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PHYTOSOCIOLOGICAL PARAMETERS OF THE EPIPHYTE COMMUNITIES IN THE OLD-GROWTH ARAUCARIA FOREST, BRAZIL

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The overtime establishment of epiphyte communities on large old-growth trees has shown that epiphyte numbers tend to rise in relation to the size of their phorophytes. The objective of our study was to perform a floristic survey of vascular epiphytes on last large old-growth trees in a subtropical forest and to compare species richness between conifers and hardwood trees. Nine phorophytes in one of the last remaining old-growth forests were selected for study. Epiphyte locations on the trees were divided into the following four ecological zones: base of the trunk: first 1.30 m above ground; mid-section of the trunk: from the trunk base to the crown base; crown base: 1.30 m below the crown; and crown. We found 30 species of epiphytes, distributed in 21 genera and 11 families. Among the distribution patterns of the epiphytes there were species predominantly occurring in the basal or mid-trunk region of the phorophytes (*Billbergia nutans*); other species occupied the upper portion of the phorophyte, between the mid-trunk and the crown (*Vriesea reitzii*). Six large trees were sufficient to estimate the sample coverage of the reference sample. The vascular epiphyte species richness was similar across large old trees, although *Ocotea porosa* appeared to have a larger crown and more epiphytes than *Araucaria angustifolia*.

Keywords: Araucaria forest, old-growth forest, old-large trees, vascular epiphyte, *Ocotea porosa*.

INTRODUCTION

Large old-growth trees are now rare in the world's forests, yet they play a crucial role in shaping forest ecosystems (Faison 2014, Lindenmayer & Laurance 2016; Lindenmayer et al. 2012, Liu et al. 2019, Scipioni et al. 2019a). Old-growth trees, characterised by their complex crowns and large trunks, provide more significant ecological services, such as carbon storage and climate regulation, compared to smaller trees. These trees provide unique habitat elements that may serve as points of reference for forest ecology management (Scipioni et al. 2022, Sillett & van Pelt 2007) and represent distinctive and essential old-growth forest habitat features for much of the fauna and flora (Pinho et al. 2020, Oliveira-Neto et al. 2022), especially their epiphytic communities that provide sheltering and food for various animals in canopies (Lowman 2004).

Epiphytes are non-parasitic plants that live on other plants, using them as support (Benzing 1990), and are fixed on phorophytes in the most varied places, from trunks to the highest branches (Benzing 2004). Epiphytes may also occur in forest undergrowth, in environments characterised by high humidity and low light (Klein 1979, Raven et al. 2001). Several morphological and physiological adaptations throughout their biological evolution enable epiphytes to survive periods of limited resources and to inhabit all strata of the tree, from the base of trunks to the outermost parts of crowns (Bonnet et al. 2014).

The Araucaria Forest, occurring predominantly in the subtropical climate, is part of the environmental gradient of the Atlantic Forest in Brazil (Oliveira-Filho et al. 2015). It is the most representative natural forest on the southern Brazilian plateau, with less than 25% of its original area size suggestion: now covering less than 25% of its original area. (Vibrans et al. 2013). Although the number of phytosociological studies on vascular epiphytes has significantly increased in recent decades (Ramos et al. 2019), there are currently no studies focused on Araucaria forests in advanced successional stages, particularly those featuring large trees with a diameter at breast height (DBH) of 1.5 meters or more and heights exceeding 30 meters. Such giant communities, with a predominance of *Ocotea porosa* (Nees & Mart.) Barroso (imbuia) and *Araucaria angustifolia* (Bertol.) Kuntze (pinheiro-brasileiro), are indicators of old-growth Araucaria forests (Rufino et al. 2022, Scipioni 2019, Scipioni et al. 2019b). Identification of life forms in the tops of these giant trees is a great challenge, requiring the use of ropes and climbing techniques to access their canopies to understand distribution of epiphytes and their role in maintaining biodiversity in such forests (Benzing 2004). There is currently an increasing focus on the preservation of biodiversity in ancient forests due to their role as biomass reservoirs and the potential to find various forms of epiphyte life, such as lichens and mosses (Gorman et al. 2019).

The spatial distribution of epiphytes is influenced by environmental factors such as variations in micro-habitats and substrates. These variations are further determined by the shape, inclination angle, and diameter of tree trunks and branches (Gorman et al. 2019, Kersten 2010, Petean 2009, Sillett 1999). According to Kersten (2010), epiphytes are components of great importance for biological diversity, not only by the richness of their species and beauty, but also by the number of niches and shelters they create for animals, especially in the canopies, with most active atmospheric flows and physiological processes. However, despite its importance, the study of the canopy of large old trees is still neglected on Brazilian subtropical forests. There is a trend towards an increase in the number of epiphytes relative to the size of trees, because of interactions between epiphytes and spatial areas of the phorophytes. Zotz and Bader (2011) suggests that a rather limited effort in the field, i.e., the sampling of about 6–8 large trees, may yield a satisfactory description of the structure of a species-rich epiphyte community in terms of the total species number when using richness estimators and evenness, in subtropical forests.

Advanced forest succession stages permit prolonged colonisation by vascular epiphytes (Kersten & Kuniyoshi 2009). Epiphyte communities in the canopies of subtropical old-growth forests, with large old trees of *Araucaria angustifolia* and *Ocotea porosa*, have not yet been studied. The objective of our study was to perform a floristic survey of the vascular epiphyte in an old growth Araucaria Forest of southern Brazil. Another question is to know how many of these host trees are needed to characterise the vascular epiphyte community.

MATERIALS AND METHODS

Study site

The study was conducted at the René Frey Ecological Park, which spans a total area of 75.9 hectares and features gently to strongly undulating terrain. Located within the urban area of Fraiburgo in the state of Santa Catarina (27° 1’ 3.26” S, 50° 55’ 46.25” W), Brazil, the park sits at an elevation of approximately 1000 meters above sea level. With the total area of 75.9 ha and gently to strongly undulating relief, it is in the urban area of the city of Fraiburgo, Santa Catarina state (27° 1’3.26”S, 50°55’46.25”W) at an altitude of ca. 1000 m above sea level. The climate of the region, Cfb in the Kḍppen classification, is warm and temperate, with the average annual temperature of 15.3 ºC and the annual mean precipitation of 1746 mm (Alvares et al. 2013). The vegetation is formed essentially by species typical of the Araucaria Forest, i.e., Coniferales and Laurales (Roderjan et al. 2002), with the largest trees represented by *Araucaria angustifolia* (Scipioni et al. 2019b) and *Ocotea porosa*. Several sections of the forest have been opened for hiking trails and clearings for recreational use. The area of our study is bordered by the city, areas of *Pinus* sp. plantations, and apple orchards.

