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UNVEILING ECOLOGICAL DYNAMICS AND PATTERNS IN AN URBAN-TO-RURAL GRADIENT OF FOREST FRAGMENTS IN THE ATLANTIC FOREST BIOME

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ABSTRACT

The floristic composition and forest structure have been extensively documented as a well-established basis for ecological studies. However, distinctions along the urban-to-rural gradient are limited for neotropical ecosystems. Therefore, we analyzed the floristic, diversity, and spatial distribution patterns of tree species along an urban-to-rural gradient of forest fragments in the Atlantic Forest Biome. Thus, a 1.0 ha area was sampled in each fragment (urban, peri-urban, and rural) based on 50 unit samples of 20.0 x 10.0 m. Data on species, diameter at breast height (DBH), total height, and position (x and y coordinates) were collected. Analyses were conducted on the secondary succession stage, phytosociology, data distribution, floristic similarity, diversity indices, and spatial distribution (total and main species). A significant floristic difference was found among the fragments along the urban-to-rural gradient ($p<0.01$), with the rural forest in a late-successional regeneration stage and the others in an intermediate stage. Urban and rural forests differed significantly in diversity ($p<0.01$). The urban fragment exhibited an aggregated species distribution up to 50.0 m, while the peri-urban fragment showed up to 30.0 m aggregation. Spatial distribution in the rural fragment was completely random. However, the distribution pattern of a considered species varies depending on the fragment type. We identified differences among the three forest fragments (floristics, diversity, and spatial distribution of species) due to the influence of the urban ecosystem. The procedures adapted to assess the secondary forest succession stage were found to be reliable to mitigate the subjectivity in Conama Resolution 02/1994.

Keywords: Mixed Ombrophilous Forest; Urban ecology; Urban forest

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DESVENDANDO DINÂMICAS E PADRÕES ECOLÓGICOS EM UM GRADIENTE URBANO-RURAL DE FRAGMENTOS FLORESTAIS NO BIOMA MATA ATLÂNTICA

RESUMO A composição florística e a estrutura florestal têm sido amplamente documentadas como uma base bem estabelecida para estudos ecológicos. No entanto, relatos de distinções ao longo do gradiente urbano-rural são limitadas para os ecossistemas neotropicais. Portanto, analisou-se os padrões de florística, diversidade e distribuição espacial de espécies arbóreas ao longo de um gradiente urbano-rural de fragmentos florestais no Bioma Mata Atlântica. Em cada fragmento (urbano, periurbano e rural) foi amostrada uma área de 1,0 ha, com base em 50 unidades amostrais de 20,0 x 10,0 m, coletando-se dados sobre espécie, DAP, altura total e posição (coordenadas x e y). Foram realizadas análises sobre estágio de sucessão secundária, fitossociologia, distribuição gráfica dos dados, similaridade florística, índices de diversidade e distribuição espacial (para todas as espécies e para as principais). Foi encontrada diferença florística significativa entre os fragmentos ao longo do gradiente urbano-rural ($p<0,01$), estando a floresta rural em estágio sucessional tardio de regeneração e os demais em estágio intermediário. As florestas urbana e rural diferiram significativamente em diversidade ($p<0,01$). O fragmento urbano exibiu distribuição agregada de espécies até 50,0 m, enquanto o fragmento periurbano apresentou comportamento de agregação até 30,0 m. No fragmento rural a distribuição espacial foi completamente aleatória. Contudo, o padrão de distribuição de uma espécie considerada varia dependendo do tipo de fragmento. Identifica-se que as diferenças entre os três fragmentos florestais (florística, diversidade e distribuição espacial das espécies) é devido à influência do ecossistema urbano. Os procedimentos adaptados para avaliar o estágio da sucessão florestal secundária mostraram-se confiáveis para mitigar a subjetividade da Resolução Conama 02/1994.

Palavras-Chave: Floresta Ombrófila Mista; Ecologia urbana; Floresta urbana

1. INTRODUCTION

As cities sprawl to rural areas, the replacement of natural ecosystems with anthropogenic areas in the urbanization process has generated a variety of habitat-altering impacts operating at different spatial and temporal scales (McDonnell & Hahs, 2008; Lowry et al., 2012; Coogan et al., 2018). It is evident that cities form a unique mosaic of habitats across these different scales, including residential, commercial, industrial, and natural infrastructure areas, among which green spaces exist (Breuste et al., 2008; Taylor & Hochuli, 2017).

These green spaces within a city are highly diverse, consisting of various green infrastructures created through landscaping practices such as squares, residential gardens, green roofs, and common-use spaces in residential buildings, but also preserved areas during the urban sprawling process as natural forest fragments (urban parks or forest remnants, whether public or private), with both of these categories presenting varying diversity of animal and plant species (Roy et al., 2012; Wolch et al., 2014; Michołap et al., 2017; Campagnaro et al., 2019).

