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Floristic-functional variation of tree component along an altitudinal gradient in araucaria forest areas, in Southern Brazil

VANESSA F. SOBOLESKI, PEDRO HIGUCHI, ANA CAROLINA DA SILVA, MARIELE A.F. DA SILVA, AMANDA S. NUNES, RODINELI LOEBENS, KARINE DE SOUZA, JHENIFFER FERRARI, CARLA L. LIMA[1] and RICARDO V. KILCA

Departamento de Engenharia Florestal, Centro de Ciências Agroveterinárias, Universidade do Estado de Santa Catarina, Av. Luiz de Camões, 2090, Conta Dinheiro, 88520-000 Lages, SC, Brazil

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ABSTRACT

We aimed to investigate the taxonomic and functional variations of tree component of Araucaria Forest (AF) areas located along an altitudinal gradient (700, 900 and 1,600 m asl), in the southern region of Brazil. The functional traits determined were leaf area, specific leaf area, wood density, maximum potential height and dispersal syndromes and deciduousness. The data were analyzed through a functional and taxonomic dissimilarity dendrograms, community-weighted mean trait values, parametric and nonparametric tests, and Principal Component Analysis. The largest floristic-structural similarity was observed between the lower altitude areas (700 and 900 m asl), whose Bray-Curtis distance was 0.63. The area at 700 m asl was characterized by a predominance of deciduous and semi-deciduous species, with a high number of self- and wind-dispersed species, whereas the area at 1,600 m asl exhibited a predominance of animal-dispersed and evergreen species. It was also observed that there were significant variations for leaf traits, basic wood density and maximum potential height. Over all altitudinal gradient, the ordinations indicated that there was no evidence of functional differentiation among dispersal and deciduousness groups. In conclusion, the evaluated Araucaria Forest areas presented high floristic-functional variation of the tree component along the altitudinal gradient.

Key words: Functional traits, altitude, similarity, subtropical forest.

INTRODUCTION

Vegetation changes along altitudinal gradients have intrigued researchers for centuries. In 1799, Alexander von Humboldt, in his scientific expedition around the world, made one of his first stops in the Canary Islands, where he climbed what was considered at the time to be the highest mountain in the world, the Teide Volcano, at 3,718 m asl. During the climb, Humboldt observed that the vegetation could be classified into five zones, depending on the altitude, soil and water availability (Helferich 2011). Since then, the topic has been revisited by several researchers in different parts of the world, whose results demonstrate that the influence of altitude on vegetation patterns is a global phenomenon (Barrera et al. 2000, Oliveira-

Correspondence to: Pedro Higuchi
E-mail: higuchip@gmail.com

Filho and Fontes 2000, Homeier et al. 2010, Valente et al. 2011). The influence occurs because changes in altitude are accompanied by changes in a series of environmental variables, such as temperature (Homeier et al. 2010), soils (Jiang et al. 2015) and humidity (Oliveira-Filho et al. 1998), with the frequency of frost considered to be one of the most limiting factors for the occurrence of plant species (Oliveira-Filho and Fontes 2000). Presently, studies that seek to understand vegetation variations as a function of altitude are important tools for forecasting climate change impacts on terrestrial ecosystems, given that historically, the immediate response of species to past climate change has been for the species to change in its geographic occurrence along attitudinal and latitudinal gradients (Davis and Shaw 2001).

To understand vegetation changes as a function of altitude, it is important to recognize that the local structure of biological communities is determined by the complex interaction among various factors that act over time and at different spatial scales (Sobral and Cianciaruso 2012). At a broad spatial scale, the regional pool of species is determined, fundamentally, for phytogeographical aspects, especially those related to historical factors, such as long-distance dispersal and vicariance events (Fiaschi and Pirani 2009). At a local spatial scale, there is an influence of factors related to environmental filters and interspecific competition, which are associated with the life strategies of the species (Webb et al. 2002, Mouillot et al. 2013, Reich 2014, Carlucci et al. 2015, Moraes et al. 2016), expressed through its functional traits. In this sense, the areas of occurrence of Araucaria Forest (AF), which is one of the main forest formations in southern Brazil, can be considered strategic for the development of this type of study. This is because this type of forest formation presents flora with different phytogeographical sources and evolutionary contexts, in addition to being heavily conditioned by altitudinal variation (Duarte et al. 2012, Higuchi et al. 2012, 2013, Duarte et al. 2014, Oliveira-Filho et al. 2015).

