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Original Paper

Indicator species and characterization of the woody and herbaceous layer in an Atlantic Forest ecotone area at the Paraná portion of Serra do Mar

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Abstract

The study aimed to evaluate the degree of conservation, analyse the structural and floristic similarity of the woody and herbaceous layers of two ecotone forest communities and evaluate the indicator species of a Mixed Ombrophilous Forest (MOF) and Dense Ombrophilous Forest (DOF). We outlined 30 sampling units of 100 m^2 in each area (West and East), where we measured three woody and one herbaceous layers. Each species was classified into ecological groups, phytogeographic distribution and conservation status. We selected other 13 studies performed on similar ecosystems to carry out cluster and indicator species analyses. We registered 213 species, arranged into 63 families. The richest families were Myrtaceae, Lauraceae and Fabaceae. In the woody layers *Araucaria angustifolia*, *Allophylus edulis* and *Cupania vernalis* highlighted in West area, while *Casearia sylvestris*, *Cyathea phalerata* and *Ilex paraguariensis* highlighted in East area. *Ctenitis paranaensis* predominates in herbaceous layer of both areas. Our cluster analysis has formed two groups (MOF; DOF), including both study areas in MOF group. The study areas are in a maturation process. Serra da Baitaca State Park presents high conservationist importance. We list indicator species of montane MOF and DOF forests in the Paraná State, which can be used for monitoring alterations in vegetation caused by environmental changes.

Key words: conservation, Dense Ombrophilous Forest, indicator species, Mixed Ombrophilous Forest, phytosociology.

Resumo

O estudo objetivou avaliar o grau de conservação, analisar a similaridade florística e estrutural dos estratos lenhosos e herbáceo de duas comunidades florestais em situação de ecótono e avaliar as espécies indicadoras de Floresta Ombrófila Mista (FOM) e Floresta Ombrófila Densa (FOD). Foram instaladas 30 parcelas de 100 m² em cada área de estudo (Oeste e Leste) e mensurados três estratos lenhosos e um herbáceo. Cada espécie foi classificada conforme o grupo ecológico, ocorrência fitogeográfica e categoria de ameaça. Foram selecionados outros 13 estudos de ecossistemas similares, para a análise de agrupamento e espécies indicadoras. Foram registradas 213 espécies pertencentes a 63 famílias. As famílias mais ricas foram Myrtaceae, Lauraceae e Fabaceae. Destacaram-se nos estratos lenhosos da área Oeste *Araucaria angustifolia*, *Allophylus edulis* e *Cupania vernalis*. Na área Leste se destacaram *Casearia sylvestris*, *Cyathea phalerata* e *Ilex paraguariensis*. *Ctenitis paranaenses* destacou-se no estrato herbáceo de ambas as áreas. A análise de agrupamento formou dois grupos (FOM; FOD), incluindo as duas áreas de estudo no grupo FOM. As áreas de estudo estão em processo de amadurecimento e o Parque Estadual Serra da Baitaca apresenta elevada importância para conservação. Foram listadas espécies indicadoras para FOM e FOD montanas no Estado do Paraná, as quais podem ser utilizadas como parâmetros no monitoramento das alterações na vegetação frente às mudanças ambientais.

Palavras-chave: conservação, Floresta Ombrófila Densa, espécies indicadoras, Floresta Ombrófila Mista, fitossociologia.

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Introduction

Ecotones are transition areas between ecological regions or distinct ecosystems, also called Ecological Stress Areas (Kark 2013). These are not simple boundaries but actually represent ecological systems with distinct environmental characteristics defined by spatial and temporal scales. Furthermore, they are further defined by the interaction between the ecosystems that form them, representing dynamic relationship zones between ecological communities (Kent *et al.* 1997). Generally, they present elevated biodiversity and several rare species, being essential for the organismic flow (Smith *et al.* 2001; Araújo 2002; Yarrow & Marín 2007). Ecotones generally occur along an environmental gradient created by climatic, orographic, edaphic changes, or other environmental factors affecting the vegetation (Kark & Van Rensburg 2006; Kark 2012).

The Serra do Mar Mountain Range, inserted in the Atlantic Forest biome (Ribeiro *et al*. 2009), represents an abrupt transition between coastal plains and the First Parana Plateau, which elevates up to 1,000 m above the plateau's mean elevation (Roderjan 1994; Maack 2012). The Serra da Baitaca Mountain Range, in the West-East direction, represents a transition zone between Mixed Ombrophilous Forest (MOF) of the first plateau and the formations under the Atlantic influence of the mountains and the coastal plain, Dense Ombrophilous Forest (DOF) (IBGE 2012).

The Atlantic Forest is a high priority biome for conservation, affected by anthropic pressures that affect the regeneration of secondary forests (Myers *et al*. 2000; Mantovani 2003; Viani *et al.* 2011). In Paraná state, most of the Serra do Mar Mountain Range is in a situation of land use transition, to the east the matrix is forest while to the west the matrix is anthropic (agricultural and urban use) (Rezende *et al*. 2018). After suffering an environmental disturbance, the secondary vegetation acquires an occupation dynamic by pioneer species, which get gradually replaced by non-pioneer species during the forest's maturation (Chazdon 2012; Oliva *et al.* 2018).

Indicator species are organisms closely associated with specific environmental conditions (Caro 2010). They are used to define strategies for forest conservation and management (Lindenmayer 1999) and to monitor the dynamics of communities and ecosystems in the face of environmental change (Siddig *et al*. 2016). The Paraná state has a high environmental vulnerability to climate change, in this context the limits of coverage of phytophysiognomies should be regularly reviewed (Viana 2015).

