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Structure, Biomass and Diversity of a Late-Successional Subtropical Atlantic Forest in Brazil

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Abstract

The highly biodiverse Atlantic Forest has been heavily exploited and its remnant areas, which are mostly composed of secondary forests, cover less than 20% of its original extension. This study analyzed the structure, aboveground biomass (AGB) and species diversity of a secondary evergreen rainforest in the state of Santa Catarina, southern Brazil. Individuals with diameter at breast height ≥ 5 cm on 22 sample plots were measured, totalizing 3.49 hectares of sampled area. A mean AGB of 201.6 Mg ha^{-1} (standard deviation = 35.5) was found; *Hyeronima alchorneoides* and *Miconia cinnamomifolia* represented 29.1% and 7.6% of the community AGB ha^{-1}, respectively. A total of 153 species distributed in 107 genera and 55 families was observed; it was estimated that 121 species (95% confidence interval: [117, 125]) occurred in one hectare. These results highlight the importance of secondary forests for biodiversity restoration/conservation and carbon sequestration.

Keywords: secondary forest, forest carbon, Mata Atlântica, hotspot.

1. INTRODUCTION AND OBJECTIVES

The Atlantic Forest is among the Earth's hotspots for biodiversity conservation, having great levels of tree species endemism (Myers et al., 2000; Lima et al., 2020). Nevertheless, historical and ongoing deforestation reduced its area to less than 20% of its original cover (Ribeiro et al., 2009), and most of its remnants consist of fragmented forests often disturbed by human activities such as selective logging (Schneider et al., 2018), cattle grazing within stands (Pereira et al., 2015), and hunting (Bragagnolo et al., 2019). However, the Atlantic Forest still holds a surprising number of arborescent species

(Lima et al., 2020), many of them with some degree of rarity in nature (Caiafa & Martins, 2010; Oliveira et al., 2019a).

Among the multiple forest types occurring in the Atlantic Forest domain, the evergreen rainforest — 'Floresta Ombrófila Densa' (IBGE, 2012) — stands out as the one with the greatest tree/shrub species richness and longitudinal range (Oliveira-Filho & Fontes, 2000). This forest type is characterized by a canopy composed of numerous tree species, multiple vertical layers, and an abundance of climbers and epiphytes (Roderjan et al., 2002; IBGE, 2012). Regarding tree/shrub species composition, evergreen rainforests have the botanical families Myrtaceae, Fabaceae, Lauraceae, Rubiaceae and Melastomataceae as the

most speciose ones (Oliveira-Filho & Fontes, 2000; Lingner et al., 2015; Brotto et al., 2019).

The state of Santa Catarina is totally inserted in the Atlantic Forest and most likely has the best studied flora among the Brazilian states. A large body of knowledge about its flora was developed based on field surveys carried out since the 1950s (e.g., Veloso & Klein, 1951, 1957, 1959, 1961, 1968; Reitz, 1965; Klein, 1978, 1980, 1984), and more recently by the Forest and Floristic Inventory of Santa Catarina (Vibrans et al., 2020). However, classical studies on structure and diversity of Atlantic Forest remnants are still needed, as stressed by Lima et al. (2015). These authors demonstrated that the existing knowledge on structure of the Atlantic Forest is based solely on sampled areas that altogether represent merely 0.01% of its total remaining area. Moreover, a substantial portion of the results of studies on this topic are registered in non-indexed vehicles, hampering the retrieval of information to carry out ecological analyses at larger scales (Caiafa & Martins, 2007; Lima et al., 2015). Local information on forest structure and diversity is also essential to underpin the sustainable use and restoration of forest resources (Zambiazi et al., 2021), regional biodiversity conservation and monitoring (Gardner, 2010), and payment for ecosystem services, such as carbon sequestration (Alarcon et al., 2017).
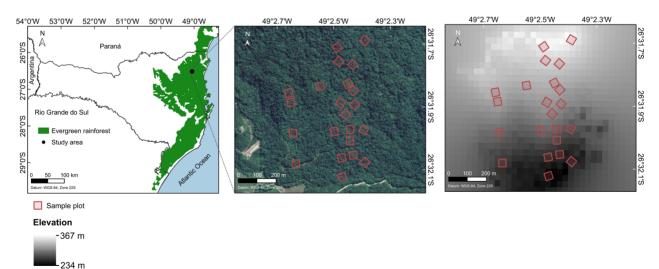
In this context, this study sought to analyze the structure, biomass and timber stocks, and species composition and diversity of a secondary evergreen rainforest stand in the state of Santa Catarina, southern Brazil. Data were gathered over a sampled area of 3.49 ha, which is nearly 4.5 times larger than the average sampled area of studies carried out in the Atlantic Forest (Lima et al., 2015).

