil and vegetation variables in areas under passive restoration post-harvest of *Pinus taeda*. The vectors (red lines) represent the significant variables ($p < 0.05$): pH = pH in water, clay = clay content and CC = canopy cover. The species and their respective abbreviations can be consulted in Table S1 (available on supplementary material <https://doi.org/10.6084/m9.figshare.26155345.v1>).

The base saturation (V) below 50% and the Al saturation greater than 50% indicate that the soils evaluated are dystrophic and allic, that is, low fertility, being deficient, mainly, in Ca, Mg, and K and with high exchangeable Al contents (> 3 mmolC dm-3) (Ronquim 2020). In addition, according to the author, under these conditions the negative colloidal loads are adsorbing exchangeable H+ and Al, and may contain aluminum at a toxic level for plants. Low levels of Ca, P, and K and high amounts of exchangeable Al were also verified by Salami *et al*. (2018) in areas post-harvest of *Pinus* sp. under passive restoration. The authors point out that the low levels of these nutrients and the high exchangeable Al are not limiting the development of native regeneration of trees and shrubs, since the nutrient cycling occurring in the litter tends to alleviate the effects of the low concentration of these nutrients in the soil. In tropical forests, characteristics such as high diversity, high biomass production, and adaptations of native species show that high levels of Al do not affect the forest development (Brunner & Sperizen 2013). We believe the miscellany formed by herbaceous and pine harvest residues (needles, branches, barks, and some trunks) contributed to the development of native vegetation in the studied areas, due to nutrient cycling promoted at the soil-litter interface and the increased rugosity of the terrain, which consequently created microhabitats for the establishment of native species. However, this is contrary to what was observed by Fockink *et al.* (2020) where the layer of needles acted as a physical barrier to the natural regeneration of native species of the Araucaria Forest.

Despite the silvicultural history with *P. taeda* and mechanized harvesting in some of these areas, the sampled soils showed low compaction, indicating few limitations to the root growth of the regenerant native plants. We found PR values below the limit considered critical for the root growth of the plants, of 2.5 MPa, as described by Furtado *et al*. (2016) for tree species. Therefore, the results of the physicochemical analysis indicate that there are no limitations to the establishment of regeneration in the soils of the studied sites, even after a history of land use for forestry.

Variations in the floristic-structural patterns of vegetation as a function of the soil have been reported by other authors in studies carried out in Araucaria Forest, mainly in response to pH and clay content (Higuchi *et al*. 2012, 2013; Silva *et al*. 2016; Gomes *et al*. 2020). We observed that the regeneration of tree species, such as *A. rugulosa*, *M. oxysepala*, and *M. euosma* was associated with sites where the CC is greater and the soil is more acidic and more clayey. Similar patterns were observed for other authors in Araucaria Forest for these species. Higuchi *et al*. (2012) observed the occurrence of *A. rugulosa* in soils that are not very steep, of low natural fertility, and with acidic pH. Gomes *et al*. (2020) found that *Myrceugenia* species adapted to high acidity, preferentially colonizing sites with dystrophic, acidic soils (pH between three and four), and low fertility. The niche of *M. euosma* is soils with low effective CEC, high acidity, and high levels of exchangeable aluminum, characteristics observed in our study area. Another important factor for the establishment of some species is shade. Higuchi *et al*. (2013) verified that colonization by *M. oxysepala* is predominant in sites with greater canopy cover, as this is a shade-adapted species. Other species, such as *S. pabstii* and *I. lentiscifolia* were associated with less clayey and less acidic soils, but differing from the sites occupied by shrub species (further to the left of the gradient), mainly due to the greater canopy cover.

Our results also demonstrate that shrub species, mainly Asteraceae, predominate in sites with low canopy cover and less acidic (even with small variation - Tab. 1) and less clayey soils. Despite their importance in the initial colonization of altered and degraded areas, studies that approach the specific relationship of shrub species with soil conditions are rare in Araucaria Forest. Some patterns are described in the literature, such as the predominance of shrub species in the initial colonization of Araucaria Forest, especially in areas with drainage and soil density limitations (Reitz & Klein 1966; Salami *et al*. 2018). Presenting abundance in our study area, *G. serrata* and *B. uncinella* are colonizers in a variety of environments, from open areas and wet grasslands to forest edges, and characterize the initial stages of ecological succession in Araucaria Forest (Cabrera & Klein 1989; Rech *et al*. 2015). However, these species are little explored in terms of their edaphic requirements. *B. uncinella* was observed with a high frequency in restoration areas post-harvest of a pine plantation, being dominant over other native species in sites with poorly drained soils, due to its ability to tolerate limiting moisture conditions and water table fluctuations, which allows for greater survival in relation to other species (Salami *et al*. 2015). Korndörfer *et al*. (2015) observed that this species contributes to the improvement in soil chemical quality in the process of colonization of open areas, due to its high litter production and high canopy cover. The presence of these shrub species in our study, in areas with limiting texture and acidity conditions, highlights the important role they play in ecological restoration; they are efficient colonizers and capable of improving the environmental quality, allowing later establishment of other groups of plants.