Due to the importance of ecotone communities and the vulnerability of Atlantic Forest ecosystems at Paraná state, the present study aimed to: (1) analyse the conservation status and the structural and floristic composition of the woody and herbaceous layers of two secondary ecotone forest communities, in a transition zone between MOF and DOF with at least 60 years old, located on the west slope of Serra da Baitaca; (2) analyse the structural and floristic similarity between MOF and DOF at the study area; (3) list indicator species between montane MOF and DOF phytophysiognomies at Paraná state.

Material and Methods

Study area

This study was carried out at the northeastern portion of the Serra da Baitaca State Park (SBSP), in the municipality of Quatro Barras, state of Paraná (PR), Brazil. We selected two sites: 1) a West area (940 m a.s.l.) with a predominance of *Araucaria angustifolia* (Bertol.) Kuntze; and 2) a East area (940 m a.s.l.) without an expressive occurrence of *A. angustifolia* (Fig. 1). The sites are 0.8 km apart from each other.

The region is located in a montane ecotone of Mixed Ombrophilous Forest (MOF) and Dense Ombrophilous Forest (DOF). The west portion of the region, the First Parana Plateau, is covered by MOF, while the DOF vegetation covers the Serra do Mar Mountain Range slopes in the eastern portion (IBGE 2012). This transition is due to the Serra da Baitaca Mountain Range localization and its topography in the east-west direction (Roderjan 1994).

According to the Köppen climatic classification, the regional climate is classified as Cfb, humid subtropical, with an average annual temperature below 18 °C, a temperate summer, without a defined dry season and with the occurrence of frosts (Alvares *et al.* 2013). The geological formation is composed of Anhagava granite and the predominant soils are Cambisols (Roderjan 1994).

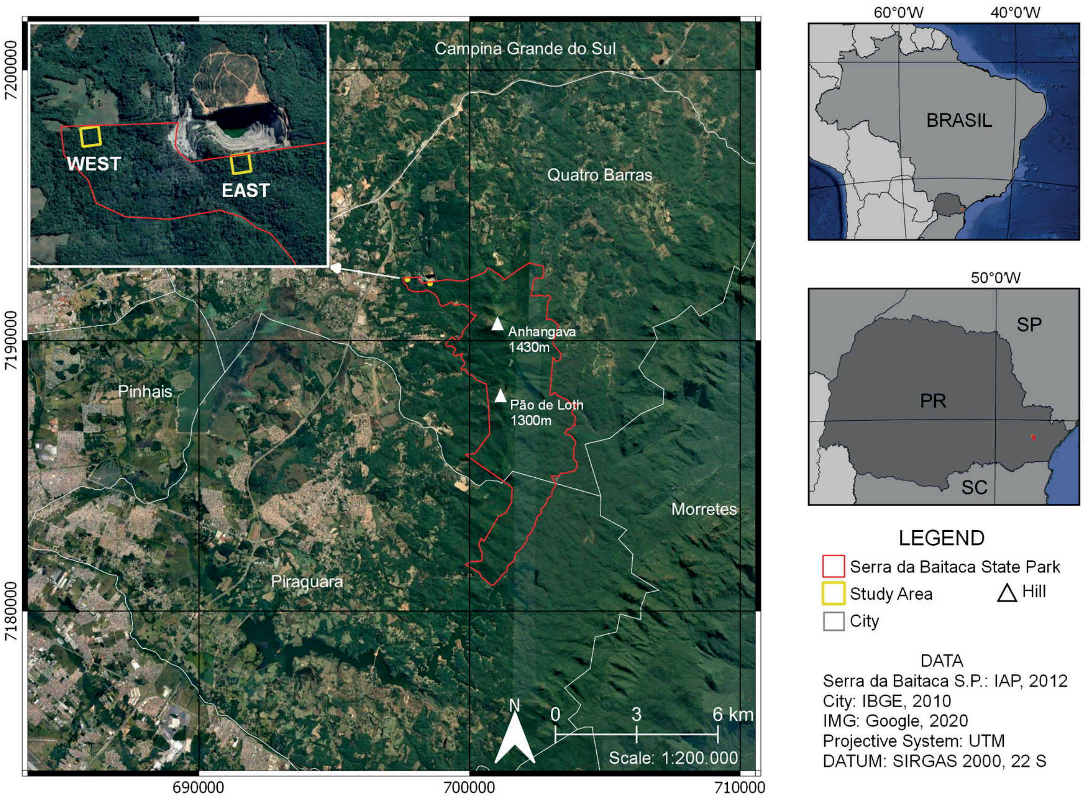

Figure 1 – Location of the study areas.

Data collection

We installed three parallel sampling lines within forest communities, 40 meters apart from each other, each with ten 100 m² (10 × 10 m) contiguous plots for each site (West and East), totalling 60 sampling units. We installed three subplots of 1 m² in each sampling unit to evaluate the herbaceous and smaller woody vegetation, totalling 180 subplots.

To collect vegetation data, we surveyed the vegetation layers using different sample sizes and inclusion criteria. Square plots of 100 m² were installed to measure trees, ferns and palms with diameter at breast height (DBH) greater than 15 cm, referred to as Woody layer 1 (WL1). Square plots of 25 m² to measure trees, ferns, palms and shrubs with diameter less than 15 cm and height greater than 1 m, called Woody layer 2 (WL2). Three 1 m² square plots in each sampling unit, to measure small-sized trees, ferns, palms and shrubs with height greater than 0.3 m and less than 1 m, referred to as Woody layer 3 (WL3). In the same 1 m² plots we measure all terrestrial herbs, called Herbaceous layer (HL).