In general, studies in areas with Araucaria Forest have focused only on phylogeographical, phytogeographical and phytosociological aspects, i.e., that consider that species are functionally similar. These studies demonstrate that this vegetation physiognomy presents high phylogenetic diversity (Duarte et al. 2014), whose organization is influenced by altitude through the annual average temperature (Duarte et al. 2012). From a taxonomic perspective, high species replacement is observed (Higuchi et al. 2012, 2013, Oliveira-Filho et al. 2015). Whereas higher areas, associated with cloud-forest conditions, exhibit low diversity and high endemism, indicating the existence of environmental filters, lower areas exhibit floristic-structural heterogeneity due to their proximity to the deciduous seasonal forest, which represents another important forest physiognomy in the region (Higuchi et al. 2012, 2013, Marcon et al. 2014, Oliveira-Filho et al. 2015). Functional approaches at the regional scale in the Araucaria Forest are nonexistent. However, based on studies conducted in other regions, changes along an altitudinal gradient are expected to occur for wood density (Chave et al. 2006), leaf traits (Read et al. 2014, Rosado et al. 2016) and the maximum potential height of trees (Barrera et al. 2000).

Thus, the present study aimed to investigate taxonomic and functional variations of the tree component of Araucaria Forest areas over an altitudinal gradient, in southern Brazil. Given the phytogeographical context, represented by the influence of the deciduous component in lower areas, and the existence of environmental filters in higher cloud forest areas, the hypothesis of the existence of functional and taxonomic changes in the region was tested. Based on previously studies, we expected that the higher altitude area had the most floristically distinctive tree component, made up by smaller animal-dispersed evergreen trees, with greater wood density, smaller leaf area and smaller specific leaf area than lower altitude areas.

MATERIALS AND METHODS

For this study, AF areas located at three altitudinal levels (approximately, 700, 900 and 1,600 m asl), in the southern region of Brazil, were considered; the sites are located, respectively, in the municipalities of Capão Alto (latitude 28°11’47” S, longitude 50°45’6” W), São José do Cerrito (latitude 27º44’16.13” S, longitude 50º28’51.35” W) and Urubici (latitude 28°04’27” S and longitude 49°37’30” W). Whereas the lowest altitude area is located in an ecotone with a deciduous seasonal forest, the highest altitude area is considered to be a cloud forest. The regional climate is type Cfb, according to the Köppen classification (Brasil 1992). All areas are in an advanced stage of succession.

Information regarding the abundance of species and their functional traits, for the three locations evaluated, were extracted from the database of the Laboratory of Dendrology of UDESC (Santa Catarina State University). This database is composed of floristic-structural data collected from permanent plots, which totaled 1 ha in each of the areas (50 plots of 10 x 20 m, in Capão Alto and São José de Cerrito, and 25 plots of 20 x 20 m, in Urubici), where all trees with a diameter at breast height (dbh) greater than or equal to 5 cm were surveyed, and of functional trait values for the most abundant species by location (20 for Capão Alto and São José de Cerrito and 19 for Urubici). The functional traits, basic wood density (g/cm^3), leaf area (cm^2) and specific leaf area (cm^2/g), were determined according to the protocols of Chave (2005) and Pérez-Harguindeguy et al. (2013). The maximum potential height, dispersal guild (animal-, wind- or self-dispersed) (Van der Pijl 1982) and deciduousness (deciduous, semi-deciduous and evergreen) were determined from observations in the field and a literature review (Negrini et al. 2012, Souza et al. 2015). For deciduousness, the field observations were based on the vegetation physiognomy classification proposed by IBGE (2012), such that species that presented a loss of up to 20% of their leaves in the unfavorable period were classified as evergreen, species that lost 20 to 50% of their leaves were classified as semi-deciduous and species with a loss of more than 50% of their leaves were classified as deciduous.