Based on our results, we believe that the greater part of the variation observed between the plots seems to be more associated with the successional gradient, especially when we observe the separation of groups of pioneer shrub species (right of the gradient) and tree species (left of the gradient) in the NMDS. The influence of the cover canopy on the composition and structure of tree vegetation is a common pattern in Atlantic Forest (Higuchi *et al*. 2013). This variable significantly influences natural regeneration in Araucaria Forest, showing the importance of luminosity as an environmental filter in the establishment of regenerants (Higuchi *et al*. 2015) and species distribution. We observed *in loco* that the plots with a predominance of shrubs were close to humid environments (for example, wetlands, floodplains, and alluvial areas) that could be limiting the establishment of some species, mainly trees that are intolerant of poorly drained soils. The recovery process of these areas may be slower, or possibly, their physiognomy is characterized by the predominance of shrub vegetation.

Considering soil and vegetation variables (Fig. 2), we can infer that better soil texture conditions possibly contributed to the establishment of tree species, considering that clay and CC are highly correlated. In areas under restoration, better texture conditions, water retention, and soil fertility allow the colonization of environments by species less tolerant to the stress caused by edaphic factors and more tolerant to shade (Chazdon 2016). This condition allows an increase in the richness of regenerating species. Thus, it is noteworthy that the greater tree regenerant richness found in environments with greater canopy cover may indicate better edaphic and microclimatic conditions and the reestablishment of the ecosystem functionality promoted by canopy coverage. Regeneration in tropical forests shows a gradual increase in species richness in response to improvements in the structure and functionality of the ecosystem (Chazdon 2013).

The low regeneration of *Araucaria angustifolia* (Bertol.) Kuntze observed in our study is a situation that deserves attention, as this species is ecologically and physiognomically important for Araucaria Forest (Kersten *et al*. 2015), and is threatened with extinction (Carlucci *et al*. 2013). Both the edaphic factors and the environmental conditions of the initial stages of succession in the restoration areas may have contributed to the low regeneration of the species. In riparian forests, the establishment of *A. angustifolia* is mainly influenced by drainage, being that in areas with higher soil moisture content the species generally establishes itself after initial colonization by hygrophyte pioneer species, while on dry slopes initial colonization occurs by itself (Reitz & Klein 1966). The only regenerant we found was on a slightly steep slope, where the drainage condition is possibly better. Cordeiro *et al*. (2020) found a predominance of the species in clayey and well-drained soils. Therefore, we believe that other factors may be contributing to this result. Other studies have also highlighted the low regeneration of this species in altered and passive restoration areas, and the authors associate this fact with factors such as historical logging, limitations on seed dispersal, and predation by rodents (Vieira & Iob 2009; Ferreira *et al*. 2012).

It is known that, beyond the soil and vegetation factors, a range of environmental variables is related to the floristic-structural patterns of natural regeneration. Higuchi *et al.* (2015) found a low relationship of physiochemical soil and canopy structure variables with natural regeneration in Araucaria Forest fragments, especially when compared to other factors of a stochastic order, such as the dispersion of propagules. In our study, the soil (pH and clay) and vegetation (CC) variables also had a low explanatory power for natural regeneration patterns. Factors such as topographic variation and proximity to propagule sources are described as determinants of natural regeneration patterns in forests, as they contribute to soil heterogeneity and the availability of propagules, respectively (Higuchi *et al*. 2013; Robinson *et al*. 2015; Kelling *et al*. 2019). In the current study, we specifically seek to understand the relationships of soil and vegetation variables with natural regeneration in areas under restoration, but we strongly recommend that efforts be made to include a greater number of environmental variables in future studies, seeking better understanding of the establishment of natural regeneration in restoration areas. In addition, we also highlight the need to carry out paired soil analyses in a reference ecosystem and in pine stands to better understand the changes caused in soil attributes.

In summary, the soil variables allowed us to verify that the quality of the soil does not present major limitations to the establishment of native species in the areas of passive restoration post-harvest of pine plantations. The areas under restoration present great richness of regenerating species and the floristic-structural heterogeneity of natural regeneration reflects successional and soil heterogeneity. Despite the low variability of the data explained by the variables (pH, clay, and CC), they exhibited relationships with the floristic-structural pattern of natural regeneration. These soil-plant relationships contribute to understanding the process of the initial establishment of regeneration of native species in restoration areas in Araucaria Forest.

Under the evaluated conditions, there were no changes to the soil caused by historical use by pine stands. Therefore, the physiochemical conditions of the soils in the areas under passive restoration post-harvest of *P. taeda* are suitable for the establishment and tree-shrub regeneration of native species of Araucaria Forest.

The soil (pH and clay) and vegetation (CC) variables are related to the floristic-structural composition of the initial natural regeneration of areas under passive restoration, despite explaining only a small variation in the observed heterogeneity. In general, regenerant tree species (*e.g.*, *A. rugulosa*, *M. oxysepala*, *E. pyriformis*) are associated with sites where high canopy cover and soils of greater acidity and clay content predominate, while pioneer-shrub species (*e.g.*, *G. serrata*, *A. laetevirens* and *Baccharis* spp.), are more predominant in open sites with less clayey and less acidic soils.

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Data availability statement

In accordance with Open Science communication practices, the authors inform that all data are available within the manuscript.

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