Data collection and division of phorophytes by ecological zones

Large trees usually host by far most epiphytes. Nine large phorophytes were selected in the study area (Flores-Palacios & García-Franco 2006, Zotz & Bader 2011). Individuals of diameter at breast height (DBH) ≥0.90 m were sampled for *Ocotea porosa* and of 1.5 m for *Araucaria angustifolia*, at the minimum distance of 25 meters between them (Kersten & Waechter 2011a). These two species are dominant and the largest trees in the old-growth Araucaria Forest. Collection and identification of epiphyte species were carried out for each phorophyte. Samples of the plants were not identified in the field were sent to the Plant Ecology Laboratory at the Federal University of Santa Catarina (UFSC). Additionally, voucher specimens were deposited in the herbarium of the Curitibanos Campus (CTBS/UFSC) in Brazil. Botanical identifications were carried out by consulting specialised bibliographies (Bonnet et al. 2014), the Flora of Brazil project (Flora do Brasil 2020), and taxonomy specialists. The classification of families of angiosperms follows APG IV (2016), and that of lycophytes and ferns, PPG (2016).

Data collection was conducted through monthly field trips from March 2018 to September 2019. The phorophytes were categorised into four ecological zones, adapted from the classification by Braun-Blanquet et al. (1932) due to the similarity of ecological zonation between the large old trees of the studied species due to the ecological zonation similarities observed among the large old trees of the studied species: 1) base of the main trunk: from ground level to 1.30 m, where the rain water is caught by the vegetation and retained the longest; 2) main trunk: between the base of the trunk and the base of the crown, where, it is exposed to winds and sunlight; 3) crown base: 1.30 m below the crown and protected from direct sunlight in exposed trees and more moist than the main trunk; and 4) crown, including branches and twigs (and reiterated trunks, in conifers), where humus is frequently collected in twig crotches.

In order to sample epiphytes in the crowns, the trees were climbed by the researchers. To map epiphytes of the crowns, arborist techniques of the two rope systems (dynamic - pulley or double-rope and static - single rope) were used. Two qualified arborist professionals helped the researchers in climbing the trees (Figure 1). Treetops were accessed by launching anchor lines over robust branches of the crown, using an aluminum arrow crossbow or a Big Shot® line launcher. A fishing line was attached to the iron tip of the arrow and mounted on a reel attached to the front of the crossbow. The Big Shot line launcher was equipped with weights (200 g) on the nylon rope (2 mm). The nylon line was used to pull a thinner rope, which subsequently facilitated the deployment of an 11 mm, 30 KN semi-static climbing rope over the branches. A pulley was attached near the top of the tree with a webbing sling through which the climbing rope was passed, reaching the ground along two paths on opposite sides of the crown. By double-tying the midpoint of the rope above the pulley, and utilising arborist-style rope lanyards, a team consisting of one climber and two researchers was able to access all areas of the crown effectively (Jepson 2000, Pelt & Sillett 2008). Between daily climbing sessions on the same tree, the rope was replaced with a nylon line.

Data analysis

The sampling sufficiency was calculated through the rarefaction index, the saturation of the sampling curve, and the sample completeness curve, using iNEXT Online - software for interpolation and extrapolation of species diversity (Chao et al. 2016) was used to perform the species accumulation curve and sample coverage (Chao et al. 2014), based on the abundance data and diversity order for species richness. Based on the number of 1000 randomisations, the confidence interval of the analysis was 95%. Sampling sufficiency was defined for interpolation and extrapolation of diversity species for all phorophytes, *Araucaria angustifolia* and *Ocotea porosa* trees. According to the degree of dependence on the phorophyte, following Benzing (1990), the species were classified as: characteristic holoepiphyte (HLC), facultative holoepiphyte (FHL), accidental holoepiphyte (AHL), primary hemiepiphyte (HMP), secondary hemiepiphyte (SHM), and facultative epiphyte (FE). Venn plots were used to characterise distributions of species richness

Figure 1 Climbing trees for the vascular epiphyte survey, *Araucaria angustifolia* trees (A–D), launching a climbing line with a big shot (E), arborists with their communication and personal protective gear (F), *Ocotea porosa* trees (G–H)

by ecological zone of the phorophyte species and in the total sampling.

The quantification of presence of epiphytes was performed by point-scoring, according from Kersten and Waechter (2011b): 1 - very small and isolated individuals; 3 - few small individuals; 5 - average-size individuals, or many small individuals; 7 - large individuals or many medium-size individuals; 10 - very large individuals or many large individuals. Quantitative evaluation of epiphyte species was conducted using absolute and relative frequencies on individual host trees (FAi, FRi); the value of epiphyte importance (Vei) was calculated using both types (FRi and FRj) of relative frequency (Waechter 1998), as follows: $FAi = (Nfi / Nfa).100$; $FRi = (Nfi / \Sigma Nfi).100$; $FAj = (Sfi / Sfa).100$; $FRj = (Sfi / \Sigma Sfi).100$ and $VEI = (FRi + FRj) / 2$, where Nfi is the number of host trees occupied by the epiphyte species *i*; Nfa the total number of host trees species in the sample; Sfi the number of host trees occupied by the epiphyte species *i*; Sfa the total number host trees species in the sample; and the value of epiphyte importance in %. These parameters translate the species capacity by means of reproduction and dispersion in the environment (FRi), and their capacity to colonize different substrata (FRj), which in turn express themselves in the ecological importance of each species (Vei) (Kersten & Waechter 2011b, Waechter 1998). The ecological importance of a species is often assessed by its role within an ecosystem, which can be influenced by both its reproductive and dispersal abilities. Species that can reproduce prolifically and disperse widely tend to have a more significant impact on their ecosystems, contributing to biodiversity and ecosystem resilience. Conversely, species with limited dispersal capabilities may be more vulnerable to habitat fragmentation and environmental changes (Quaresma et al. 2017, Abdelaal et al. 2024) for which only two previous studies have been published. We performed a group comparative analysis for the number of vascular epiphytes species by comparing the species of trees. The statistical analyses included a descriptive analysis of the data and a data normality test. Therefore, the independent samples t-test (parametric) was performed to test the hypothesis (*Araucaria* ≠ *Ocotea*). The analysis was conducted using Jamovi software (Jamovi 2022).

RESULTS

Floristic composition

The vascular epiphyte community was represented by 11 families, 19 genera and 30 species. Polypodiaceae and Piperaceae were the richest families, with 9 (30%) and 6 (20%) species, respectively. *Peperomia* (6 sp.), *Pleopeltis* (4 sp.) and *Pecluma* (3 sp.) were the most represented genera (Table 1). Judging by the sample-size-based rarefaction, extrapolation sampling curve, and sample completeness curve, the vascular epiphyte representation was sufficiently sampled in the sample coverage by the number of observed species (30 sp.; default level = 0.95), representing 97% of the species diversity in nine large old trees. From the sixth phorophytes sampled, the species diversity of vascular epiphytes can be considered a sufficient sample, representing 95% of the species in the old-growth Araucaria Forest. Epiphytic species observed in *Araucaria angustifolia* and *Ocotea porosa* trees were, respectively, 25 ± 10.47 sp. and 23 ± 4.34 sp., with 89% and 96% of the sample coverage estimator of the reference sample (Figure 2A & 2B).

