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Environmental factors affect population structure of tree ferns in the Brazilian subtropical Atlantic Forest

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ABSTRACT

Tree ferns are important elements of tropical forests, mainly because they are common and provide microhabitats for epiphytic plants. Due to their ecological importance, the aim of this study was to evaluate population structure, distribution, and influence of environmental variables on tree ferns in the state of Santa Catarina, southern Brazil. All tree ferns with a diameter at breast height ≥ 10 cm on 418 sampling units (SUs) systematically distributed throughout the study area were measured (total sampled area of 153.4 ha). Population structure was evaluated through classical phytosociological parameters and the relationships among dominance and environmental variables were evaluated through multiple linear regression models. *Dicksonia sellowiana* presented the greatest importance value among all species (IV = 13.19 %), followed by *Alsophila setosa* (IV = 4.37 %) and *Cyathea phalerata* (IV = 2.71 %). Altitude and mean rainfall of the driest quarter were significantly related to the dominance of *D. sellowiana* in most of the SUs. The mean temperature of the driest quarter and aspect were significantly related to the dominance of Cyatheaceae. Our study demonstrates that tree ferns are important elements of forest communities in the state of Santa Catarina.

Keywords: Cyatheaceae, Dicksoniaceae, environmental variables, population structure, regression analysis, tree ferns

Introduction

Tree ferns are important elements of diverse plant formations, especially of tropical forests (Tryon & Tryon 1982). Ferns affect the dynamics of the ecosystem in which they occur, influencing the regeneration of woody species and nutrients cycling (Brock *et al*. 2016); they also participate in the ecological succession process (Arens & Baracaldo 1998). Furthermore, they contribute to forest biomass stocks, accounting for more than 6 % of the total aboveground biomass in sites with a great density of individuals (Medeiros & Aidar 2011). Tree ferns are also important because many epiphytic plants (*e.g.*, *Asplenium mucronatum*, *Pecluma truncorum*, and *Trichomanes anadromum*) use their caudices as exclusive support (Moran *et al*. 2003; Schmitt & Windisch 2005; 2010; Fraga *et al*. 2008).

In the neotropics, most tree ferns species belong to Cyatheaceae or Dicksoniaceae (Pteridophyte Phylogeny Group 1 2016). Cyatheaceae is the richest family, with approximately 640 species worldwide (Pteridophyte Phylogeny Group 1 2016) and 43 species occurring in Brazil (Weigand & Lehnert 2016). This family is distributed over tropical and temperate areas in America, Australia, New Zealand, and Malaysia (Large & Braggins 2004). Dicksoniaceae has 35 species worldwide (Pteridophyte Phylogeny Group 1 2016) and two species in Brazil (Della & Vasques 2017). It is distributed in tropical and southern temperate regions (Large & Braggins 2004).

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In the state of Santa Catarina, southern Brazil, Cyatheaceae is the second family with the largest number of individuals in the subtropical evergreen rainforest. Two species of this family, namely *Alsophila setosa* and *Cyathea phalerata*, are among the ten most abundant arborescent species in this forest type (Lingner *et al*. 2013). In turn, the most abundant species in the Araucaria forest is *Dicksonia sellowiana*, followed by *Araucaria angustifolia* (Meyer *et al*. 2013). According to Bystriakova *et al*. (2011), Cyatheaceae species prefer hot and humid sites. Dicksoniaceae species, in turn, prefer sites with higher altitude and lower temperatures, and tolerate frosts (Mantovani 2004; Gasper *et al*. 2011).

In the last decades, tree ferns were intensively exploited due to their fibers and ornamental value, causing the depletion of natural populations (Windisch 2002; Santiago *et al*. 2013). Continuous exploitation can lead to the elimination of these individuals in nature due to their slow growth, as well as the loss of specific epiphytes occurring on them. Although, the ecological importance of tree ferns has been highlighted in the literature (Arens & Baracaldo 1998; Moran *et al*. 2003; Schmitt & Windisch 2005; 2010; Fraga *et al*. 2008; Medeiros & Aidar 2011), studies about this plant group are still scarce. In Brazil, most studies regarding tree ferns were conducted in the Atlantic Forest domain, focusing mainly on phenology (Schmitt & Windisch 2005; 2007; Schmitt *et al*. 2009; Neumann *et al*. 2014) and population structure (Mantovani 2004; Schmitt & Windisch 2007; Gasper *et al*. 2011). Relationships among environmental variables and the distribution and population structure of ferns were investigated by Tuomisto *et al*. (2019) in the Amazon; notwithstanding, the authors did not focus exclusively on tree ferns, but rather on all types of ferns. This demonstrates that there is a lack of information about the influence of environmental factors on tree fern populations.

Therefore, we analyzed population structure, distribution, and influence of environmental variables on tree ferns, aiming to answer the following questions: (1) Are tree ferns a relevant element of subtropical Atlantic Forest communities? (2) Which environmental variables are significantly related to the dominance of tree fern species? According to previous studies, tree ferns occur abundantly in the Atlantic Forest (Gasper *et al*. 2011; Lingner *et al*. 2013; Meyer *et al*. 2013) and their occurrence is influenced by temperature and rainfall-related variables (Mantovani 2004; Bystriakova *et al*. 2011). Hence, we expect to find similar results in the present study.