2. MATERIALS AND METHODS

2.1. Study area

The study area consists of a 42-ha private property in the state of Santa Catarina, southern Brazil (26°32'01"S, 49°02'30"W), located within the evergreen rainforest region (Figure 1) (Klein, 1978; Oliveira-Filho et al., 2015). Based on historical aerial imagery from 1957 and 1978, it is possible to describe the area as a mosaic of secondary forests in different successional stages (Figures 1, 2 and S1), resulting from the abandonment of agricultural patches and pastures. A small portion of study area was enriched in the late 1970s with seedlings of *Hyeronima alchorneoides*, *Miconia cinnamomifolia*, and *Nectandra* spp. — typical species with economic value of secondary forests in the region. The natural regeneration of non-commercial species nearby the planted seedlings was slashed with a machete in the first years.

According to the Köppen classification, the climate in the study area is classified as Cfa — humid subtropical oceanic climate with hot summers, without dry seasons (Alvares et al., 2013). The average annual temperature varies between 20 and 22 °C, and the average annual rainfall between 1,600 and 1,900 mm; average monthly absolute minimum temperatures may reach –3 °C in the coldest months (Wrege et al., 2012). According to the Brazilian Soil Classification System, two soil types are predominant in the area: *Cambissolo Háplico Tb A moderado* and *Neossolo Litólico A moderado* (Embrapa, 2004). The slope varies between 10 to 40%, and the elevation above sea level between 205 to 426 m.

Figure 1. Study area location within the subtropical evergreen rainforest and location of the sample plots in the study area. The satellite image was acquired in 2021, and the elevation data were retrieved from the SRTM digital elevation model.

Figure 2. Vertical profile of the secondary subtropical evergreen rainforest in the study area.

2.2. Forest inventory data

Forest inventory data were gathered on 21 sample plots, each with an area of 1,600 m² (40 m × 40 m), plus a 40 m × 30 m sample plot, totaling 3.49 ha of sampled area (Figure 1). All living and standing dead trees, palms and tree ferns with diameter at breast height (dbh) ≥ 5 cm on the sample plots had their dbh measured. Species identification was mostly made in the field by trained foresters; taxa not identified in the field were collected and later identified by consulting the Dr. Roberto Miguel Klein Herbarium (FURB) and experts. Species names were verified with the 'flora' R package (Carvalho, 2021), which consults the Flora do Brasil 2020 (2021) database and checks for misspellings or no longer valid names. The sample plot elevation above sea level ranges from 242 to 359 m; it increases from the base of the hillside towards the north direction (Figure 1).

2.3. Data analysis

The aboveground biomass (AGB) for each stem was predicted using the allometric model constructed by Uller et al. (2019) based on 105 individuals harvested in the study area (Eq. 1):

$$\widehat{AGB} = 1.2802e{-}04 \cdot dbh^{2.1642} \cdot h^{0.5072} \cdot \rho^{0.9999} \tag{1}$$

where $\widehat{AGB}$ is the predicted dry aboveground biomass (kg), dbh is the diameter at breast height (cm), h is the total height (m), and ρ is the wood specific gravity (kg m⁻³).

The total height for each stem was predicted through a Korf nonlinear model (Flewelling and Jong 1994) constructed with data from 420 trees that had both their dbh and h measured in the study area: $\hat{h} = 1.30 + 77\,47 \cdot \exp\left(-4.51 \cdot dbh^{-0.34}\right)$; the model has a pseudo-R² of 0.75 and a root mean square error of 2.46 m. The ρ for each species record in the dataset was retrieved from Oliveira et al. (2019b).