We identified the recorded species in all layers based on relevant literature and with the assistance of specialists in some groups. The taxonomic classification follows the Angiosperm Phylogeny Group (APG IV 2016) and the Pteridophyte Phylogeny Group (PPG 2016). Fertile material was collected, herborized, and deposited at the Escola de Florestas Curitiba Herbarium (EFC).

For the WL1 and WL2 we measured the Circumference at Breast Height (CBH) using a measuring tape. For the WL3 we measured the Total Height (TH). For the herbaceous layer we made a visual estimate of the species coverage rate adapted from the Braun-Blanquet (1964) scale. This scale was used because it is commonly applied in phytosociological studies (Chmura & Salachna 2016), making the data comparison with other surveys easier.

The species were classified into ecological layers (Ephemerous Pioneers, Lasting Pioneers, Facultative, Non-Pioneers) based on their shade tolerance, seed size, dispersal syndrome, growth rate, and longevity. This approach followed Secco (2017), who based himself on the works of Budowski (1965), Whitmore (1990), Finegan (1984) and Calegari *et al*. (2013).Taxa not identified at the species level were not classified, except for the members of Myrtaceae, which, even if identified only at the genus level, could be classified as Non-Pioneers because they are known to occur in the dominanted strata of more conserved communities of Mixed Ombrophilous Forest (MOF) and Dense Ombrophilous Forest (DOF) (Roderjan *et al.* 2002).

The species occurrence classification was based on the distribution of collections from the visited herbaria, and the data available in the Species Link database (CRIA 2021). For the occurrence classification, we only considered collection records from Paraná, except for rare species, in which we took into account all records from Brazil. The species' classification criteria were based on Reginato & Goldenberg (2007), considering both vegetation formations relevant for the present study (MOF and DOF). Therefore, species were classified as follows: 1) Preferential: with most records concentrated in one of the vegetation types (MOF or DOF); 2) Both: records are evenly distributed between both vegetation types; and 3) Undetermined: due to the small number of records, it is not possible to indicate its distribution pattern.

We highlight that some species classified as Preferential for either MOF and DOF are also widely distributed across the Semidecidual Seasonal Forest (SSF). However, in this study, these species were only accessed regarding MOF and DOF. The extinction-level of threatened species was determined according to Martinelli & Moraes (2013).

Data analysis

Data were entered into electronic spreadsheets and analyzed using the R statistical programming language (R Core Team 2021). Sample sufficiency was calculated using two distinct approaches, one based on structure and the other on richness. We calculated the density and dominance stratified sampling error for the structural sampling sufficiency, with the latter calculated only for WL1 and WL2. These values were calculated using the sampling.analysis function (Higuchi 2019), allowing for a probability of 95% and an error of 20%. Alternatively, for richness sampling sufficiency, we calculated the interpolation and extrapolation curves using the iNEXT package (Hsieh *et al.* 2016), considering only taxa identified at the species level.

We calculated the phytosociological parameters using the fitoR function (Dalagnol *et al.* 2017) for the WL1 and WL2. For the WL3, we calculated density, frequency, and importance values that considered only these two descriptors. For the HL, dominance was replaced by the coverage rate (Braun-Blanquet 1964).

The floristic-structural dissimilarity was calculated considering previous studies for the region (Tab. 1; Fig. 2). We considered the absolute density for phytosociological studies at arboreal layers in montane patches of MOF, DOF or ecotone areas in the Paraná portion of the Serra do Mar Mountain Range and surroundings.

We considered only the montane portions of the altitudinal gradient studies (Roderjan 1994; Blum 2006). The studies that analyzed vegetation on different soil types (Schorn 1992; Seger *et al.* 2005), we considered only communities growing on Cambisols. Finally, the only study that looked at vegetation classification in the region (Santos 2014), we excluded alluvial formations.

Taxonomic names have been updated for species listed in the selected phytosociological studies. Taxa not identified or identified only at the family and genus level were excluded from our analysis. Exotic species were also excluded.

We created an abundance matrix that considered the absolute density of each study. Based on this matrix, we created a dissimilarity matrix using the Bray & Curtis distance (1957). Using the dissimilarity matrix, we performed a cluster analysis using the Unweighted Pair Group Method with Arithmetic Mean (UPGMA) and created a dendrogram and a cophenetic matrix using the Vegan package (Oksanen *et al.* 2020).

Based on the cluster analysis, we performed the indicator species analysis. In this approach, the degree of specificity for a given habitat and the degree of fidelity or frequency of occurrence within the same habitat are determined for each species with their sum resulting in the IndVal value (Dufrene & Legendre 1997). The IndVal values were calculated according to Cáceres & Legendre (2009), using the indicspecies package (Cáceres & Jansen 2016). The statistical significance was randomly tested using the Monte Carlo method, considering 999 permutations and a significance value of 0.01.

Results

Structural sample sufficiency was reached for all layers. For WL1, the abundance and basal area sampling errors were 6.7% and 9.1%, respectively.

Table 1 – Relationship between the selected studies to analyse their dissimilarity and indicator species. * Coordinates UTM (22S) Datum SIRGAS 2000.

