



Abiotic effects on the cover and richness of corticolous lichens on *Araucaria angustifolia* trunks

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ABSTRACT

Lichens play a key role in natural ecosystems, as they can function as primary producers, recycle minerals and fix nitrogen. Despite their environmental importance, little is known about lichen ecology in Brazil, and especially about how abiotic factors may influence their spatial distribution. In this study, we aimed to verify how the cover and richness of corticolous lichens on *Araucaria angustifolia* trunks vary between two different habitats (Forest and Grassland). The photoquadrat sampling method was applied to *A. angustifolia* trunks. The Coral Point Count software with Excel extensions (CPCe) was used to analyze photographs for lichen cover and richness. Additionally, a redundancy analysis was conducted to estimate how five abiotic and two biotic variables affected the spatial distribution of lichens. Twenty-five morphospecies were identified, none of them occurring exclusively in the Grassland habitat. Canopy openness, air humidity and tree trunk rugosity were important parameters influencing lichen distribution; therefore, spatial segregation of growth forms can be explained by environmental selectivity. Foliose lichens require more air humidity, which explains their predominance in the Forest habitat. Canopy openness in Grassland habitat favors fruticose lichens, which depend on factors such as wind for reproduction.

Keywords: Ascomycota, corticolous lichens, environmental selectivity, fungi, lichen ecology, niche overlap

Introduction

Lichens are symbiotic organisms formed by the association of one or more fungi (Ascomycota and/or Basidiomycota) and microalgae (Cyanophyceae or Chlorophyta groups; Beck *et al.* 1998; Marcelli 2006; Spribille *et al.* 2016). Lichens exist in a great diversity of shapes and sizes, and are considered a key group in ecosystem functioning for their role as primary producers (Büdel *et al.* 2014; Munir *et al.* 2015), atmospheric nitrogen fixers (Nash 2008) and for contributing to the cycling and incorporation of soil minerals (Cornelissen *et al.* 2007; Nash 2008; Concostrina-Zubiri *et al.* 2013). Furthermore,

lichens are important bioindicators of environmental quality (Lemos *et al.* 2007; Gauslaa 2014; Perlmutter *et al.* 2017).

Lichens develop close interactions with living surfaces, such as tree trunks (Brodo 1973). These biological substrates provide favorable environmental conditions for lichen growth, such as substrate complexity and light conditions that are generally adequate for physiological responses by lichens (Brodo 1973; Nascimbene *et al.* 2009). In addition, the structural complexity of tree trunks, considering tree age and size, influence lichen richness, as older tree trunks tend to be rougher and favor establishment (Nascimbene *et al.* 2009).

Although lichens are present in different environments, their abundance and distribution are influenced by abiotic

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factors that facilitate their development (Honda & Vilegas 1998; Gauslaa 2014). Light availability and wind speed are among the most important factors, as they influence photosynthetic processes and spore/propagule dispersal, respectively (Heinken 1999; Palmqvist 2000; Nash 2008; Gauslaa 2014). Secondly, air humidity and temperature determine colonization success, since they enable the photobiont to develop symbiotic interactions (Brodo 1973; Benítez *et al.* 2012; Gauslaa 2014). To determine how abiotic conditions influence the success of biological interactions is a key factor in understanding lichen distribution and abundance (Fedrowitz *et al.* 2012; Gauslaa 2014). The effects of abiotic factors on lichen distribution and richness are well known globally, as well as the importance of forest ecosystems as a matrix for lichen colonization and dispersal (Moning *et al.* 2009; McMullin *et al.* 2010; Gauslaa 2014). However, there are few studies on these factors in Brazilian ecosystems (Martins *et al.* 2011; Käffer & Martins 2014), especially considering different habitats in Mixed Ombrophilous Forest (araucaria forest), for which there is scarce knowledge on lichen ecology (e.g. Fleig & Grüniger 2008; Käffer *et al.* 2009; 2010; 2015; Koch *et al.* 2012; Hampp *et al.* 2018).