Holoepiphytes (27 species, 90%) and angiosperms (18 species; 60%) were the dominant categories of the epiphyte vascular community on giant trees in the Araucaria Forest. A pioneer shrub species (*Urera baccifera* (L.) Gaudich. ex Wedd.) was found at the base of the araucaria trunks (Table 1). At the base of large trees, there is an environment of opportunity for pioneer plants with substrate and light, due to their size, high crowns, and extensive buttressing with thick and cracked bark.

Ecological zones and distribution of epiphytes

The number of epiphyte species per phorophyte was 13.3 ± 3.0. *Ocotea porosa* (13.8 ± 3.2) tends to have greater numbers compared to *Araucaria angustifolia* (12.7 ± 3.2), with 18 species of vascular epiphytes on a single tree, against 15 on *Araucaria angustifolia*. There was no difference in species richness between the two ($p = 0.639$; $\alpha = 0.05$), though they have different biological structures in crowns and anatomy. *Araucaria angustifolia* has a straight cylindrical trunk, with horizontal branches and a chalice-shaped crown, while *Ocotea porosa*, of lower height, has a greater number of inclined vertical branches. Also, due to denser crowns in certain large *Ocotea porosa*, and reiterated trunks of *Araucaria angustifolia*, there is lower incidence of sunlight in of their ecological zones, enabling survival of epiphyte species not tolerant of direct sunlight, such as species of *Peperomia*.

Of the 30 epiphyte species recorded on all the studied phorophytes, 13 were non-specific, occurring in all the ecological zones. Of those occupying only one ecological zone, six were recorded in the trunks and three in the crown (Figure 3). Separated by the phorophyte species, 25 were recorded for *Araucaria angustifolia*, of which 7 were common to all ecological zones. Separated by specific ecological zones, 9 species were at the trunk base and 3 in the crown. *Ocotea porosa* had 23 species, nine of which are common to the four ecological zones and, notably, three exclusives to the crown.

Among the distribution patterns of the epiphytes there were species predominantly occurring in the basal or mid-trunk region of the phorophytes (e.g., *Billbergia nutans* H.Wendl. ex Regel, *Campyloneurum nitidum* C.Presl, *Selaginella* sp., *Rumohra adiantiformis* (G.Forst.) Ching, *Sinningia douglasii* (Lindl.) Chautems, *Pecluma recurvata* (Kaulf.) M.G.Price); other species more frequently occupied the upper portion of the phorophyte, between the mid-trunk and the crown (e.g., *Vriesea reitzii* Leme & And. Costa, *Tillandsia stricta* Sol. ex Ker Gawl., *Microgramma squamulosa* (Kaulf.) de la Sota, *Bulbophyllum regnellii* Rchb.f.); and several others evenly distributed among all of the ecological zones (e.g., *Peperomia tetraphylla* Hook. & Arn., *Pecluma pectinatiformis* (Lindm.) M.G.Price, *Campyloneurum austrobrasilianum* (Alston) de la Sota). It was not possible to determine the distribution pattern for rare species, observed on one or even three phorophytes. Indicator species analysis did not identify species preference in host trees ($p < 0.01$).

Table 1 Phytosociological parameters of the epiphyte communities in the old-grow Araucaria Forest

Species	NF_i	Nz	Community phytosociological parameters (%)					Phytosociological parameters by ecological zones (%)							
			VI_e	AFi	RF_i	AC_i	RC_i	AFbt	AFmt	AFcb	AFc	RFbt	RFmt	RFbc	RFc
Billbergia nutans H.Wendl. ex Regel	9	21	11.3	100.0	7.5	38.6	15.1	77.8	66.7	55.6	33.3	11.3	9.7	12.5	4.84
Rhipsalis neves-armondii K.Schum.	7	23	10.2	77.8	5.8	37.3	14.6	44.4	66.7	77.8	66.7	6.5	9.7	17.5	9.68
Campyloneurum nitidum C.Presl	8	15	7.7	88.9	6.7	22.5	8.8	66.7	55.6	11.1	33.3	9.7	8.1	2.5	4.84
Lepismium houlletianum (Lem.) Barthlott	6	14	6.7	66.7	5.0	21.6	8.5	44.4	44.4	11.1	55.6	6.5	6.5	2.5	8.06
Pleopeltis hirsutíssima (Raddi) de la Sota	8	16	5.9	88.9	6.7	13.0	5.1	22.2	66.7	22.2	66.7	3.2	9.7	5.0	9.68
Vriesea reitzii Leme & And. Costa	5	11	5.6	55.6	4.2	18.2	7.1	11.1	33.3	22.2	55.6	1.6	4.8	5.0	8.06
Tillandsia stricta Sol. ex Ker Gawl	7	20	5.6	77.8	5.8	13.6	5.3	33.3	66.7	55.6	66.7	4.8	9.7	12.5	9.68
Pecluma recurvata (Kaulf.) M.G.Price	5	8	5.0	55.6	4.2	15.1	5.9	22.2	44.4	11.1	11.1	3.2	6.5	2.5	1.61
Microgramma squamulosa (Kaulf.) de la Sota	5	9	4.6	55.6	4.2	12.7	5.0	11.1	22.2	11.1	55.6	1.6	3.2	2.5	8.06
Peperomia tetraphylla Hook. & Arn.	8	16	4.3	88.9	6.7	4.9	1.9	55.6	44.4	44.4	33.3	8.1	6.5	10.0	4.84
Bulbophyllum regnellii Rchb.f.	7	8	4.1	77.8	5.8	6.2	2.4	11.1	11.1	22.2	44.4	1.6	1.6	5.0	6.45
Sinningia douglasii (Lindl.) Chautems	4	7	3.3	44.4	3.3	8.3	3.3	44.4	22.2	0.0	11.1	6.5	3.2	0.0	1.61
Selaginella sp.	5	9	3.1	55.6	4.2	5.2	2.1	55.6	33.3	11.1	0.0	8.1	4.8	2.5	0.00
Pecluma pectinatiformis (Lindm.) M.G.Price	5	8	2.8	55.6	4.2	3.7	1.4	22.2	22.2	22.2	22.2	3.2	3.2	5.0	3.23
Campyloneurum austrobrasilianum (Alston) de la Sota	3	5	2.8	33.3	2.5	7.7	3.0	11.1	11.1	22.2	11.1	1.6	1.6	5.0	1.61
Rumohra adiantiformis (G.Forst.) Ching	4	6	2.5	44.4	3.3	4.3	1.7	33.3	22.2	0.0	11.1	4.8	3.2	0.0	1.61
Pleopeltis mínima (Bory) J.Prado & R.Y.Hirai	4	6	2.3	44.4	3.3	3.1	1.2	0.0	22.2	11.1	33.3	0.0	3.2	2.5	4.84
Lepismium warmingianum (K.Schum.) Barthlott	2	4	2.2	22.2	1.7	7.1	2.8	0.0	22.2	22.2	0.0	0.0	3.2	5.0	0.00
Asplenium gastonis Fée	2	2	1.4	22.2	1.7	3.1	1.2	0.0	0.0	0.0	22.2	0.0	0.0	0.0	3.23
Tradescantia sp.	3	3	1.4	33.3	2.5	0.9	0.4	33.3	0.0	0.0	0.0	4.8	0.0	0.0	0.00
Tillandsia tenuifolia L.	2	2	1.2	22.2	1.7	1.9	0.7	0.0	0.0	0.0	22.2	0.0	0.0	0.0	3.23