Species-specific double-entry (dbh and h) models constructed by Uller et al. (2021) were used to predict the AGB for *Cecropia glaziovii*, *Cyathea* spp. and *Euterpe edulis* individuals, as well as the single-entry (h) model constructed by Moreira-Burger and Delitti (2010) for *Syagrus romanzoffiana*. These models were used because Uller et al. (2021) showed that generic models may yield predictions with strong systematic deviances for species with different growth forms and/or with particular morphological features. The total height of individuals of these species were predicted using species-specific nonlinear models (Table S1).

The total volume (VOL; stem plus branches with diameter ≥ 5 cm) for each stem was predicted through an updated version of the model constructed by Oliveira et al. (2018) based on 419 trees harvested in the study area (Eq. 2):

$$\widehat{VOL} = 4.0987e{-}05 \cdot dbh^{2.2740} \cdot h^{0.7434} \tag{2}$$

where $\widehat{VOL}$ is the predicted total volume (m³), dbh is the diameter at breast height (cm), and h is the total height (m). The total height of each stem was predicted by the model mentioned above.

Means of tree density (ind. ha⁻¹), basal area (m² ha⁻¹), AGB (Mg ha⁻¹), and growing stock volume (VOL; m³ ha⁻¹) were calculated based on plot level predictions scaled to hectare. Non-woody individuals (i.e., tree ferns and palm trees) and *C. glaziovii* individuals were excluded from the calculation of mean VOL ha⁻¹. Means were computed independently considering individuals with dbh ≥ 5 cm and individuals with dbh ≥ 10 cm to allow for comparisons with other studies. It should be mentioned that uncertainty in tree-level model predictions of AGB and VOL was not accounted for in estimates per unit area.

Phytosociological parameters were predicted for each species as per Mueller-Dombois & Ellenberg (2002), namely, absolute density (AD), relative density (RD), absolute dominance (ADo), relative dominance (RDo), absolute frequency (AFq), and relative frequency (RFq). Additionally, the absolute AGB (AAGB) and relative AGB (RAGB) were predicted. The percentage of importance (PI) was calculated as the mean over RD, RDo, RAGB, and RFq. These parameters were predicted considering individuals with dbh ≥ 5 cm.

Based on the observed abundance of individuals of each species, three measures of Hill numbers of order *q* were estimated with the aid of the 'iNEXT' R package (Hsieh et al., 2020): species richness (*q* = 0), Shannon diversity (*q* = 1, exponential of Shannon entropy), and Simpson diversity

(*q* = 2, inverse of Simpson concentration). Rarefaction and extrapolation curves for the Hill numbers were also constructed using the referred package. For the latter curves, a two-fold extrapolation of the reference sample was carried out, as suggested by Chao et al. (2014). In addition, using the 'endpoint' argument of the 'iNEXT' function, Hill numbers of order *q* = 0, *q* = 1 and *q* = 2 were estimated considering 1724 individuals (dbh ≥ 5 cm), which is the estimated mean tree density per hectare for the study area (see below). The estimates were compared to diversity estimates reported by studies in the region that measured one hectare of forest. This analysis provides approximate results because uncertainty in the estimation of mean tree density was not accounted for.