Araucaria angustifolia (Araucariaceae) is described as a predominant phytoecological unit in Mixed Ombrophilous Forest (Rondon Neto *et al.* 2002). Its distribution covers higher altitude areas between Rio Grande do Sul and Paraná states in southern Brazil, as well as small disconnected areas in São Paulo, Rio de Janeiro and Minas Gerais (Hueck 1953). The species has high ecological relevance, although the total cover of Mixed Ombrophilous Forest has been significantly reduced due to logging and conversion to agriculture (Borgo & Silva 2003; Medeiros *et al.* 2005). *Araucaria angustifolia* is important for the recruitment of different epiphytic and arboreal species, increasing local diversity (Borgo & Silva 2003; Fogaça *et al.* 2016). Ecological studies with corticolous lichens associated with *A. angustifolia* are still incipient (see Käffer *et al.* 2010), although it is acknowledged that the dominance of a particular lichen morphospecies may be indicative of certain environmental conditions (Nimis *et al.* 2002; Will-Wolf *et al.* 2006; Giordani *et al.* 2009) and anthropogenic effects on natural areas (Dettki & Esseen 1998; Das *et al.* 2012; Li *et al.* 2013; Bähring *et al.* 2016).

Lichens exist in different growth forms as a result of the symbiotic interaction. These are defined as morphotypes. Crustose lichens are sessile and adhered to the substrate; foliose lichens grow leafy, lobular structures anchored in the substrate by a thallus or rhizine; and fruticose lichens have little contact with the substrate and grow as pendent, sub-pendent or shrub-like thallus (Hinds & Hinds 2007; Nash 2008). The symbiont species in the interaction determines the lichen morphospecies, while the spatial distribution of each growth form may be correlated with the habitat where the symbiosis was established. This is justified by the influence of abiotic factors on the development,

maintenance or replication of the symbiosis (Fedrowitz *et al.* 2012).

This study aimed to evaluate the influence of abiotic factors (i.e. canopy openness, air humidity, distance to a river, air temperature and wind speed) on the cover and richness of lichen morphospecies and growth forms associated with *A. angustifolia* (araucaria hereafter) in two different habitats in Mixed Ombrophilous Forest (Forest and Grassland). We hypothesized that differences in abiotic factors and vegetation structure between these habitats result in differences in lichen cover and richness.

Materials and methods

Study area

Field work was conducted in November 2017, in the daytime (9am - 5pm), on the Reunidas Campo Novo farm, located in the municipality of Bom Retiro (27°53'58.28"S 49°26'11.06"W), state of Santa Catarina, in southern Brazil (Fig. 1A). The climate is temperate oceanic, Cfb in the Köppen-Geiger classification system (see Pandolfo *et al.* 2002). Annual mean rainfall varies between 1500-1700 mm, mean temperature between 17-18 °C, and mean air humidity between 82-84 % in the summer (Pandolfo *et al.* 2002). Photoquadrat sampling was applied on araucaria trees in two Mixed Ombrophilous Forest habitats at a minimum distance of 360 meters ("Forest" and "Grassland" hereafter). These areas are located next to the João Paulo river. The Forest habitat is situated upstream and represented by riparian vegetation, characterized by high frequency of *Araucaria angustifolia* (Bertol.) Kuntze trees. The Grassland habitat is located downstream and characterized by the prevalence of herbaceous vegetation, mostly grasses with shrubs, and sparse *A. angustifolia* trees (Fig. 1B).

Data collection

In each habitat, four linear transects placed 30 meters apart were set up with the use of a measuring tape. The transects were 50 m long and 10 m wide (comprising an area of 500 m²). The photoquadrat sampling method (Fig. 1C) was applied to all araucaria trees in the transects at least 3 m distant from other araucaria trees and circumference at breast height (CBH) larger than 50 cm.

Canopy openness (measured with a spherical densitometer; Forest Model-C), air humidity (analogic hygrometer, Incoterm, %), distance from the river (measuring tape, meters), air temperature (thermometer, °C) and wind speed (anemometer Instrutherm THD-500, meters/second) were measured for each araucaria tree. All abiotic variables were measured within a three-hour interval on the northern side of the trunk, at a height of 1.3 meters from the ground. The biotic variables CBH (cm) and trunk rugosity were measured in the same spot



of the photoquadrat. Rugosity was visually estimated and categorized as low, medium or high. “Low” rugosity was characterized by smooth irregularities on the trunk, “medium” for shallow grooves and/or light cortex peeling, and “high” as deep grooves and advanced process of cortex peeling (Fig. 2).