For the analysis of the floristic-structural and functional distribution along an altitudinal gradient, a heatmap was generated that was built from two dissimilarity dendrograms, one for floristic-structural composition among areas and another for the functional traits of all species. The floristic-structural dissimilarity dendrogram was based on studied species of each location, through the Bray-Curtis distance and UPGMA (unweighted pair group method with arithmetic mean) clustering method. The functional dissimilarity dendrogram was generated using Gower distance, which was later transformed to Euclidean distance using the method of Cailliez (1983), and Ward’s algorithm. In addition, for each of the plots of each location, the community-weighted mean (CWM) for the functional traits values was calculated. Thus, the functional traits for continuous variables (wood density, leaf area, specific leaf area and maximum potential height) were compared among the different altitudes using parametric tests (ANOVA and Tukey test) in the case of normal data and using nonparametric tests (Kruskall-Wallis and a *post-hoc* test for multiple comparisons) for non-normal data. The species in each altitudinal level were ordered through a Principal Component Analysis (PCA) according to their continuous functional traits (leaf area, specific leaf area and maximum potential height) in order to investigate the existence of functional differences among dispersal and deciduousness ecological groups and to contextualize *Araucaria angustifolia* in relation to other co-existing species.

All analyses were conducted in the statistical programming environment R (R Core Team 2015), using the vegan (Oksanen et al. 2015), FD (Laliberté and Legendre 2010, Laliberté et al. 2014), pgirmess (Giraudoux 2015) and calibrate (Graffelman 2015) packages.

RESULTS

The largest floristic-structural similarity was observed among the lowest altitude areas (Fig. 1), whose Bray-Curtis distance was 0.63. The highest area (1,600 m asl) exhibited low similarity with lower altitudinal levels, not sharing any species with the 700 m asl area and presenting a Bray-Curtis floristic distance of 0.89 with the 900 m asl area. The most abundant species at each altitudinal level were *Parapiptadenia rigida, Allophylus edulis* and *Nectandra megapotamica* at 700 m asl; *Casearia decandra, Matayaba elaeagnoides* and *Lithrea brasiliensis* at 900 m asl; and *Myrceugenia glaucescens, Ocotea pulchella* and *Ilex microdonta* at 1,600 m asl. This floristic difference among the areas was also accompanied by functional replacement, with the area at 700 m asl presenting a prevalence of deciduous and semi-deciduous species, with a high concentration of self- and wind-dispersed species, and the area at 1,600 m asl primarily consisting of animal-dispersed and evergreen species. As for the intermediate altitude area, at 900 m asl, there was greater variation of these traits, indicating greater functional diversity in this location.

The eigenvalues of functional PCA ordination of species for 1,600, 900 and 700 m asl areas (Fig. 2) were, respectively, 1.67, 1.65 and 1.67 for Axis 1; and 1.16, 1.00, 1.04 for Axis 2. *Araucaria angustifolia*, that is the most representative species of the study phytophysiognomy, was absent in the lower area, but, in general, for 900 and 1,600 m asl areas, it was related to species with relatively smaller specific leaf area and higher maximum potential height. Over all altitudinal gradient, the ordinations indicated that there was no evidence of functional differentiation among dispersal and deciduousness groups.

When functional traits are compared separately among areas, it is observed that in addition to the differences in the pattern of leaf renewal and dispersal syndrome already observed in Fig. 1, there are also significant variations ($p < 0,05$) in leaf traits (leaf area and specific leaf area), basic wood density and maximum potential height (Fig. 3). Whereas the community at 1,600 m asl presented the smallest values for leaf area, the community at the lowest altitude was characterized by the largest maximum potential height, lowest basic wood density and largest specific leaf area. As previously noted in Fig. 1, Fig. 3e and 3f show an increase in the representation of evergreen and animal-dispersed species in higher areas.

