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THE SLOPE DOES NOT INFLUENCE UNDERSTORY COMMUNITY ON A BRAZILIAN MONTANE ATLANTIC FOREST

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Abstract. Canestraro, B. K. & R. A. Kersten. 2018. The slope does not influence understory community on a Brazilian Montane Atlantic Forest. *Darwiniana*, nueva serie 6(1): 5-23.

The understory is a component of great relevance to the flora and structure of tropical forests. Mountain environments, through physical factors, can show differences in the structure and composition of this stratum. We aimed to analyze whether there is a correlation between the slope and the understory plant community. A transition area between the Montane Dense Ombrophilous Forest and the Araucaria Forest in the Atlantic Forest in South of Brazil was analyzed. 63 plots of 1 m² were made, being equally subdivided into three slope classes (0-25%, 40-60%, and >80%). 93 species, 63 genera and 42 families were recorded. The richest families were Myrtaceae (15 species), followed by Lauraceae (7), Dryopteridaceae (6), and Rubiaceae (5). The most frequent life forms were arboreal (43 species), followed by herbaceous (24) and shrubby (11). 58 species were transient and 35 were resident. The richness and diversity indices showed no significant differences between the structure and composition of the slope classes. The ordination analysis could not distinguish any slope class grouping. This is possibly justified by the environmental homogeneity of the sampled area created by the density and regularity of the canopy, climatic stability, high organic matter and shallow soil.

Keywords. Araucaria Forest; Dense Ombrophilous Forest; floristics; lower stratum; phytosociology.

Resumen. Canestraro, B. K. & R. A. Kersten. 2018. La pendiente no influye en la comunidad del sotobosque del Bosque Atlántico Montano de Brasil. *Darwiniana*, nueva serie 6(1): 5-23.

El sotobosque es un componente de gran relevancia para la flora y estructura de los bosques tropicales. Los ambientes montañosos, a través de factores físicos, pueden reflejar diferencias en la estructura y composición de este estrato. El objetivo del estudio fue evaluar si existe una correlación entre la pendiente del terreno y la comunidad de plantas del sotobosque. Se analizó una zona de transición entre la Floresta Ombrófila densa y la Selva de Araucaria en el Bosque Atlántico en el sur de Brasil. Se delimitaron 63 parcelas de 1 m², subdivididas por igual entre tres clases de pendiente (0-25%, 40-60% y >80%). Se registraron 93 especies, 63 géneros y 42 familias. Las familias más ricas fueron Myrtaceae (15 especies), Lauraceae (7), Dryopteridaceae (6) y Rubiaceae (5). Las formas de vida más frecuentes fueron arbórea (43 especies), seguido de herbácea (24) y arbustiva (11). Se registraron 58 especies transitorias y 35 residentes. Los índices de riqueza y diversidad no mostraron diferencias significativas entre la estructura y la composición de las clases de pendientes. Los análisis de ordenamiento no distinguieron diferentes grupos para las clases de pendiente. Esto posiblemente se justifica por la homogeneidad ambiental del área muestreada generada por la densidad y regularidad del dosel, la estabilidad climática de la región, el alto contenido de materia orgánica y los suelos superficiales.

Palabras clave. Bosque Atlántico Montano; fitosociología; florística; Selva de Araucaria; sotobosque.

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INTRODUCTION

The Dense Ombrophilous Forest, also known as Atlantic Rain Forest, is one of the main phytogeographic units of the Brazilian Atlantic Forest hotspot. It is located in the east portion of Brazil and of Paraná State from 0 to 1,650 m a.s.l., including the Serra do Mar mountain range. This forest type is directly influenced by the warm and humid air mass from the Atlantic Ocean and by the evenly distributed rainfall throughout the year, which provides a climate with thermal stability (Maack,1968; Leite, 2002; Roderjan et al., 2002). The Subtropical Atlantic Forest (or Araucaria Forest), integrating the Brazilian Atlantic Forest hotspot, is characterized by the coexistence of the tropical and temperate flora and by the components *Araucaria angustifolia* (Bertol.) Kuntze, *Podocarpus lambertii* Klotzsch ex Endl., Lauraceae and Myrtaceae. It is distributed on highlands (750 – 1,300 m a.s.l) westwards from the Serra do Mar (Maack,1968; Roderjan et al., 2002). The climate is always humid with low temperatures and frosts are common in winter (Leite, 2002).

Environmental factors are usually considered the main causes of the large diversity of plant communities, either for canopy and for understory (Pereira et al., 2007). Some of these factors are: edges (Pereira et al., 2007; Silva et al., 2008), light gradients (Poulsen, 1996; Záchia & Waechter, 2011; Enoki & Abe, 2004; Inácio & Jarenkow, 2008), soil moisture (Záchia & Waechter, 2011; Cardoso & Schiavini, 2002; Enoki & Abe, 2004), soil properties (Beatty, 1984; Roderjan, 1994; Záchia & Waechter, 2011), litter thickness (Beatty, 1984; Poulsen, 1996), temperature (Roderjan, 1994), and also topography (Poulsen & Balslev, 1991; Záchia & Waechter, 2011; Enoki & Abe, 2004; Pereira et al., 2007; Silva et al., 2008).

In order to understand the local flora and the participation of each environmental factor within the richness and structure of the community is of utmost importance to embrace distinct growth forms in phytosociological studies (Moro & Martins, 2011). In tropical forests, the lower stratum is an important element, both on diversity and ecology (Cestaro et al., 1986; Andrade, 1992; Kozera et al., 2009). Specific studies on the understory layer, such as the herbaceous and shrubby components, are significantly scarcer than those on the arboreal layer (Gentry & Dodson, 1987; Munhoz & Araújo, 2011). However, research on the non-woody understory component (herbs, shrubs and climbers) had increased substantially in recent years (Andrade, 1992; Silva et al., 2008; Polisel et al., 2014), mainly in the South of Brazil (Cestaro et al., 1986; Kozera, 2001; Müller & Waechter, 2001; Kozera & Rodrigues, 2005; Silva & Britez, 2005; Inácio & Jarenkow, 2008; Kozera et al., 2009; Blum, 2010; Záchia & Waechter, 2011). Fine-scale heterogeneity is still ignored in the study of community response to gradients and available data remain insufficient for the understanding of abundance, distribution, richness, and diversity of species.

Studies on the flora of the mountain regions and at different geographical scales become interesting due to the gradual phytophysiognomy change over the altitudinal gradient. Variations in topography result in differences in the physiognomy and structure of interior habitats (Grytnes & Vetaas, 2002; Carvalho et al., 2007; Silva et al., 2008). Considering a smaller scale, the microrelief can lead to a mosaic of soil and to a vegetation pattern in the understory (Beatty, 1984). Specific researches on the relationship between the topography and the understory community are very scarce (Poulsen, 1996; Záchia & Waechter, 2011). Some studies have analyzed the arboreal and shrubby community (Blum, 2006) and the herbaceous group (Blum, 2010) along the altitudinal gradient in a Mountain range in Paraná State; slope however was just mentioned on descriptions but never taken in consideration by researchers. On the other hand, the studies of Enoki & Abe (2004), Pereira et al. (2007), Silva et al. (2008) and Záchia & Waechter (2011) analyzed the topography as a variable within the ecosystem. Thus, there are no studies emphasizing the role of the microrelief on the lower stratum community in forests of the mountain regions of Brazil.