The photoquadrat sampling method was adapted from the method described by Kohler & Gill (2006), previously

applied in studies on marine benthic organisms. A polyvinyl chloride (PVC) rectangle was placed on the northern side of the trunk, and one 25 x 10 cm (250 cm²) photograph was taken at a minimum distance of 40 cm between the rectangle and the camera (Canon G15). The photographs were analyzed in the laboratory using Coral Point Count software with Excel extensions (CPCe 4.0 version 2006). Richness of morphospecies and cover of each of the

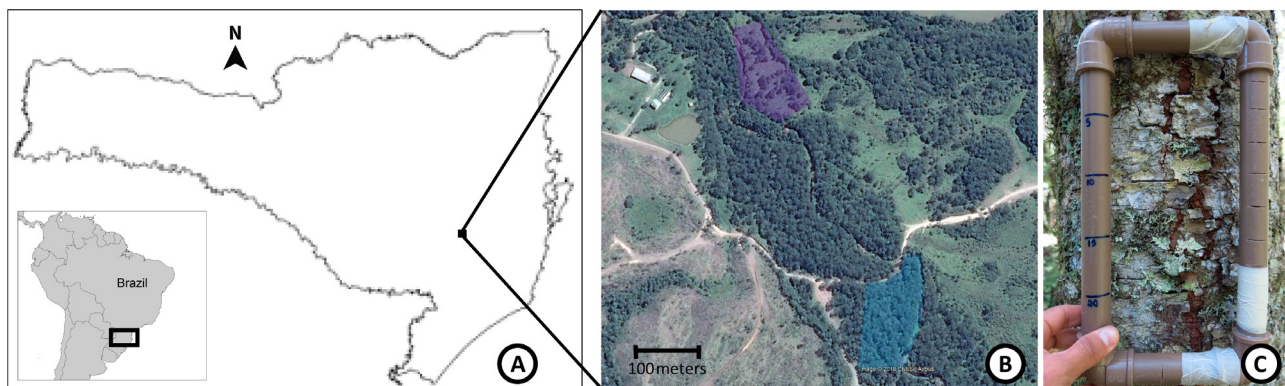


Figure 1. Location map of the study area and sampling method used for estimating lichen cover and richness. **A.** Map of Santa Catarina State, with the location of Bom Retiro (Black square); **B.** Study area on the Reunidas Campo Novo farm; blue and purple polygons define Forest and Grassland habitats, respectively; **C.** The photoquadrat used to obtain images for each araucaria tree sampled.