Materials and methods

Study area

The study area was defined as the state of Santa Catarina State (Fig. 1), which has ~29 % of its territory covered by native forests (Vibrans *et al*. 2013). According to the Köppen-Geiger climate classification, two climate types can be found in the state: Cfa – fully humid temperate climate with a hot summer, and Cfb – fully humid temperate climate with a warm summer (Alvares *et al*. 2013). In the evergreen rainforest, high temperatures, humidity and precipitation are found, and biologically dry periods are absent. The Araucaria forest has moderately hot summers and a long winter period (Leite 2002). Precipitation is abundant in the western region of the state, reaching over 2,000 mm.year^{-1} (Wrege *et al*. 2012). The semi-deciduous forest, located in the west of Santa Catarina, is characterized by temperature seasonality (Leite 2002).

Data collection

We obtained tree fern community data from the Forest and Floristic Inventory of Santa Catarina (IFFSC; see more details in Vibrans *et al*. 2010). Between 2007 and 2010, the IFFSC gathered data using a systematic sampling design; each sampling unit (SU) was located at the intersections of a 10 km × 10 km grid. The SF required a 5 km × 5 km grid to guarantee representativeness (Fig. 1). Each SU was composed of a cluster with a nominal area of 4,000 m², where the diameter at breast height (DBH) ≥ 10 cm and total height of each individual were measured.

We selected eight tree ferns species: *Alsophila setosa* Kaulf, *Cyathea atrovirens* (Langsd. & Fisch.) Domin, *Cyathea corcovadensis* (Raddi) Domin, *Cyathea delgadii* Sternb., *Cyathea phalerata* Mart., *Cyathea hirsuta* C.Presl, *Sphaeropteris gardneri* Hook., and *Dicksonia sellowiana* Hook. The climatic data were obtained from WorldClim v2.0 (Fick & Hijmans 2017). In addition, altitude, slope and aspect data were obtained from the Brazilian Geomorphometric Database (INPE 2017). In total, 24 environmental variables with approximately 1 km of spatial resolution were used (Tab. 1).

Data analysis

To assess the importance of tree ferns in the forest types of Santa Catarina, phytosociological parameters were calculated (dominance, density, frequency and importance value; Müeller-Dombois & Ellenberg 1974). Although the parameters for all the species occurring on the SUs were computed, only parameters related to tree fern species were considered in this study. We also assigned the individuals to height and diameter classes.

The influence of environmental variables on the tree ferns was analyzed using multiple linear regression models, using dominance (m².ha^{-1}) as the response variable and environmental variables as predictor variables. GWR (Geographically Weighted Regression) and OLS (Ordinary Least Squares) models were fitted and compared. Collinear variables with variance inflation factor > 10 were removed from the models using the 'vif' function of the 'usdm' R package (Naimi *et al*. 2014). Models with the smallest Corrected Akaike Information Criterion (AICc) (Burnham & Anderson 2002) were selected. In addition, the global significance of the models was evaluated ($\alpha = 0.05$), and F tests were performed to verify whether there was a significant improvement of the GWR residuals over the OLS residuals (Fotheringham *et al*. 2002). The regression models were fitted only for species that occurred at least on 30 SUs. *Cyathea atrovirens*, *Cyathea hirsuta* and *Sphaeropteris gardneri* were disregarded.

Moran's I correlograms were built for the OLS model residuals aiming to search for significant spatial structure in them, which would suggest that spatial