Therefore, the hypotheses of this study are: a) the understory community is influenced by microrelief and show distinct structure, composition and diversity on different slope classes and b) the spatial distributions of plant species are related to particular topographic features.

MATERIALS AND METHODS

The "Serra do Mar" region is the elevation of the crystalline complex which predominates rocky outcrops from Pre-Cambrian period and slopes strongly dissected by the drainage that forms different sizes of valleys (Maack, 1968). The relief is mountainous with steep slopes, rocky shallow soils (Entisoils Orthend, Histosoils and Inceptisoils - Soil Survey Staff, 1999), rich in organic matter and with heterogeneous litter thickness (Roderjan, 1994; Portes et al., 2001; Blum, 2010).

The study was conducted on the western hillside of Anhangava Mountain (1,432 m), the summit of the "Parque Estadual da Serra da Baitaca" on the "Serra do Mar" mountain range, Paraná State, Brazil. The studied area is restricted to the middle third hillside of the mountain and presents a dissected microrelief (Figs. 1 and 2). The vertices of the area are point A (25°23'18.9"S; 49°00'36.8"W), B (25°23'20.3"S; 49°00'37.1"W), C (25°23'20.5"S; 49°00'37.7"W) and D (25°23'18.8"S; 49°00'39.6"W), totaling 3,350 m^2 and varying from 1,086 m a.s.l. at point D to 1,108 m a.s.l. at point B (Fig. 1). The studied area has two convergent drainage canals, one of which is a long and deep seasonal waterway (section A1 and point D in Fig. 1, 2 and 3). Close to the area there is a perennial stream. The points A and B are placed in a 1.5 m wide path towards the mountain peak with closed canopy (Fig. 1). Longitudinal sections of relief profile can be seen in figure Fig. 3.

The climate is classified as *Cfb* (Koeppen's classification) (Roderjan, 1994). The mean annual temperatures of the coldest month vary between -3°C and 18°C and in the hottest month from 10°C to 22°C, with high rates of evenly distributed annual rainfall (Roderjan, 1994).

The vegetation is classified as Montane Atlantic Rain Forest (Montane Dense Ombrophilous Forest) (Roderjan et al., 2002). However, considering the short distance and the altitude, the environment is directly influenced by the Araucaria Forest (which extends until 1,000 m), and therefore the area should be considered an ecotone (Roderjan, 1994; Portes et al., 2001). The area is in the interior of an extensive forest fragment, in advanced regeneration stage and has no evidence of recent deforestation or selective logging (Figs. 1 and 3).

The following plant life forms were considered components of the understory: herbs, shrubs, juvenile trees and climbers (not connected to the phorophyte). The species were classified into two ecological groups (residents and transients) according to their typical stratum of permanence.

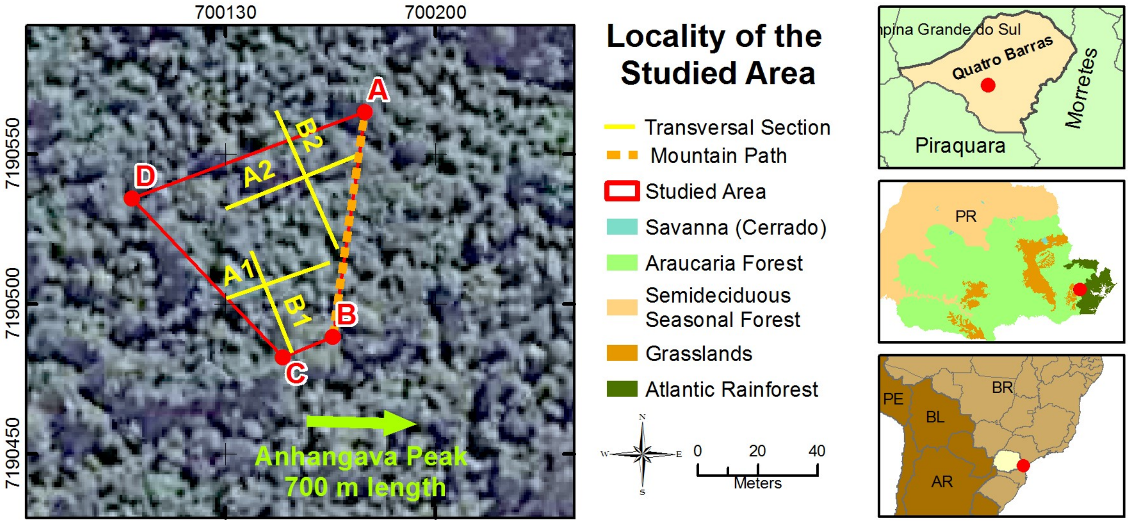

Fig. 1. Location of the studied site in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Color version at http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/762/751

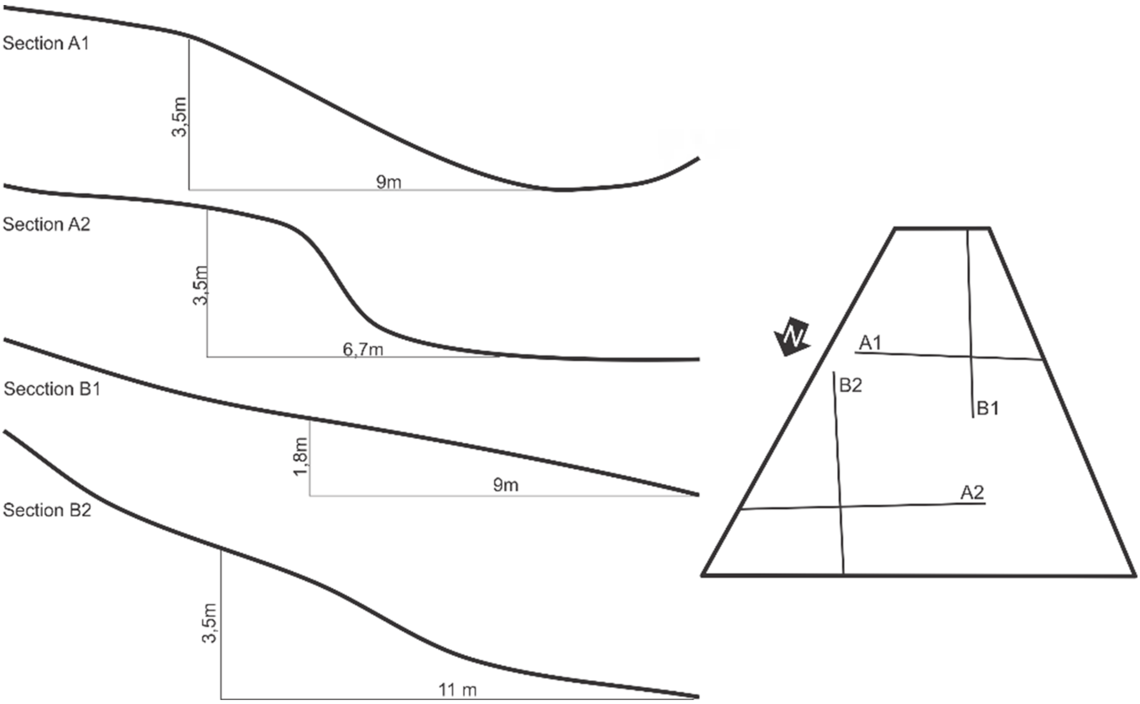

Fig. 2. Relief profile (according to the four sections in figure 1) of the studied site in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil.