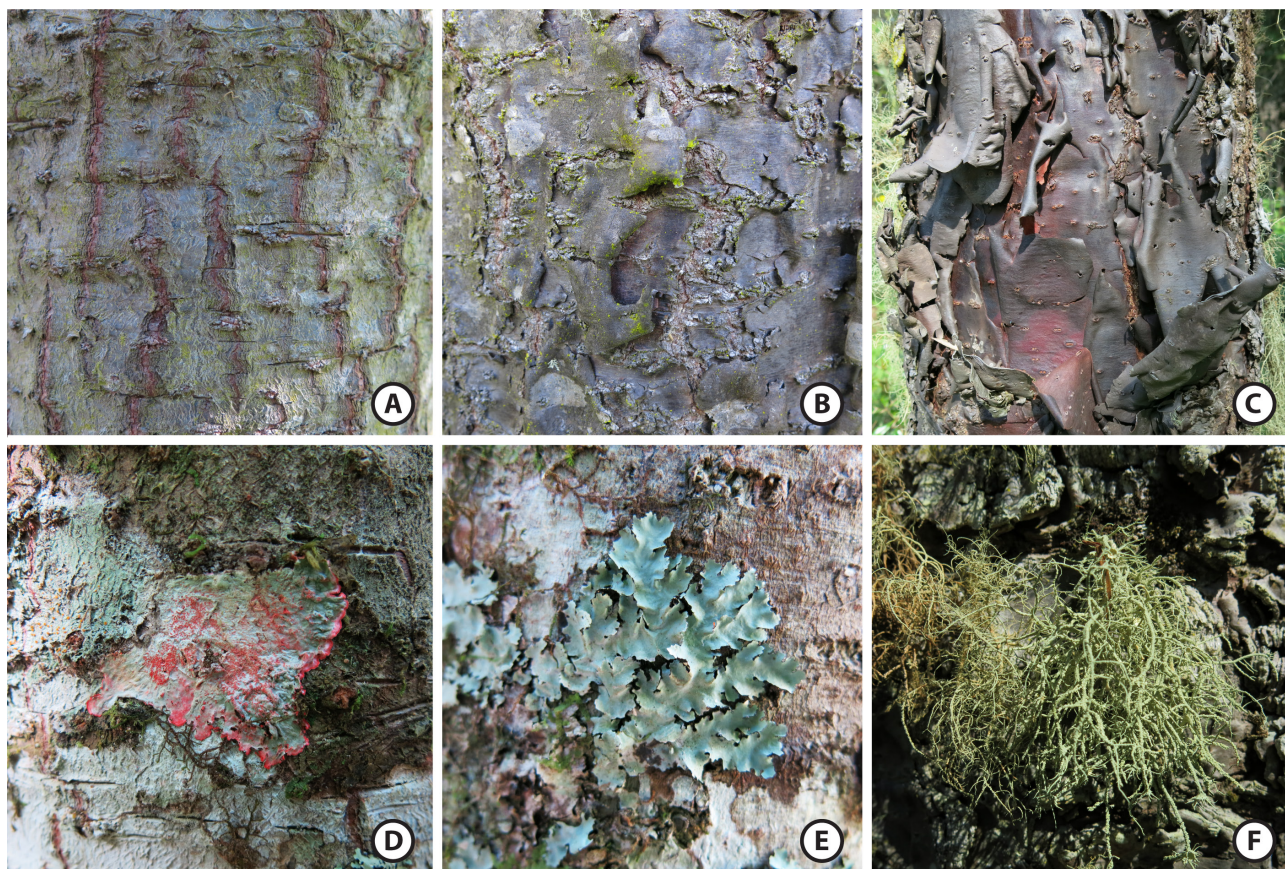


Figure 2. Rugosity categories of *Araucaria angustifolia* trunks (**A.** low rugosity, **B.** medium rugosity, **C.** high rugosity); and growth forms of lichens sampled in Mixed Ombrophilous Forest (**D.** crustose, morphospecies *Herpothallon* cf. *rubrocinctum*, **E.** foliose, morphospecies *Parmotrema* sp., **F.** fruticose, morphospecies *Usnea* sp.).

three lichen growth forms were obtained by 30 randomly distributed points on each photo. The lichens at each point were identified and classified in one of the three growth forms: crustose, foliose or fruticose (Fig. 2). When the point fell on the cortex, bryophytes or pteridophytes, the element was termed “other”. Once the lichens at each point were identified, the proportion of cover of each growth form was estimated in each photo by extrapolation using the CPCE software. The total cover of 100% corresponds to the sum of all organisms identified in every photoquadrat, and the total cover of each growth form corresponds to the average of each growth form for all trees sampled in “Forest” and “Grassland”.

Statistical analyses

We performed a principal coordinate analysis (PCoA) to verify how the samples (tree trunks) were arranged regarding abiotic variables and a permutation analysis of variance (PERMANOVA) to test the null hypothesis that Forest and Grassland do not differ on abiotic terms. Abiotic variables were transformed by standardization to decrease data dispersion. We also performed a PCoA and a PERMANOVA to verify and test how lichen composition (morphospecies) varied between habitats.

To verify whether total cover and richness; and the cover of growth forms (*i.e.* crustose, foliose and fruticose) varied between habitats, we performed a Welch’s t-test. To verify the influence of abiotic variables on lichen composition we performed a redundancy analysis (RDA) and a subsequent analysis of variance (ANOVA) of the canonical axes. All analyses were performed using the “vegan” (Oksanen *et al.* 2013) and “ggplot2” (Wickham 2009) packages of R software (R Core Team 2017).

Results

A total of 80 araucaria trunks were sampled, 40 in each habitat (Forest and Grassland), on which 25 morphospecies of lichens were found. Seven of these were crustose, 11 foliose, and seven fruticose. While no morphospecies were exclusive to Grassland, 13 occurred only in Forest (Tab. 1). Although registered in the photographs, the morphospecies *Ramalina cf. usnea* and *Phyllopsora sp.* were not captured in the random point placement method due to restricted cover (Tab. 1).