3. RESULTS

3.1. Means of forest attributes per unit area

A mean tree density of 1724 ind. ha⁻¹ (standard deviation [SD] = 364), mean basal area of 32.2 m² ha⁻¹ (SD = 4.9), mean AGB of 201.6 Mg ha⁻¹ (SD = 35.5), and mean VOL of 320.7 m³ ha⁻¹ (SD = 77.3) were found, considering all living individuals with dbh ≥ 5 cm. Considering all living individuals with dbh ≥ 10 cm, a mean tree density of 773 ind. ha⁻¹ (SD = 151), mean basal area of 27.8 m² ha⁻¹ (SD = 4.6), mean AGB of 187.8 Mg ha⁻¹ (SD = 35.2), and mean VOL of 306.8 m³ ha⁻¹ (SD = 78.1) were found. Medians and quartiles of sample plot predictions are shown in Figure 3.
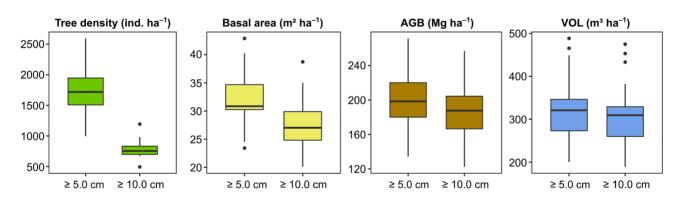

Figure 3. Medians and quartiles of sample plot predictions for different forest attributes considering two minimum dbh inclusion criteria.

3.2. Forest structure

H. alchorneoides, Cyathea delgadii, Euterpe edulis, M. cinnamomifolia, and *Clusia criuva* were the five species with the greatest percentage of importance (PI) (Table 1). The first three species were found on all sample plots, whereas *M. cinnamomifolia* was found on 82% of the sample plots. *C. criuva* was abundant in the less developed parts of the community, occurring on about one-third of the sample plots (Table 1). *H. alchorneoides* and *M. cinnamomifolia* represented 21.2% and 6.1% of the total basal area ha^{-1}, respectively. The two species together represented 36.7% of the total AGB ha^{-1} (Table 1). Although *Nectandra membranacea* – a typical species of subtropical secondary evergreen rainforests – was not among the species with the greatest absolute density, it was observed on every sample plot. The understory shade-tolerant species *Psychotria nuda* and *Psychotria suterella* were observed on almost every sample plot, and together represented 7.8% of the total tree density ha^{-1}. Notably, the climax species *Virola bicuhyba* and *Cabralea canjerana* were amidst the 10 species with the largest PI; the former was the fourth tree species with the greatest AGB ha^{-1} (Table 1). Phytosociological parameters for all species are found in Supplementary Material (Table S2).

The stem dbh distribution of the entire community followed a negative exponential distribution (Figure 4). *M. cinnamomifolia* had a unimodal stem dbh distribution, where small individuals (dbh < 10 cm) were scarce. In turn, *H. alchorneoides* had similar numbers of stems per dbh class up to the intermediate classes, with a major drop in number of stems in the subsequent classes.

Table 1. Phytosociological parameters per species.