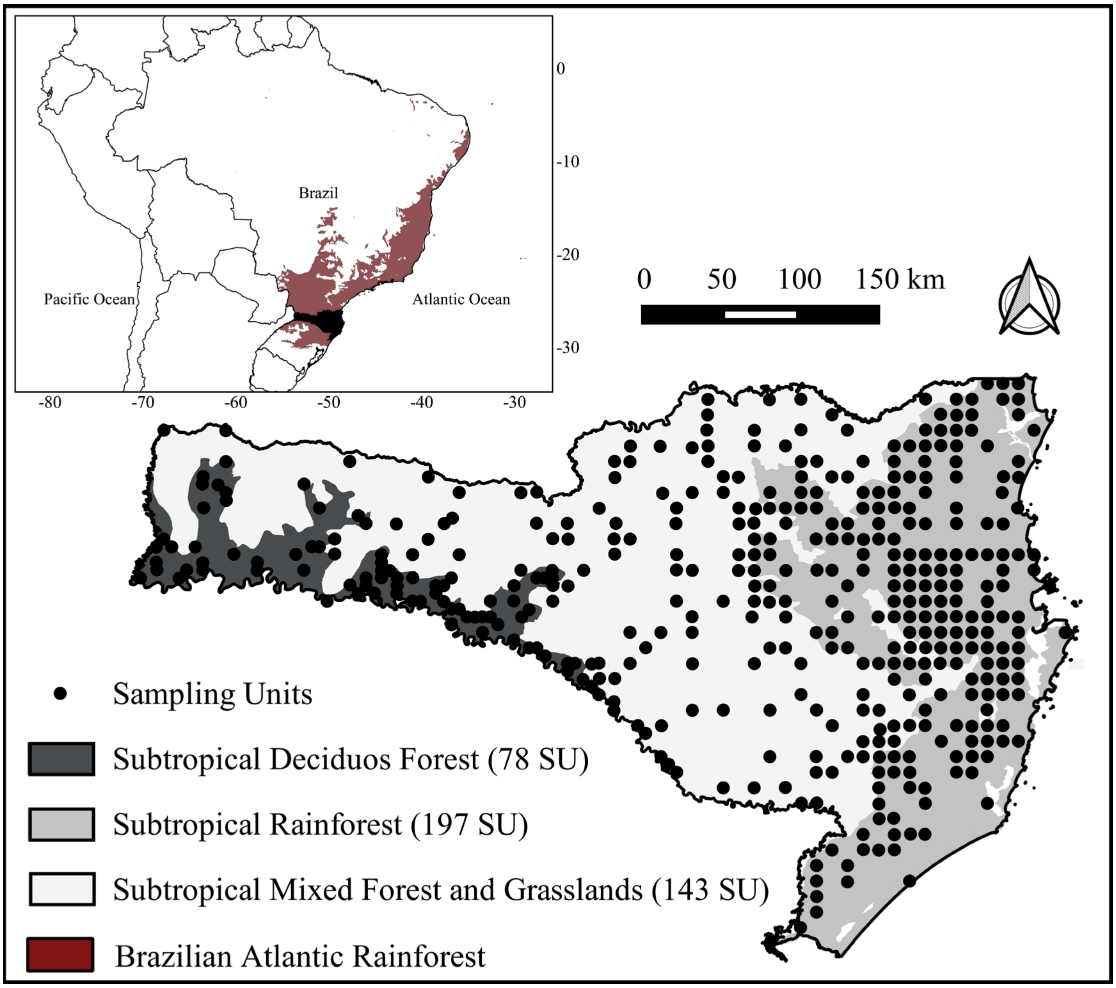

Figure 1. Study area (state of Santa Catarina, southern Brazil) and sampling units of the IFFSC.

Table 1. Environmental variables used in the Regression Analyses for Santa Catarina State, southern Brazil. Source: 1: *Worldclim*; 2: INPE.

Code	Description	Unit	Code	Description	Unit
Bio1	Annual Mean Temperature[1]	°C	Bio13	Precipitation of Wettest Month[1]	mm
Bio2	Mean Diurnal Range[1]	°C	Bio14	Precipitation of Driest Month[1]	mm
Bio3	Isothermality[1]	%	Bio15	Precipitation Seasonality[1]	mm
Bio4	Temperature Seasonality[1]	°C	Bio16	Precipitation of Wettest Quarter[1]	mm
Bio5	Max Temperature of Warmest Month[1]	°C	Bio17	Precipitation of Driest Quarter[1]	mm
Bio6	Min Temperature of Coldest Month[1]	°C	Bio18	Precipitation of Warmest Quarter[1]	mm
Bio7	Temperature Annual Range[1]	°C	Bio19	Precipitation of Coldest Quarter[1]	mm
Bio8	Mean Temperature of Wettest Quarter[1]	°C	Rad_win	Solar radiation in winter[1]	$KJ.m^{-2}.day^{-1}$
Bio9	Mean Temperature of Driest Quarter[1]	°C	Rad_sum	Solar radiation in summer[1]	$KJ.m^{-2}.day^{-1}$
Bio10	Mean Temperature of Warmest Quarter[1]	°C	-	Altitude[2]	m
Bio11	Mean Temperature of Coldest Quarter[1]	°C	-	Slope[2]	%
Bio12	Annual Precipitation[1]	mm	-	Aspect[2]	%

variables could be useful predictors. Default parameters were used to select the number of distance classes in the correlogram. A significance test for each distance class was performed using 999 Monte Carlo permutations. The global significance of the correlograms was tested using $\alpha = 0.05$ corrected using Bonferroni's approach (Fortin & Dale 2005). The residuals of the OLS models did not present any significant spatial structure according to this procedure. The normality of the residuals was tested using the D'Agostino-Pearson test (Zar 1999). The assumptions of linearity, homoscedasticity and residuals' independence were checked through residual plots (Hair *et al*. 2009). For the GWR models, the adaptive Gaussian kernel function for geographical weighting based on the minimization of AICc was applied (Fotheringham *et al*. 2002). These analyses were performed using SAM v4.0 (Rangel *et al*. 2010).