continued

Table 1 Continued

Species	NF_i	Nz	Community phytosociological parameters (%)					Phytosociological parameters by ecological zones (%)							
			VI_e	AFi	RF_i	AC_i	RC_i	AFbt	AFmt	AFcb	AFc	RFbt	RFmt	RFbc	RFc
Peperomia catharinae Miq.	2	3	1.0	22.2	1.7	0.9	0.4	22.2	11.1	0.0	0.0	3.2	1.6	0.0	0.00
Pleopeltis pleopeltidis (Fée) de la Sota	2	2	1.0	22.2	1.7	0.6	0.2	11.1	0.0	0.0	11.1	1.6	0.0	0.0	1.61
Urera bacífera (L.) Gaudich. ex Wedd.	1	1	0.8	11.1	0.8	2.2	0.8	11.1	0.0	0.0	0.0	1.6	0.0	0.0	0.00
Pleopeltis pleopeltifolia (Raddi) Alston	1	2	0.8	11.1	0.8	1.9	0.7	0.0	0.0	11.1	11.1	0.0	0.0	2.5	1.61
Aechmea recurvata (Klotzsch) L.B.Sm.	1	1	0.7	11.1	0.8	1.5	0.6	0.0	0.0	0.0	11.1	0.0	0.0	0.0	1.61
Peperomia pereskiaefolia (Jacq.) Kunth	1	1	0.5	11.1	0.8	0.3	0.1	11.1	0.0	0.0	0.0	1.6	0.0	0.0	0.00
Peperomia trineuroides Dahlst.	1	1	0.5	11.1	0.8	0.3	0.1	11.1	0.0	0.0	0.0	1.6	0.0	0.0	0.00
Peperomia glabela (Sw.) A.Dietr.	1	1	0.5	11.1	0.8	0.3	0.1	11.1	0.0	0.0	0.0	1.6	0.0	0.0	0.00
Peperomia trineura Miq.	1	1	0.5	11.1	0.8	0.3	0.1	11.1	0.0	0.0	0.0	1.6	0.0	0.0	0.00

Nfi = number of host trees occupied by the epiphyte species, Nz = number of phorophyte zones occupied by the epiphyte species, Vei = value of epiphytic importance, AFi = Absolute Frequency, RFi = Relative Frequency, ACi = Average Estimate of Absolute Coverage, RCi = Average Relative Coverage Estimate, AFbt = Absolute frequency on the base of the trunk, AFmt = Absolute frequency on the main trunk, AFbc = Absolute frequency on the base crown, AFc = Absolute frequency on the crown, RFbt = Relative frequency on the base trunk, RFmt = Relative frequency on the main trunk, RFbc = Relative frequency on the base crown, RFc = Relative frequency on the crown

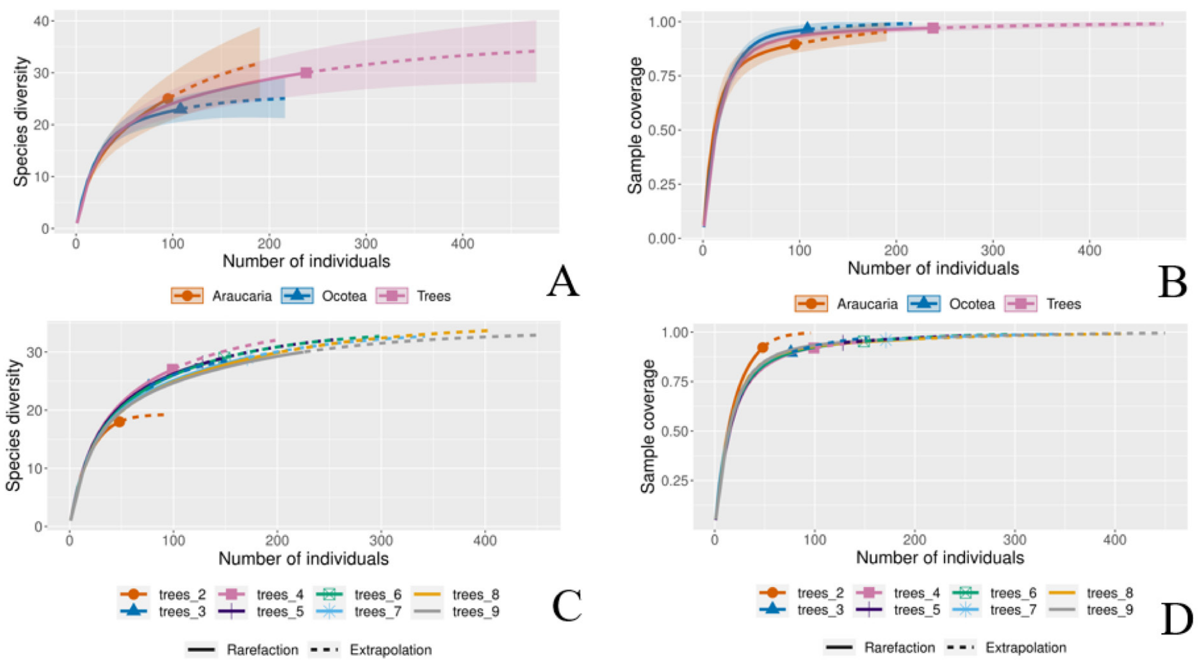

Figure 2 The rarefaction and sample sufficiency extrapolation curves based on the sample size: Araucaria: *Araucaria angustifolia* (n = 4 trees, code = Ara), Ocotea: *Ocotea porosa* (n = 5 trees, code = Oco) and all trees (n = 9, Trees, tree_x amount of phorophytes in the analysis). Sample-size-based rarefaction and extrapolation sampling curve (2A & 2C) and sample completeness curve (2B & 2D). Sample size (continuous line) and extrapolation (dashed line), with 95% confidence intervals represented by the shaded regions.