DISCUSSION

The results found confirm the hypothesis that across an altitudinal gradient, the Araucaria Forest (AF) areas present high floristic and functional variation, which can be explained by past phytogeographical aspects and environmental heterogeneity. From the perspective of the vegetation traits studied, the highest (1,600 m asl) and lowest (700 m asl) areas are considered to be the two extremes of the gradient of changes observed, with these areas not sharing any of the species analyzed. Therefore, the lowest area was characterized by a predominantly deciduous/semi-deciduous tree component with taller trees, lower wood density, greater leaf area and greater specific leaf area, with species typical of a deciduous seasonal forest (Higuchi et al. 2012), whereas the highest area was characterized by an evergreen and animal-dispersed tree component, with smaller trees, with less leaf area and less

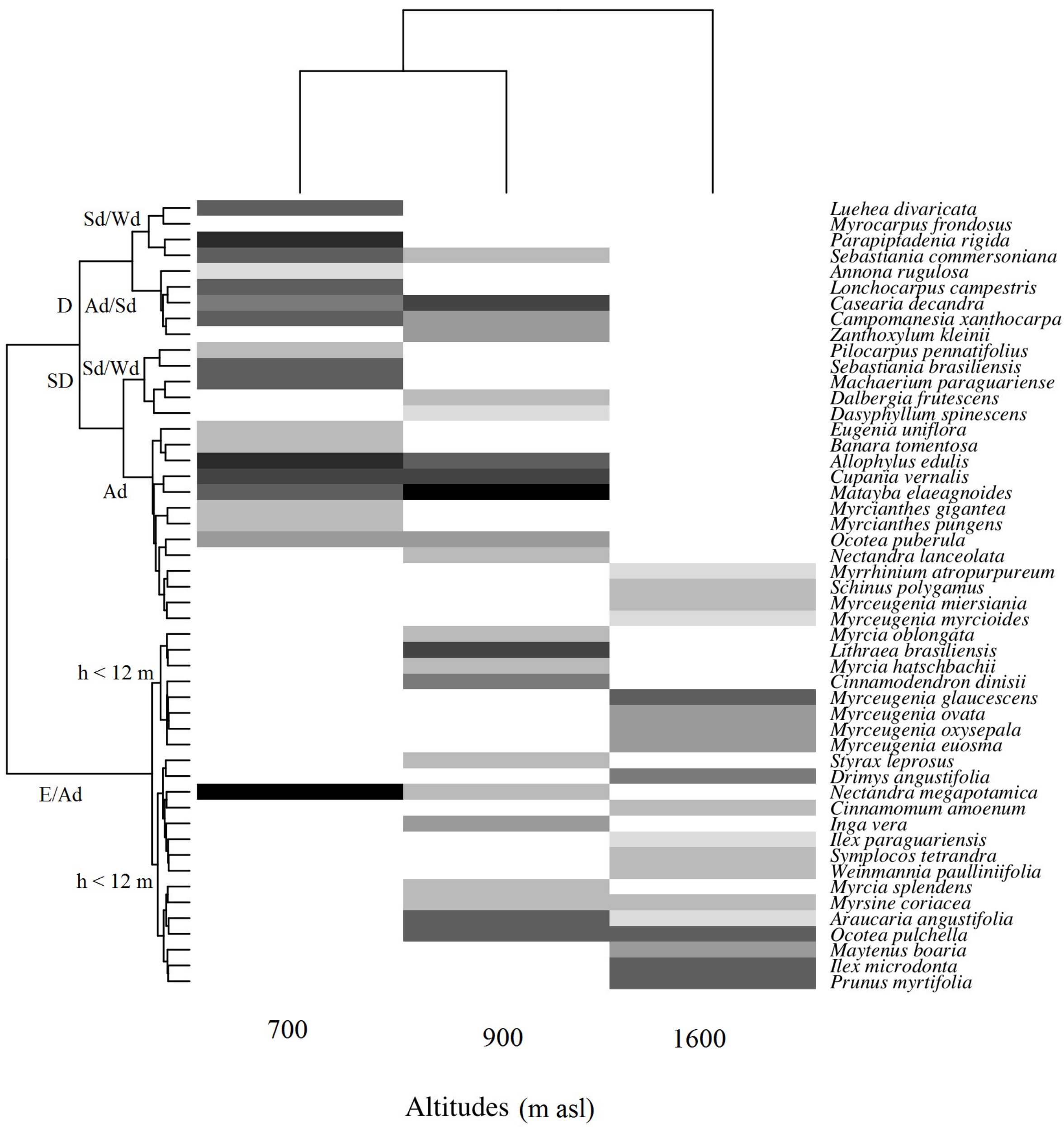

Figure 1 - Heatmap showing the distribution of tree species in araucaria forest areas, across an altitudinal gradient, in the southern plateau of Santa Catarina, Brazil. Darker shades indicate a greater abundance of species. The dendrogram at the top indicates the floristic-structural similarity among areas and the dendrogram on the side indicates the functional similarity among species (SD = semi-deciduous; D = deciduous; E = evergreen; Sd = self-dispersed; Wd = wind-dispersed; Ad = Animal-dispersed, h = tree height).