Moreover, we performed a variance partition analysis to assess how much of the variability of the dominance of tree ferns was explained by the (a) "pure" spatial structure; (b) spatially-structured environmental variables; and (c) "pure" environmental variables (Peres-Neto & Legendre 2010). The statistical significance of fractions (a) and (c) was tested using ANOVA models based on 999 permutations and $\alpha = 0.05$ (Dray *et al*. 2006). The variance partition was conducted as per Clappe *et al.* (2018) using the ade4 R package (Dray & Dufour 2007; R Development Core Team 2011).

Results

Population structure

In total, 10,632 individuals (Cyatheaceae = 5,129; Dicksoniaceae = 5,503) were observed. *Dicksonia sellowiana* presented the greatest importance value among all species (IV = 13.19 %). This species also had the largest Relative Dominance (6.96 %) and the greatest Relative Density (5.59 %) (Tab. 2, Fig. 2).

The diameter distributions of the five species with the greatest density followed a right asymmetry distribution (Fig. 3), with exception of *Alsophila setosa*, whose individuals were predominantly in the class of 10-15 cm (96.88 %). *Dicksonia sellowiana* showed the largest diametric amplitude, with most of the individuals in the class of 20-25 cm (33.58 %). The mean diameter over all species was 16.22 cm (± 7.66 cm); *D. sellowiana* presented the largest mean diameter (23.02 cm ± 7.2 cm).

Most individuals reached up to 5 m of height (Fig. 4), with a mean of 3.94 m (± 2.16 m). *Cyathea delgadii* had a less common distribution, because it has a distribution close to the normal distribution, while the others have right asymmetry, with a peak in the class of 6-7 m (20.79 %). For this reason, this species presented a greater mean height (6.28 m ± 2.54 m).

Regression models

According to the AICc, OLS models presented better performance for all species (Tab. 3). No spatial structure in the dominance data of this species was found. For *D. sellowiana*, temperature and rainfall variables were significantly related to the dominance of the individuals. Regarding Cyatheaceae, temperature variables, solar radiation and aspect variables were significant (Tab. 4).

Variance partitioning

The variance partition indicated that the dominance of tree ferns is significantly influenced by "pure" environmental variables (c) ($F_{(df = 8)} = 13.41$; $p < 0.01$) and "pure" space (a) ($F_{(df = 8)} = 22.18$; $p < 0.01$). Pure environmental factors explained the largest portion of the data variance (6.99 %), followed by the "pure" space (4.94 %) and by the spatially structured environmental variables (2.5 %). Unexplained factors (residuals) accounted for 85.57 % of the data variance.

Discussion

The increased density of tree ferns found in the subtropical Atlantic Forest indicate that the current environmental conditions in this domain are adequate for the occurrence of such plants, as observed by other authors (Catharino *et al*. 2006; Reginato & Goldenberg 2007; Conoletti *et al*. 2009; Klauberg *et al*. 2010; Ferreira *et al*. 2012; Lima *et al*. 2011; Silva *et al*. 2013). This result answered our first question, indicating that tree ferns species, such as *Dicksonia sellowiana*, *Alsophila setosa* and *Cyathea phalerata*, are very common in the studied forest types.

Inasmuch as *Araucaria angustifolia* is often regarded as the most abundant species in the Araucaria forest (Seger *et al*. 2005; Cordeiro & Rodrigues 2007), *Dicksonia sellowiana* proved to be the most abundant species in this forest type. The increased values of the phytosociological parameters of *D. sellowiana* were a consequence of the great number of observed individuals, which sometimes assemble as monodominant clusters on some SUs (Gasper *et al*. 2011). According to the last authors, the abundance of *D. sellowiana* on some SUs is related to temperature variation conditioned by high altitude (> 1,000 m) and, in fact, it proved to be a factor strongly associated with the occurrence of individuals of this species.

The small diameter and low height observed in most individuals are characteristic of tree ferns because they present slow growth, with growth rates of a few centimeters per year (Schmitt & Windisch 2006; 2012). From an ecological perspective, these features indicate that the populations tend to be stable and growing (Condit *et al*. 1998), and most likely the species found suitable sites for their development (Schmitt & Windisch 2007). According to Young & León (1989), these features are also common because young individuals present greater mortality rates than mature individuals.

Tree ferns can be found in all forest types in Santa Catarina. Nevertheless, Cyatheaceae has preference for the evergreen rainforest, where temperatures are higher compared to the Araucaria forest, where more intense frost events occur and *Dicksonia sellowiana* prevails (Mantovani 2004; Bystriakova *et al*. 2011; Gasper *et al*. 2011). These preferences are manifestations of the ecological demands of the two families, as reported by Tryon & Tryon (1982) and Gasper *et al*. (2011). The small abundance of tree ferns observed in the state's extreme west, especially in the semi-deciduous forest, may be influenced by precipitation seasonality driven by drier winters than other regions of the state (Wrege *et al*. 2012). The drought period may be restrictive for the tree ferns species considered in this study because they (1) are generally associated with sites with abundant and constant humidity (Mantovani 2004); (2) require water for reproduction; and (3) do not have adaptations for drought periods, such as loss of leaves (Sharpe & Mehltreter 2010).