Therefore, the value of green spaces in urban ecosystems is indisputable, as urban vegetation is essential for providing ecosystem services, aesthetic benefits, and recreational opportunities, contributing to the quality of life for the population (Brander & Koetse, 2011; Buchel & Frantzeskaki, 2015). In turn, landscape elements are crucial for the successful development of sustainable urban strategies, which are more effective when green areas are well-connected in the landscape (Dobbs et al., 2011; Xiao et al., 2018).

The assessment of urban ecosystems has

gained prominence in recent decades, both in urban and landscape planning, as these areas support a high diversity of animals and plants adapted to habitat changes (Sattler et al., 2010; Seto et al., 2012). These areas are consequently often referred to as "novel ecosystems" (Catford et al., 2012), as environmental variables and the composition of forest fragments significantly differ between preserved and anthropogenic ecosystems.

Among the studies on urban ecosystems, those focusing on urban forests and trees stand out in floristic surveys and phytosociological analyses of urban forest remnants (Cordeiro et al., 2011; Brun et al., 2017; Nunes et al., 2018; Reis et al., 2021). Therefore, an essential first step to effectively manage urban environments is to comprehensively and holistically understand urban diversity, considering that urbanization is one of the main causes of local and regional plant diversity loss (Seto et al., 2012; Nock et al., 2013; Newbold et al., 2015; Blood et al., 2016; Norton et al., 2016).

It is also crucial to understand how plant species are distributed along the urban-to-rural gradient. Studies which compare ecosystems along disturbance gradients or different levels of urban disturbance, such as the urban-to-rural gradient, can provide valuable insights into urban ecosystem processes (Nielsen et al., 2016; English et al., 2022). This can be accomplished through phytosociological analysis, allowing to characterize and compare tree floristic compositions (Cordeiro et al., 2011; Higuchi et al., 2016; Brun et al., 2017; Nunes et al., 2018).

Concerning this, several studies have indicated that urban forest fragments are altered environments and less diverse compared to rural forest fragments or forests in conservation units (Nock et al., 2013; Blood et al., 2016; Lopes et al., 2018; English et al., 2022). However, other research suggests that urban forest fragments can be potential areas for biodiversity conservation (Mello et al., 2016; Molin et al., 2017) and that conservation strategies are crucial for the Atlantic Forest Biome due to its high degradation level (Molin et al., 2017; Guerra et al., 2020). Hence, our research goal was to determine the floristic, diversity, and spatial distribution patterns of tree species along an urban-to-rural gradient of forest fragments in the Atlantic Forest Biome within the Mixed Ombrophilous Forest Ecosystem.

2. MATERIAL AND METHODS

We performed this study with data from three forest remnants along a landscape of neotropical forest in an urban-to-rural gradient (Figure 1), within the Mixed Ombrophilous Forest ecosystem, constituting one of the ecosystems in the Atlantic Forest Biome characterized as the most degraded and threatened biome in Brazil (Guerra et al., 2020). The urban fragment is isolated in the landscape and covers 1.30 ha. It is in an area with high building density surrounded by four streets and sidewalks in the city center of Irati, Paraná, Brazil. The peri-urban fragment is connected in the landscape and spans 32.0 ha. It is situated in a transitional area between urban and rural environments, with nearby constructions and roadways, being part of the Unicentro university campus in Irati. The third fragment is connected in the landscape and covers an area > 1,500.00 ha. It is located within a federal conservation unit (Flona de Irati) at the border of agricultural cultivation in the rural area of Fernandes Pinheiro municipality.

Considering the constraint of the urban area due to its total area of just over 1.0 ha, we sampled the three areas at a total of 1.0 ha each as a standardization procedure for this study. Thus, 50 plots of 20.0 x 10.0 m were established in each of these locations for the floristic survey. Natural regeneration was assessed in the five central plots of each forest fragment, across three distinct tree layers: Class 1: plants from 0.20 m to 1.0 m in height, in five sample units of 1.0 m x 5.0 m; Class 2: plants > 1.0 m and ≤ 3.0 m in height, in five sample units of 10.0 x 1.0 m;

Class 3: plants > 3.0 m in height and less than 5.0 cm in diameter at breast height (DBH), in five sample units of 20.0 x 1.0 m.