Species	AD	RD	ADo	RDo	AAGB	RAGB	AFq	RFq	PI
Hyeronima alchorneoides Allemão	147	8.44	6.93	21.15	58.67	29.10	100.00	1.90	15.15
Cyathea delgadii Sternb.	207	11.89	1.49	4.54	2.73	1.35	100.00	1.90	4.92
Euterpe edulis Mart.	222	12.72	1.05	3.20	2.25	1.12	100.00	1.90	4.73
Miconia cinnamomifolia (DC.) Naudin	48	2.78	2.01	6.12	15.36	7.62	81.82	1.56	4.52
Non-identified taxa	44	2.51	1.66	5.06	11.29	5.60	95.45	1.82	3.75
Clusia criuva Cambess.	65	3.75	1.21	3.68	7.08	3.51	31.82	0.61	2.89
Annona dolabripetala Raddi	38	2.17	1.15	3.50	4.79	2.37	90.91	1.73	2.44
Psychotria nuda (Cham. & Schltdl.) Wawra	87	4.96	0.39	1.20	1.15	0.57	100.00	1.90	2.16
Nectandra membranacea (Sw.) Griseb.	25	1.45	0.93	2.85	4.86	2.41	100.00	1.90	2.15
Virola bicuhyba (Schott ex Spreng.) Warb.	30	1.69	0.87	2.66	5.41	2.68	81.82	1.56	2.15
Cabralea canjerana (Vell.) Mart.	37	2.12	0.67	2.05	3.70	1.84	95.45	1.82	1.96
Alchornea triplinervia (Spreng.) Müll.Arg.	23	1.33	0.75	2.30	3.85	1.91	68.18	1.30	1.71
Bathysa australis (A.St.-Hil.) K.Schum.	46	2.61	0.51	1.56	2.16	1.07	81.82	1.56	1.70
Cupania oblongifolia Mart.	23	1.31	0.54	1.66	4.07	2.02	90.91	1.73	1.68
Guapira opposita (Vell.) Reitz	36	2.05	0.43	1.32	1.44	0.71	95.45	1.82	1.48
Casearia sylvestris Sw.	22	1.26	0.47	1.43	3.17	1.57	68.18	1.30	1.39
Psychotria suterella Müll.Arg.	50	2.84	0.21	0.65	0.57	0.28	90.91	1.73	1.38
Miconia formosa Cogn.	27	1.54	0.38	1.17	2.57	1.28	72.73	1.38	1.34
Matayba intermedia Radlk.	14	0.80	0.40	1.22	3.42	1.70	63.64	1.21	1.23
Cedrela fissilis Vell.	10	0.56	0.44	1.35	2.60	1.29	68.18	1.30	1.12
Trichilia lepidota Mart.	19	1.07	0.33	1.00	2.26	1.12	63.64	1.21	1.10
Dead trees	18	1.05	0.54	1.64	0.00	0.00	81.82	1.56	1.06
Schizolobium parahyba (Vell.) Blake	7	0.38	0.53	1.62	2.92	1.45	40.91	0.78	1.06
Myrcia pubipetala Miq.	15	0.89	0.28	0.87	1.91	0.95	77.27	1.47	1.04
Platymiscium floribundum Vogel	15	0.84	0.28	0.85	1.80	0.89	72.73	1.38	0.99
Allophylus petiolulatus Radlk.	24	1.38	0.19	0.59	0.93	0.46	77.27	1.47	0.97
Casearia decandra Jacq.	17	1.00	0.26	0.79	1.98	0.98	54.55	1.04	0.95
Casearia obliqua Spreng.	21	1.22	0.29	0.88	1.68	0.83	40.91	0.78	0.93
Psychotria carthagenensis Jacq.	14	0.82	0.30	0.90	2.06	1.02	45.45	0.87	0.90
Sloanea guianensis (Aubl.) Benth.	17	0.97	0.19	0.59	1.34	0.67	72.73	1.38	0.90
Other species	377	21.67	7.05	21.55	43.59	21.68	2950.24	56.27	30.36
Total	1724	100.00	32.73	100.00	201.61	100.0	5254.79	100.00	100.00

AD = absolute density (ind. ha^{-1}); RD = relative density (%), ADo = absolute dominance (m² ha^{-1}); RDo = relative dominance (%); AAGB = absolute aboveground biomass (Mg ha^{-1}); RAGB = relative aboveground biomass (%); AFq = absolute frequency (%); RFq = relative frequency (%); PI = percentage of importance (%), that is the mean over RD, RDo, RAGB, and RFq.
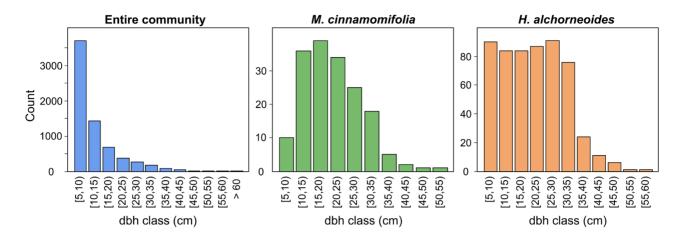
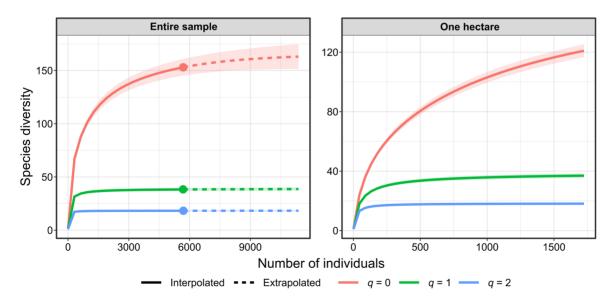**Figure 4.** Stem dbh distributions for the entire community, *M. cinnamomifolia*, and *H. alchorneoides*.