The PCoA and PERMANOVA analyses showed that abiotic factors and lichen composition are different in Forest and Grassland (Fig. 3). Furthermore, in the samples located in Grassland a more diffuse pattern was observed for abiotic factors, with few samples overlapping Forest. On the other hand, samples in Forest presented a more diffuse pattern in lichen composition.

Lichen total cover differed between habitats ($T=21.8$; $DF=79.1$; $p<0.01$), being higher in Forest (mean=47.9; standard error= ± 2.5) than in Grassland (46.8 ± 3.4). Total richness also differed ($T=14$; $DF=93.2$; $p<0.01$), being higher in Forest (4.6 ± 0.3) than in Grassland (3.88 ± 0.26). The crustose growth form differed in cover ($T=5.6$; $DF=79.2$; $p<0.01$) and richness ($T=-2.5$; $DF=117.8$; $p=0.01$) between habitats, being higher in Grassland (Fig. 4). The foliose growth form also differed in cover ($T=7.1$; $DF=79.1$; $p<0.01$), but did not differ in richness ($T=0.3$; $DF=93.3$; $p=0.75$); cover was higher in Forest (Fig. 4). Conversely, the fruticose growth form differed in cover ($T=7.8$; $DF=79.1$; $p<0.01$), but did not differ in richness ($T=0.1$; $DF=99.2$; $p=0.94$); cover was higher in Grassland (Fig. 4).

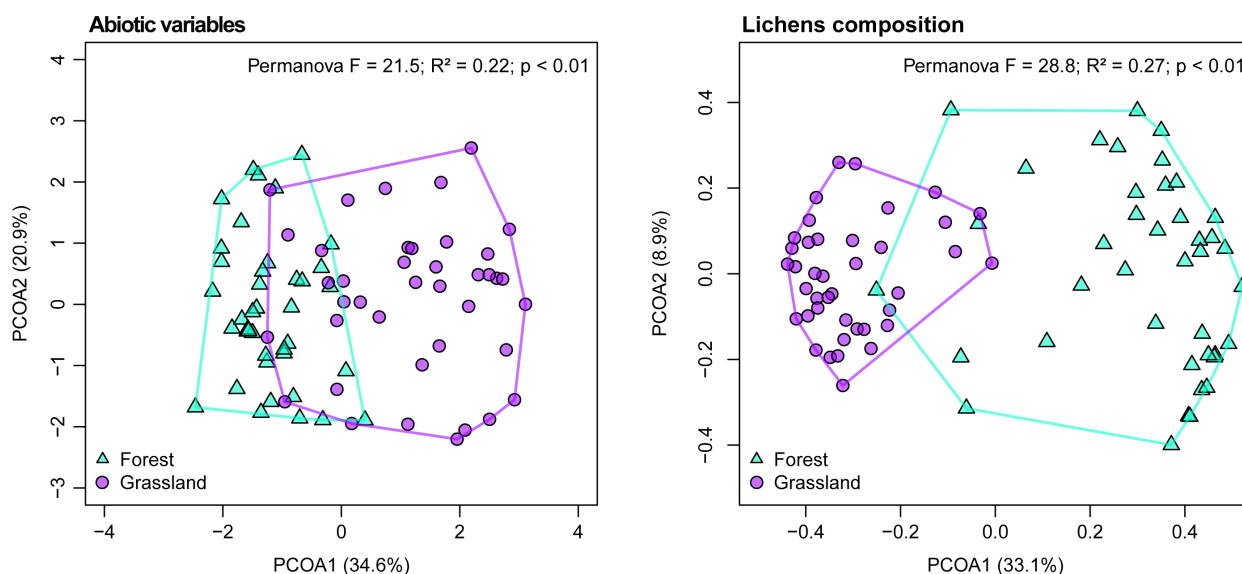


Figure 3. Principal coordinate analysis (PCoA) and permutational analysis of variance (PERMANOVA) performed with the abiotic variables and the composition of lichen morphospecies sampled in two habitats: “Forest” (Blue triangles) and “Grassland” (purple circles) in Mixed Ombrophilous Forest.

Table 1. Morphospecies and growth forms of lichens on *Araucaria angustifolia* trunks sampled in two habitats (“Forest” and “Grassland”) in Mixed Ombrophilous Forest.