Juvenile individuals which have temporary permanence in the lower stratum and occupy higher stratum when mature (trees and climbers) were classified as transients. Otherwise, species that normally complete their cycle in this stratum (herbs or small shrubs) were classified as residents (Gilliam et al., 1994). Both groups are typical of the lower stratum, although the transients are not exclusive to it (Gilliam & Roberts, 2003).

For each species the following characteristics were determined: physical habitat (terrestrial or epipetric), ecological habit (transient or resident) and the biological forms: herbaceous (erect, rhizomatous, creeping, rosulate, and caespitose), shrubby (erect, scandent and rosulate), arboreal, climber, and accidental herbaceous (rosulate), according to Mueller-Dombois & Ellenberg (1974). Accidental herbs are components of the lower stratum because they use the soil in some parts of their life cycle (which is commonly epiphytical) and can also be classified as facultative terrestrial herbs (Poulsen & Balslev, 1991).

Fertile individuals were collected, preserved and herborized according to usual methods and deposited in the Municipal Botanical Museum of Curitiba (MBM) herbarium. Specimens were identified to the lowest taxonomical level (when possible), using specialized literature, specialist assistance and consultancy from MBM's collection. Indeterminate taxa were treated as distinct morpho-species. The scientific names, authors and classification system followed BFG (2015) and Prado et al. (2015).

In order to analyze the influence of the slope on the structure and composition of species, we delimited three classes of slope: 0-25 %, 40-60 % and > 80%. We did not perform analyses on slopes outside of these classes' intervals. The slope rate was determined through a levelling rod, a wood stick and a level. Each plot comprised 1 m² of area (Munhoz & Araújo, 2011) and the measurements were within this area. As the plots had a fixed length (100cm), the height of the declivity (in cm) is equal to the percentage of the slope. We sampled 21 plots in each class of slope, with a total area of 63 m².

Fig. 3. Picture of the studied site, showing the drainage canal (point D of figure 1) in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Color version at http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/762/751

The multiple plots system (Mueller-Dombois & Ellemberg, 1974) was used. The 1m² quadrats were placed randomly and directly on the ground of the forest, following the relief topography and were positioned with at least 2 m between each other. Due to the constant shift on microrelief and the small length of the considered slopes it was not possible to follow any systematic sampling scheme. All individuals between 20 cm and 2 m height and with perimeter at breast height (1.3 m) less than 5 cm were included; for tree ferns the only criterion was stature. Woody individuals below 20 cm were treated as seedlings and ignored by the analysis due to their uncertain identification. The relative plant cover (%) was estimated by each species' vertical projection of occupation including those individuals non-rooted inside the plot, but with cover projection inside of it.

The phytosociological parameters collected for each species were frequency, leaf cover and dominance. The importance value (IV) was calculated based on the relatives' frequency and dominance (Mueller-Dombois & Ellenberg, 1974). The community diversity was calculated through the indices of Evenness (J), Shannon (H') and Simpson (1/D and 1-D) (Magurran, 2011) and the richness was calculated by the Margalef (Dα) and Chao-1 indices (Chao, 1984). Those calculations were made using PAST 3.0-ORD (Hammer et al 2001) when software allowed and graphs with error bars were displayed. In order to compare diversities, we applied the diversity profiles method using the on-line version of the iNext R-package (Chao et al, 2016). To understand diversity through a single index is to project multidimensional complexity onto a one-dimensional ordinal scale.

One way to surpass this problem is to quantify diversity by means of diversity profiles which is a curve showing the simultaneous values of a large collection of diversity indices. (Patil, 2014)

Considering species abundance on the plots, we performed an ordination analysis using Detrended Correspondence Analysis (DCA) downweighting rare species (Hill & Gauch, 1980). We used MRPP and PerMANOVA as an “a posteriori test” for all slopes classes, and for making the paired (two-by-two) comparisons (Anderson, 2005). Species with single occurrences (singletons) were excluded in both cases. The calculations were made using the PC-ORD program, version 6.0 (McCune & Mefford, 2011). We also compared floristic composition similarity using the Jaccard Index (IJ) (Mueller-Dombois & Ellenberg, 1974) and a modified version of this index, excluding the singletons.

RESULTS AND DISCUSSION

Floristic composition

We recorded 354 individuals belonging to 93 species, 63 genera and 42 families (Tab. 1). Three taxa were identified to family level (Myrtaceae) and four taxa to genus level due to their sterile state. From the total, 75 species, 48 genera and 33 families were Angiosperms and 18 species, 15 genera and 9 families were ferns. Lycophytes and Gymnosperms were not found. The richest families were Myrtaceae (15 species), Lauraceae (7), Dryopteridaceae (6) and Rubiaceae (5) and their sum represents 35% of the total richness (Tab. 1). Myrtaceae, Lauraceae and Rubiaceae were the most representative families on the Araucaria Forest (Kozera et al., 2006; Scheer & Blum 2011; Lima et al.,2012; Ribeiro et al., 2013) and also on a transitional area between Dense Ombrophilous Forest and Araucaria Forest (Reginato & Goldenberg, 2007).

The richest herbaceous family was Dryopteridaceae, as observed by Kozera & Rodrigues (2005), Kozera *et al.* (2006), Inácio & Jarenkow (2008), Paciencia (2008), Kozera *et al.* (2009), Blum (2010) and Lima *et al.* (2012). The most representative genera were *Ocotea* (6 species) and *Eugenia* (5), as observed by Ribeiro *et al.* (2013) in a fragment of Araucaria Forest.

The arboreal and shrubby strata were composed of taxa of both Araucaria and Dense Ombrophilous Forest (Roderjan et al., 2002; Blum, 2006; Scheer & Blum, 2011). While *Cinnamodendron dinisii*, *Casearia decandra* and *Eugenia uniflora* are typical of Araucaria Forest, *Pouteria bullata*, *Myrsine umbellata, Guatteria australis* and *Cyathea phalerata* represent the Dense Ombrophilous Forest type (Scheer & Blum, 2011).

Habitats and biological forms

Considering physical habitats, 85 species were exclusively terrestrial, four were exclusively epipetric and four used both substrates (Tab. 1). Regarding the biological forms, the arboreal type was represented by 43 species (46%), followed by herbaceous (including herbaceous/climber) with 24 species (25.8%), shrubby with 11 species (11.8%), arboreal/shrubby with 10 species (10.7%), exclusively climber with four species (4%) and only one accidental herbaceous epiphyte (1%) (Tab. 1). A similar proportion of biological forms was found by Gentry & Dodson (1987) in a tropical wet forest in Ecuador and by Andrade (1992), Kozera et al. (2006) and Lima et al. (2012) in the Atlantic Forest hotspot, excluding epiphytic species (Kozera et al., 2006; Lima et al., 2012). The low contribution of climbers was an evidence of a forest with a perennial and continuous canopy, as observed by Polisel et al., 2014 in an Araucaria Forest.

The most common habit of herbs was rhizomatous (11 species), followed by rosulate habit (7) (Tab. 1) as observed by Kozera & Rodrigues (2005) and Záchia & Waechter (2011) in different Atlantic Forest physiognomies. Among the obligatory herbs, 67% were composed of ferns and only 36% were angiosperms, in contrast to the proportion of ferns and flowering plants found by Kozera et al. (2009) and Blum (2010) on Dense Ombrophilous Forest and Záchia & Waechter (2011) in a coastal Atlantic Forest. Within the woody species, the erect biological form represented most records not only for trees (43), but also for shrubs (7) and trees/shrubs (10), as observed by Kozera & Rodrigues (2005) in a coastal Atlantic Forest.