We performed a floristic survey to assess information on tree diversity, with species richness and diversity estimated for

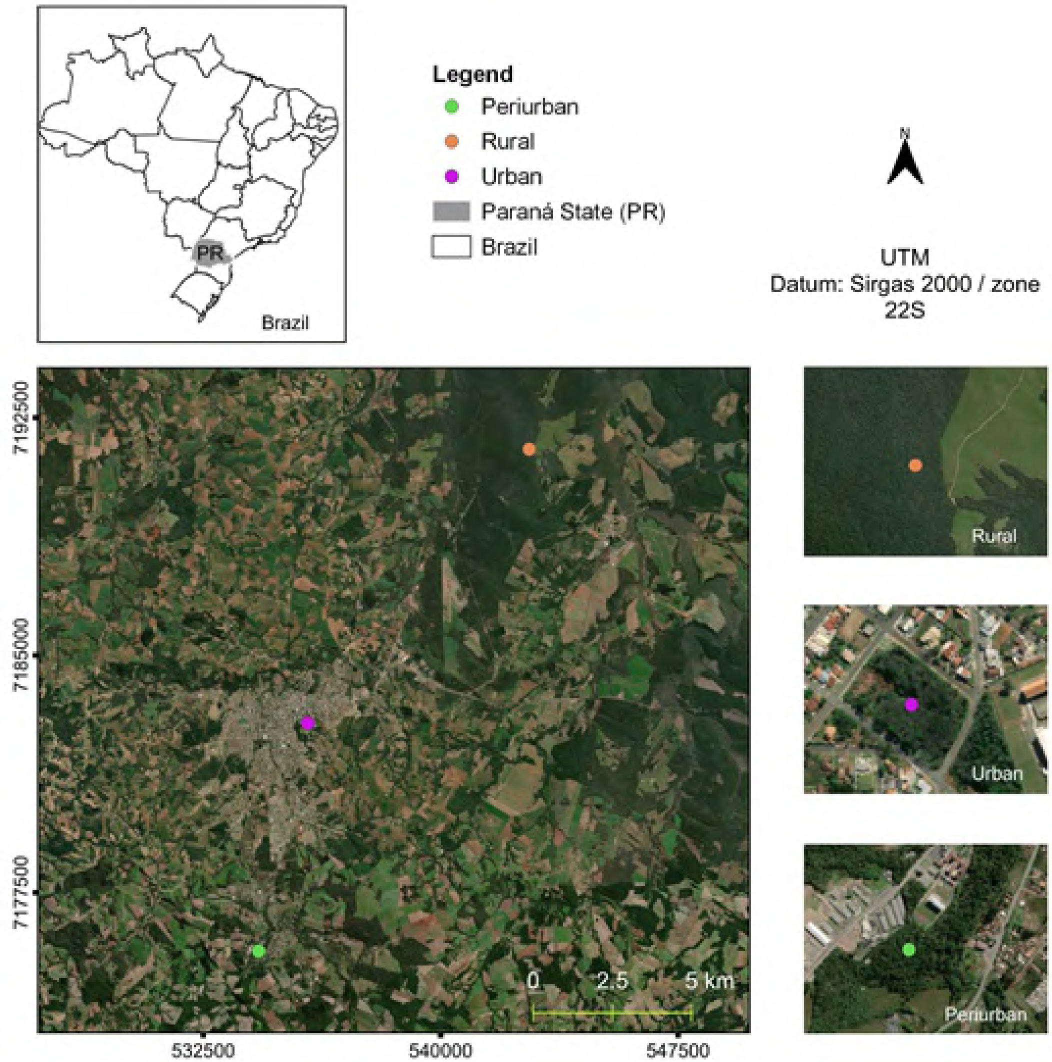

Figure 1. Study areas sampled along the urban-to-rural gradient
Figure 1. Áreas de estudo amostradas ao longo do gradiente urbano-rural

each location. All trees with diameter at breast height (DBH) ≥ 10 cm were measured in each of the 50 sample units. We estimated the DBH from the perimeter at breast height (PBH) with a tape measure for each tree, and the total tree height was estimated by an EC2 digital clinometer. When the use of the clinometer was not possible due to canopy density, total height was estimated from a stick reference of a 3.0 m high. Species identification was performed during data acquisition, while biological material was collected for those which could not be identified to facilitate species identification and storage in the herbarium of the Department of Forest Engineering at Unicentro, Irati Campus.

A horizontal and vertical structure analysis was conducted using the total height and DBH of each forest fragment sampled. We categorized data distribution into classes to promote better visualization of tree distribution in the study areas and their regenerative capacity. DBH data were divided into diameter classes with a 5 cm interval, and total height data were divided into height classes of 5 meters interval.

We used a phytosociological analysis to describe the floristic composition of the forest fragments and classified species according to its Importance Value (IV) based on relative frequency (RF), relative density (RD), and dominance (DM), following the methodology described by Moro & Martins (2011). All phytosociological calculations were performed in a spreadsheet using Microsoft Excel 2019.

We estimated species diversity using different indices, as each index is related to a different purpose in describing environments, and a single index is unable to describe the specific structure of a community (Magurran, 2011). Four indices from four different classes were used: Richness, expressed by the Margalef index; Dominance, expressed by the Simpson index; Evenness, expressed by the Pielou index; and Information, expressed by the Shannon-Wiener index (Magurran, 2011).