Code	Country	Coordinates*	Elevation	Inclusion criteria	Reference
ECO_01	Piraquara	703731 / 7179476	1020–1040	CBH ≥ 10 cm	Reginato & Goldenberg (2007)
ECO_02	Piraquara	701844 / 7177239	950–1050	CBH ≥ 10 cm	Lacerda (1999)
DOF_01	Morretes / SJP	703148 / 7152903	800	CBH ≥ 30 cm	Schorn (1992)
DOF_02	Morretes	731486 / 7164730	800–900	CBH ≥ 31.4 cm	Blum (2006)
DOF_03	Morretes	731618 / 7164451	1000	CBH ≥ 31.4 cm	Blum (2006)
DOF_04	Morretes (with gaps)	731720 / 7164287	1100	CBH ≥ 31.4 cm	Blum (2006)
DOF_05	Quatro Barras	701047 / 7190552	1100	CBH ≥ 10 cm	Roderjan (1994)
MOF_01	Pinhais	688040 / 7188674	900	CBH > 15	Seger *et al.* (2005)
MOF_02	Curitiba	669901 / 7187019	900	CBH > 10	Kozera *et al.* (2006)
MOF_03	Curitiba (Edge)	676940 / 7184265	900	CBH ≥ 31.4 cm	Santos (2014)
MOF_04	Curitiba (MOF 1)	676940 / 7184265	900	CBH ≥ 31.4 cm	Santos (2014)
MOF_05	Curitiba (MOF 2)	676940 / 7184265	900	CBH ≥ 31.4 cm	Santos (2014)
MOF_06	Curitiba	677567 / 7184428	900	CBH > 10	Reginato *et al.* (2008)
WEST	Quatro Barras (west)	697737 / 7192232	940	CBH > 15	Present study (2023)
EAST	Quatro Barras (east)	698556 / 7192081	950	CBH > 15	Present study (2023)

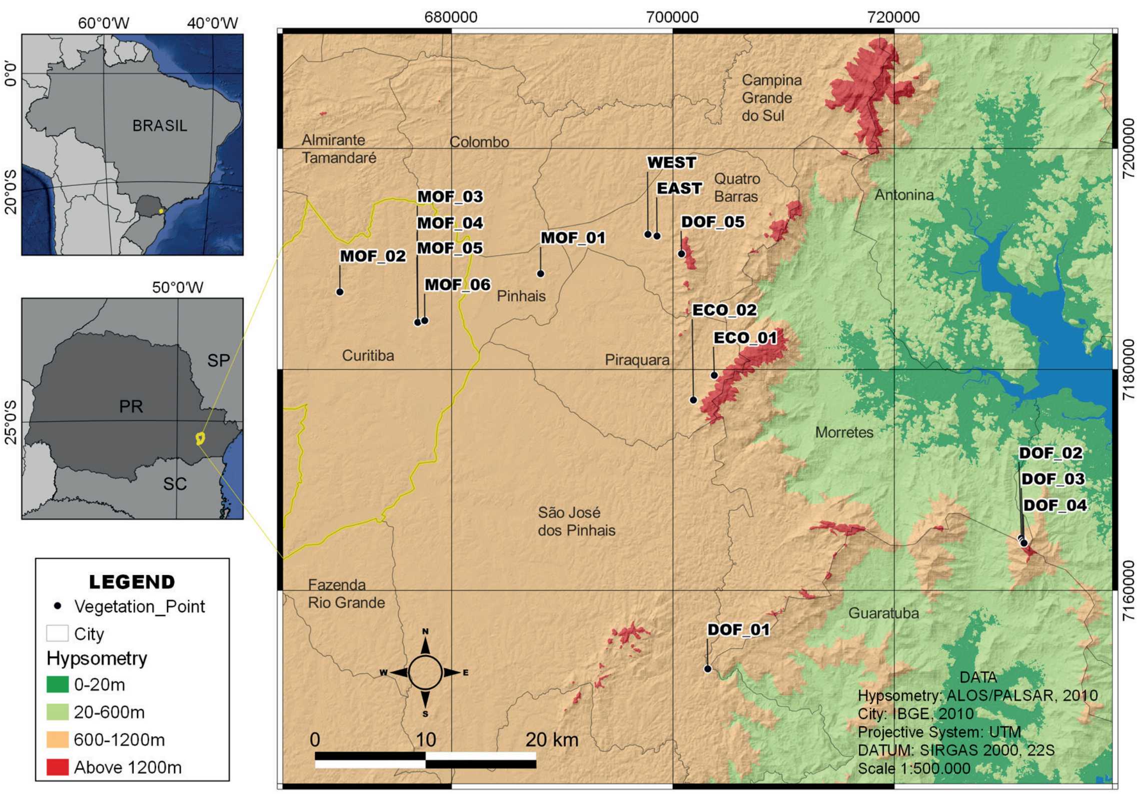

Figure 2 – Location of the selected studies used in the dissimilarity and indicator species.

The WL2 layers showed 7.9% and 8.4% for abundance and basal area, respectively. For WL3 and EH, the abundance sampling errors were 8.2% and 16.4%, respectively.

When the number of sampled individuals was increased by 10%, the richness increased by less than 5% in most layers, with higher values only in the East WL3 and in the West herbaceous (5.5% and 6%, respectively). Even though these values were above the limit (Sanquetta *et al.* 2014), they were regarded as enough sufficiency of richness sampling.

A total of 213 taxa were recorded in the four layers, of which199 were identified to the species level, distributed among 63 families and 114 genera (Tab. S1, available on supplementary material <https://doi.org/10.6084/m9.figshare.21948215.v1>). A total of 152 species were measured in the WL1 layer, 147 in WL2, 66 in WL3 and 18 in the herbaceous. The most species-rich family was Myrtaceae (51), which accounted for 23.6% of the total richness, followed by Lauraceae (13), Fabaceae (12), Rubiaceae (10), Salicaceae (10), and Solanaceae (9). In total, these six families accounted for 48.6% of the total richness. The richest genera were *Myrcia* (21), *Eugenia* (15), and *Ocotea* (9).