Among the five species with the highest Importance Value (IV), four were herbs and sum 33.1% of the IV. Within the 20 species with highest IV, nine were herbs and sum 45.6% of the IV, whereas ten species are trees and shrubs and sum 25.5% of the IV (Tab. 1 and 2). It is possible to notice a gradual increase in the richness and in the IV of herbs from the flat (class 1) towards the slope (class 3) slope (Tab. 1 and 2). Záchia & Waechter (2011) observed this same pattern in a coastal forest.

Fifty-eight species (62%) were classified as transients and 35 (37%) as residents (Tab. 1). According to Kozera et al. (2006), in Ombrophilous Forests, the arboreal stratum (transient habit) is the most representative component of the community. Gomes-Westphalen et al. (2012) studying the Atlantic Forest understory, have also found a considerable amount of transient species (regenerative strata). However, among the 20 species with the highest IV, 13 were resident and seven were transient (Tab. 2), showing that the most significant species are resident, while the transient component is still rich, yet less expressive. The four most important species in class 3 (>80%) were resident (Tab. 2).

Community Similarity and Diversity

Pseuderanthemum riedelianum was the most important species with the highest IV within all three slope classes, due to its high frequency and dominance (Fig. 4). *Parodiolyra micrantha* and *Ctenitis paranaensis* featured between the six highest IVs; however, the species appeared in distinct orders within the slope classes (Fig. 4). Another species of *Ctenitis* (*C. distans*) also played an important role in the structure of an Araucaria Forest fragment, as seen by Rigon et al. (2011). *Pseuderanthemum riedelianum* and *Parodiolyra micrantha* have also exhibited relevant participation in the Submontane Dense Ombrophilous Forest communities in the study of Kozera & Rodrigues (2005). Poulsen & Balslev's study (1991), on the understory herbs of the Amazon Forest, showed that a Poaceae (*Pariana radiciflora*) had the highest cover value, indicating that grasses are important components of the lower stratum, as well as *Parodiolyra micrantha*'s performance in this study. The tree *Rudgea jasminoides* was very important in this study (Tab. 2) and also presented a high IV in different Montane Araucaria Forest remnants as analyzed by Ribeiro et al. (2013). Were recorded

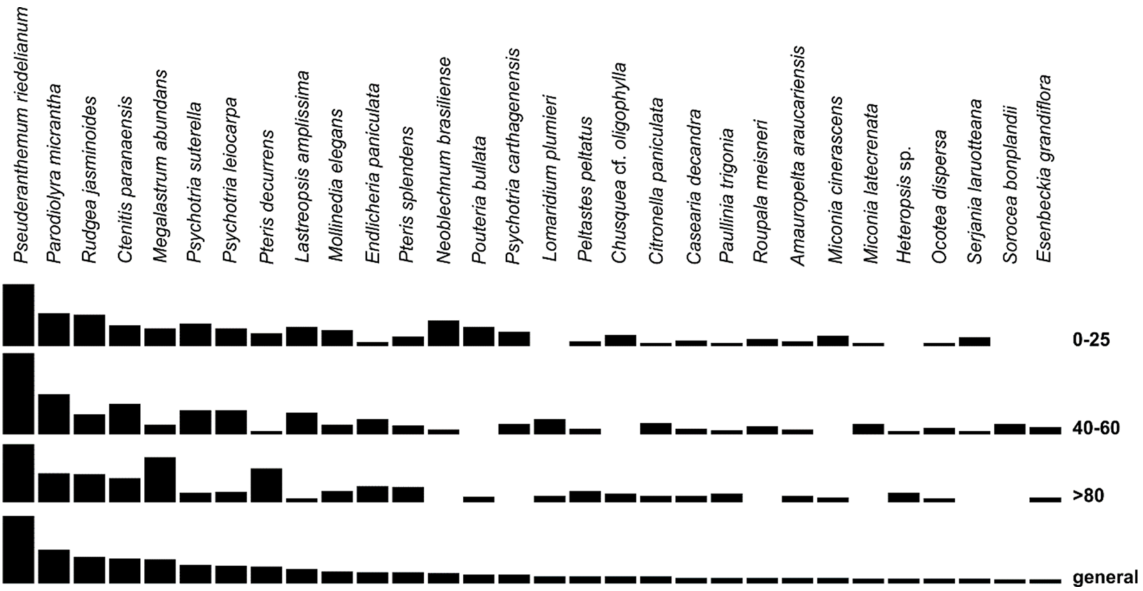

Fig. 4. Importance values of the 30 most important species (80% of the importance value) compared to the three slope classes and in general in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil.

47 singletons species (50%) (found only once on the survey) and 10 doubletons. Rubiaceae was the most frequent family in the lower stratum for both Araucaria Forest and Dense Ombrophilous Forest, agreeing with a forestry survey by Roderjan et al. (2002).

In steep slopes (>80% slope), the fern *Megalastrum abundans* accomplished the highest dominance (15%) (Tab. 2), possibly due to its large fronds, which increase cover value. The ferns were among the species with the highest cover values (Tab. 2), due to their compound and large leaves, when compared with most of angiosperms leaves. The class > 80% of slope showed high leaf cover index by herbs and especially by ferns, probably due to its short and narrow roots that establish well on slopes, as observed by Záchia & Waechter (2011) (Tab. 2).

In general, the most frequent families were Acanthaceae (54 from 63 plots), followed by Rubiaceae (45), Dryopteridaceae (42) and Poaceae (31). Of the total, the five most important species corresponded to 38% of the Importance Value whereas 80% of the IV was achieved by the 29 main species. There were species exclusive to each class; however their IVs were not sufficiently relevant to show significant differences between the communities.

The richness was very similar among the slope classes, in spite of the fact that the Chao-1 indicated highest richness for class 3 (>80%) (Tab. 3, Fig. 5). In contrast, Silva et al. (2008) found distinct richness rates comparing three understory topographical sites. The dominances were also similar (Tab. 3). The number of sampled individuals was higher in class 40-60% (129) and lower in class 0-25% (105) (Tab. 3). The leaf cover index was lower in class >80% (31) and higher in class 40-60% (41.7) (Tab. 3).