Each study area was divided into five sample units of 100.0 m x 20.0 m to allow comparison between the three forest fragments, ensuring repetition in each one. Comparison between forest fragments in both floristic composition and diversity was performed using the Non-metric Multidimensional Scaling (NMDS) procedure. We created an abundance matrix of species in each sample unit of each study area to compare floristic compositions. In addition, a matrix was created for diversity comparison using the values of each diversity index observed in each sample unit of each study area. We used the altGower dissimilarity method and the Analysis of Similarity (Anosim) with 999 permutations for both analyses. All statistical analyses were performed in the R statistical programming language (R Development Core Team), through the R Studio interface version 4.0.0, using the vegan and ggplot2 packages.

We also suggested the successional stage of each area to better understand the forest fragments' conservation status. Conama Resolution number 2 of 1994 (Table 1) served as a basis for defining the successional stage for the Mixed Ombrophilous Forest. However, due to the subjectivity of some criteria outlined in this regulation, an adaptation was performed for a more controlled assessment of the successional stage, considering the ranges and characteristics of various variables measured or observed in the forest fragments. Then, a matrix based on the quantitative values obtained for each assessed variable (Table 1) in each forest fragment was created for cluster analysis. The Euclidean distance and the 'ward.D2' method for linkages were employed, using the factoextra package in the R software, considering a cophenetic correlation > 0.85.

Table 1. Variables used for classification of the successional stages of forest fragments in the urban-to-rural gradient, according to Conama Resolution number 2 of 1994 (Conama, 1994)

Tabela 1. Variáveis utilizadas para classificação dos estágios sucessionais dos fragmentos florestais no gradiente urbano-rural, segundo a Resolução Conama nº 2 de 1994 (Conama, 1994)

Variables assessed in the forest	Stage of Secondary Forest Succession			Variables used
	Early	Intermediate	Late	
Number of tree layers	1	1 – 2	> 2	AV
Number of Species	1 a 10	5 – 30	> 30	AV
Basal Area ($m^2.ha^{-1}$)	8 a 20	15 – 35	> 30	MV
Total height (m)	Up to 10	8 – 17	> 15	MV
DBH amplitude (cm)	10	25	40	MV

Cont...

Cont...

Variables assessed in the forest	Stage of Secondary Forest Succession			Variables used
	Early	Intermediate	Late	
DBH distribution (cm)	5 a 15	10 – 40	20 - 60	MV
Tree growth	Fast	Moderate	Slow	---
Tree longevity	Short	Median	Large	---
DBH variation	Short	Median	Large	CV%
Total height variation	Short	Median	Large	CV%
Plant type	Heliophytes	Facultative	Ombrophilous	---
Epiphytes	Rare	Little	Abundant	Class
Herbaceous vines	Abundant	Little	Rare	---
Woody vines	Absent	Rare	Present	Class
Grasses	Abundant	Little	Rare	---
Tree regeneration	Rare	Little	Abundant	---
Litter thickness	Thin	Inconstant	Inconstant	CV%
Litter decomposition	Little	Changeable	Intense	---

Note: AV (absolute value observed at each forest fragment), MV (mean value observed per unit sample at each forest fragment), CV% (coefficient of variation observed among unit samples at each forest fragment), Class (values ranging from 1 to 3 according to the successional stage - 1 for early and 3 for late).

In order to obtain information on how the trees' spatial distribution sets and consequently understand ecological relationships between species, such as competition, dispersal, and natural associations (Araújo et al., 2016), metric coordinates were recorded for each sampled tree at each unit sample related to the X and Y axes. We subsequently selected the two most important species in each area from the phytosociological analysis which occurred in the other study areas for comparison of their spatial distribution.

Finally, we performed spatial distribution pattern analyses of species using Ripley's K function, with a focus on interaction processes between species in forest dynamics (Capretz et al., 2012; Araújo et al., 2016). The analyses were performed for the total number of species in each study area and for three groups of two most frequent species in the forest fragments, aiming to compare distribution patterns. The Splancs package and the Khat function in R Studio version 4.0.0 were used for these analyses, as they allow implementing an edge correction to prevent the occurrence of spatial distribution of forest species outside the analyzed forest area (Rowlingson & Diggle, 2004).

3. RESULTS

A total of 1,768 trees were measured, representing 78 species and 35 families. Among the locations, 510 trees were sampled in the urban area (21 species and 14 families), 521 trees in the peri-urban area (31 species and 17 families), and 737 trees in the rural area (57 species in 26 families, with eight unidentified species).

The 10 most sampled species in the urban forest fragment represent 96.47% of the Importance Value. The 10 most sampled species represent 83.52% of the Importance Value in the peri-urban and 68.63% in the rural forest fragment (Table 2). There is floristic similarity between the urban and peri-urban forest fragments, with the rural forest fragment being significantly different ($p < 0.01$) from the urban forest fragment (Figure 2).