Most species were non-pioneers (72.4%), followed by the facultative ecological group (16.8%). Lasting pioneers represented 6.5% and ephemeral pioneers 3.7%. In the layers WL1, 2, and 3, non-pioneer species represented 60%, 81.8%, and 89.5% of the respective density in the West area, and 60.3%, 85.7%, and 91.3% of the respective density in the East area. The proportion of non-pioneer species increased gradually in the above mentioned layers.

Almost half of the species occurred in Ombrophilous Dense and Mixed Forests (48.6%). There were similar values for species showing preferences for these vegetation types (22% and 21%, respectively). Only 7% of the species were not classified according to their distribution, as they were identified only at the genus level, and 1.4% of species were identified as indeterminate taxa.

Ten species were recorded as threatened in some extinction-level (Martinelli & Moraes 2013), four of which are Vulnerable (VU): *Ocotea catharinensis*, *Cedrela fissilis*, *Myrcia pileata*, and *Casearia paranaensis*; and six Endangered (EN): *Annona dolabripetala*, *Araucaria angustifolia*, *O. odorifera*, *O. porosa*, *Myrcia legrandii*, and *Pouteria bullata*.

Phytosociological analysis - west

A total of 102 species were recorded in the WL1 layer with a density of 2,323.3 ind./ha and basal area of 62.7 m²/ha. For the WL2, 93 species were recorded with a density of 13,880 ind./ha and a basal area of 4.8 m²/ha. And for the WL3, 49 species were found and a density of 5,666.7 ind./ha. See Tabs. S2-S9 (available on supplementary material <https://doi.org/10.6084/m9.figshare.21948215.v1>) for all layers phytosociological parameters.

A total of 139 species were found in the three woody layers of the West area. Of these, 32 species were found in the three layers, 36 exclusively in WL1, 24 exclusively in WL2, and only six exclusively in WL3. A total of 30 species were found in layers WL1 and WL2, four in layers WL1 and WL3, and seven in layers WL2 and WL3 layers.

The species with the highest importance value in the WL1 layer was *Araucaria angustifolia*, which showed high dominance, as did *Schinus terebinthifolia* and *Psidium longipetiolatum* (Fig. 3a). Some species

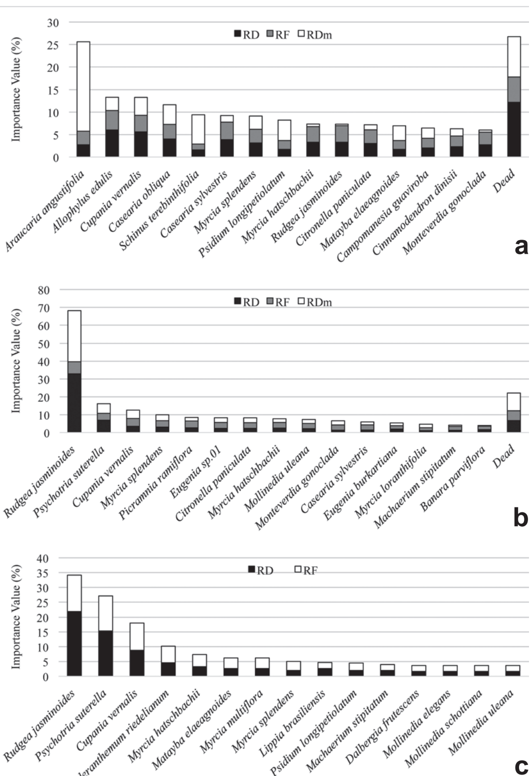

Figure 3 – a-c. Phytosociologycal parameters of the 15 species with the highest IV of the woody layer in the west area of Serra da Baitaca, PR – a. woody 1; b. woody 2; c. woody 3. RD = Relative Density; RF = Relative Frequency; RDm = Relative Dominance; (P) = Pioneer.

had higher density and frequency but low dominance, such as *Allophylus edulis*, *Casearia sylvestris*, *Myrcia hatschbachii*, *Rudgea jasminoides*, and *Monteverdia gonoclada*, which indicates species with low stature and regular horizontal occurrence.

Rudgea jasminoides was the most important species in WL2, representing almost 1/3 of all measured individuals in this layer, and occurring in more than 90% of the sampling units with more than 1/4 of the total dominance (Fig. 3b). The species *Psychotria suterella*, *Cupania vernalis*, and *Myrcia splendens* were also highlighted in this layer.

In the WL3 layer, two species from the Rubiaceae family, *Rudgea jasminoides* and *Psychotria suterella*, had the highest importance value (Fig. 3c). The species *Cupania vernalis* and *Pseuderanthemum riedelianum* also had high importance value in this layer.

Phytosociological analysis - east

A total of 120 species were recorded in the WL1 layer, with a density of 2,219.8 ind./ha and a basal area of 60.6 m²/ha. In WL2, 121 species were observed, with a density of 10,559.9 ind./ha. A total of 165 species were found in the three woody layers in the East area. Of these, 27 species occurred in all three layers, 33 exclusively in WL1, 24 in WL2, and only ten exclusively in WL3. Additionally, 59 species were recorded jointly in WL1 and WL2 a single species in the WL1 and WL3 layers, and nine species in the WL2 and WL3 layers.

The species with the highest VI in the WL1 layer was *Casearia sylvestris*, mainly due to its higher density, which represents 9% of the total individuals (Fig. 4a). The second highest importance value was for *Cyathea phalerata*, which had a high density. The third highest VI value was observed for *Ilex paraguariensis*, which stood out for its large basal area. Some species, such as *Casearia sylvestris*, *Cyathea phalerata*, *Rudgea jasminoides* and *Cupania vernalis*, were represented by individuals of lower stature that were well distributed in the study area, showing high density and frequency but low dominance. Other species, such as *Ilex paraguariensis*, *Aspidosperma olivaceum*, *Pseudobombax grandiflorum*, *Machaerium hatschbachii* and *Sloanea garckeana*, were represented by tall and sparsely distributed individuals.

