# Vascular epiphytes on large old-growth trees: the influence of ecological zones in epiphyte species composition

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## Abstract

The over time 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 (0.9 - 2.1 m in diameter and 22 - 40 m in height) in one of the last remaining old-growth forests were selected for study. Epiphyte locations on the trees were divided into the following 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 (e.g., *Billbergia nutans*); other species occupied the upper portion of the phorophyte, between the mid-trunk and the crown (e.g., *Vriesea reitzii*). The relationship between size in large old host trees and vascular epiphyte species richness is not positive and linear. Vascular epiphyte species richness by host trees species was indifferent among large old trees species, even though *Ocotea porosa* (hardwood) has an apparently larger crown greater and show more abundance of epiphytes than that of *Araucaria angustifolia* (conifer).

## 1. Introduction

Large old-growth trees in the world's forests are rare today but remain critically important to the structuring of forest ecosystems (Faison, 2014; Lindenmayer et al., 2012; Lindenmayer and Laurance, 2016; Liu et al., 2019; Scipioni et al., 2019b). Old-growth trees, with their complex crowns and big trunks, supply more important ecological services (carbon storage and climate regulation) than smaller ones. These trees provide unique habitat elements that may serve as points of reference for forest ecology management (Scipioni et al., 2022; Sillett and van Pelt, 2007) and represent distinctive and essential old-growth forest habitat features for much of the fauna and flora (Pinho et al., 2020), especially their epiphytic communities that provide sheltering and food for various animals in canopies (Lowman and Rinker, 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 characterized 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 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 (Vibrans et al., 2013). Even though the number of phytosociological studies of vascular epiphytes has significantly increased in recent decades (Ramos et al., 2019), studies of Araucaria forests in an advanced succession stage, with large trees of 1.5 m DBH (diameter at breast height, 1.30 m) and over 30 meters in height, are non-existent. Such giant trees, 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 Vaz et al., 2022; Scipioni, 2019; Scipioni et al., 2019a). 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 also currently a growing concern with the preservation of biodiversity in ancient forests because of their capacity as biomass reservoirs and possibilities of finding in them various forms of epiphyte life (e.g., lichens, mosses) (Gorman et al., 2019).

Environmental factors determining spatial distribution of epiphytes are differences in micro-habitats and substrates, determined by the shape, angulation 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 in the Subtropical Forests of Brazil. 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.

Advanced stages of forest succession allow for a longer period of colonization by vascular epiphytes (Kersten and Kuniyoshi, 2009). Epiphyte communities in the canopies of Subtropical Forests of old-growth, with large old trees of *Araucaria angustifolia* and *Ocotea porosa*, have yet not 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 and compare vascular epiphyte diversity between the two dominant giant tree species. The base of the trunk has many vascular epiphytes in the large old *Araucaria angustifolia* trees, although in a visual pre-analysis it shows less vascular epiphytes in the extension of the main trunk and crown compared to large old *Ocotea porosa* trees. Thus, the study hypothesis is that the distinct structures of trunk and crown between these species of conifer and hardwood in long-lived trees (>250 yr) may present similar diversity of vascular epiphyte species due to the longer colonization time on the trees. Another question is: how many of these host trees are needed to characterize the vascular epiphyte community?

# 2. Materials And Methods

### 2.1 Study site

The study was carried out at the René Frey Ecological Park. 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 (Fig. 1) at an altitude of ca. 1,000 m above sea level. The climate of the region, Cfb in the Koppen classification, is warm and temperate, with the average annual temperature of 15.3ºC and the total annual precipitation of 1,746 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., 2019a) 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 bounded by the city, areas of *Pinus* sp. plantations, and apple orchards.

### 2.2 Data collection and division of phorophytes by ecological zones

Large trees usually harbor by far the majority of epiphytes. Nine large phorophytes were selected in the study area (Flores-Palacios and García-Franco, 2006; Zotz and Bader, 2011). Individuals of diameter at breast height (DBH) equal to or greater than 0.90 m were sampled for *Ocotea porosa* (Nees & Mart.) Barroso and of 1.5 m for *Araucaria angustifolia* (Bertol.) Kuntze (Table 1, Fig.1), at the minimum distance of 25 meters between them (Kersten and 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 not identified in the field were sent to the Plant Ecology Laboratory of the Federal University of Santa Catarina (UFSC), and vouchers were deposited at the herbarium of the Curitibanos Campus (CTBS/UFSC). Botanical identifications were carried out by consulting specialized bibliographies (Bonnet et al., 2014), the Flora of Brazil project (Flora do Brasil 2020, 2020), and taxonomy specialists. The classification of families of angiosperms follows APG IV (2016), and that of lycophytes and ferns, PPG (2016).

Data collection, with monthly field trips, was carried out from March 2018 to September 2019. The phorophytes were divided into the following four ecological zones, adapted from Braun-Blanquet *et al.* (1932) due to the similarity of ecological zonation between the large old trees of the studied species (Fig. 2): 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.