Species considered rare in the phytosociological analysis of the urban forest fragment were among the most abundant in the peri-urban and rural places (*Casearia sylvestris* Sw. and *Matayba elaeagnoides* Radlk.). The same was observed with species considered rare in the peri-urban fragment listed among the most abundant in the rural fragment (*Nectrandra megapotamica* (Spreng.) Mez and *Curitiba prismatica* (D. Legrand) Salywon & Landrum).

Table 2. Observed values for the relative frequency (Fr), relative density (De), relative dominance (Do), and Importance Value Index (VI) for the top 10 species sampled in the forest fragments in the urban-to-rural gradient
Tabela 2. Valores observados para a frequência relativa (Fr), densidade relativa (De), dominância relativa (Do) e Índice de Valor de Importância (VI) para as 10 principais espécies amostradas nos fragmentos florestais no gradiente urbano-rural

Species Sampled	Fr	De	Do	VI
Urban Forest Fragment				
Parapiptadenia rigida (Benth.) Brenan.	37.25	37.25	61.81	45.44
Gymnanthes klotzschiana Müll.Arg.	19.22	19.22	7.27	15.23
Bauhinia forficata Link	13.73	13.73	9.37	12.27
Ocotea puberula (Rich.) Nees	9.02	9.02	10.22	9.42
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl.	5.69	5.69	1.69	4.36
Campomanesia xanthocarpa O.Berg	3.14	3.14	1.75	2.68
Luehea divaricata Mart.	2.35	2.35	2.34	2.35
Ligustrum lucidum W.T.Aiton	1.96	1.96	2.01	1.98
Hovenia dulcis Thunb.	1.76	1.76	1.04	1.52
Casearia decandra Jacq.	1.57	1.57	0.52	1.22
Peri-urban Forest Fragment				
Parapiptadenia rigida (Benth.) Brenan.	14.2	14.2	31.56	19.99
Cinnamodendron dinisii Schwacke	14.2	14.2	12.69	13.70
Allophylus edulis (A.St.-Hil. et al.) Hieron. ex Niederl.	13.05	13.05	6.88	10.99
Gymnanthes klotzschiana Müll.Arg.	11.52	11.52	5.97	9.67
Matayba elaeagnoides Radlk.	7.68	7.68	10.62	8.66
Eugenia uniflora L.	5.76	5.76	3.18	4.90
Araucaria angustifolia (Bertol.) Kuntze	2.88	2.88	7.86	4.54
Casearia decandra Jacq.	4.99	4.99	2.1	4.03
Campomanesia xanthocarpa O.Berg	4.61	4.61	2.85	4.02
Casearia silvestris Eichler	3.26	3.26	2.53	3.02
Rural Forest Fragment				
Araucaria angustifolia (Bertol.) Kuntze	9.36	9.36	38.07	18.93
Nectandra grandiflora Nees & Mart.	11.67	11.67	8.36	10.56
Ilex paraguariensis A.St.-Hil	8.28	8.28	4.49	7.01
Cinnamodendron dinisii Schwacke	6.92	6.92	6.77	6.87
Matayba elaeagnoides Radlk.	6.65	6.65	7.24	6.84
Ocotea odorifera Rohwer	5.43	5.43	2.39	4.42
Ocotea puberula (Rich.) Nees	3.12	3.12	5.56	3.93
Curitiba prismatica (D,Legrand) Salywon & Landrum	4.88	4.88	1.47	3.75
Nectandra megapotamica Mez	3.66	3.66	3.44	3.59
Casearia sylvestris Eichler	3.53	3.53	1.14	2.73

We identified some invasive exotic species in the urban (four species) and peri-urban (two species) forest fragments. Two of the main invasive species in the Mixed Ombrophilous Forest ecosystem were among the most frequent in the urban forest fragment (*Ligustrum lucidum* W.T. Aiton and *Hovenia dulcis* Thunb.), with 10 and 9 trees per hectare, respectively, with DBH > 0.10m.

In the urban forest fragment, 20 species were sampled in the regenerating layer, with eight of them being new in the floristic composition and unrelated to species present in the mature tree layer (*Apuleia leiocarpa* J.F.Macbr.; *Campomanesia guazumifolia* (Cambess.) O.Berg; *Casearia lasiophylla* Eichler; *Cinnamomum amoenum* (Nees & Mart.) Kosterm.; *Cordia ecalyculata* Vell.;