Just as in the West area, *Rudgea jasminoides* and *Psychotria suterella* showed the greatest IV to the WL2 layer, but with lower expressivity and dominance of the first species (Fig. 4b). In the third place, *Sorocea bonplandii* was highlighted with a high dominance in WL2.

Pseuderanthemum riedelianum had the highest importance value in WL3, mainly because of its high density (Fig. 4c). *Psychotria suterella* also stood out with the second highest IV.

Herbaceous Layer

In the West area, seven species were recorded with a density of 3,000 ind./ha and coverage of 13.6% of the area. *Ctenitis paranaensis* was highlighted with 48.1% and 55.5% of the density and total coverage, respectively (Fig. 5a). Additionally, the herbaceous bamboo *Taquara micrantha* and the Commelinaceae *Commelina obliqua* were also highlighted.

In the East area, 17 species were recorded with a density of 7,444.4 ind./ha and coverage of 42.4%. Ferns are highlighted, such as *Ctenitis*

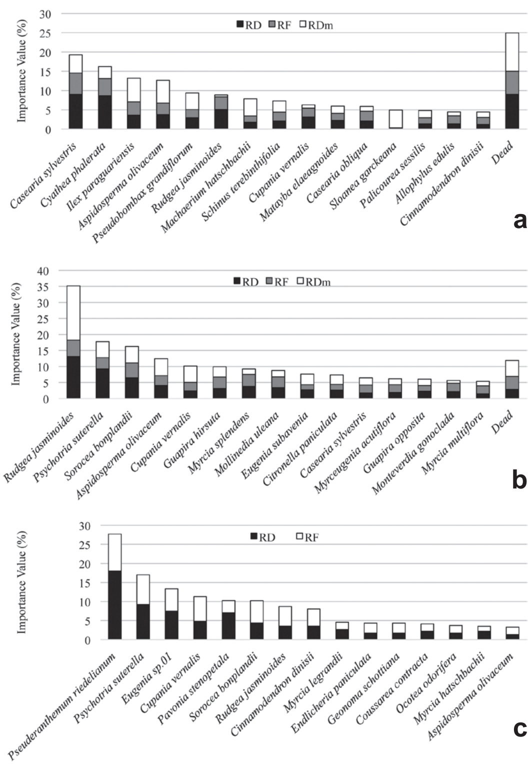

Figure 4 – a-c. Phytosociologycal parameters of the 15 species with the highest IV of the woody layer in the east area of Serra da Baitaca, PR – a. woody 1; b. woody 2; c. woody 3. RD = Relative Density; RF = Relative Frequency; RDm = Relative Dominance; (P) = Pioneer.

paranaensis and *Lastreopsis amplissima* (Fig. 5b). The first species represented 28.3% and 39% of density and total coverage, respectively. The second species accounted for 20.9% of the density and 17.8% of the total coverage.

Cluster analysis

The cophenetic coefficient in the dendrogram (Fig. 6) was 0.93, with two groups formed (based on the 92% dissimilarity margin): a group of Mixed Ombrophilous Forest (MOF) studies and a group of Dense Ombrophilous Forest (DOF) studies. Both groups had only 8% similarity, which demonstrates the floristic and structural heterogeneity between MOF and DOF.

Both areas in the present study were classified as MOF in the working groups, indicating that the WL1 layer of both areas is floristically and structurally similar to MOF. The floristic and structural similarities between the two study areas reached 50%.

The study with the highest floristic and structural similarity concerning the two areas of this study was ECO_02 (Lacerda 1999), performed at South of the Serra do Marumbi Mountain Range, about 15 km away, reaching 31.8% of similarity with the East area and 24.9% with the West area.

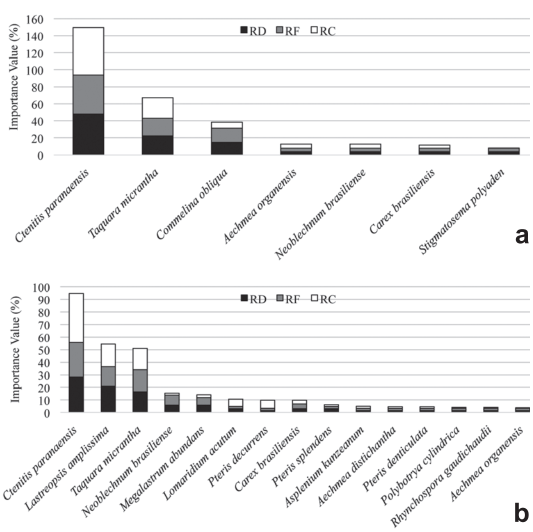

Figure 5 – a-b. Phytosociologycal parameters of the species with the highest IV of the herbaceous layer at Serra da Baitaca, PR – a. west area; b. east area. RD = Relative Density; RF = Relative Frequency; RC = Relative Cover.

Indicator species analysis

Indicator species analysis considered 324 species, with 14 indicative species (p-value < 0.01), 11 of MOF and three of FOD (Tab. 2). Two species had IndVal = 1, *Araucaria angustifolia* and *Campomanesia xanthocarpa*, showing maximum MOF specificity and fidelity, which shows that they are good indicators for this vegetation type *Casearia sylvestris*, *Jacaranda puberula*, and *C. decandra* showed maximum fidelity and high specificity to MOF. *Allophylus edulis*, *Matayba elaeagnoides*, *Myrcia hatschbachii* and *Sapium glandulosum* showed maximum specificity and high fidelity to MOF, which was also observed for *Weinmannia paulliniifolia* in DOF. *Cupania vernalis* and *Ilex paraguariensis* also showed high fidelity but low specificity in both vegetation types.