**Table 1** Location, height (H), and diameter (DBH) of the phorophytes selected for sampling of vascular epiphytes at the René Frey Ecological Park, Fraiburgo, SC, Brazil.

| Phorophytes (Code) | DBH (m) | H (m) | Geographic location |
|---|---|---|---|
| *Araucaria angustifolia* (Ara1) | 2.13 | 40.06 | 27°01'03,3" S, 50°55'46" W |
| *Araucaria angustifolia* (Ara2) | 1.89 | 36.5 | 27°01'02,8" S, 50°55'42,7"W |
| *Araucaria angustifolia* (Ara3) | 1.70 | 36.0 | 27°01' 03.2"S, 50° 55' 35.5"W |
| *Araucaria angustifolia* (Ara4) | 1.50 | 28.0 | S27°01'03,4", 50°55'45"W |
| *Ocotea porosa* (Oco1) | 1.86 | 24.4 | 27°01'02,1"S, 50°55'47"W |
| *Ocotea porosa* (Oco2) | 1.75 | 22.2 | 27°01'01.8"S 50°55'43.4"W |
| *Ocotea porosa* (Oco3) | 1.56 | 33.0 | 27°0,1'02,6"S, 50°55'45,6"W |
| *Ocotea porosa* (Oco4) | 1.41 | 20.97 | 27°01'01,7"S, 50º55'43,6"W |
| *Ocotea porosa* (Oco5) | 0.91 | 24.4 | 27°1'3.02"S, 50°55'49.75"W |

To sample epiphytes in the crowns, 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 (Fig. 3). 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 tied to the iron tip of the arrow and was mounted on a reel attached to the front of the crossbow. Big Shot line launcher was armed with weights (200g) on the nylon rope (2 mm). The nylon rope (2 mm) was used to pull a nylon line and then an 11 mm 30 KN semi-static climbing rope over 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 with the use of arborist-style rope lanyards, a team of one climber and two researchers was able to gain access to all parts of the crown (Jepson, 2000; Pelt and Sillett, 2008). Between daily climbing sessions on the same tree, the rope was replaced by a nylon line.

## 2.3 Data analysis

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 randomizations, the confidence interval of the analysis was 95%. Sampling sufficiency was defined for interpolation and extrapolation of species diversity for all phorophytes, *Araucaria angustifolia* trees and *Ocotea porosa* trees.

According to the degree of dependence on the phorophyte, following Benzing (1990), the species were classified as: characteristic holoepíphyte (HLC), facultative holoepíphyte (FHL), accidental holoepíphyte (AHL), primary hemiepíphyte (HMP), secondary hemiepiphyte (SHM), and facultative epiphyte (FE). To characterize distributions of species richness by ecological zone of the phorophyte species and in the total sampling, Venn plots were used.

The quantification of presence of epiphytes was performed by point-scoring, according from Kersten and Waechter (2011): 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: $FAi = (Nfi / Nfa).100$; $FRi = (Nfi / \sum Nfi).100$; $FAj = (Sfi / Sfa).100$; $FRj = (Sfi / \sum Sfi).100$ 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 and Waechter, 2011b; Waechter, 1998).

Ordination analyses were performed to identify preference of vascular epiphytes species in host trees species (Ara and Oco, table 1). Nonmetric Multidimensional Scaling (NMS) used the values frequency of each the vascular epiphytes species by host trees. All species were used in the analysis. Stress in relation to dimensionality (number of axes) was analyzed by the Monte Carlo test with random data from 999 runs. Indicator species analysis (Dufrene and Legendre, 1997) was performed to determine indicator species in the host trees. All analyzes were performed using the PC-Ord 6 program (McCune and Mefford, 2011), according to Peck's recommendations (2010).

# 3. Results

## 3.1 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 3). 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 six 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 (Fig. 4 A, B). From the six 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 (Table 2, Fig. 4 C, D). There is no positive and linear relationship between size in large old host trees and vascular epiphyte species richness and diversity (Fig. 4 E). NMS ordination diagram showing host trees without species grouping pattern between them and the independence of richness and diversity of vascular epiphytes in large old trees (Fig 4 F). Stress in relation to dimensionality resulted in two axes, mean values of the axes: 1 in 37.688 (*p*: 0.0530) and 2 in 13.946 (*p*: 0.1720).

**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.

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) was occasionally found at the base of the araucaria trunks (Table 3). 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.

**Table 3** Families and species of vascular epiphytes on giant trees at the René Frey Ecological Park, Fraiburgo, SC, Brazil, and their ecological categories (E.C.). The life form on the phorophyte: HLC (characteristic holoepiphyte); HMP (primary hemiepiphyte); and FE (facultative epiphyte). (Aa) *Araucaria angustifolia* and (Op) *Ocotea porosa*. Ecological zones: 1. base of the main trunk; 2. main trunk; 3. crown base; 4. crown. Grey mark: presence of the species.

| Family | Species (Herbarium Code - CTBS) | E.C. | Aa | | | | Op | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| LYCOPHYTES and FERNS | | | | | | | | | | |
| Aspleniaceae (1;1) | *Asplenium gastonis* Fée (4578) | HLC | | | | | | | | |
| Dryopteridaceae(2;2) | *Rumohra adiantiformis* (G.Forst.) Ching | HLC | | | | | | | | |
| Polypodiaceae (4;9) | *Campyloneurum austrobrasilianum* (Alston) de la Sota (4587) | HLC | | | | | | | | |
| | *Campyloneurum nitidum* (Kaulf.) C. Presl (4602) | HLC | | | | | | | | |
| | *Microgramma squamulosa* (Kaulf.) de la Sota (4661) | HLC | | | | | | | | |
| | *Pecluma pectinatiformis* M.G.Price (4585) | FE | | | | | | | | |
| | *Pecluma recurvata* (Kaulf.) M.G.Price (4607) | HLC | | | | | | | | |
| | *Pleopeltis hirsutissima* (Raddi) de la Sota (4600) | HLC | | | | | | | | |
| | *Pleopeltis minima* J. Prado & R.Y. Hirai (4586) | HLC | | | | | | | | |
| | *Pleopeltis pleopeltidis* (Fée) de la Sota | HLC | | | | | | | | |
| | *Pleopeltis pleopeltifolia* (Raddi) Alston (4660) | HLC | | | | | | | | |
| Selaginellaceae(1;1) | *Selaginella* sp. P.Beauv. (4620) | HLC | | | | | | | | |