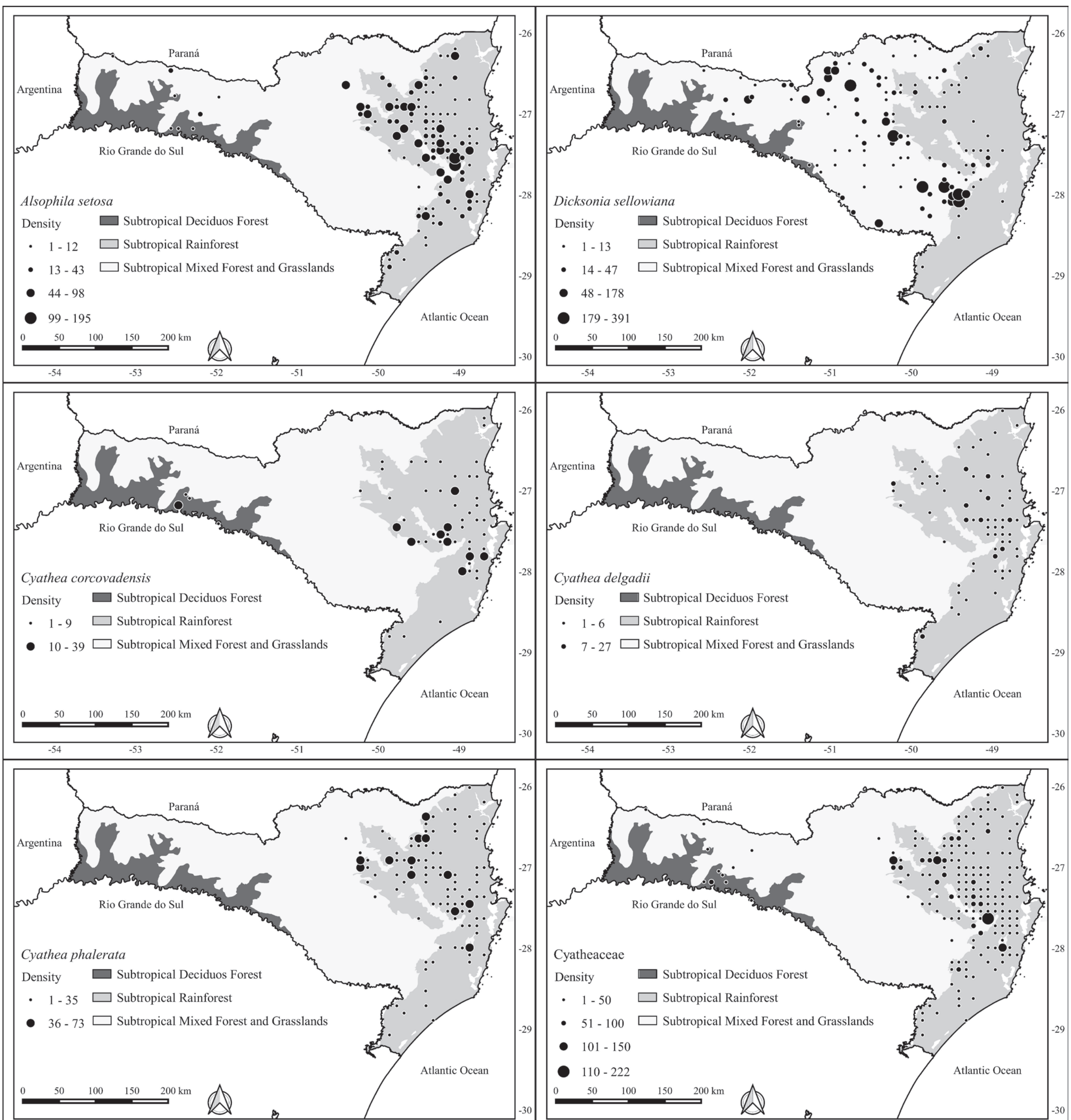

Figure 2. Distribution of tree fern species in the state of Santa Catarina, southern Brazil.

Table 2. Phytosociological parameters of tree fern species in the IFFSC, considering all species sampled. N: number of individuals; SU: number of sampling units in which the x species occurs; AD: Absolute Density (n/ha); RD: Relative Density (%); AF: Absolute Frequency (%); RF: Relative Frequency (%); ADo: Absolute Dominance (m²/ha); RDo: Relative Dominance (%); VI: Value of importance; SR: Subtropical Rainforest; SMF: Subtropical Mixed Forest; SDF: Subtropical Deciduous Forest.