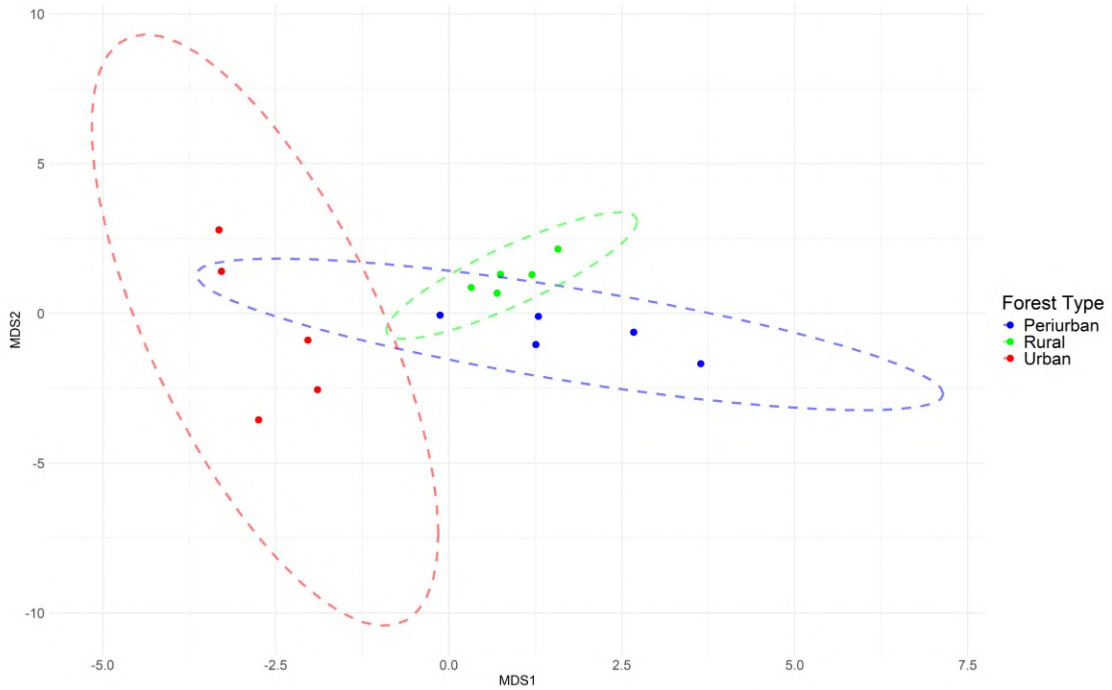

Figure 2. Floristic similarity among urban, peri-urban, and rural forest fragment groups using NMDS analysis, altGower dissimilarity method (solution reached with 20 runs, stress = 0.1199), Anosim with 999 permutations ($R^2 = 0.63$ and p-value = 0.001)

Figura 2. Similaridade florística entre grupos de fragmentos florestais urbanos, periurbanos e rurais usando análise NMDS, método de dissimilaridade altGower (solução alcançada com 20 execuções, stress = 0,1199), Anosim com 999 permutações ($R^2 = 0,63$ e p-valor = 0,001)

Eugenia pyriformis Cambess.; *Eugenia uniflora* L.; *Lonchocarpus muehlbergianus* Hassl.). Only four of the sampled species had regenerating individuals in all three evaluated layers: *Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl.; *Cinnamomum amoenum* (Nees & Mart.) Kosterm.; *Cordia ecalyculata* Vell.; *Parapiptadenia rigida* (Benth.) Brenan.

In the peri-urban forest fragment, eight species were in the regenerating layer, with two of them being new in the floristic composition and unrelated to species present in the upper tree layer (*Celtis iguanaea* (Jacq.) Sarg.; *Eugenia uniflora* L.). Moreover, four species presented regenerating individuals in all three evaluated tree layers: *Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl.; *Cupania vernalis* Cambess.; *Eugenia uniflora* L.; *Matayba elaeagnoides* Radlk.

In the rural forest fragment, 15 species were in the regenerating layer, with eight of them being new in the floristic composition and unrelated to species present in upper tree layer (*Dalbergia frutescens* (Vell.) Britton.; *Calyptranthes concinna* DC.; *Celtis iguanaea* (Jacq.) Sarg.; *Eugenia uniflora* L.; *Piper aduncum* L.; *Rudgea jasminoides* (Cham.) Müll. Arg.; *Solanum granulosoleprosum* Dunal; *Solanum mauritianum* Scop.). Only four of the sampled species had regenerating individuals in all three evaluated layers: *Calyptranthes concinna* DC.; *Eugenia uniflora* L.; *Nectandra megapotamica* Mez.; *Pleroma* sp.

Key species related to the late-successional stage were sampled in all evaluated forest fragments. The most frequent species in the urban and peri-urban fragments (*P. rigida*), along with a species among the most frequent in the peri-urban and rural fragments (*A. angustifolia*), are listed as key species of a late-successional stage according to Conama Resolution number 2 of 1994 (Conama, 1994).