specific leaf area, and species typical of montane cloud forests (Higuchi et al. 2012). The 900 m asl area presented a greater variation of these traits, suggesting that this area represents a transition zone between the two extremes.

Through the representation of deciduous elements in the areas, the AF was shown to be taxonomically and functionally influenced by the deciduous seasonal forest (DSF), with such influence decreasing as altitude increases. As

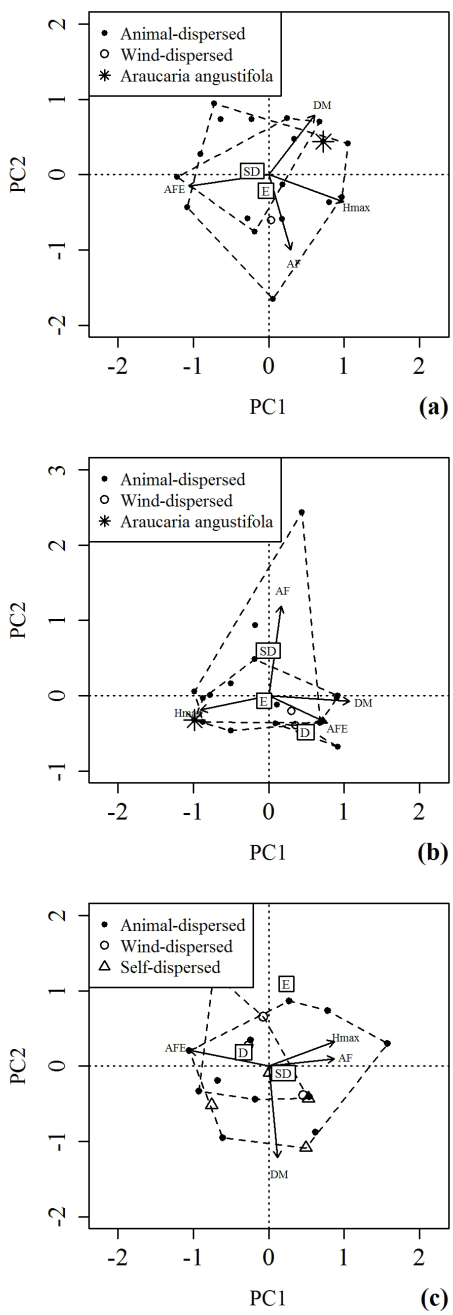

Figure 2 - Ordinations produced by Principal Component Analysis of species according to their functional traits in araucaria forest areas, over an altitudinal gradient (**a** – 1,600 m asl; **b** – 900 m asl and **c** – 700 m asl), along the southern plateau of Santa Catarina, Brazil comparison. Dashed lines connect species with the same deciduousness condition (SD = semi-deciduous; D = deciduous; E = evergreen; DM = Basic Wood Density; AFE = Specific Leaf Area; Hmax = Maximum Potential Height; AF = Leaf Area).

observed by Higuchi et al. (2013), the presence of the DSF in the region is related to a forest expansion process, in a north-south direction, through the Parana-Uruguay River basins (Rambo 1951), which occurred during the Holocene. Thus, because a large extension of the same river basins is shared, without the presence of geographical and climate barriers, the AF and DSF share a large number of species (Higuchi et al. 2013) as a result, which reflects on the functional aspects of the tree component.