Morphospecies	Growth form	Habitats	
		Forest	Grassland
<i>Chrysothrix</i> sp.1	Crustose	X	X
<i>Chrysothrix</i> sp. 2	Crustose	X	X
<i>Graphis</i> sp.	Crustose	X	X
<i>Herpothallon</i> cf. <i>roseocinctum</i>	Crustose	X	-
<i>Herpothallon</i> cf. <i>rubrocinctum</i>	Crustose	X	-
<i>Phyllopsora</i> sp.	Crustose	-	-
Trypetheliaceae	Crustose	X	X
cf. <i>Heterodermia</i>	Foliose	X	-
cf. <i>Lobariella</i> sp.	Foliose	X	-
<i>Dirinaria</i> sp.	Foliose	X	-
<i>Heterodermia</i> cf. <i>leucomela</i>	Foliose	X	-
<i>Heterodermia</i> sp.	Foliose	X	-
<i>Parmotrema</i> cf. <i>clavuliferum</i>	Foliose	X	-
<i>Parmotrema</i> sp.1	Foliose	X	-
<i>Parmotrema</i> sp.2	Foliose	X	-
<i>Parmotrema</i> sp.3	Foliose	X	X
<i>Physcia</i> sp.	Foliose	X	-
<i>Punctelia</i> sp.	Foliose	X	-
<i>Ramalina</i> sp.	Fruticose	X	-
<i>Ramalina</i> cf. <i>sprengelii</i>	Fruticose	X	X
<i>Ramalina</i> cf. <i>usnea</i>	Fruticose	-	-
<i>Usnea</i> cf. <i>rubicunda</i>	Fruticose	X	X
<i>Usnea</i> sp.1	Fruticose	X	X
<i>Usnea</i> sp.2	Fruticose	X	X
<i>Usnea</i> sp.3	Fruticose	X	X

The RDA analysis showed that canopy openness, air humidity and trunk rugosity were the main abiotic factors influencing cover of the three growth forms (Fig. 5). The foliose growth form was more related to Forest, being positively influenced by humidity and CBH, while the fruticose growth form showed the opposite pattern, being more related to Grassland and positively influenced by canopy openness. The crustose growth form was related to both habitats and inversely related to trunk rugosity (Fig. 5).

Discussion

In this study, we verified that the cover and richness of corticolous lichens on *A. angustifolia* trunks are determined by the environment in which the tree is growing, as a consequence of abiotic variables that can influence the selectivity of lichens for substrate type. The highest total cover and richness of lichens was found in Forest, where samples presented a more scattered pattern, indicating higher variation in species composition compared to Grassland. In terms of growth form, the cover by foliose lichens was higher in Forest, while the cover by fruticose and crustose lichens was higher in Grassland.

The spatial segregation of lichen growth forms between habitats may be indicative of lichen dispersal limitation (Werth *et al.* 2006) and/or the effect of abiotic factors on reproductive strategies. Lichens can reproduce asexually (*i.e.* soredia and isidia) and sexually; and may also produce