3.3. Species diversity

Among all observed native taxa, 153 were identified at the species level, distributed in 107 genera and 55 families. The families Fabaceae (19 spp.), Myrtaceae (17), Lauraceae (11), Rubiaceae (11) and Euphorbiaceae (7) were the most speciose and represented 42.5% of all taxa identified at the species level.

It was estimated that 121 species (95% confidence interval [CI]: [117, 125]) occurred in one hectare (Figure 5). The exponential of the Shannon diversity, exp(H'), was estimated to be 37 species per hectare (95% CI: [36, 38]), whereas the inverse of Simpson concentration, 1/D, was estimated to be 18

species per hectare (95% CI: [17, 19]) (Figure 5). This means that the community has the same diversity as a community composed of 37 or 18 equally-common species per hectare depending on the metric, which gives different weights to lesser common species (Jost, 2006).

It was estimated that 163 species (95% CI: [152, 175]) would be observed if the reference sample would be extrapolated two-fold. Therefore, on average, 10 new species would be observed if the sample size would be doubled. The exp(H') was estimated to be 39 species (95% CI: [37, 40]) based on the extrapolated sample, whereas the 1/D was estimated to be 18 species (95% CI: [17, 19]) (Figure 5).

Figure 5. Rarefaction and extrapolation curves for Hill numbers of order $q = 0$ (species richness), $q = 1$ (exponential of Shannon diversity), and $q = 2$ (inverse of Simpson concentration).

4. DISCUSSION

4.1. Forest attributes

The mean tree density found in this study was similar to that reported by Maçaneiro et al. (2015) for a mature evergreen rainforest (ERF) remnant in Santa Catarina, where selective logging of *Ocotea catharinensis* ('canela-preta') and other species with economic value was conducted ~85 years ago. On the other hand, they found a greater basal area (40.4 m² ha⁻¹) than us (32.2 m² ha⁻¹), a result that could be attributed to the degree of development of the community they studied, in which the climax species *Sloanea guianensis*, *Euterpe edulis*, *Tapirira guianensis*, *Ocotea aciphylla* and *Vantanea compacta* together represented one-third of total basal area (Maçaneiro et al., 2015). Likewise, Guislon (2017) found a basal area of 60.4 m² ha⁻¹ for a mature ERF within a protected area in Santa Catarina, where *O. catharinensis* and senescent *Alchornea triplinervia* individuals represented nearly half of the total basal area.

Vibrans et al. (2022), based on data (dbh ≥ 10 cm) gathered by the Forest and Floristic Inventory of Santa Catarina (IFFSC), reported a mean basal area of 22.3 m² ha⁻¹ (95% CI: [21.3, 23.3]) for the ERF in the state, which is a substantially smaller value than that we found (27.8 m² ha⁻¹). Using the IFFSC data and the same allometric model employed in this study, a mean AGB of 117.6 Mg ha⁻¹ (95% CI: [109.7, 125.5]) was calculated for the same forest type (unpublished data). Vibrans et al. (2020) asserted that a relevant portion of ERF remnants in Santa Catarina consists of stands with reduced α-diversity and biomass stocks. In fact, the community we studied appears to be in a later succession stage than the average secondary ERF in the state. Although the mean AGB ha⁻¹ we found was larger than the 88th percentile of AGB ha⁻¹ predictions for the IFFSC sample plots in the ERF, Vibrans et al. (2022) highlighted the existence of mature ERF remnants with AGB stocks greater than 300 Mg ha⁻¹ in northern Santa Catarina. Therefore, about two-thirds of the AGB accumulation potential of the remnant we studied has been actualized.

The expressive growing stock volume we found merits comment. The management of secondary forests has been highlighted as a win-win activity that would generate income for landowners and promote forest conservation (Fantini & Siminski, 2016; Zambiazi et al., 2021). According to our data, *H. alchorneoides* and *M. cinnamomifolia* have, on average, 83.0 m³ ha⁻¹ and 23.2 m³ ha⁻¹ of total timber volume in the study area, respectively. Hence, these species have great potential for being managed in secondary forests due to their increased abundance and stocks, good quality wood, among other desirable features (Schuch et al., 2008, 2011; Zambiazi et al., 2021).