The diversity indices showed structural similarity between the classes of slope (Tab. 3, Fig. 5). The other analyzed indices were not capable of showing differences between the community classes, however the diversity was higher in class >80%, due to its higher richness and evenness and lower dominance (Tab. 3). The Simpson's index average (1-D) was 0.95 (increasing scale from 0 to 1), emphasizing the high diversity of the sampled area, despite the similarities between the classes (Tab. 3, Fig 5). Záchia & Waechter (2011) found higher diversity in steep slopes due to the greater richness and evenness of the community

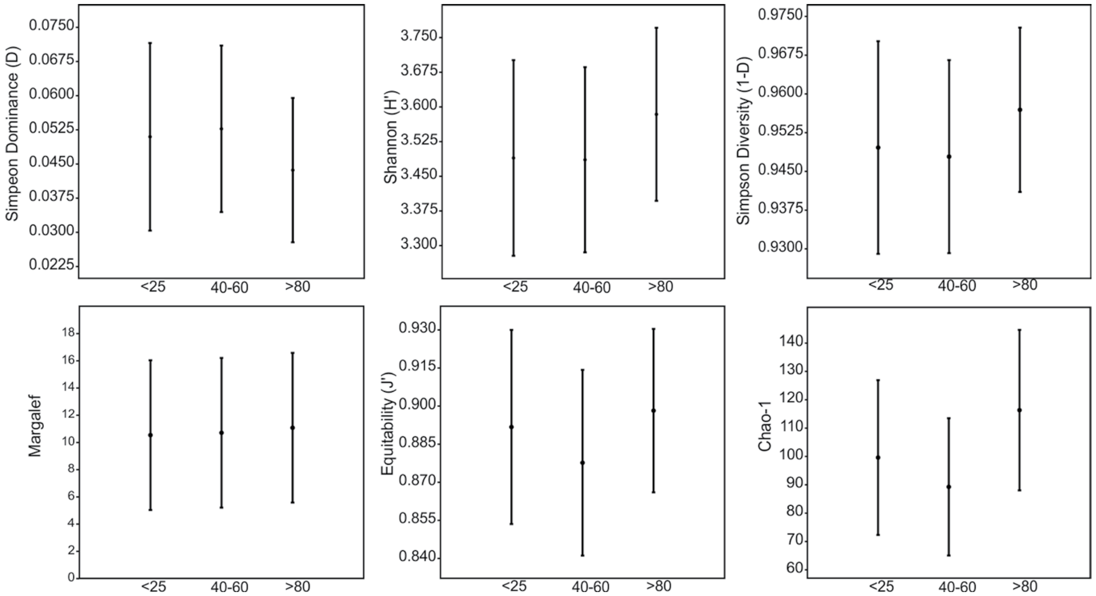

Fig. 5. Comparison of different diversity parameters of the three slope classes in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil.

in a costal environment. Silva et al. (2008), studying the edge *vs.* the interior understory community, reported homogeneous diversity indices in different topographical interior sites, however the lower slopes were more diverse, followed by the terraces.

The diversity profiles also indicated that the slope communities were very similar on species richness (q=0), Shannon Diversity index (q=1) and Simpson Diversity Index (q=2) (Fig. 6).

The ordination analysis (DCA) indicated that the plots were very similar despite the slope classes and that the groups were completely overlapped (Fig. 7). The low A-value on MRPP (A = 0,011) indicates that heterogeneity within groups equals expectation by chance and PerManova indicates that only 2.7% of variance is explained by slope classes variable.

The plots on class 0-25% (red triangles in Fig. 7) presented higher heterogeneity, whereas the plots on class 40-60% (green circles in Fig. 7) were more homogeneous. The analysis showed the presence of several generalist and broadly distributed species within the plots, in other words, the sampled area was considered statistically homogeneous. The great distance between the points indicates distinct structural and floristic communities.

Paciencia (2008) analyzed the ferns' and lycophytes' community in altitudinal gradients in the "Serra do Mar" Mountains in Paraná. This study showed, by another correspondence analysis (NMDS), that the community was influenced by altitudinal variations among the gradients; however those localities with low altitudinal variations had similar compositions and structures.

Low floristic diference was also observed among slope classes. The Jaccard Indexes were high (0-25% - 40-60% = 0.37; 0-25% - >80% = 0.35; 40-60% - >80% = 0.39), but lower than expected due to the high number of singletons (50%). When those were excluded, the indexes were much higher (0-25% - 40-60% = 0.64; 0-25% - >80% = 0.60; 40-60% - >80% = 0.65).

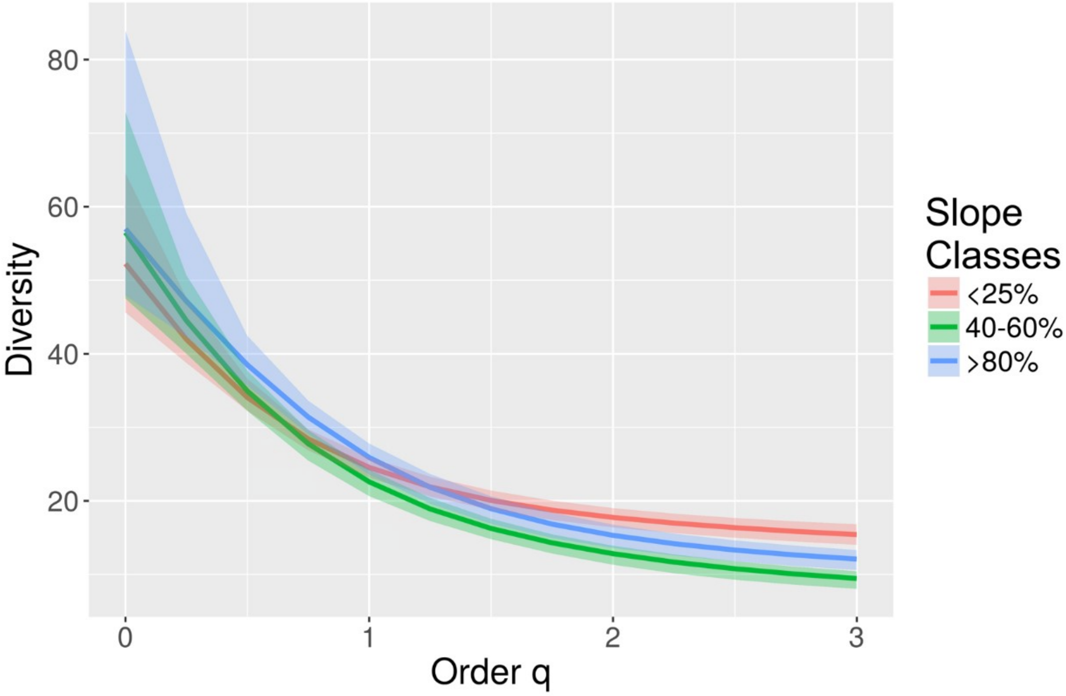

Fig. 6. Diversity profile comparing slope classes in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Color version at http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/762/751