However, other key species of intermediate or late-secondary successional stage were observed in both the urban and peri-urban fragments (*Ocotea puberula* (Rich.) Nees, *Casearia decandra* Jacq., *Casearia sylvestris* Sw., *Campomanesia xantocarpha* (Mart.) O.Berg, *Cupania vernalis* Cambess., *Eugenia uniflora* L., *Calyptranthes concinna* DC., *Matayba elaeagnoides* Radlk, *Gymnanthes klotzschiana* Müll.Arg.), even outside the list of the 10-most frequent species (Felitto et al., 2017).

Regarding the successional stages and the criteria used to evaluate the forest fragments (Table 3), two groups were formed based on the cluster analysis, (Figure 3), one group consisting of the rural fragment and the other of the urban and peri-urban fragments. This analysis indicates that the rural area is in a different successional stage from the others. Based on the values of the evaluated variables (Table 3), we can suggest that the rural forest fragment is in a late-secondary successional stage, while the urban and peri-urban ones are in an intermediate succession stage, as the values for the urban and peri-urban areas are similar and discrepant from the rural area.

The DBH distribution for the three study areas (Figure 4) shows the same trend, forming a reverse J-shaped curve which represents a possible balance between seedling establishment and mortality, generally related to a balanced forest

Table 3. Criteria and values used for evaluating the successional stage of the urban, peri-urban, and rural forest fragments

Tabela 3. Critérios e valores utilizados para avaliar o estágio sucessional dos fragmentos florestais urbanos, periurbanos e rurais

Criteria used	Forest Fragment		
	Urban	Peri-urban	Rural
Mean Basal Area ($m^2.ha^{-1}$)	6.46	6.37	7.53
Basal Area amplitude	4.68	3.14	0.89
Basal Area CV%	30.58	19.88	5.10
Mean Total Height (m)	12.08	12.31	9.13
Total Height amplitude	21.00	25.00	22.00
Total Height CV%	32.53	31.02	45.91
Mean DBH (cm)	24.65	24.75	22.19
DBH amplitude	104.03	75.99	74.36
DBH CV%	57.50	52.00	58.35
Epiphytes	1.00	1.00	3.00
Woody vines	1.00	1.00	2.00
Mean litter thickness (cm)	1.48	1.58	1.37
Litter thickness amplitude	2.60	2.90	5.50
Litter thickness CV%	41.43	48.35	82.97
Number of Trees	510.00	521.00	737.00
Number of Species	21.00	31.00	57.00
Number of Families	14.00	17.00	26.00
Margalef (mean value)	3.21	4.79	9.69
Simpson (mean value)	0.21	0.09	0.05
Shannon-Wiener (mean value)	1.98	2.73	3.34
Number of tree layers	2.00	2.00	3.00

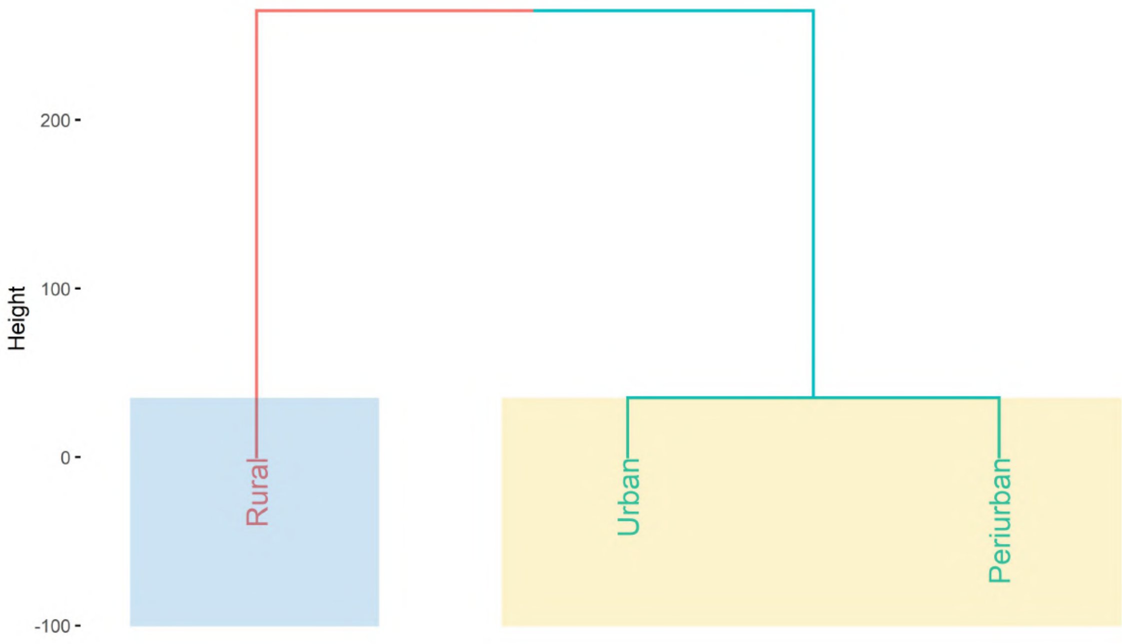

Figure 3. Groups of secondary succession stages (cophenetic correlation = 0.9947, ward.D2 linkage, euclidean distance)
Figura 3. Grupos de estádios de sucessão secundária (correlação cofenética = 0,9947, ligação ward.D2, distância euclidiana)