| Family | Species (Herbarium Code - CTBS) | E.C. | Aa | | | | Op | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| ANGIOSPERMS | | | | | | | | | | |
| Bromeliaceae(4;5) | *Aechmea recurvata* (Klotzsch) L.B.Sm. (4664) | HLC | | | | | | | | |
| | *Billbergia nutans* H.Wendl. ex Regel (4631) | HLC | | | | | | | | |
| | *Tillandsia stricta* Sol.ex Ker Gawl. (4654) | HLC | | | | | | | | |
| | *Tillandsia tenuifolia* L. (4638) | HLC | | | | | | | | |
| | *Vriesea reitzii* Leme & A.F.Costa (4655) | HLC | | | | | | | | |
| Cactaceae(2;3) | *Lepismium houlletianum* (Lem.) Barthlott (4621) | HLC | | | | | | | | |
| | *Lepismium warmingianum* (K.Schum.) Barthlott (4603) | HLC | | | | | | | | |
| | *Rhipsalis neves-armondii* K. Schum. (4639) | HLC | | | | | | | | |
| Commelinaceae(1;1) | *Tradescantia* sp. L. emend. M. Pell. (4593, 4594) | HMP | | | | | | | | |
| Gesneriaceae(1;1) | *Sinningia douglasii* (Lindl.) Chautems | HLC | | | | | | | | |
| Orchidaceae(1;1) | *Bulbophyllum regnellii* Rchb.f | HLC | | | | | | | | |
| Piperaceae(1;6) | *Peperomia catharinae* Miq. (4577) | HLC | | | | | | | | |
| | *Peperomia glabella* (Sw.) A.Dietr. | HLC | | | | | | | | |

| Family | Species (Herbarium Code - CTBS) | E.C. | Aa | | | | Op | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| | *Peperomia pereskiiaefolia* (Jacq.) Kunth (4624) | HLC | | | | | | | | |
| | *Peperomia tetraphylla* (G.Forst.) Hook. & Arn. (4630) | HLC | | | | | | | | |
| | *Peperomia trineura* Miq. | HLC | | | | | | | | |
| | *Peperomia trineuroides* Dahlst. (4583) | HLC | | | | | | | | |
| Urticaceae(1;1) | *Urera baccifera* (L.) Gaudich. | FE | | | | | | | | |

### 3.2 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 not found difference in species richness between the two, thought 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 some of their ecological zones, enabling survival of some epiphyte species not tolerant of direct sunlight, such, for example, 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 (Fig. 5). 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 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*, *Campyloneurum nitidum*, *Selaginella* sp., *Rumohra adiantiformis*, *Sinningia douglasii*, *Pecluma recurvata*); other species more frequently occupied the upper portion of the phorophyte, between the mid-trunk and the crown (e.g., *Vriesea reitzii*, *Tillandsia stricta*, *Microgramma squamulose*, *Bulbophyllum regnellii*); and several others evenly distributed among all of the ecological zones (e.g., *Peperomia tetraphylla*, *Pecluma pectinatiformis*, *Campyloneurum austrobrasilianum*). 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 ($p < 0.01$).

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. 19 species were found on the main truck, most of them medium-sized individuals, or small individuals grouped together (8 spp). At the base of the crown, 17 species of variable size and coverage area were found. Of the

21 species present in the crown, nine were medium-sized or small individuals in clumps, with a wide coverage area (Table 3). Bromeliaceae and Cactaceae were the families that stood out among the angiosperms, with *Billbergia nutans* and *Rhipsalis neves-armondii* obtaining the highest importance values (Table 4). With high values of frequency and coverage areas, the former is more abundant at the base of the trunk, while the latter at the base of the crown. *Lepismium houlletianum*, *Vriesea reitzii*, and *Tillandsia stricta* were also widely distributed species. *Campyloneurum nitidum*, *Pleopeltis hirsutissima* and *Pecluma recurvata*, by forming dense clusters in different ecological zones of the phorophytes, were the most important species within the fern group.

Table 4 - Phytosociological parameters of the epiphyte communities in the old-grow Araucaria Forest. 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.

| 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* | 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* | 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* | 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* | 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 hirsutissima* | 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* | 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* | 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* | 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* | 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* | 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* | 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* | 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* | 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* | 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* | 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 minima* | 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* | 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* | 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* | 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 |
| *Peperomia catharinae* | 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* | 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 baccifera* | 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* | 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* | 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* | 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* | 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 glabella* | 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* | 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 |

## 4. 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 and 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 in the way an ecosystem responds to them (Lutz et al., 2013). In this study, araucaria giant trees in an old-growth Araucaria Forest, with their unique set of architectural and morphological characteristics of trees, offer different conditions on base main trunks and reiterated trunks with large diameter that are favorable epiphyte plants, thus contributing to their diversity (Scipioni et al., 2022)

Because of difficulties of access requiring use of specialized 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 recognizing 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 shown in Appendix A (Supplementary Material), 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* (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 (Appendix A). 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 (Fig.1 C) 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 and 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 and Krömer, 2001; Díaz et al., 2010; Mancinelli and 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., 2022, 2019a) and fissured barks are important to certain groups of vascular epiphytes (e.g., bromeliads) (Ceballos et al., 2016).

The prevalence of holoepiphytes, characterized 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 (Lüttge, 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 and Zanin, 2003), as can be seen in Fig. 5 and Table 3.

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 and Waechter, 2002; Kersten and 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 characterized 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.

# Declarations

### Author contributions

MCS: Conceptualization, Methodology, Visualization, Investigation, Formal analysis, Resources, Funding acquisition, Writing-Reviewing and Editing. EAM: Investigation, Formal analysis Writing-Reviewing and Editing. VLSTF: Methodology, Investigation, Writing-Original draft preparation, Formal analysis, Writing-Reviewing. EAM: Methodology, Investigation, Formal analysis Writing-Reviewing and Editing. EC: Methodology, Formal analysis, Visualization, Writing-Reviewing and Editing. VS: Investigation and Writing-Reviewing.

### Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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**Data availability**

Data will be made available on request.

# References

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

Alvares, C.A., Stape, J.L., Sentelhas, P.C., De Moraes Gonçalves, J.L., Sparovek, G., 2013. Köppen's climate classification map for Brazil. Meteorologische Zeitschrift 22, 711–728. https://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. https://doi.org/10.1111/boj.12385

Becker, D.F.P., Müller, A., Schmitt, J.L., 2015. Influência dos forófitos Dicksonia sellowiana e Araucaria angustifolia sobre a comunidade de epífitos vasculares em floresta com araucária. Floresta 45, 781–790. https://doi.org/10.5380/rf.v45i4.37082

Benzing, D.H., 2004. Vascular Epiphytes, in: Lowman, M., Rinker, H.B. (Eds.), Forest Canopies. Academic Press, pp. 175–211. https://doi.org/10.1016/B978-012457553-0/50014-9

Benzing, D.H., 1995. The phisical mosaic and plant variety in forest canopies . Selbyana 16, 159–168.

Benzing, D.H., 1990. Vascular epiphytes: general biology and related biota. Cambridge University Press, Cambridge.

Bianchi, J.S., Bento, C.M., Kersten, R. de A., 2012. Epífitas vasculares de uma área de ecótono entre as Florestas Ombrófilas Densa e Mista, no Parque Estadual do Marumbi, PR. Estudos de Biologia 34. https://doi.org/10.7213/estud.biol.6121

Bohn, F.J., Huth, A., 2017. The importance of forest structure to biodiversity-productivity relationships. R Soc Open Sci 4. https://doi.org/10.1098/rsos.160521

Bonnet, A., Caglioni, E., Schmitt, J.L., Gasper, A.L. de, Andrade, S. de, Grosch, B., Cristofolini, C., Oliveira, C.P.L. de, Lingner, D.V., Stival-Santos, A., Korte, A., Verdi, M., Sevegnani, L., Vibrans, A.C., 2014. Epífitos da Floresta Ombrófila Densa de Santa Catarina: um guia de campo, Inventário Florístico Florestal de Santa Catarina, Vol VI. Edifurb, Blumenau.

Braun-Blanquet, J., Fuller, G.D., Conard, H.S., 1932. Plant Sociology: the study of plant communities. New York and London, McGraw-Hill book company, inc., New York.

Ceballos, S.J., Chacoff, N.P., 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, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K., Ellison, A.M., 2014. Rarefaction and extrapolation with Hill numbers: A framework for sampling and estimation in species diversity studies. Ecol Monogr 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.

Díaz, I.A., Sieving, K.E., Peña-Foxon, M.E., Larraín, J., Armesto, J.J., 2010. Epiphyte diversity and biomass loads of canopy emergent trees in Chilean temperate rain forests: A neglected functional component. For Ecol Manage 259, 1490–1501.

https://doi.org/10.1016/j.foreco.2010.01.025

Dittrich, V.A. de O., Kozera, C., Menezes-Silva, S., 1999. Levantamento floristico dos epífitos vasculares do Parque Barigüi, Curitiba, Paraná, Brasil. Iheringia 52, 11–21.

Dufrene, M., Legendre, P., 1997. Species assemblages and indicator species: the need for a flexible asymmetrical approach. Ecol Monogr 67, 345–366.

Faison, E.K., 2014. Large old tree declines at broad scales: A more complicated story. Conserv Lett 7, 70–71. https://doi.org/10.1111/conl.12075

Fichtler, E., Clark, D.A., 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/10.1646/03027

Flora do Brasil 2020, 2020. Jardim Botânico do Rio de Janeiro [WWW Document].

Flores-Palacios, A., García-Franco, J.G., 2006. The relationship between tree size and epiphyte species richness: Testing four different hypotheses. J Biogeogr. https://doi.org/10.1111/j.1365-2699.2005.01382.x

Gonçalves, C.N., Waechter, J.L., 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 Bot Brasilica 16, 429–441.

Gorman, A.J., Kerhoulas, L.P., Polda, W.T., Kerhoulas, N.J., 2019. Epiphyte diversity, abundance, and distribution in an old sitka spruce crown. Evansia 36, 12. https://doi.org/10.1639/0747-9859-36.1.12

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

Kersten, R. de A., 2010. Epífitas vasculares - histórico, participação taxonômica e aspectos relevantes, com ênfase na Mata Atlântica. Hoehnea 37, 9–38.

Kersten, R. de A., Kuniyoshi, Y.S., 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, R. de A., Silva, S.M., 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, R. de A., Waechter, J.L., 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, in: Felfili, J.M., Eisenlohr, P.V., Melo, M.M. da R.F. de, Andrade, L.A. de, Meira Neto, J.A.A. (Eds.), Fitossociologia No Brasil: Métodos e Estudos de Casos. Ed. UFV, Viçosa, pp. 479–503.

Kersten, R. de A., Waechter, J.L., 2011b. Métodos quantitativos no estudo de comunidades epifíticas, in: Felfili, J.M., Eisenlohr, P.V., Melo, M.M. da R.F. de, Andrade, L.A. de, Meira Neto, J.A.A. (Eds.), Fitossociologia No Brasil: Métodos e Estudos de Casos. Ed. UFV, Viçosa, pp. 231–254.

Klein, R.M., 1979. Ecologia da flora e vegetação do Vale do Itajaí. Sellowia 31, 1–164.