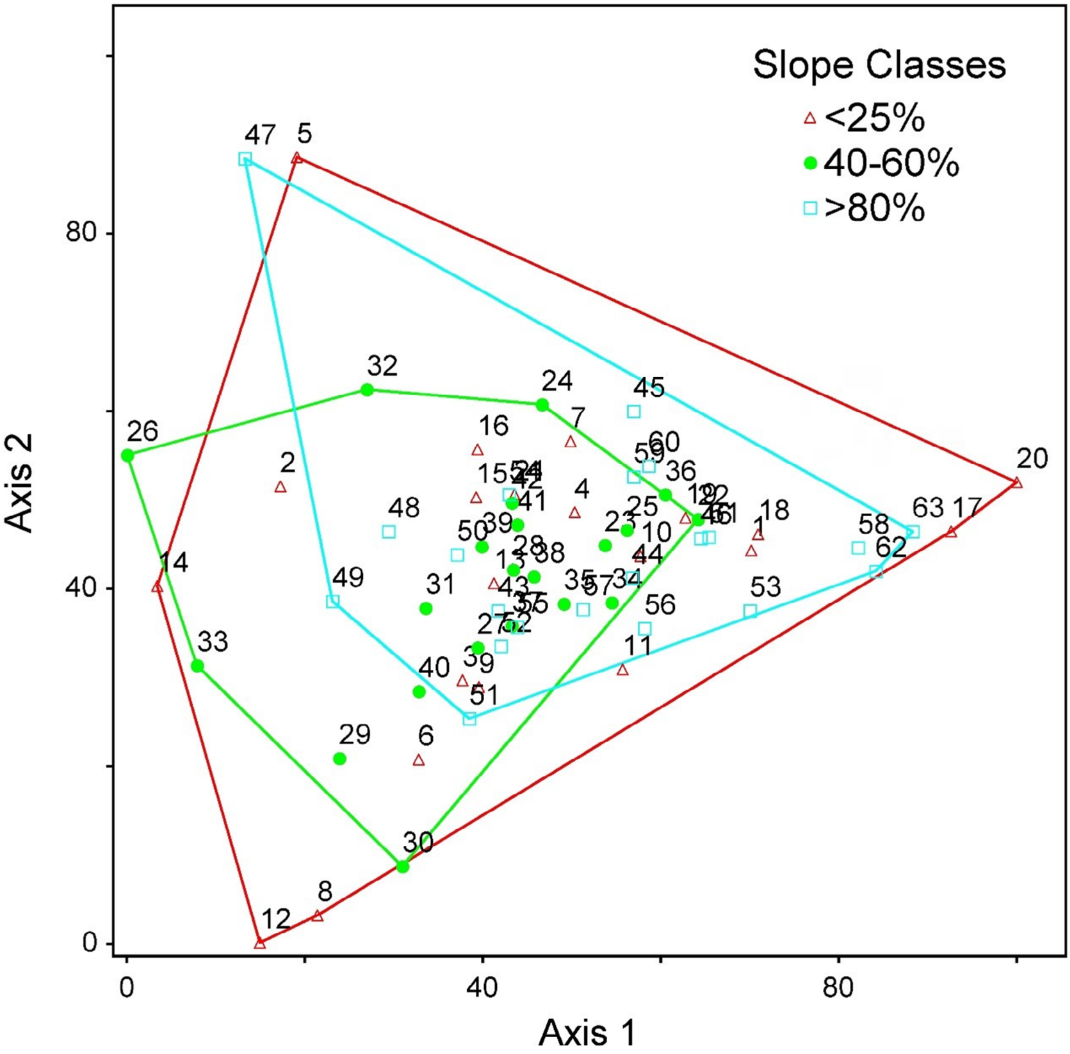

Fig. 7. Detrended Correspondence Analysis (DCA) comparing slope classes in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Color version at http://www.ojs.darwin.edu.ar/index.php/darwiniana/article/view/762/751

Slope and abiotic factors

The relief of the Montane Dense Ombrophilous Forest involves steep slopes, contributing to shallow soils with little effective depth (Roderjan, 1994; Roderjan et al., 2002; Blum, 2006). The studied area shows a thick layer of litter, especially in flat areas, which can be related to the low temperatures of the region that slow down the organic matter decomposition in forest environments (Beatty, 1984; Blum, 2006). The relief heterogeneity creates distinct microenvironments for the understory community (Whitmore, 1990 *apud* Blum 2010); however, the small size of our sampled area did not capture this feature. Forest shallow and poor developed soils ("Entisols") and high organic matter combined with homogeneous shading and a regular 22 m-high canopy can provide undifferentiation within the understory community (Beatty, 1984; Roderjan, 1994; Portes et al., 2001; Scheer & Blum, 2011).

The effect of this homogeneous and dense canopy (Figs. 1 and 2) is understory protection against high solar radiation, wind and air masses exposure and rain impact, preventing abrupt variation in soil humidity and temperature (Roderjan, 1994), thus contributing to less niche diversification and herb biodiversity (Blum, 2010; Polisel et al., 2014). In addition, the understory environment and the light availability strongly affect the herbaceous layer (Beatty, 1984; Poulsen & Balslev,1991; Gilliam & Roberts, 2003; Silva et al., 2008; Blum 2010) and the regenerative stratum (Enoki & Abe, 2004). The inconspicuous difference among diversity indices are evidence of this environmental homogeneity (Tab. 3) (Pereira et al., 2007; Inácio & Jarenkow, 2008; Silva et al., 2008). The meaningless variation in the herbaceous layer structure is a result of the perennial canopy of the forest, since the low solar incidence in the understory doesn't cause differentiation on the structure and composition of the lower stratum (Enoki & Abe, 2004; Inácio & Jarenkow, 2008; Blum, 2010). Furthermore, the invariable climatic factors such as air humidity, temperature and rainfall are responsible for the climatic stability of the Anhangava Mountain region as analyzed by Roderjan (1994).

However, Poulsen & Balslev (1991) found correlation between the relief and the composition of the understory herbaceous layer in a tropical forest and Záchia & Waechter (2011) successfully associated the understory community and the topography in a coastal Atlantic Forest in South of Brazil; both studies analyzed small scale topography (variations between 8 to 19 m). Záchia & Waechter (2011) evaluated different variables as luminosity and soil composition and humidity, thus reflecting distinct environmental conditions and plant communities. Silva et al. (2008) demonstrated the edge effect is more responsible for the diversification of the composition and structure of the understory community than the topographical gradient in an area of 100m elevation range. Nonetheless, Pereira et al. (2007) analyzed both edge effect and topography related to tree community and presented a correlation between tree distribution and topography, probably due to its influence on soil fertility and its properties and ground-water regime. Pereira et al. (2007) studied a mountainous area between 800 and 1,000 m.a.s.l. Daws et al. (2002) stated that the environmental heterogeneity resulting from microtopography variation could explain the high species richness in a tropical forest in Panama, by providing distinct hydrologically defined niches. These authors analyzed the correlation of the microtopographic position (at a small scale) and the water regime of a river in plateaus and slopes. However, in Anhangava sampled area the plots were not influenced by water bodies.

Although some authors had found that the distribution of understory species was influenced mainly by microtopography (Beatty, 1984) and that variations in topography result in diversification in the structure of interior habitats (Carvalho et al., 2007; Silva et al., 2008) we found no difference among the slope classes. Assuming these findings, the present study refutes the proposed hypotheses, probably due to the specific environmental characteristics found in the studied region on Anhangava Mountain.

CONCLUSIONS

The richness of young trees reveals the relevance of the transient component in the lower stratum and in the diversity composition of forest areas. Herbaceous individuals are less frequent, yet with great family number. Among the species with the highest Importance Value, most are resident, however the two richest families are exclusively transient.

Despite the inconspicuous higher diversity observed in the slope class >80%, the analyses of diversity, richness and DCA show the differences of structure and composition are not significative and there is no correlation between the slope and the understory plant community, thus refuting the two proposed hypotheses. Furthermore, less than 3% of the variance is explained by the slope (PerMANOVA test). This lack of correlation with the slope variable probably occurs due to the influence of the climatic and environmental homogeinity in a well-preserved fragment in the Atlantic Forest of South of Brazil.

Table 1. The understory community and its habitats and life forms in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Physical habitat: EP –epipetric and TE – terrestrial. Growth form: ARB – arboreal, CAH – caespitose herb, CLI – climber, CRH – creeping herb, ERH – erect herb, ERS – erect shrub, RAH – rosulate accidental herb, RHH – rhizome herb, ROH – rosulate herb, ROS –rosulate shrub, SCS – scandent shrub. Ecological habitat: RE –resident, TR –transient.