Table 2 Species diversity of vascular epiphytes on large old-growth trees

Quantity of trees	1	2	3	4	5	6	7	8	9
n	34	48	76	99	128	149	171	203	225
S. obs	16	18	24	27	28	29	29	30	30
SC	0.8936	0.9217	0.8965	0.9200	0.9458	0.9535	0.9594	0.9658	0.9735

n = number of observed individuals in the reference sample (sample size), S. obs = number of observed species in the reference sample, SC = estimator of the sample coverage of the reference sample

Estimate of species coverage area showed the predominance of very small individuals at the base of the trunk (10 spp.), a total of 24 species in this ecological zone. Nineteen species were found on the main trunk, with most being medium-sized individuals, while eight species consisted of small individuals grouped together. At the base of the crown, seventeen species of variable size and coverage area were found. Of the twenty-one species present in the crown, nine were medium-sized or small individuals in clumps, with a wide coverage area (Table 1). Bromeliaceae and Cactaceae were the families that stood out among the angiosperms, with *Billbergia nutans* and *Rhipsalis neves-armondii* K.Schum. obtaining the highest importance values (Table 1). With high values of frequency and coverage, the former is more abundant at the base of the trunk, while the latter is found more frequently at the base of the crown. *Lepismium houlletianum* (Lem.) Barthlott, *Vriesea reitzii*, and *Tillandsia stricta* were also widely distributed species. *Campyloneurum nitidum*, *Pleopeltis hirsutissima* (Raddi) de la Sota, and *Pecluma*

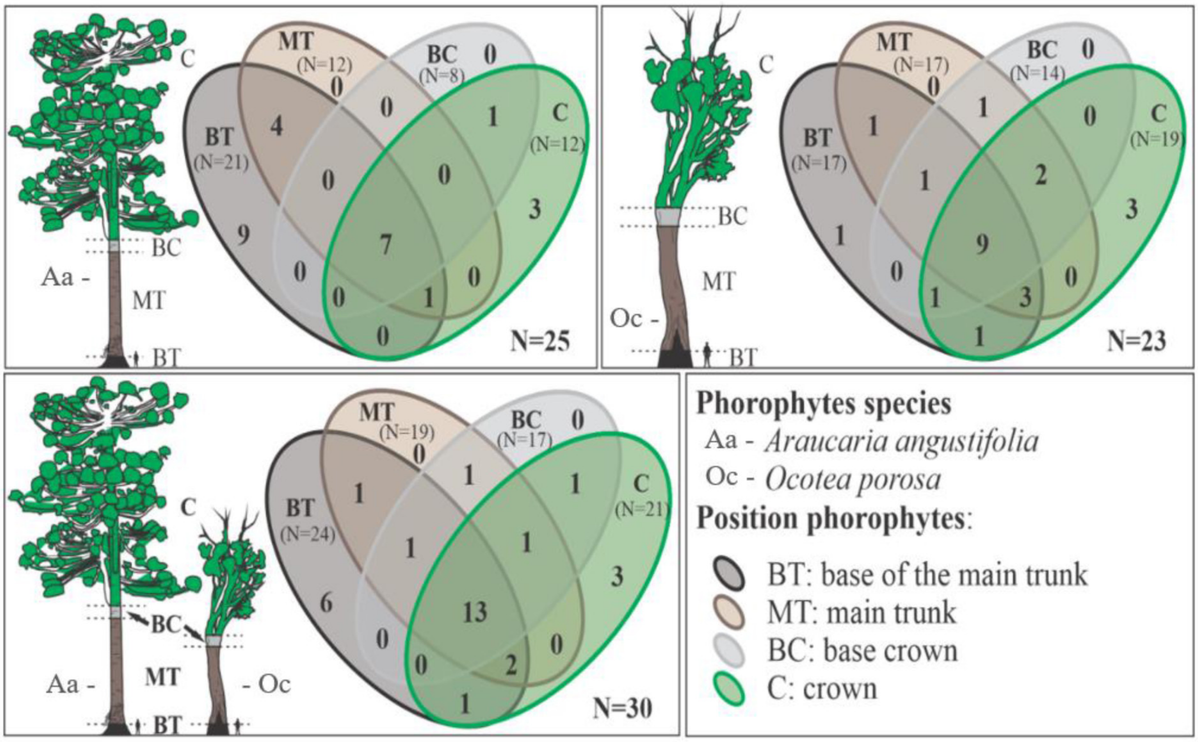

Figure 3 Venn diagram of commonly distributed and exclusive epiphyte species numbers on large old trees (drawing by the author)

recurvata are significant within the fern group due to their ability to form dense clusters across various ecological zones of their phorophytes.

DISCUSSION

Large old trees play an important role in the forest ecosystems, contributing to the vegetation heterogeneity, population dynamics, and essential ecosystem services, such as potential control over the carbon cycle on a global level (Bohn & Huth 2017, Lutz et al. 2018, Mensah et al. 2020, Zhang et al. 2016). Studies have shown that they are highly sensitive to environmental disturbances and play a significant role on the ecosystems respond to these changes (Lutz et al. 2013). In this study, the giant Araucaria trees in an old-growth Araucaria Forest, characterised by their unique architectural and morphological traits, create distinct conditions on their main trunks and reiterated trunks with large diameters that are favorable epiphyte plants, thus contributing significantly to the diversity of epiphytes within the ecosystem. The architectural complexity of these trees provides various microhabitats that support a wide range of epiphyte species, enhancing overall biodiversity (Scipioni et al. 2022).

Due to the difficulties of access requiring the use of specialised climbing techniques for data collection (Lowman 2004), studies addressing diversity of epiphytes on large forest trees are rare (Sillett 1999). Due to the decline in the number of giant trees in the Atlantic Forest of Brazil and recognising them not only as isolated individuals, but as complex systems, we present complementary data that reinforce the need for conservation of old-growth forests and their associated life forms that are under constant threat.

Compared with other surveys of the same forest physiognomy, species richness of vascular epiphyte species on 9 giant phorophytes may be considered high. In a survey of *Araucaria angustifolia*, without criteria for exclusively large phorophyte species, Ruiz (2017) identified 25 species of vascular epiphytes on 30 phorophytes, lower mean species richness per phorophyte. Similarly, Becker et al. (2015), evaluating the presence of vascular epiphytes in an Araucaria Forest, found 27 species distributed on 20 phorophytes of *Araucaria angustifolia* and *Dicksonia sellowiana* Hook. (tree fern). This corroborates Zotz and Bader's (2011) claim that sampling around 6 to 8 large trees can provide a satisfactory analysis of an epiphyte community in terms of the total number of species, α-diversity, and evenness. The absence of indicator species among host old large tree species is the result of the saturation of vascular epiphyte species on them, and consequently, the need for few phorophytes for characterization of vascular epiphytic flora in old-growth Araucaria Forest.