Lindenmayer, D.B., Laurance, W.F., 2016. The ecology, distribution, conservation and management of large old trees. Biological Reviews. https://doi.org/10.1111/brv.12290

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., 2012. Global decline in large old trees. Science (1979) 338, 1305–1306. https://doi.org/10.1126/science.1231070

Lindenmayer, D.B., Laurance, W.F., Franklin, J.F., Likens, G.E., Banks, S.C., Blanchard, W., Gibbons, P., Ikin, K., Blair, D., Mcburney, L., Manning, A.D., Stein, J.A.R., 2014. New policies for old trees: Averting a global crisis in a keystone ecological structure. Conserv

Lett 7, 61–69. https://doi.org/10.1111/conl.12013

Liu, J., Lindenmayer, D.B., Yang, W., Ren, Y., Campbell, M.J., Wu, C., Luo, Y., Zhong, L., Yu, M., 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, M., Rinker, H.B., 2004. Forest Canopies, 2nd ed. Academic Press.

Lowman, M.D., 2004. Tarzan or Jane? A Short History of Canopy Biology, in: Lowman, M., Rinker, H.B. (Eds.), Forest Canopies: Second Edition. Academic Press, pp. 453–464. https://doi.org/10.1016/B978-012457553-0/50030-7

Lüttge, U., 1989. Vascular Plants as Epiphytes: Evolution and Ecophysiology, Springer. ed. Berlin, Heidelberg.

Lutz, J.A., Furniss, T.J., Johnson, D.J., Davies, S.J., Allen, D., Alonso, A., Anderson-Teixeira, K.J., Andrade, A., Baltzer, J., Becker, K.M.L., Blomdahl, E.M., Bourg, N.A., Bunyavejchewin, S., Burslem, D.F.R.P., Cansler, C.A., Cao, K., Cao, M., Cárdenas, D., Chang, L.W., Chao, K.J., Chao, W.C., Chiang, J.M., Chu, C., Chuyong, G.B., Clay, K., Condit, R., Cordell, S., Dattaraja, H.S., Duque, A., Ewango, C.E.N., Fischer, G.A., Fletcher, C., Freund, J.A., Giardina, C., Germain, S.J., Gilbert, G.S., Hao, Z., Hart, T., Hau, B.C.H., He, F., Hector, A., Howe, R.W., Hsieh, C.F., Hu, Y.H., Hubbell, S.P., Inman-Narahari, F.M., Itoh, A., Janík, D., Kassim, A.R., Kenfack, D., Korte, L., Král, K., Larson, A.J., Li, Y., Lin, Y., Liu, S., Lum, S., Ma, K., Makana, J.R., Malhi, Y., Mcmahon, S.M., Mcshea, W.J., Memiaghe, H.R., Mi, X., Morecroft, M., Musili, P.M., Myers, J.A., Novotny, V., de Oliveira, A., Ong, P., Orwig, D.A., Ostertag, R., Parker, G.G., Patankar, R., Phillips, R.P., Reynolds, G., Sack, L., Song, G.Z.M., Su, S.H., Sukumar, R., Sun, I.F., Suresh, H.S., Swanson, M.E., Tan, S., Thomas, D.W., Thompson, J., Uriarte, M., Valencia, R., Vicentini, A., Vrška, T., Wang, X., Weiblen, G.D., Wolf, A., Wu, S.H., Xu, H., Yamakura, T., Yap, S., Zimmerman, J.K., 2018. Global importance of large-diameter trees. Global Ecology and Biogeography 27, 849–864. https://doi.org/10.1111/geb.12747

Lutz, J.A., Larson, A.J., Freund, J.A., Swanson, M.E., Bible, K.J., 2013. The importance of large-diameter trees to forest structural heterogeneity. PLoS One 8. https://doi.org/10.1371/journal.pone.0082784

Mancinelli, W.S., Esemann-Quadros, K., 2007. Levantamento de epífitos vasculares em quatro forófitos em diferentes altitudes no Morro da Tromba, SC. Cad. Inic. Pesq. 9, 205–208.

McCune, B., Mefford, M.J., 2011. PC-ORD. Multivariate Analysis of Ecological Data.

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

Oliveira, J.M., Roig, F.A., Pillar, V.D., 2010. Climatic signals in tree-rings of Araucaria angustifolia in the southern Brazilian highlands. Austral Ecol 35, 134–147. https://doi.org/10.1111/j.1442-9993.2009.02018.x

Oliveira-Filho, A.T., Budke, J.C., Jarenkow, J.A., Eisenlohr, P. v., Neves, D.R.M., 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. https://doi.org/10.1093/jpe/rtt058

Padilha, P.T., Santos Junior, R. dos, Custódio, S.Z., Oliveira, L.C. de, Santos, R. dos, Citadini-Zanette, V., 2015. Comunidade epifítica vascular do Parque Estadual da Serra da Furada, sul de Santa Catarina, Brasil. Ciência e Natura 37, 64–78. https://doi.org/10.5902/2179460x14368

Peck, J.E., 2010. Multivariate Analysis for Community Ecologists: Step-by-step using PC-ORD. Sofware Desing, Glenden Beach.