Region	Species	Ranking	N	SU	AD	RD	AF	RF	ADo	RDo	VI
All study area	*Dicksonia sellowiana*	1	5503	128	36.0079	5.5953	30.622	0.6416	1.7512	6.9607	13.1975
	Alsophila setosa	6	2890	120	18.9102	2.9385	28.7081	0.6015	0.2087	0.8297	4.3696
	Cyathea phalerata	21	1596	103	10.4431	1.6228	24.6411	0.5163	0.1443	0.5735	2.7126
	Cyathea delgadii	99	303	63	1.9826	0.3081	15.0718	0.3158	0.0305	0.1211	0.745
	Cyathea corcovadensis	106	310	55	2.0284	0.3152	13.1579	0.2757	0.0275	0.1094	0.7003
	Cyathea atrovirens	394	22	10	0.144	0.0224	2.3923	0.0501	0.0021	0.0082	0.0807
	Sphaeropteris gardneri	544	6	3	0.0393	0.0061	0.7177	0.015	0.0011	0.0043	0.0254
	Cyathea hirsuta	671	2	1	0.0131	0.002	0.2392	0.005	0.0001	0.0005	0.0076
	TOTAL	-	10632	-	69.5686	10.8104	115.5501	2.421	2.1655	8.6074	21.8387
SR	*Alsophila setosa*	2	2689	108	38.2673	5.2738	54.8223	0.9214	0.4239	1.6862	7.8814
	Cyathea phalerata	5	1576	101	22.4282	3.0909	51.269	0.8617	0.3092	1.23	5.1826
	Cyathea delgadii	53	301	62	4.2836	0.5903	31.4721	0.529	0.0652	0.2592	1.3785
	Dicksonia sellowiana	58	247	36	3.5151	0.4844	18.2741	0.3071	0.1075	0.4277	1.2192
	Cyathea corcovadensis	93	189	40	2.6897	0.3707	20.3046	0.3413	0.0374	0.1488	0.8608
	Cyathea atrovirens	289	21	10	0.2989	0.0412	5.0761	0.0853	0.0043	0.017	0.1435
	Sphaeropteris gardneri	434	6	3	0.0854	0.0118	1.5228	0.0256	0.0023	0.0093	0.0467
	Cyathea hirsuta	573	2	1	0.0285	0.0039	0.5076	0.0085	0.0003	0.0011	0.0136
	TOTAL	-	5031	361	71.5967	9.867	183.2486	3.0799	0.9501	3.7793	16.7263
SMF	*Dicksonia sellowiana*	1	5252	89	95.268	15.6138	62.2378	1.7027	4.7154	17.5955	34.912
	Alsophila setosa	69	167	8	3.0293	0.4965	5.5944	0.1531	0.0333	0.1242	0.7737
	Cyathea corcovadensis	113	70	11	1.2698	0.2081	7.6923	0.2104	0.0196	0.0732	0.4918
	Cyathea phalerata	214	18	3	0.3265	0.0535	2.0979	0.0574	0.0054	0.0201	0.131
	Cyathea delgadii	279	5	2	0.0907	0.0149	1.3986	0.0383	0.0022	0.0081	0.0612
	TOTAL	-	5512	113	99.9843	16.3868	79.021	2.1619	4.7759	17.8211	36.3697
SDF	*Cyathea corcovadensis*	88	51	4	1.8593	0.3716	5.1282	0.1328	0.018	0.0823	0.5867
	Alsophila setosa	105	34	4	1.2395	0.2477	5.1282	0.1328	0.0119	0.0543	0.4349
	Dicksonia sellowiana	152	4	3	0.1458	0.0291	3.8462	0.0996	0.0047	0.0216	0.1503
	TOTAL	-	89	11	3.2446	0.6484	14.1026	0.3652	0.0346	0.1582	1.1719