FAMILY (N° of species) *Species*	**Physical habitat**	**Growth form**	**Ecological habitat**
ACANTHACEAE (1)			
Pseuderanthemum riedelianum (Nees) Radlk.	TE, EP	ERH	RE
ANEMIACEAE (1)			
Anemia phyllitidis (L.) Sw.	TE	ROH	RE
ANNONACEAE (1)			
Guatteria australis A. St.-Hil.	TE	ARB	TR
APOCYNACEAE (1)			
Peltastes peltatus (Vell.) Woodson	TE	CLI	TR
AQUIFOLIACEAE (1)			
Ilex taubertiana Loes.	TE	ARB	TR
ARACEAE (2)			
Heteropsis sp.	TE, EP	CLI	TR
Philodendron meridionale Buturi & Sakur.	TE	CRH, CLI	RE
ARECACEAE (1)			
Geonoma schottiana Mart.	TE	ROS	RE
ASTERACEAE (1)			
Dasyphyllum spinescens (Less.) Cabrera	TE	ARB	TR
BEGONIACEAE (1)			
Begonia fruticosa (Klotzsch) A.DC.	EP	CRH, CLI	RE
BLECHNACEAE (2)			
Lomaridium plumieri (Desv.) C. Presl	TE	ROH, CLI	RE
Neoblechnum brasiliense (Desv.) Gasper & V.A.O. Dittrich	TE	ROH	RE
BROMELIACEAE (1)			
Aechmea aff. *organensis* Wawra	TE	RAH	RE
CANELLACEAE (1)			
Cinnamodendron dinisii Schwacke	TE	ARB	TR
CARDIOPTERIDACEAE (1)			
Citronella paniculata (Mart.) R.A. Howard	TE	ARB	TR
COMMELINACEAE (1)			
Dichorisandra hexandra (Aubl.) C.B. Clarke	TE	ERH	RE
CYATHEACEAE (2)			
Alsophila setosa Kaulf.	TE	ROS	RE
Cyathea phalerata Mart.	TE	ROS	RE
CYPERACEAE (2)			
Carex sp.	TE	CAH	RE
Pleurostachys gaudichaudii Brongn.	EP	RHH	RE

Table 1. (Continuation). The understory community and its habitats and life forms in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Physical habitat: EP –epipetric and TE – terrestrial. Growth form: ARB – arboreal, CAH – caespitose herb, CLI – climber, CRH – creeping herb, ERH – erect herb, ERS – erect shrub, RAH – rosulate accidental herb, RHH – rhizome herb, ROH – rosulate herb, ROS –rosulate shrub, SCS – scandent shrub. Ecological habitat: RE –resident, TR –transient.

FAMILY (Nº of species) *Species*	**Physical habitat**	**Growth form**	**Ecological habitat**
DENNSTAEDTIACEAE (1)			
Dennstaedtia obtusifolia (Willd.) T. Moore	TE	RHH	RE
DRYOPTERIDACEAE (6)			
Ctenitis paranaensis (C. Chr.) Lellinger	TE	RHH	RE
Lastreopsis amplissima (C. Presl) Tindale	TE	RHH	RE
Megalastrum abundans (Rosenst.) A.R. Sm. & R.C. Moran	TE	ROH	RE
Mickelia scandens (Raddi) R.C. Moran, Labiak & Sundue	EP	RHH, CLI	RE
Polybotrya cylindrica Kaulf.	TE	RHH, CLI	RE
Stigmatopteris heterocarpa (Fée) Rosenst.	TE, EP	ROH	RE
ELAEOCARPACEAE (1)			
Sloanea garkeana K. Schum.	TE	ARB	TR
FABACEAE (2)			
Dalbergia frutescens (Vell.) Britton	TE	SCS	TR
Inga virescens Benth.	TE	ARB	TR
LAURACEAE (7)			
Endlicheria paniculata (Spreng.) J.F. Macbr.	TE	ARB	TR
Ocotea catharinensis Mez	TE	ARB	TR
Ocotea dispersa (Nees & Mart.) Mez	TE	ARB	TR
Ocotea odorifera Rohwer	TE	ARB	TR
Ocotea silvestris Vattimo-Gil	TE	ARB	TR
Ocotea teleiandra (Meisn.) Mez	TE	ARB	TR
Ocotea sp.	TE	ARB	TR
LINDSAEACEAE (1)			
Lindsaea virescens Sw.	TE	RHH	RE
MELASTOMATACEAE (4)			
Leandra acutiflora (Naudin) Cogn.	TE	ARB, ERS	TR
Miconia cinerascens Miq.	TE	ARB, ERS	TR
Miconia latecrenata (DC.) Naudin	TE	ARB, ERS	TR
Miconia sellowiana Naudin	TE	ARB	TR
MONIMIACEAE (3)			
Mollinedia elegans Tul.	TE	ERS	RE
Mollinedia schottiana (Spreng.) Perkins	TE	ERS	RE
Mollinedia uleana Perkins	TE	ERS	RE
MORACEAE (1)			
Sorocea bonplandii (Baill.) W.C. Burger et al.	TE	ARB, ERS	TR

Table 1. (Continuation). The understory community and its habitats and life forms in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Physical habitat: EP –epipetric and TE – terrestrial. Growth form: ARB – arboreal, CAH – caespitose herb, CLI – climber, CRH – creeping herb, ERH – erect herb, ERS – erect shrub, RAH – rosulate accidental herb, RHH – rhizome herb, ROH – rosulate herb, ROS –rosulate shrub, SCS – scandent shrub. Ecological habitat: RE –resident, TR –transient.

FAMILY (Nº of species) *Species*	**Physical habitat**	**Growth form**	**Ecological habitat**
MYRTACEAE (15)			
Curitiba cf. *prismatica* (D. Legrand) Salywon & Landrum	TE	ARB	TR
Eugenia cf. *handroana* D. Legrand	TE	ARB	TR
Eugenia cf. *prasina* O.Berg	TE	ARB	TR
Eugenia cf. *ramboi* D. Legrand	TE	ARB	TR
Eugenia cf. *repanda* O. Berg	TE	ARB	TR
Eugenia cf. *uniflora* L.	TE	ARB	TR
Myrceugenia cf. *acutiflora* (Kiaersk.) D. Legrand & Kausel	TE	ARB	TR
Myrceugenia cf. *miersiana* (Gardner) D. Legrand & Kausel	TE	ARB	TR
Myrceugenia myrcioides (Cambess.) O. Berg	TE	ARB	TR
Myrcia hatschbachii D. Legrand	TE	ARB	TR
Myrcia splendens (Sw.) DC.	TE	ARB	TR
Myrcia sp	TE	ARB	TR
Myrtaceae sp1	TE	ARB	TR
Myrtaceae sp2	TE	ARB	TR
Myrtaceae sp3	TE	ARB	TR
NYCTAGINACEAE (1)			
Guapira opposita (Vell.) Reitz.	TE	ARB, ERS	TR
OCHNACEAE (1)			
Ouratea parvifolia (A.DC.) Baill.	TE	ARB, ERS	TR
ORCHIDACEAE (1)			
Sauroglossum elatum Lindl.	TE	ROH	RE
POACEAE (2)			
Chusquea cf. *oligophylla* Rupr.	TE	ERS	RE
Parodiolyra micrantha (Kunth) Davidse & Zuloaga	TE, EP	CAH	RE
POLYPODIACEAE (1)			
Campyloneurum minus Fée	EP	RHH	RE
PRIMULACEAE (2)			
Myrsine gardneriana A.DC.	TE	ARB	TR
Myrsine umbellata Mart.	TE	ARB	TR
PROTEACEAE (1)			
Roupala meisneri Sleumer	TE	ARB	TR
PTERIDACEAE (2)			
Pteris decurrens C. Presl	TE	RHH	RE
Pteris splendens Kaulf	TE	RHH	RE

Table 1. (Continuation). The understory community and its habitats and life forms in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. Physical habitat: EP –epipetric and TE – terrestrial. Growth form: ARB – arboreal, CAH – caespitose herb, CLI – climber, CRH – creeping herb, ERH – erect herb, ERS – erect shrub, RAH – rosulate accidental herb, RHH – rhizome herb, ROH – rosulate herb, ROS –rosulate shrub, SCS – scandent shrub. Ecological habitat: RE –resident, TR –transient.