Pelt, R. Van, Sillett, S.C., 2008. Crown development of coastal Pseudotsuga menziesii, including a conceptual model for tall conifers. Ecol Monogr 78, 283–311. https://doi.org/10.1890/07-0158.1

Petean, M.P., 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, B.X., Peres, C.A., Leal, I.R., Tabarelli, M., 2020. Critical role and collapse of tropical mega-trees: A key global resource. Adv Ecol Res 62, 253–294. https://doi.org/10.1016/bs.aecr.2020.01.009

PPG I, 2016. A community-derived classification for extant lycophytes and ferns. J Syst Evol 54, 563–603. https://doi.org/10.1111/jse.12229

Ramos, F.N., Mortara, S.R., Monalisa-Francisco, N., Elias, J.P.C., Neto, L.M., Freitas, L., Kersten, R. de A., Amorim, A.M., Matos, F.B., Nunes-Freitas, A.F., Alcantara, S., Alexandre, M.H.N., de Almeida-Scabbia, R.J., de Almeida, O.J.G., Alves, F.E., de Oliveira Alves, R.M., Alvim, F.S., de Andrade, A.C.S., de Andrade, S., Aona, L.Y.S., Araujo, A.C., de Araújo, K.C.T., Ariati, V., Assis, J.C., de Azevedo, C.O., Barbosa, B.F., Barbosa, D.E.F., Barbosa, F. dos R., de Barros, F., Basilio, G.A., Bataghin, F.A., Bered, F., Bianchi, J.S., Blum, C.T., Boelter, C.R., Bonnet, A., Brancalion, P.H.S., Breier, T.B., Brion, C. de T., Buzatto, C.R., Cabral, A., Cadorin, T.J., Caglioni, E., Canêz, L., Cardoso, P.H., de Carvalho, F.S., Carvalho, R.G., Catharino, E.L.M., Ceballos, S.J., Cerezini, M.T., César, R.G., Cestari, C., Chaves, C.J.N., Citadini-Zanette, V., Coelho, L.F.M., Coffani-Nunes, J.V., Colares, R., Colletta, G.D., Corrêa, N. de M., da Costa, A.F., da Costa, G.M., Costa, L.M.S., Costa, N.G.S., Couto, D.R., Cristofolini, C., da Cruz, A.C.R., Del Neri, L.A., di Pasquo, M., dos Santos Dias, A., Dias, L. do C.D., Dislich, R., Duarte, M.C., Fabricante, J.R., Farache, F.H.A., de Faria, A.P.G., Faxina, C., Ferreira, M.T.M., Fischer, E., Fonseca, C.R., Fontoura, T., Francisco, T.M., Furtado, S.G., Galetti, M., Garbin, M.L., de Gasper, A.L., Goetze, M., Gomes-da-Silva, J., Gonçalves, M.F.A., Gonzaga, D.R., Silva, A.C.G. e, Guaraldo, A. de C., Guarino, E. de S.G., Guislon, A.V., Hudson, L.B., Jardim, J.G., Jungbluth, P., Kaeser, S. dos S., Kessous, I.M., Koch, N.M., Kuniyoshi, Y.S., Labiak, P.H., Lapate, M.E., Santos, A.C.L., Leal, R.L.B., Leite, F.S., Leitman, P., Liboni, A.P., Liebsch, D., Lingner, D.V., Lombardi, J.A., Lucas, E., Luzzi, J. dos R., Mai, P., Mania, L.F., Mantovani, W., Maragni, A.G., Marques, M.C.M., Marquez, G., Martins, C., Martins, L. do N., Martins, P.L.S.S., Mazziero, F.F.F., Melo, C. de A., de Melo, M.M.F., Mendes, A.F., Mesacasa, L., Morellato, L.P.C., Moreno, V. de S., Muller, A., Murakami, M.M. da S., Cecconello, E., Nardy, C., Nervo, M.H., Neves, B., Nogueira, M.G.C., Nonato, F.R., de Oliveira-Filho, A.T., de Oliveira, C.P.L., Overbeck, G.E., Marcusso, G.M., Paciencia, M.L.B., Padilha, P., Padilha, P.T., Pereira, A.C.A., Pereira, L.C., Pereira, R.A.S., Pincheira-Ulbrich, J., Pires, J.S.R., Pizo, M.A., Pôrto, K.C., Rattis, L., Reis, J.R. de M., Reis, S.G. dos, da Rocha-Pessôa, T.C., Rocha, C.F.D., Rocha, F.S., Rodrigues, A.R.P., Rodrigues, R.R., Rogalski, J.M., Rosanelli, R.L., Rossado, A., Rossatto, D.R., Rother, D.C., Ruiz-Miranda, C.R., Saiter, F.Z., Sampaio, M.B., Santana, L.D., Santos, J.S. dos, Sartorello, R., Sazima, M., Schmitt, J.L., Schneider, G., Schroeder, B.G., Sevegnani, L., Júnior, V.O.S., da Silva, F.R., da Silva, M.J., Silva, M.P.P., Silva, R.G., Silva, S.M., Singer, R.B., Siqueira, G., Soares, L.E., de Sousa, H.C., Spielmann, A., Tonetti, V.R., Toniato, M.T.Z., Ulguim, P.S.B., van den Berg, C., van den Berg, E., Varassin, I.G., da Silva, I.B.V., Vibrans, A.C., Waechter, J.L., Weissenberg, E.W., Windisch, P.G., Wolowski, M., Yañez, A., Yoshikawa, V.N., Zandoná, L.R., Zanella, C.M., Zanin, E.M., Zappi, D.C., Zipparro, V.B., Zorzanelli, J.P.F., Ribeiro, M.C., 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, P.H., Evert, R.F., Eichhorn, S.E., 2001. Biologia vegetal, 6th ed. Guanabara Koogan, Rio de Janeiro.

Roderjan, C.V., Galvão, F., Kuniyoshi, Y.S., Hatschbach, G.G., 2002. As unidades fitogeográficas do estado do Paraná, Brasil. Ciencia & Ambiente 24, 75–92.

Rogalski, J.M., Zanin, E.M., 2003. Composição florística de epífitos vasculares no estreito de Augusto César, Floresta Estacional Decidual do Rio Uruguai, RS, Brasil. Revista Brasil. Bot. 26, 551–556.