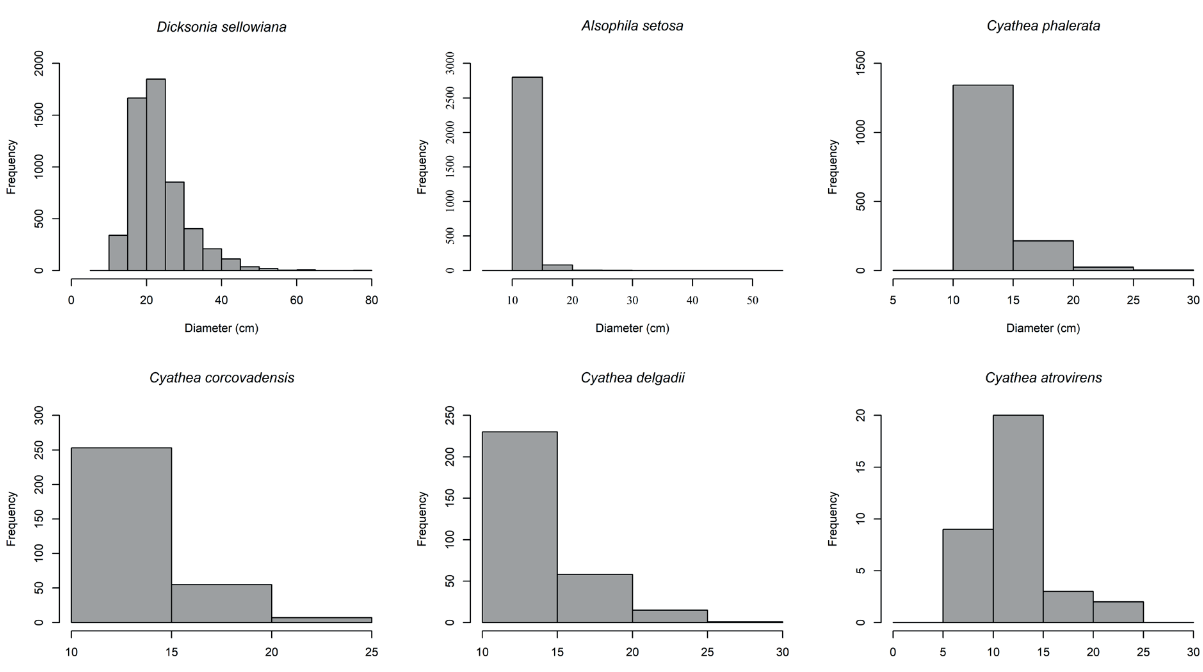

Figure 3. Diametric distribution of tree fern species in the state of Santa Catarina, southern Brazil.

Aspect, temperature and precipitation are correlated with tree ferns dominance (Bystriakova *et al*. 2011). Indeed, we found a significant correlation between tree fern dominance and these variables. The negative correlation of Cyatheaceae dominance with aspect indicates that this family prefers less sloped sites (Jones *et al*. 2007). The influence of temperature and precipitation variables on Cyatheaceae species was reported by other authors (Tryon & Tryon 1982; Fernandes 1997). The positive correlation of *Dicksonia sellowiana* with precipitation (Bio18) indicates that it prefers humid sites, as observed by Mantovani (2004) and Mallmann *et al*. (2018). Moreover, the positive correlation with the mean temperature of the driest quarter (Bio8) indicates that sites with higher temperatures do not completely inhibit the occurrence of *Dicksonia sellowiana*. This may be explained by the fact that the species grows under the forest canopy.

The percentage of variance explained by the predictor variables we selected was smaller than other studies (*e.g.*, Gasper *et al*. 2015; Saiter *et al*. 2015). The large unexplained fraction (residuals) suggests that we did not address other relevant variables that may influence the distribution patterns of the species, such as distance from the ocean (Saiter *et al*. 2015), biotic interactions such as herbivory (Aide 1988), and soil chemical properties that influence germination, such as pH (Marcon *et al*. 2014; 2017) and fertility (Jones *et al*. 2007).

Tree ferns are abundant in Santa Catarina, mainly in the evergreen rainforest where *Alsophila setosa* is expressive, and in the Araucaria forest where *Dicksonia sellowiana* predominates. Cyatheaceae and Dicksoniaceae occupy distinct habitats in Santa Catarina. The dominance of *Dicksonia sellowiana* was related to temperature and rainfall variables. For Cyatheaceae, different environmental variables were related to each species; some presented relationships with slope (*Alsophila setosa*), and others with aspect (*Cyathea delgadii*), temperature (*Alsophila setosa*, *Cyathea corcovadensis* and *Cyathea phalerata*), precipitation (*Alsophila setosa* and *Cyathea delgadii*) and solar radiation (*Alsophila setosa* and *Cyathea phalerata*). These results extend our knowledge on ecological patterns of this plant group,