Discussion

In addition to characterizing the floristic and structure of several forest sinuses with high conservation value in the context of the Atlantic Forest Biome, this study has contributed with information that confirms the indicator aspect of certain species for montane MOF and DOF ecosystems of Paraná state, which can be used as parameters for monitoring alterations in vegetation in the face of environmental changes (Viana 2015).

The three richest families and genera in both study areas corroborate the study by Scheer & Blum (2011) to the WL1 layer of MOF and DOF. The richest families were Myrtaceae and Lauraceae, with high importance in mature forests (Tabarelli & Mantovani 1999). Ten threatened species were also found, indicating that the Serra

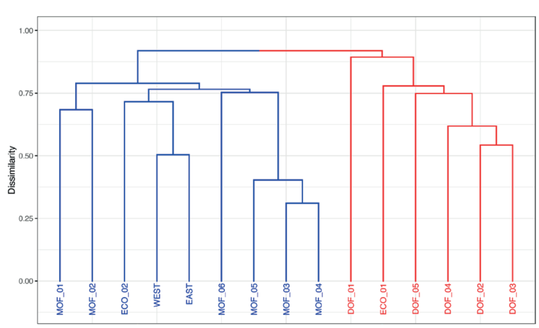

Figure 6 – Dendrogram generated by the cluster analysis (UPGMA) based on the Bray-Curtis distance of studies developed in Montane MOF and DOF near the Serra do Mar Mountain Range.

Table 2 – Indicator species of Montane MOF and DOF in the gradient First Paranaense Plateau - Serra do Mar Mountain Range, from the indicator analysis (IndVal).

Species	IndVal	p-value
Montane Mixed Ombrophilous Forest		
Araucaria angustifolia	1	0.001
Campomanesia xanthocarpa	1	0.001
Casearia sylvestris	0.997	0.001
Jacaranda puberula	0.988	0.001
Casearia decandra	0.961	0.002
Allophylus edulis	0.943	0.004
Matayba elaeagnoides	0.943	0.002
Myrcia hatschbachii	0.943	0.004
Sapium glandulosum	0.943	0.008
Myrcia splendens	0.933	0.004
Cinnamodendron dinisii	0.93	0.009
Montane Dense Ombrophilous Forest		
Weinmannia paulliniifolia	0.913	0.008
Ocotea catharinensis	0.896	0.003
Sloanea lasiocoma	0.874	0.001

da Baitaca State Park is of high importance for the conservation of the Atlantic Forest flora (Tabarelli *et al*. 2005).

The gradual increase in density of non-pioneer species in the woody layers (WL1–WL3) indicates a substitution of ecological groups, a restart of the understory, and a shift to mature forest (Chazdon 2012). In this scenario, pioneer species occupy only edge environments (Murcia 1995) and natural clearings (Tabarelli & Mantovani 1997; Hubbell *et al.* 1999).

The co-occurrence of MOF and DOF preferential species confirms the ecotone situation of the study area (Kent *et al.* 1997). Almost half of the species (48.6%) showed a wide distribution. A similar pattern was observed by Reginato & Goldenberg (2007) in an ecotone area of MOF-DOF, where these species represented 52.8%. For the ecotone between MOF and SSF in the state of Paraná, the percentage of species distributed in both vegetation types was higher, up to 71% (Seki *et al.* 2022), indicating a lower species sharing between MOF and DOF compared to MOF and SSF.

In the WL1 layer from the West area, the higher VI was for *Araucaria angustifolia*, the same pattern observed in phytosociological studies in montane MOF (Rondon Neto *et al.* 2002; Seger *et al*. 2005; Silva *et al.* 2012; Santos 2014). This species occurs in most of the three southern Brazilian states and in some patches in southeastern Brazil, occupying plateaus above 500 m, where MOF occurs (Souza *et al*. 2007; Zanette *et al*. 2017).

Rudgea jasminoides was highlighted in the WL2 layer, resulting in similar patterns to other studies in DOF (Schorn 1992; Blum 2006; Canestraro & Kersten 2018; Pastório *et al.* 2018). This species occurs in different stages of forest regeneration (Tabarelli & Mantovani 1997) in southern and southeastern Brazil, as well as in the state of Mato Grosso and Paraguay (Zappi 2003). In MOF communities in an advanced stage of succession, the species showed higher IV in the regenerating shrub layer (similar to WL2), considered typical of the forest understory (Felitto *et al*. 2017).

Rudgea jasminoides, *Psychotria suterella* and *Cupania vernalis* were highlighted in the WL2 and WL3 layers of the West area. Cardoso-Leite (1995), in a DOF study in the state of São Paulo, observed the highest VI for *R. jasminoides* and *P. suterella* in the shrub layer and a higher VI for *P. suterella* in seedlings, corroborating our study. Blum (2006) also highlighted that Rubiaceae are mainly found in the shaded layers of the forest, showing high structural importance (Pastório *et al.* 2018).

Cupania vernalis had the second highest number of individuals in natural regeneration in MOF from the State of Santa Catarina and represented the second largest VI in altitudes below 1,000 m and the third highest VI for altitudes between 1,000 and 1,200 m (Meyer *et al.* 2013).

In the WL1 layers in the East area, *Casearia sylvestris* was highlighted with the highest structural importance in a study performed in an ecotonal area of MOF and SSF (Seki *et al*. 2022) and also in an MOF remnant (Rondon Neto *et al.* 2002). It showed a high VI in MOF (Dias *et al.* 1998; Seger *et al.* 2005; Reginato *et al.* 2008; Santos 2014) and SSF studies (Silva *et al.* 1995).