FAMILY (Nº of species) *Species*	**Physical habitat**	**Growth form**	**Ecological habitat**
RUBIACEAE (5)			
Coussarea contracta (Walp.) Mull. Arg.	TE	ARB, ERS	TR
Psychotria carthagenensis Jacq.	TE	ARB	TR
Psychotria leiocarpa Cham. & Schltdl.	TE	ERS	RE
Psychotria suterella Mull. Arg.	TE	ERS	RE
Rudgea jasminoides (Cham.) Mull. Arg.	TE	ARB	TR
RUTACEAE (2)			
Esenbeckia grandiflora Mart.	TE	ARB	TR
Zanthoxylum rhoifolium Lam.	TE	ARB	TR
SALICACEAE (3)			
Casearia decandra Jacq.	TE	ARB	TR
Casearia obliqua Spreng.	TE	ARB	TR
Casearia sylvestris Sw.	TE	ARB	TR
SAPINDACEAE (3)			
Cupania vernalis Cambess.	TE	ARB	TR
Paullinia trigonia Vell.	TE	CLI	TR
Serjania laruotteana Cambess.	TE	CLI	TR
SAPOTACEAE (2)			
Chrysophyllum gonocarpum (Mart. & Eichler ex Miq.) Engl.	TE	ARB	TR
Pouteria bullata (S.Moore) Baehni	TE	ARB	TR
SOLANACEAE (1)			
Solanum megalochiton Mart.	TE	ERS	RE
SYMPLOCACEAE (3)			
Symplocos estrellensis Casar.	TE	ARB, ERS	TR
Symplocos tenuifolia Brand	TE	ARB, ERS	TR
Symplocos tetranda Mart.	TE	ARB, ERS	TR
THELYPTERIDACEAE (2)			
Amauropelta araucariensis (Ponce) Salino & T.E.Almeida	TE	ROH	RE
Thelypteris hatschbachii A.R. Sm.	TE	RHH	RE

Table 2. Phytosociological parameters of the 20 species with the highest importance values for each class of the understory community in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil. ADo: absolute dominance, RDo: relative dominance, AF: absolute frequency, RF: relative frequency, IV: importance value.

	Species	Slope 0-25%					Slope 40-60%					Slope >80%					General
		ADo	RDo	AF	RF	IV	ADo	RDo	AF	RF	IV	ADo	RDo	AF	RF	IV	IV
1	*Pseuderanthemum riedelianum*	100,4	11,5	17	16,2	13,9	184	21,0	20	15,5	18,3	76	11,7	17	14,2	12,9	15,0
2	*Parodiolyra micrantha*	69	7,9	7	6,7	7,3	58,5	6,7	14	10,9	8,8	44	6,8	7	5,8	6,3	7,5
3	*Rudgea jasminoides*	54	6,2	8	7,6	6,9	27,5	3,1	7	5,4	4,3	42	6,5	7	5,8	6,1	5,8
4	*Ctenitis paranaensis*	45	5,2	4	3,8	4,5	68,5	7,8	7	5,4	6,6	40	6,1	5	4,2	5,2	5,4
5	*Megalastrum abundans*	50	5,7	2	1,9	3,8	12	1,4	3	2,3	1,8	97	14,9	6	5,0	10,0	5,2
6	*Psychotria suterella*	68	7,8	2	1,9	4,9	71	8,1	3	2,3	5,2	14	2,2	2	1,7	1,9	4,0
7	*Psychotria leiocarpa*	50	5,7	2	1,9	3,8	71	8,1	3	2,3	5,2	6	0,9	4	3,3	2,1	3,7
8	*Pteris decurrens*	28	3,2	2	1,9	2,6	1	0,1	1	0,8	0,4	70	10,8	5	4,2	7,5	3,5
9	*Lastreopsis amplissima*	30,5	3,5	5	4,8	4,1	46	5,3	5	3,9	4,6	2	0,3	1	0,8	0,6	3,1
10	*Mollinedia elegans*	50	5,7	1	1,0	3,3	21	2,4	2	1,6	2,0	25	3,8	1	0,8	2,3	2,6
11	*Endlicheria paniculata*	3	0,3	1	1,0	0,6	21	2,4	5	3,9	3,1	16	2,5	5	4,2	3,3	2,4
12	*Pteris splendens*	17,5	2,0	2	1,9	2,0	17	1,9	2	1,6	1,7	20	3,1	4	3,3	3,2	2,3
13	*Neoblechnum brasiliense*	80	9,2	2	1,9	5,5	9	1,0	1	0,8	0,9	0	0,0	0	0,0	0,0	2,1
14	*Pouteria bullata*	31	3,6	5	4,8	4,2	0	0,0	0	0,0	0,0	3	0,5	2	1,7	1,1	1,7
15	*Psychotria carthagenensis*	27	3,1	3	2,9	3,0	15	1,7	3	2,3	2,0	0	0,0	0	0,0	0,0	1,7
16	*Lomaridium acutum*	0	0,0	0	0,0	0,0	43	4,9	2	1,6	3,2	9	1,4	1	0,8	1,1	1,4
17	*Peltastes peltatus*	5	0,6	1	1,0	0,8	3	0,3	2	1,6	0,9	9	1,4	4	3,3	2,4	1,4
18	*Chusquea* cf. *oligophylla*	30	3,4	1	1,0	2,2	0	0,0	0	0,0	0,0	12	1,8	2	1,7	1,8	1,3
19	*Citronella paniculata*	1	0,1	1	1,0	0,5	20	2,3	3	2,3	2,3	9	1,4	1	0,8	1,1	1,3
20	*Casearia decandra*	2	0,2	2	1,9	1,1	3	0,3	2	1,6	0,9	4	0,6	2	1,7	1,1	1,1

Table 3. Parameters of richness and diversity for each slope class of the understory community in a transitional area of Atlantic Rain Forest and Araucaria Forest in the Serra do Mar mountain range in South of Brazil.

Parameters	*Slope classes*		
	0-25%	*40-60%*	*>80%*
Number of species	50	53	54
Number of individuals	105	129	120
Dominance (D)	0.05107	0.05282	0.04375
Simpson index (1/D)	19.58	18.93	22.86
Simpson index (1-D)	0.9489	0.9472	0.9563
Shannon index (H')	3.488	3.484	3.582
Margalef index (Dα)	11	11	11
Evenness (J)	0.8916	0.8775	0.8981
Chao-1 index	99.6	89.25	116.3
Leaf cover	41.5	41.7	31

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