The greater diversity of epiphyte species in our study must be related to the larger size and age of the sampled phorophytes (~250–600 years) (Fichtler et al. 2003, Oliveira et al. 2010). It showed the highest epiphyte richness in a forest of the same physiognomy compared to other studies with the highest number of sampled trees. Although several studies of the Araucaria Forest have shown a greater species richness of the epiphytes, such results are generally influenced by the size of the area and number of sampled phorophytes. Flores-Palacios and García-Franco (2006) have demonstrated a positive and linear relationship between the phorophyte size and the species richness of epiphytes they support, concluding that the relationship is valid both for certain species of phorophytes, and for the tree communities as a whole. However, the positive and linear correlation in large old trees is not observed (DBH > 0.9 m), demonstrating high richness variability (Figure 2C) due to species saturation in certain trees and others with potential space for colonization of new vascular epiphytes. Our sampling effort was based on the size of the phorophytes, performed on nine trees. With the sampling sufficiency, shown in the rarefaction curve, it was possible to demonstrate reduced chances of finding new species in new surveys. However, diversity can vary when large old trees are regularly distributed in the forest and with broader sampling in conifers and hardwoods, which have different size and form of crowns, trunks, and tree bark texture, covering more ecological zones for vascular epiphytic species.

The size and age of the phorophytes determine vertical microclimatic gradients (stratification) within the tree, as well as within the forest as a whole (Shaw 2004), allowing the canopy biota to find larger and heterogeneous colonizable spaces (Benzing 1995, Sillett & van Pelt 2007), as has been observed in *Ocotea porosa*, with more epiphyte species found in the canopy and justifying their association with great species richness (Acebey & Krḍmer 2001, Díaz et al 2010, Mancinelli & Esemann-Quadros 2007, Padilha et al. 2015) on large old trees. Whereas in *Araucaria angustifolia*, the association of species richness was the highest with the base of the trunk of giant individuals due to buttressing (Scipioni et al. 2019b & 2022) and fissured barks are important to certain groups of vascular epiphytes (e.g., bromeliads) (Ceballos et al. 2016).

The prevalence of holoepiphytes, characterised by the epiphyte habit throughout their entire life cycle and by specific attributes for fixation and permanence on the phorophytes (Benzing 1990), over other categories of epiphytes is commonly demonstrated in several studies (Bianchi et al. 2012, Dittrich et al. 1999).

Vertical distribution of epiphytes over the ecological zones of large phorophytes was variable and may be due to such factors as humidity, luminosity, and availability of space, in addition to a greater tree ramification, which augments surface for their attachment and their abundance (Benzing 1990). Predominant species in the basal region are generally more dependent on the understory moisture or more sensitive to luminosity in the canopy.

Among the limiting resources of the canopy, there is also the relative scarcity of nutrients, due to the absent or incipient soil, substrate instability, but mostly to water stress (Lūttge 1989). Studies have shown that humidity is one of the main factors with the greatest influence on the structure of epiphyte communities, especially those of ferns (Becker et al. 2015), corroborating our findings of the lower number of species of this group in the upper portion of large old trees. Nevertheless, an expressive number of epiphyte species occurs in the treetops of old trees exceeding 30 m in height, reinforcing the hypothesis that the vertical division of phorophytes into ecological zones exerts a strong influence on vascular epiphytes, due to their preference for distinct habitats with gradients of light and humidity, with some species occurring exclusively or preferentially in certain segments of the phorophyte (Rogalski & Zanin 2003), as can be seen in Figure 3 and Table 1.

Among the botanical families of epiphytes with higher values of importance on large old trees, with morphophysiological characteristics adapted to conditions of greater physiological stress in acquiring water and nutrients (Benzing 1990) stood out Bromeliaceae, Cactaceae, and Polypodiaceae, confirming other studies carried out in the Atlantic Forest (Gonçalves & Waechter 2002, Kersten & Silva 2001), which showed, besides the above named families, the prominence of Orchidaceae, Piperaceae, and Gesneriaceae. These families are of a wide geographic distribution, with centers of diversity in southern and southeastern Brazil. Not requiring specific conditions for their establishment and being morpho-physiologically very adaptable, they occupy phorophytes with higher frequency, regardless of the ecological zone for establishment. Such mechanisms of capture, storage, and reduction of water loss as photosynthetic metabolism CAM, reduced leaves, presence of trichomes, tissue succulence, poikilohydry, rosette leaves forming tanks, among others (Bonnet et al. 2014), allow for their presence in diverse habitat niches provided by the large old trees.

Subtropical large old-growth trees are characterised by great abundance and species richness of vascular epiphytes. From the base of the trunk to the canopy they have clustered epiphytes of high number of individuals. Large old-growth trees have bromeliad colonies occupying areas greater than 1 m^2 at the base of the trunk, something that is uncommon in trees of sizes less than 1 m in diameter (DBH), representing important phorophytes for the epiphytic community, providing shelter for flora and fauna, carbon sequestration, water retention and nutrient recycling, as well as elements that favor the biodiversity of vascular epiphytes in the old-growth Araucaria Forest. Such trees are rare and endangered in Brazil (Scipioni 2019, Scipioni et al. 2019a & 2019b). Scientific studies and environmental policies to protect these elements of the landscape have become urgent (Lindenmayer et al. 2014). Our study did not find new species of vascular epiphytes on large old-growth trees. However, it has high richness due to the number of individuals sampled when compared to other studies. Large old trees may still harbor new species of plants, fungi and animals and represent a research frontier that should be prioritized in regions with high losses of forest cover (>50%) worldwide.

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REFERENCES

Abdelaal M, Al-Huqail Aa, Alghanem SMS et al. 2024. Population status, habitat preferences and predictive current and future distributions of three endangered Silene species under changing climate. *Frontiers in Plant Science* 15: 1–12. https://doi.org/10.3389/fpls.2024.1336911

Acebey A & Krömer T. 2001. Diversidad y distribucíon vertical de epífitas en losalrededores del campamento Rio Eslabón y de la laguna Chalalán, Parque Nacional Madidi, Dpto. La Paz, Bolivia. *Revista de la Sociedad Boliviana de Botánica* 3: 104–123.

Alvares Ca, Stape Jl, Sentelhas PC et al. 2013. Kḍppen’s climate classification map for Brazil. *Meteorologische Zeitschrift* 22 : 711–728. http//dx.doi.org/10.1127/0941-2948/2013/0507.

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

Becker DFP, Mũller A & Schmitt JL. 2015. Influência dos forófitos *Dicksonia sellowiana* e *Araucaria angustifolia* sobre a comunidade de epífitos vasculares em floresta com araucária. *Floresta* 45: 781–790.