Cyathea phalerata was also highlighted to show high structural importance in an ecotone of MOF and DOF (Reginato & Goldenberg 2007). According to Schwartz & Gasper (2020), this species is widely distributed in the state of Santa Catarina in the DOF, in the MOF, and in areas close to the DOF. *Ilex paraguariensis* had the highest VI in the study by Roderjan (1994) in DOF at the same study area of the present study and a higher VI in MOF (Silva & Marconi 1990).

In the WL2 layer *Sorocea bonplandii* was structurally important, corroborating Seki *et al.* (2022), who studied the understory of an ecotonal area between MOF and SSF, and Barros (2006), who studied the lower and intermediate layers of DOF. This species occurs sparsely within the Atlantic forest dominating the understory (Ruschel *et al*. 2006).

In WL3 the most important species was *Pseuderanthemum riedelianum* corroborating Canestraro & Kersten (2018) in a survey of the understory of DOF, in the same area of the present study. In fact, this species occurs mostly near the southern coast of the states of Paraná, Santa Catarina, and São Paulo in DOF and Restinga vegetation (Rodrigues & Souza 2022).

In both areas, *Ctenitis paranaensis* was predominant in the herbaceous layer, showing high density and coverage. This species also showed high importance in a DOF study in Serra da Baitaca (Canestraro & Kersten 2018). It is a species endemic to the Atlantic forest, occurring in MOF and DOF (Viveros & Salinos 2015).

The result of the cluster analysis was similar to that of obtained by Reginato & Goldenberg (2007), who made a floristic distinction between the MOF and the DOF groups, highlighting the floristic differences between these vegetation types.

Despite the geographical proximity of the FOD_05 study (Roderjan 1994) to the present study area, it was clustered in the DOF group, showing only 11.8% of floristic and structural similarity with the West area and 24.8% with the East area. This low floristic and structural similarity is probably influenced by the higher altitude (1,100 m) of the FOD_05 study in comparison with the West (940 m) and East (950 m) areas, showing higher proximity with a high montane DOF from the peaks of the mountain range. The altitudinal gradient affects the local environment, especially the climate, resulting in differentiations in the vegetation along the altitudinal range (Blum *et al*. 2011).

From the MOF indicative species, *Araucaria angustifolia*, *Campomanesia xanthocarpa*, *Allophylus edulis*, *Casearia decandra*; *Myrcia hatschbachii*, and *Cinnamodendron dinisii* are highlighted as preferential or dominant in MOF (Legrand & Klein 1977; Sleumer 1980; Roderjan *et al*. 2002; Coelho 2022; Salazar *et al*. 2020; Lannoy *et al*. 2021).

In contrast, *Casearia sylvestris*, also an indicator of MOF, is a generalist, occurring in the Amazon, Cerrado, and Atlantic forest, including in MOF and DOF (Sleumer 1980; Oliveira-Filho & Ratter 1995). *Jacaranda puberula* occurs in all vegetation types of the Atlantic forest (Gentry 1992). *Matayba elaeagnoides* occurs in MOF and SSF, but is less frequent in DOF (Coelho *et al*. 2017). *Sapium glandulosum* occurs throughout Brazil, including in MOF and DOF (Cordeiro & Esser 2022). *Myrcia splendens* occurs in all vegetation types of the State of Paraná (Lannoy *et al*. 2021).

For DOF, *Weinmannia paulliniifolia* stood out as common in the understory of the montane portions of this vegetation type (Roderjan *et al*. 2002), and *Ocotea catharinensis* was identified as frequent in DOF and rare in MOF and SSF (Brotto *et al*. 2013). *Sloanea lasiocoma*, on the other hand, occurs in the Atlantic forest, mostly in MOF and DOF (Sampaio & Souza 2014).

Cupania vernalis is considered frequent and common in both vegetation types in open or closed areas of MOF or DOF (Reitz 1980), as is *Ilex paraguariensis*, which follows the same pattern

(Silva *et al*. 2018). This species was considered an indicator of montane gradient in the FOD of the Serra da Prata (Blum & Roderjan 2007).

Through ecological niche modeling, Wrege *et al*. (2017) pointed to the maintenance of DOF areas, but replacement of MOF by SSF in Paraná state. Saraiva *et al*. (2021) predicted f 43% to 64% losses of vegetation cover for the entire extent of the MOF ecoregion in the face of future climate change.

In this sense, the importance of defining indicator species for each phytophysiognomy is highlighted, in order to monitor the dynamics of vegetation and update the definition of its boundaries (Viana 2015). To this end, the species *Araucaria angustifolia* and *Campomanesia xanthocarpa* are good indicators of montane MOF; *Allophylus edulis*, *Myrcia hatschbachii*, and *Cinnamodendron dinisii* are indicators of MOF; and *Weinmannia paulliniifolia* and *Ocotea catharinensis* are indicators of DOF.

The studied forest communities are in a maturation process, and the Serra da Baitaca State Park shows high importance for conservation;

The study areas comprise species occurrences of both Mixed Ombrophilous Forest (MOF) and Dense Ombrophilous Forest (DOF), but the WL1 layer (trees, ferns and palms) shows higher floristic and structural similarity to MOF;

In the transition zone between MOF and DOF, in the Serra do Mar in the state of Paraná, the species *Araucaria angustifolia* and *Campomanesia xanthocarpa* were considered good indicators of montane MOF; *Allophylus edulis*, *Myrcia hatschbachii*, and *Cinnamodendron dinisii* were considered indicators of MOF; and *Weinmannia paulliniifolia* and *Ocotea catharinensis* were considered indicators of DOF.

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