4.2. Forest structure and composition

Klein (1980, 1984) discussed several possible successional trajectories of the ERF in Santa Catarina, highlighting *M. cinnamomifolia* as one of the most relevant light-demanding species in early- and mid-successional subtropical ERF stands, often being the most abundant species. Given its requirement for open areas to successfully regenerate and its relatively short life cycle, this species is progressively replaced by *H. alchorneoides*, *Alchornea triplinervia*, among others (Klein, 1980). Accordingly, the distribution of stem dbh we found for *M. cinnamomifolia* suggests that it is being replaced by shade-tolerant species, as small individuals (dbh < 10 cm) were found to be scarce (Figure 4). This species had the seventh largest RD, but still had the second largest RDo (Table 1), indicating the presence of adult/senescent individuals. In fact, Schorn and Galvão (2009) showed that the dynamics of mid-successional subtropical ERFs in Santa Catarina is accelerated by the death of *M. cinnamomifolia* individuals.

Notedly, *H. alchorneoides* was the most representative species in terms of AGB, alone accounting to nearly one-third of the community stock. Although the enrichment with saplings of this species carried out in the late 1970s may have contributed to its current dominance, it was mentioned by Klein (1980) as one of the most important species in late-successional ERFs, and as one of the shade-tolerant species that benefits from the environmental conditions shaped by mature *M. cinnamomifolia* individuals. *H. alchorneoides*, in turn, prepares the environment for *S. guianensis*, which, along with *E. edulis* and other shade-tolerant species, prepares the environment for more selective Lauraceae species, such as *Ocotea catharinensis*, *Ocotea odorifera*, and *Cryptocarya* spp. (Klein, 1980; Maçaneiro et al., 2015; Brotto et al., 2019). Klein (1980) observed that at this late successional stage – that is, when *H. alchorneoides* dominates and *S. guianensis* begins to appear – several Myrtaceae species join the community, a phenomenon we detected in the study area; this family had the second greatest number of species. However, the number of Myrtaceae species observed by Maçaneiro et al. (2015) in 1 ha of mature subtropical ERF is greater than the number we observed in 3.49 ha by a factor of 1.6. Similarly, Caglioni et al. (2015) found more Myrtaceae species in 0.33 ha of subtropical ERF within a protected area than we found. Indeed, this family can be regarded as an indicator of overall species diversity and biological conservation value (Lucas & Bünger, 2015).

Maçaneiro et al. (2015) did not find an expressive density of *H. alchorneoides* (12 ind. ha⁻¹), but rather a great density of *S. guianensis* (107 ind. ha⁻¹), *E. edulis* (442 ind. ha⁻¹), and *Garcinia gardneriana* (66 ind. ha⁻¹) associated with climax

Lauraceae species, which together represented 19% of the community total basal area ha⁻¹. Likewise, Caglioni et al. (2015) found an increased density of *S. guianensis* associated with *E. edulis*, but only 15 ind. ha⁻¹ of *H. alchorneoides*. Lauraceae species represented only 5.6% of the total basal area ha⁻¹ of the community we studied, and *Nectandra membranacea* – a typical soft-wood species of secondary subtropical ERFs – was the most representative (RDo = 2.9%). Overall, these evidences suggest that the community we studied is less developed relative to the communities studied by Veloso & Klein (1968), Klein (1980), Caglioni et al. (2015), Maçaneiro et al. (2015), and Guislon (2017). According to our data, it was predicted that *O. catharinensis* – one of the most important climax species in the region (Veloso & Klein, 1968) – has only 2 ind. ha⁻¹ and represents merely 0.4% of the total AGB ha⁻¹. Klein (1980) stated that *O. catharinensis* would often represent up to one-third or even half of the growing stock volume of pristine subtropical ERF stands. Accordingly, Brotto et al. (2019) found that this species represents ~25% of the total stem volume of a montane ERF remnant within a protected area in the state of Paraná, southern Brazil.