Benzing DH. 1995. The phisical mosaic and plant variety in forest canopies. *Selbyana* 16: 159–168.

Benzing DH. 2004. Vascular Epiphytes. Pp 175–211 in Lowman M & Rinker HB. (eds.*) Forest Canopies* (Second Edition). Elsevier Academic Press, Burlington.

Benzing DH. 1990. *Vascular epiphytes: general biology and related biota.* Cambridge University Press, Cambridge.

Bianchi JS, Bento CM & Kersten RA. 2012. Epífitas vasculares de uma área de ecótono entre as Florestas Ombrófilas Densa e Mista, no Parque Estadual do Marumbi, PR. *Estudos de Biologia* 4: 37–44. https://doi.org/10.7213/estud.biol.6121.

Bohn FJ & Huth A. 2017. The importance of forest structure to biodiversity-productivity relationships. *Royal Society Open Science*, 4: 160521. https://doi.org/10.1098/rsos.160521.

Bonnet A, Caglioni E, Schimitt JL et al. 2014. *Epífitos da Floresta Ombrófila Densa de Santa Catarina: um guia de campo.* Edifurb, Blumenau.

Braun-Blanquet J, Fuller GD & Conard HS 1932. *Plant Sociology: the study of plant communities.* McGraw-Hill book company Inc., New York.

Ceballos SJ, Chacoff NP & Malizia, A 2016. Interaction network of vascular epiphytes and trees in a subtropical forest. *Acta Oecologica* 77: 152–159. https://doi.org/10.1016/j.actao.2016.10.007.

Chao A, Gotelli NJ, Hsieh TC et al. 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. *Ecological Monographs*, 84: 45–67. https://doi.org/10.1890/13-0133.1.

Chao A, Ma K & Hsieh T. 2016. *INEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity*. https://chao.shinyapps.io/iNEXTOnline

Díaz IA, Sieving KE, Peña-Foxon ME et al. 2010. Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: A neglected functional component. *Forest Ecology and Management*, 259: 1490–1501. https://doi.org/10.1016/j.foreco.2010.01.025.

Dittrich VAO, Kozera C & Menezes-Silva S. 1999. Levantamento floristico dos epífitos vasculares do Parque Barigũi, Curitiba, Paraná, Brasil. *Iheringia* 52: 11–21.

Faison EK. 2014. Large old tree declines at broad scales: A more complicated story. *Conservation Letters* 7: 70–71. https://doi.org/10.1111/conl.12075.

Fichtler E, Clark DA & Worbes M. 2003. Age and Long-term Growth of Trees in an Old-growth Tropical Rain Forest, Based on Analyses of Tree Rings and 14C. *Biotropica* 35: 306–317. https://doi.org/10.1111/j.1744-7429.2003.tb00585.x.

Flora Do Brasil 2020. Jardim Botânico do Rio de Janeiro. Reflora - Virtual Herbarium. https://floradobrasil.jbrj.gov.br/reflora/herbarioVirtual/

Flores-Palacios A & García-Franco JG 2006. The relationship between tree size and epiphyte species richness: Testing four different hypotheses. *Journal of Biogeography* 33: 323–330.

Gonçalves CN & Waechter JL 2002. Epífitos vasculares sobre espécimes de Ficus organensisi isolados no norte da planície costeira do Rio Grande do Sul: padrões de abundância e distribuição. *Acta Botanica Brasilica* 16: 429–441.

Gorman AJ, Kerhoulas LP, Polda WT et al. 2019. Epiphyte diversity, abundance, and distribution in an old sitka spruce crown. *Evansia* 36: 12–22. https://doi.org/10.1639/0747-9859-36.1.12.

Jamovi 2022. *The Jamovi project*, version 2.3. [Computer Software]. https://www.jamovi.org

Jepson J. 2000. *The tree climber's companion: a reference and training manual for professional tree climbers*. 2. ed. Beaver Tree Publishing, Longville.

Kersten RA. 2010. Epífitas vasculares - histórico, participação taxonômica e aspectos relevantes, com ênfase na Mata Atlântica. *Hoehnea* 37: 9–38.

Kersten RA & Kuniyoshi YS. 2009. Conservação das florestas na bacia do alto Iguaçu, Paraná – avaliação da comunidade de epífitas vasculares em diferentes estágios serais. *Floresta* 39: 51–66.

Kersten RA & Silva SM. 2001. Composição florística e estrutura do componente epifítico vascular em floresta da planície litorânea na Ilha do Mel, Paraná, Brasil. *Revista Brasileira de Botânica* 24: 213–226.

Kersten RA & Waechter JL. 2011a. Florística e Estrutura de Epífitas Vasculares na Transição entre as Florestas Ombrófilas Densa e Mista da Vertente Oeste da Serra do Mar Paranaense, Brasil. Pp. 479–503 in Felfili, JM et al. (eds.) *Fitossociologia no Brasil: métodos e estudos de casos.* Editora UFV, Viçosa.

Kersten RA & Waechter JL. 2011b. Métodos quantitativos no estudo de comunidades epifíticas. Pp. 231–254 in Felfili, JM et al. (eds). *Fitossociologia no Brasil: métodos e estudos de casos.* Editora UFV, Viçosa.

Klein RM. 1979. Ecologia da flora e vegetação do Vale do Itajaí. *Sellowia*, 31: 1–164.

Lindenmayer Db, Laurance Wf, Franklin JF et al. 2014. New policies for old trees: Averting a global crisis in a keystone ecological structure. *Conservation Letters* 7: 61–69. https://doi.org/10.1111/conl.12013.

Lindenmayer DB & Laurance WF. 2016. The ecology, distribution, conservation and management of large old trees. *Biological Reviews,* 92(3): 1434-1458. http://doi.wiley.com/10.1111/brv.12290.

Lindenmayer DB, Laurance WF & Franklin JF. 2012. Global decline in large old trees. *Science* 338: 1305–1306. http://doi.org/10.1126/science.1231070.

Liu J, Lindenmayer DB, Yang W et al. 2019. Diversity and density patterns of large old trees in China. *Science of The Total Environment* 655: 255–262. https://doi.org/10.1016/j.scitotenv.2018.11.147.

Lowman MD. 2004. Tarzan or Jane? A Short History of Canopy Biology. Pp. 453–464 in: Lowman M. & Rinker HB. (eds.) *Forest Canopies* (Second Edition). Elsevier Academic Press, Burlington.

Lüttge U. 1989. *Vascular Plants as Epiphytes: Evolution and Ecophysiology*. Springered, Berlin and Heidelberg.

Lutz JA, Furniss TJ, Johnson DJ et al. 2018. Global importance of large-diameter trees. *Global Ecology and Biogeography* 27: 849–864. https://doi.org/10.1111/geb.12747.