Rufino Vaz, D., Dobner, M., Callegari Scipioni, M., Nicoletti, M.F., Arce, J.E., 2022. Old-growth and secondary Araucaria Forest characterization. Trees, Forests and People 9. https://doi.org/10.1016/j.tfp.2022.100306

Ruiz, E.C.Z., 2017. Biomassa e flora epifítica de copas de Araucaria angustifolia (Master's thesis). Universidade  Estadual do Centro-Oeste, Irati.

Scipioni, M.C., 2019. Monumental tree trunks as indicators of forest degradation in southern Brazil. Ciência Florestal 29, 1–14. https://doi.org/10.5902/1980509835588

Scipioni, M.C., Dobner, M., Longhi, S.J., Vibrans, A.C., Schneider, P.R., 2019a. The last giant Araucaria trees in southern Brazil. Sci Agric 76, 220–226. https://doi.org/10.1590/1678-992x-2017-0264

Scipioni, M.C., Higuchi, P., Fockink, G.D., Allen, C.D., 2022. Old-growth structural attributes associated with the last giant subtropical conifers in South America. Austral Ecol 47, 1271–1285. https://doi.org/10.1111/aec.13212

Scipioni, M.C., Salomão, R. de P., Vibrans, A.C., Uller, H.F., 2019b. Decline in giant tree numbers: status report for Santa Catarina state and perspectives for Brazil. Floresta e Ambiente 26, 1–5. https://doi.org/10.1590/2179-8087.003919

Shaw, D.C., 2004. Vertical organization of canopy biota, in: Lowman, M.D., Rinker, H.B. (Eds.), Forest Canopies. Academic Press, Boston, pp. 73–101.

Sillett, S.C., 1999. Tree Crown Structure and Vascular Epiphyte Distribution in Sequoia Sempervirens Rain Forest Canopies. Selbyana 20, 76–97.

Sillett, S.C., van Pelt, R., 2007. Trunk Reiteration Promotes Epiphytes and Water Storage in an Old-Growth Redwood Forest Canopy. Ecol Monogr 77, 335–359.

Vibrans, A.C., McRoberts, R.E., Moser, P., Nicoletti, A.L., 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 Sens Environ 130, 87–95. https://doi.org/10.1016/j.rse.2012.10.023

Waechter, J.L., 1998. Epifitismo vascular em uma floresta de restinga do Brasil Subtropical. Ciência e Natura 20.

Zhang, Z., Papaik, M.J., Wang, X., Hao, Z., Ye, J., Lin, F., Yuan, Z., 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, M.Y.B., 2011. Sampling Vascular Epiphyte Diversity – Species Richness and Community Structure. Ecotropica 17, 103–112.

# Figures

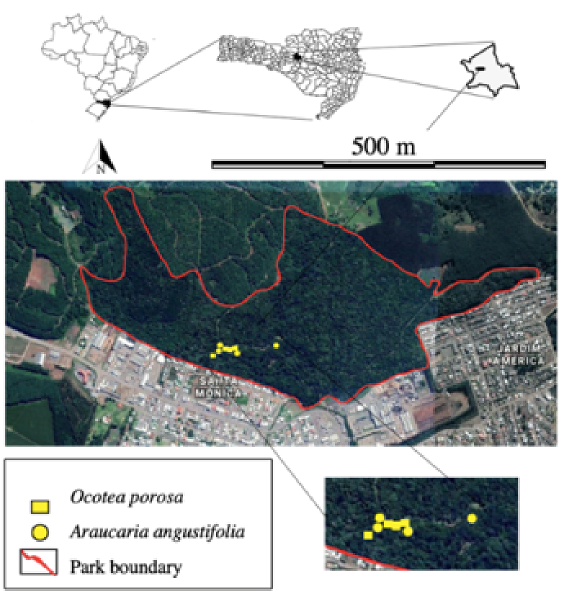
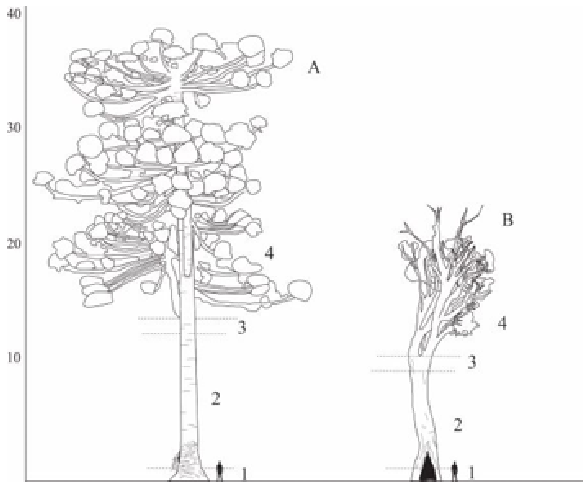



**Figure 1**

Study area at the René Frey Ecological Park, Fraiburgo, Santa Catarina, Brazil.




#### Figure 2

Division of phorophytes by ecological zones of epiphyte communities, (A) *Araucaria angustifolia*and (B) *Ocotea porosa*. Ecological zones: 1) base of the main trunk 2) main trunk, 3) crown base, and 4) crown. Tree scale (meters). Drawing by the authors.


#### Figure 3

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).