Deciduousness represents an adaptation strategy related to survival during an unfavorable period of the year, in regions with seasonal climate (Givnish 2002). In southeastern and midwestern Brazil, this strategy is related with water seasonality, whereas in the south, deciduousness represents an adaptation to the annual thermal amplitude (Pennington et al. 2009). Moreover, this strategy is usually associated with greater soil fertility (Jiang et al. 2015) because the replenishment of leaf biomass lost through leaf fall requires high-energy expenditure, which is only possible in environments with greater primary productivity. Therefore, a reduction in the representation of deciduous species with increased altitude may be related to climate and soil changes. In this case, the combination of low temperatures and nutrient-poor soils, common in cloud forests (Marcon et al. 2014, Jiang et al. 2015), may represent a limiting condition for the occurrence of species that are typical of the DSF. The absence of evidence that dispersal and deciduousness syndromes differed regarding functional traits suggests that the studied ecological groups can share similar life-strategies, allowing them to compete and to develop in similar type of habitat (e.g., closed and opened canopy) within each altitudinal level.

The patterns observed for maximum potential height, leaf area and specific leaf area in the highest area represent the functional expression imposed by limiting environmental conditions, characterized by

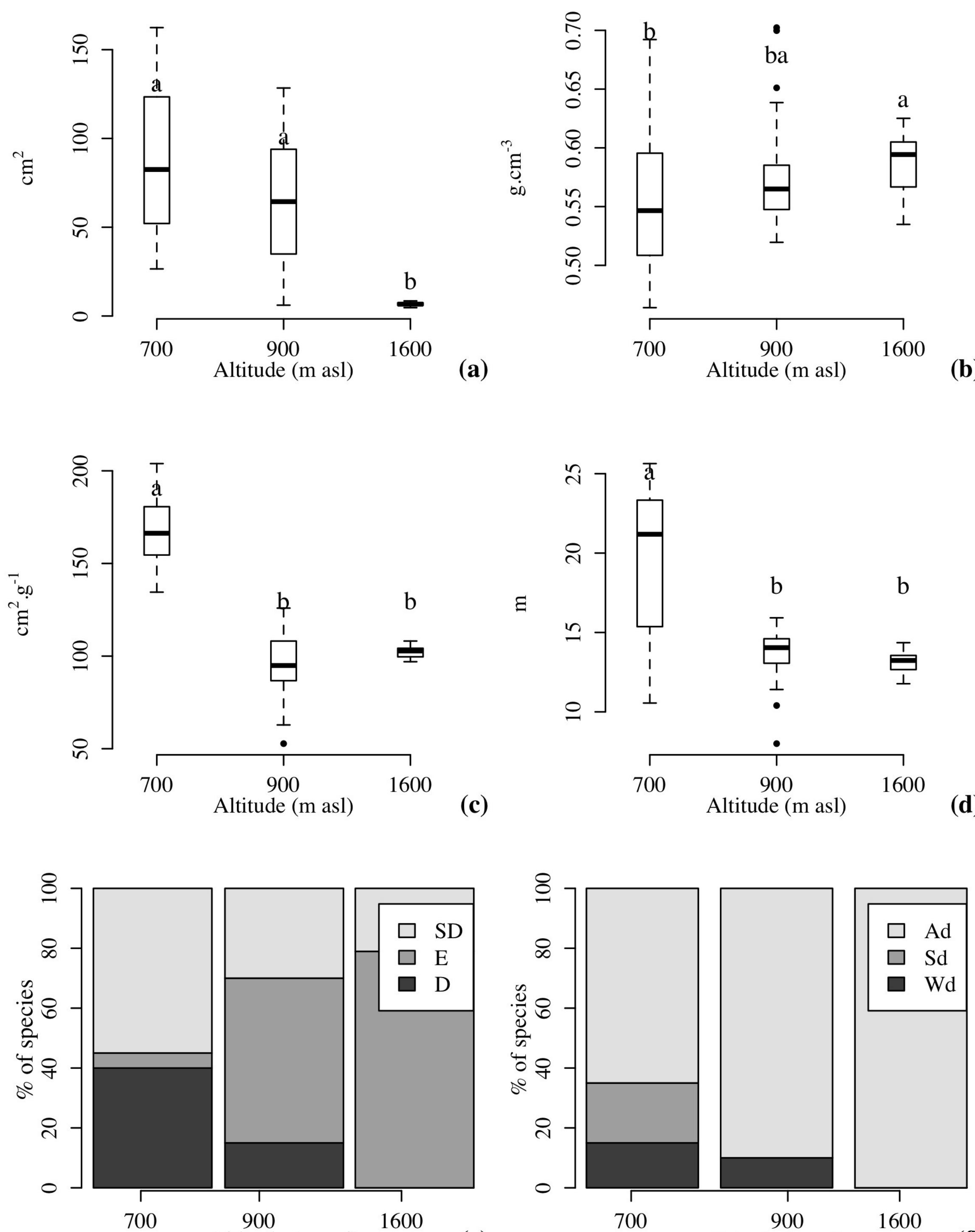

Figure 3 - Comparison of functional traits of tree species (**a** - Leaf Area; **b** - Basic Wood Density; **c** - Specific Leaf Area; **d** - Maximum Potential Height; **e** - Pattern of Leaf Renewal; and **f** - Dispersal Guilds) in araucaria forest areas, over an altitudinal gradient, along the southern plateau of Santa Catarina, Brazil. Boxplots followed by different letters present significant differences by nonparametric post hoc tests for multiple comparison (SD = semi-deciduous; D = deciduous; E = evergreen; Sd = self-dispersed; Wd = wind-dispersed; Ad = Animal-dispersed).

low temperature, constant clouds and low natural soil fertility (Marcon et al. 2014). This pattern has been described in the literature (Barrera et al. 2000, for maximum potential height and leaf area; Jiang et al. 2015 and Rosado et al. 2016, for specific leaf area), such that it can be inferred that this functional convergence is the result of environmental filters characterized by decreased temperature, leading to a lower growth capacity (Körner 2007) and greater occurrence of frost (Barrera et al. 2000).