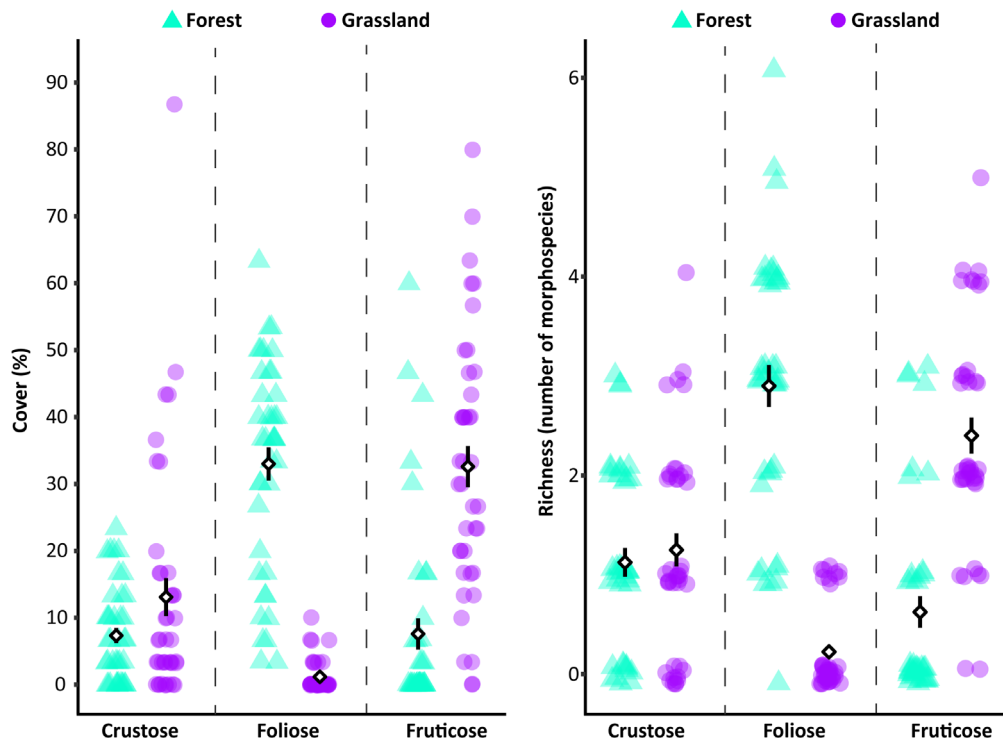


Figure 4. Scatterplot of cover (%) and richness of lichen growth forms (crustose, foliose and fruticose) associated with *Araucaria angustifolia* tree trunks sampled in two habitats: “Forest” (blue triangles) and “Grassland” (purple circles) in Mixed Ombrophilous Forest. Black and white diamonds and black bars represent mean and standard errors, respectively.



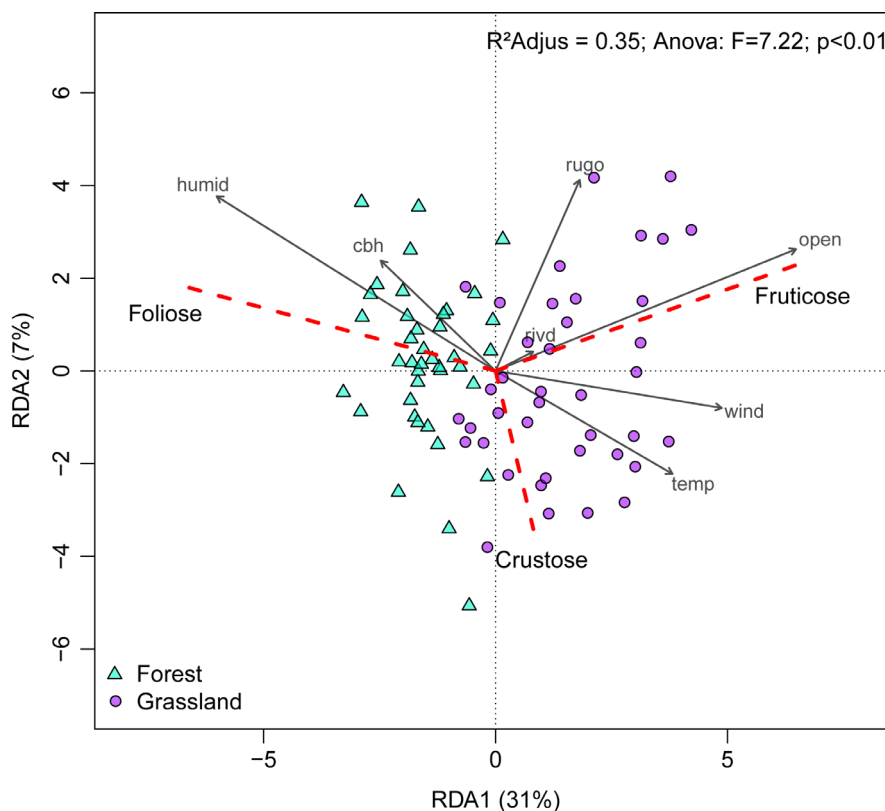


Figure 5. Redundancy analysis (RDA) between abiotic variables and lichen growth forms associated with *Araucaria angustifolia* tree trunks, sampled in two habitats (“Forest” and “Grassland”) in Mixed Ombrophilous Forest. Arrows indicate abiotic variables: “open” – canopy openness; “cbh” – circumference at breast height; “rugo” – trunk rugosity; “temp” – air temperature (°C); humid – air humidity (%); wind – wind speed (m/s). Red dashed lines represent the three growth forms of lichens (crustose, foliose and fruticose).