We found that *E. edulis*, one of the most important species composing the intermediate layer of the subtropical ERF (Klein, 1978, 1980), had a smaller density (222 ind. ha⁻¹) than those found in other studies (330 to 645 ind. ha⁻¹; Colonetti et al., 2009; Bosa et al., 2015; Maçaneiro et al., 2015; Melo Júnior et al., 2017). The smaller density we found is related to historical and recent extractivism without permission of the landowner, given that *E. edulis* usually occurs abundantly in humid environments over flat or moderately sloped terrains, such as those found in our study area. The understory species *Psychotria nuda* and *Psychotria suterella*, which are abundant in mature ERF stands dominated by *O. catharinensis*, *S. guianensis* and *E. edulis*, may also be abundant in late-successional forests, as pointed out by Klein (1980). The author argued that their short life cycle and fast regeneration dynamics, in addition to more stable microclimatic conditions within the forest, explain why the understory tends to evolve towards an association of shade-tolerant species in a faster pace relative to the canopy layer.

4.3. Species diversity

Our estimates of species richness and exp(H') per hectare (121 and 37 spp., respectively) are within the expected for late-successional subtropical ERFs; according to the meta-analysis conducted by Maçaneiro et al. (2016) based on 12 studies carried out in the ERF of Santa Catarina, the former measure varies between 106 and 149 species and the latter between 11 to 64 species. The community we studied has a quite similar exp(H') than that found by Maçaneiro et al. (2015) for a mature ERF in Santa Catarina; in terms of species richness though, the community studied by these authors had nearly 20% more species per hectare than we found.

As stressed by Maçaneiro et al. (2016) and Oliveira & Vibrans (2020), the abundance of dominant species often found in old-growth subtropical Atlantic forests is negatively correlated with diversity metrics (e.g., Shannon and Simpson diversity metrics). Therefore, late-successional forests may have greater species diversity than old-growth forests, although the structural complexity, overall plant richness and AGB stocks of the latter are usually greater (Liebsch et al., 2008; Oliveira & Vibrans, 2020; Siminski et al., 2021).

5. CONCLUSIONS

Four conclusions may be drawn from this study. First, the studied subtropical ERF remnant can generally be described as a late-successional forest, given the dominance of the shade-tolerant species *Hyeronima alchorneoides* and the small populations of typical climax Lauraceae species. Second, the remnant has a substantially larger AGB stock than the average for the ERF in Santa Catarina, but still has potential of further accumulation, especially with the recovery of populations of climax species. Third, *H. alchorneoides* and *Miconia cinnamomifolia* accumulated more than one-third of the community AGB ha⁻¹ – an indication of their potential for enrichment plantings aimed to enhance forest productivity. Because of their desirable silvicultural features and market acceptance, these two species represent valuable resources for forest management in the region. Fourth, species richness in the study area is within the expected for secondary forests in the region – that is, more than 100 arborescent species per hectare –, and therefore corroborates the potential of such forests for biodiversity recovery, which is simultaneously achieved with carbon sequestration and other ecosystem services.

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SUPPLEMENTARY MATERIAL

The following online material is available for this article:
Figure S1. Historical aerial imagery from 1957 and 1978 for the study area. Scale: 1:4,500. Datum: WGS-84, UTM Zone 22S.
Table S1. Species-specific nonlinear models to predict total height (ĥ, in meters). The models were constructed using the data collected by the following authors (cited in the manuscript) – Uller et al. (2021) and Moreira-Burger and Delitti (2010). dbh = diameter at breast height (cm).
Table S2. Phytosociological parameters per species. AD = absolute density (ind. ha^{-1}); RD = relative density (%), ADo = absolute dominance (m² ha^{-1}); RDo = relative dominance (%); AAGB = absolute aboveground biomass (Mg ha^{-1}); RAGB = relative aboveground biomass (%); AFq = absolute frequency (%); RFq = relative frequency (%); PI = percentage of importance (%), that is the mean over RD, RDo, RAGB, and RFq.

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