Wood density, which represents one of the primary traits of woody species because it summarizes a large set of functional aspects (Chave et al. 2006, Swenson and Enquist 2007), was smallest in the lowest area. There is no consensus in the literature regarding the response of this attribute to altitude variation. For the neotropical region, Chave et al. (2006) observed the opposite pattern, with a negative relationship between altitude and wood density. Zhang et al. (2011) and Jiang et al. (2015), in China, and Rosado et al. (2016), in Brazil, also did not find a clear relationship between altitude and wood density. Thus, it is inferred that at a regional scale, variations of this trait can be conditioned by specific conditions of the vegetation physiognomy evaluated, such as the phylogenetic structure of the community, because studies have demonstrated that wood density represents a phylogenetically conserved trait (Swenson and Enquist 2007, Zhang et al. 2011).

For 900 and 1,600 m asl areas, *Araucaria angustifolia*, that is the most representative species of the studied phytophysiognomy, was associated with taxa that showed relatively greater maximum potential height and smaller specific leaf area. While a greater maximum potential height may represent a competitive advantage to light acquisition (Falster and Westoby 2003), a smaller specific leaf area is frequently observed for species occurring in dry or cold climate (Reich et al. 1997, 2003). In fact, *Araucaria angustifolia* is described as an open area colonizer species, common in south Brazil highlands, playing an important role as a nurse element in forest expansion process (Korndörfer et al. 2015).

We conclude that the evaluated Araucaria Forest areas exhibited high floristic-functional heterogeneity of the tree component along an altitudinal gradient. The factors that can explain this pattern include those related to past phytogeographical events, such as the expansion and occupation of the seasonal forest in the region due to past climate changes, and the existing environmental differences, such as the presence of cloud-forest conditions, low temperatures and nutrient-poor soils in the highest area.

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