vegetative propagules (Bowler & Rundel 1975; Seymour *et al.* 2005). These forms of reproduction result in different dispersal strategies. Sexual spores can be dispersed to long distances by wind and rain (Bowler & Rundel 1975), whereas asexual reproduction limits dispersal distance but generates new thallus quicker than sexual spores after deposition on a substrate (Seymour *et al.* 2005). For instance, the fruticose growth form was observed in higher proportion in Grassland with a positive influence of canopy openness. Generally, this growth form is known to undergo symbiotic reproduction (*i.e.* many species of *Usnea* with fibrils), may have low dispersal capacity, and the growth of new individuals is dependent on the transport of fragments by vectors such as wind (Hinds & Hinds 2007). The open canopy in Grassland facilitates dispersal of lichens by wind, which may explain the dominance of the fruticose growth form in this habitat. On the other hand, the foliose anatomy generates high adherence to the substrate, protecting the photobiont between the fungus cortical layers (Büdel & Scheidegger 2008), thus requiring lower wind exposure and higher retention of humidity for the physiological maintenance of the algae (Hinds & Hinds 2007; Koch *et al.* 2013). Hence, this growth form is favored by lower canopy openness that can act as a physical barrier against desiccation. Thus, we could infer that abiotic

parameters influence dispersal ability and limit lichen establishment (Bowler & Rundel 1975; Scheidegger & Werth 2009).

Trunks of araucaria trees with high rugosity were less colonized by crustose lichens. The crustose growth form is characterized by high adherence to the substrate (Hinds & Hinds 2007), therefore its occurrence is probably limited on trees with a high extent of bark peeling. This was corroborated by the presence of crustose lichens exclusively related to medium and low trunk rugosity in both habitats and less correlated with abiotic parameters. The crustose form is resistant to low light availability and can tolerate water oversaturation due to morphological adaptations (Lakatos *et al.* 2006). Thus, we may infer that the substrate (characteristics of araucaria trunks) was more relevant in the distribution of crustose lichens than other abiotic conditions.

These observations led to the hypothesis that the distribution of corticolous lichens in Forest and Grassland may be due to the existence of different optimum conditions required for their establishment and growth (Marcelli 1998; Gauslaa 2014). Especially considering abiotic conditions, water availability or saturation is a key parameter, as it influences CO₂ exchange on the surface of the lichen thallus (Harris 1971; Lakatos *et al.* 2006) and acts as a

dispersal mechanism for reproductive stages (Scheidegger & Werth 2009). For instance, in conditions of low humidity, higher canopy openness and higher substrate rugosity (observed in Grassland), there is less substrate available for establishment and less water for the physiological maintenance of the photobiont. These conditions may reduce richness in Grassland when compared to Forest. However, an increase in humidity would create a niche overlap with other species that require increased water availability to survive, such as mosses and ferns (Friedel *et al.* 2006). The niche overlap concept (Pianka 1974) assumes that an environment in which species share their resources may support a more diverse community than those where this partition of resources does not occur. Pianka's theory reinforces our finding that Forest has the highest species richness considering that the increase in humidity can favor lichen growth, but can also lead to competition for space, affecting their coexistence.

The higher richness of lichen morphospecies observed in Forest was possibly related to the interaction among the abiotic variables in this habitat. These variables were more constant (*i.e.* lower range of values) than in Grassland, which could favor a diversification of morphospecies. In contrast, the high variability of each abiotic factor in Grassland could act as a "filter effect". In this case, reduced richness may be related to the ability of species to establish and disperse in this habitat. The filter effect is corroborated by the composition of lichens in each area, with high segregation of the foliose growth form in Forest. Conversely, the interaction of abiotic parameters was more important for determining the composition of crustose and fruticose lichens.

Our study reinforces the importance of abiotic factors in the spatial distribution and species composition of lichen communities on *Araucaria angustifolia* trunks. As a consequence, we highlight the relevance of conservation of populations of the endangered species *A. angustifolia* (Brasil 2008), as well as of the protection of Mixed Ombrophilous Forest remnants in southern Brazil.

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