Lutz JA, Larson AJ, Freund JA, Swanson M & Bible KJ. 2013. The importance of large-diameter trees to forest structural heterogeneity. *PLoS ONE* 8: 1–13. https://doi.org/10.1371/journal.pone.0082784.

Mancinelli WS & Esemann-Quadros K. 2007. Levantamento de epífitos vasculares em quatro forófitos em diferentes altitudes no Morro da Tromba, SC. *Caderno de Iniciação Científica* 9: 205–208.

Mensah S, Salako VK & Seifert T. 2020. Structural complexity and large-sized trees explain shifting species richness and carbon relationship across vegetation types. *Functional Ecology* 34: 1731–1745. https://doi.org/10.1111/1365-2435.13585.

Oliveira JM, Roig FA & Pillar VD. 2010. Climatic signals in tree-rings of Araucaria angustifolia in the southern Brazilian highlands. *Austral Ecology* 35: 134–147.

Oliveira-Filho AT, Budke JC, Jarenkow JA et al. 2015. Delving into the variations in tree species composition and richness across South American subtropical Atlantic and Pampean forests. *Journal of Plant Ecology* 8: 242–260. http:// 10.1093/jpe/rtt058.

Oliveira-Neto NE, Raymundo D, Altomare M, et al. 2022. Large Trees Driving Neighbourhood Assembly Through Simultaneous Facilitative and Competitive Effects in a Woodland Savanna. *Journal* *of Tropical Forest Science* 34: 267–273. https://doi.org/10.26525/jtfs2022.34.3.267.

Padilha PT, Santos R, Custódio SZ et al. 2015. Comunidade epifítica vascular do Parque Estadual da Serra da Furada, sul de Santa Catarina, Brasil. *Ciēncia e Natura* 37: 64–78.

Pelt R Van & Sillett SC. 2008. Crown development of coastal Pseudotsuga menziesii, including a conceptual model for tall conifers. *Ecological Monographs* 78: 283–311.

Petean MP. 2009. *As epífitas vasculares em uma área de floresta ombrófila densa em Antonina, PR. Tese (Doutorado em Engenharia Florestal) - Setor de Ciencias Agrárias,* Universidade Federal do Paraná, Curitiba.

Pinho BX, Peres CA, Leal I & Tabarelli M 2020. Critical role and collapse of tropical mega-trees: A key global resource. *Advances in Ecological Research* 62: 253–294 http://dx.doi.org/10.1016/bs.aecr.2020.01.009.

Ppg IA 2016. Community-derived classification for extant lycophytes and ferns. *Journal of Systematics and Evolution* 54: 563–603. https://doi.org/10.1111/jse.12229.

Quaresma Ac, Piedade MTF, Feitosa YO et al. 2017. Composition, diversity and structure of vascular epiphytes in two contrasting Central Amazonian flood plain ecosystems. *Acta Botanica Brasilica* 31: 686–697. https://doi.org/10.1590/0102-33062017abb0156

Ramos FN, Mortara SR, Monalisa-Francisco N et al. 2019. Atlantic epiphites: a data set of vascular and non-vascular epiphyte plants and lichens from the Atlantic Forest. *Ecology* 100: e02541. https://doi.org/10.1002/ecy.2541.

Raven PH, Evert RF & Eichhorn SE. 2001. *Biologia vegetal.* 6. ed. Guanabara Koogan, Rio de Janeiro.

Roderjan CV, Franklin G, Kuniyoshi YS & Hatschbach GG. 2002. As unidades fitogeográficas do estado do Paraná, Brasil. *Ciēncia & Ambiente* 24: 75–92.

Rogalski JM & Zanin EM. 2003. Composição florística de epífitos vasculares no estreito de Augusto César, Floresta Estacional Decidual do Rio Uruguai, RS, Brasil. *Revista Brasileira de Botânica* 26: 551–556.

Rufino DV, Dobner MJR, Scipioni MC et al. 2022. Old-growth and secondary Araucaria Forest characterization. Trees, *Forests and People* 9: 1–13. https://doi.org/10.1016/j.tfp.2022.100306.

Ruiz ECZ. 2017. *Biomassa e flora epifítica de copas de Araucaria angustifolia.* 96p. Master's thesis - Universidade Estadual do Centro-Oeste, Irati.

Scipioni MC, Salomão RP, Vibrans AC et al. 2019a. Decline in giant tree numbers: status report for Santa Catarina state and perspectives for Brazil. *Floresta e Ambiente* 6: 1–5. https://doi.org/10.1590/2179-8087.003919.

Scipioni MC. 2019. Monumental tree trunks as indicators of forest degradation in southern Brazil. *Ciēncia Florestal* 29: 1–14. https://doi.org/10.5902/1980509835588.

Scipioni MC, Higuchi P, Folckink D & Allen CD. 2022. Old-growth structural attributes associated with the last giant subtropical conifers in South America. *Austral Ecology* 47: 1271–1285. https://doi.org/10.1111/aec.13212.

Scipioni MC, Dobner M, Lonchi SJ et al. 2019b. The last giant Araucaria trees in southern Brazil. *Scientia Agricola* 76: 220–226. https://doi.org/10.1590/1678-992X-2017-0264.

Shaw DC. 2004. Vertical organization of canopy biota. Pp. 73–101 in Lowman M. & Rinker HB. (eds.) *Forest Canopies* (Second Edition). Elsevier Academic Press, Burlington.

Sillett SC. 1999. Tree Crown Structure and Vascular Epiphyte Distribution in Sequoia Sempervirens Rain Forest Canopies. *Selbyana* 20: 76–97.

Sillett SC & Van Pelt R. 2007. Trunk Reiteration Promotes Epiphytes and Water Storage in an Old-Growth Redwood Forest Canopy. *Ecological Monographs* 77: 335–359. https://doi.org/10.1890/06-0994.1.

Vibrans AC, Mcroberts RE, Moser P et al. 2013. Using satellite image-based maps and ground inventory data to estimate the area of the remaining Atlantic forest in the Brazilian state of Santa Catarina. *Remote Sensing of Environment* 130: 87–95 http://dx.doi.org/10.1016/j.rse.2012.10.023.

Waechter J L. 1998. Epifitismo vascular em uma floresta de restinga do Brasil Subtropical. *Ciēncia e Natura* 20: 43–66.

Zhang Z, Papaik MJ, Wang X et al. 2016. The effect of tree size, neighborhood competition and environment on tree growth in an old-growth temperate forest. *Journal of Plant Ecology* 10: 970–980. https://doi.org/10.1093/jpe/rtw126.

Zotz G & Bader MYB. 2011. Sampling Vascular Epiphyte Diversity – Species Richness and Community Structure. *Ecotropica* 17: 103–112.