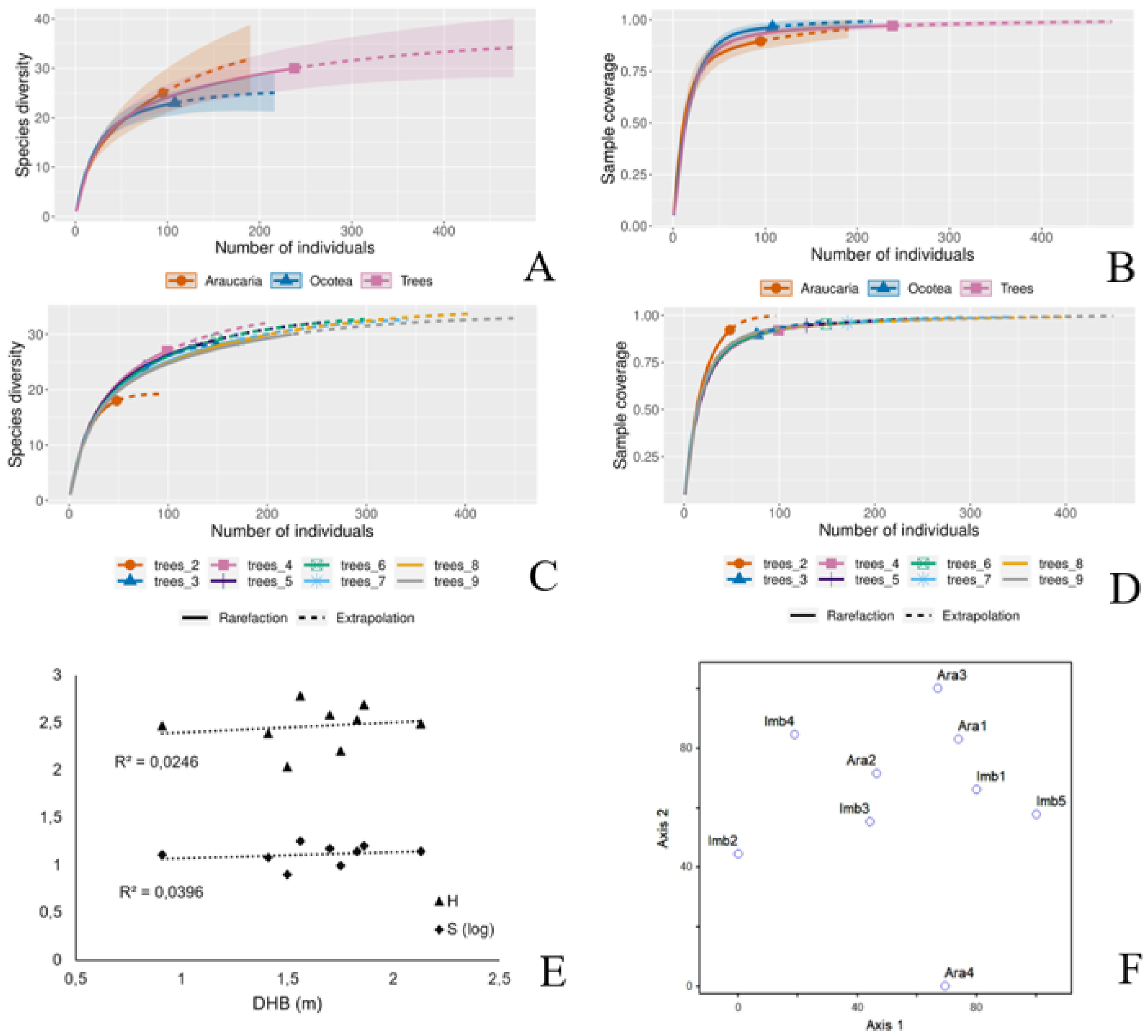



**Figure 4**

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 (A and C) and sample completeness curve (B and D). Sample size (continuous line) and extrapolation (dashed line), with 95% confidence intervals represented by the shaded regions. (E) Species richness and Shannon´s diversity index by host trees with their respective size in diameter. (F) Ordination analysis (NMS) of host trees species in vascular epiphytes community (code trees in Table 1).

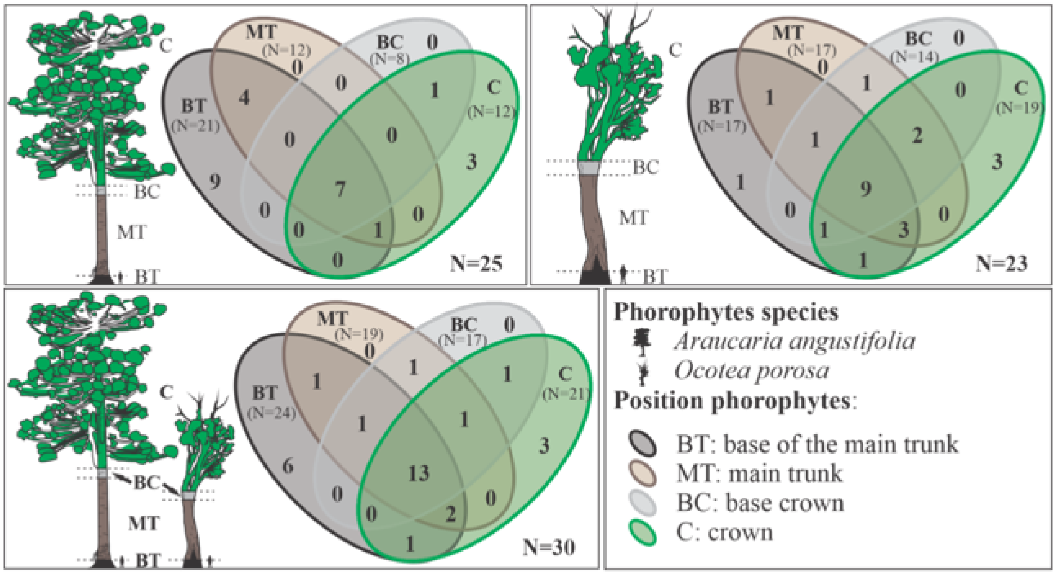



**Figure 5**

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

## Supplementary Files

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- AppendixA.docx