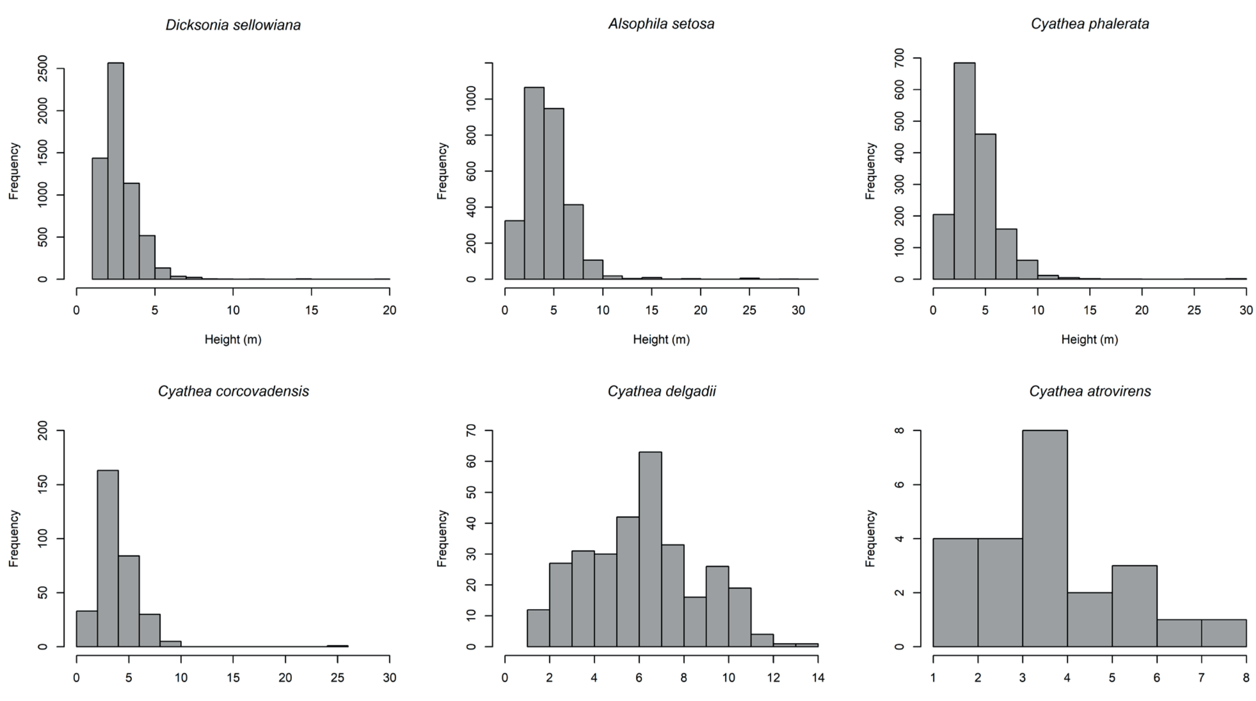

Figure 4. Hypsometric distribution of tree fern species in the state of Santa Catarina, southern Brazil.

Table 3. Statistical parameters for OLS and GWR models for tree ferns in Santa Catarina State. AICc: corrected Akaike Information Criterion; r: correlation coefficient; r^2: coefficient of determination; r^2 aj: coefficient of determination adjusted; F: *F*-test value; p: *p*-value.

Species	*Dicksonia sellowiana*		*Alsophila setosa*		*Cyathea corcovadensis*		*Cyathea delgadii*		*Cyathea phalerata*		Cyatheaceae	
Parameters	GWR	OLS	GWR	OLS	GWR	OLS	GWR	OLS	GWR	OLS	GWR	OLS
AICc	-589.09	-593.38	-1,149.03	-1,130.74	-656.65	-663.52	-758.31	-768.58	-1,022.62	-1,031.52	-1,627.09	-1,647.96
r	0.693	0.627	0.63	0.467	0.532	0.429	0.616	0.403	0.53	0.437	0.553	0.454
r^2	0.48	0.393	0.397	0.218	0.283	0.184	0.38	0.163	0.281	0.191	0.306	0.206
r^2 aj	0.417	0.373	0.25	0.169	0.2	0.184	0.246	0.135	0.197	0.174	0.2	0.179
F (r^2)	7.005	15.809	2.55	4.463	2.793	11.039	2.551	3.883	3.031	7.613	2.757	6.441
p	<0.001	<0.001	<0.001	<0.001	0.016	0.002	0.007	0.013	<0.001	<0.001	<0.001	<0.001

Table 4. Standard coefficients for OLS model variables for tree ferns in Santa Catarina State. VIF: Variance Inflation Factor; t: *t*-value; p: *p*-value

Species	Variable	Standard Coefficient	VIF	t	p
Alsophila setosa	Constant	0	0	1.611	0.11
	Aspect	-0.162	1.145	-1.811	0.073
	Slope	-0.219	1.218	-2.379	0.019
	Bio4	0.201	1.61	1.892	0.061
	Bio8	-0.316	1.928	-2.722	0.008
	Bio9	-0.267	1.54	-2.58	0.011
	Bio18	0.209	1.541	2.019	0.046
	Rad_win	-0.323	2.012	-2.725	0.007
Cyathea corcovadensis	Constant	0	0	4.068	<0.001
	Bio9	-0.429	1	-3.323	0.002
Cyathea delgadii	Constant	0	0	-1.078	0.286
	Aspect	-0.269	1.024	-2.253	0.028
	Bio12	-0.53	3.309	-2.465	0.017
	Bio18	0.456	3.313	2.119	0.038
Cyathea phalerata	Constant	0	0	3.71	<0.001
	Bio8	-0.39	1.288	-3.763	<0.001
	Rad_win	-0.185	1.217	-1.832	0.07
	Rad_sum	-0.187	1.078	-1.976	0.051
Cyatheaceae	Constant	0	0	2.987	0.003
	Slope	-0,113	1.165	-1.552	0.123
	Aspect	-0,117	1.225	-2.371	0.019
	Bio4	0,123	1.047	1.776	0.077
	Bio8	-0,261	2.593	-2.4	0.017
	Bio9	-0,213	2.142	-2.155	0.033
	Rad_win	-0,2	1.858	-2.177	0.031
	Rad_sum	-0,154	1.584	-1.807	0.072
Dicksonia sellowiana	Constant	0	0	5.202	<0.001
	Bio4	-0.629	2.376	-5.786	<0.001
	Bio8	-0.676	3.704	-4.98	<0.001
	Bio9	0.678	4.005	4.801	<0.001
	Bio12	-0.293	1.503	-3.386	<0.001
	Bio18	0.387	3.627	2.884	0.005

and can be used to elaborate conservation actions for each species according to their ecological preferences.

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