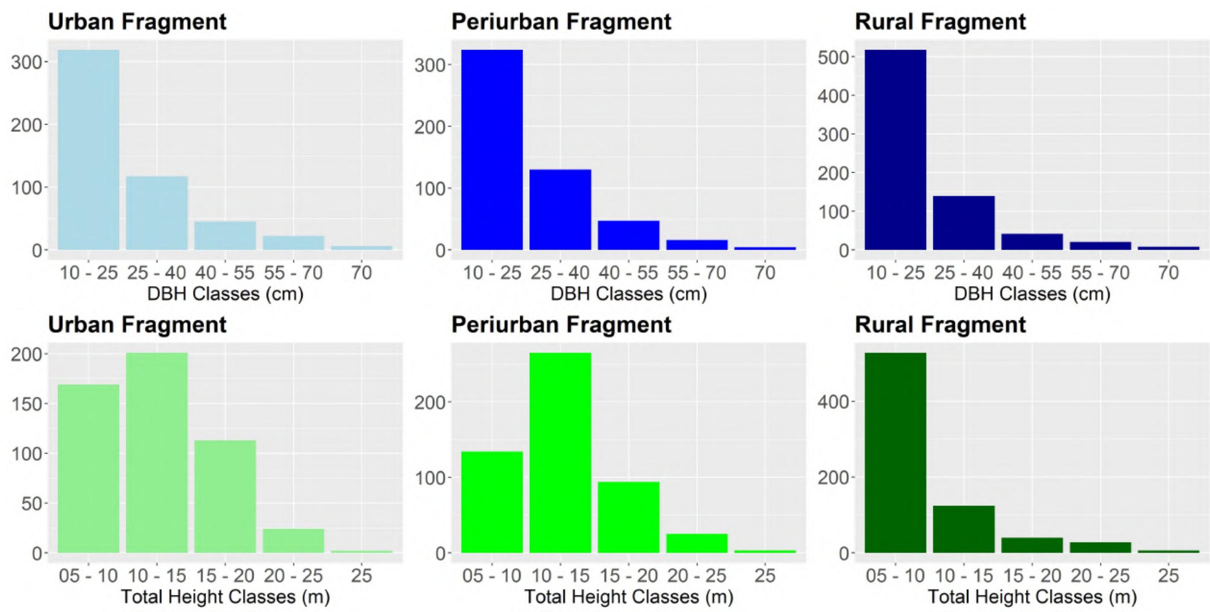

Figure 4. DBH and total height distribution for urban, peri-urban, and rural forest fragments
Figura 4. Distribuição do DAP e da altura total em fragmentos florestais urbanos, periurbanos e rurais

structure (Pearce et al., 2013). We observed that the distribution pattern regarding total height classes (Figure 4) is unimodal, indicating that most trees are in intermediate height classes with a lower proportion of smaller trees, except for the rural forest fragment, which shows a reverse J-shaped pattern.

The urban and peri-urban forest fragments showed similar diversity indices

(Table 4), with lower species richness (Margalef), higher species composition uniformity (Simpson), and lower diversity (Shannon-Wiener) compared to the rural forest fragment. There is a more prominent variation in diversity data among sample units in the urban forest fragment compared to the others (Table 4). We observed that there was significant dissimilarity ($p < 0.01$) among the study locations in terms of diversity index values (Figure 5). The diversity index values for the rural forest fragment stand out compared to those observed in the urban forest fragment (Figure 6), being significantly different (Figure 5). There is greater species richness and evenness among individuals, with lower species dominance in the rural forest fragment. The higher species dominance in the urban forest fragment (Figure 6) is related to the higher importance value observed for the species *P. rigida* in this study area, representing 45.44% of the total (Table 2).

Table 4. Summary of observed values for diversity indices in the five sample units of each evaluated forest fragment

Tabela 4. Resumo dos valores observados para os índices de diversidade nas cinco unidades amostrais de cada fragmento florestal avaliado

Fragment	Values	Margalef	Simpson	Pielou	Shannon
Urban	Minimum	1.68	0.19	0.68	1.56
	Mean	2.31	0.25	0.72	1.75
	Maximum	3.15	0.29	0.81	1.87
	CV%	27.66	14.35	7.75	8.31
Peri-urban	Minimum	3.10	0.10	0.83	2.33
	Mean	3.78	0.11	0.86	2.49
	Maximum	4.43	0.12	0.88	2.59
	CV%	16.03	8.12	2.16	4.35
Rural	Minimum	5.94	0.06	0.86	2.98
	Mean	6.99	0.06	0.87	3.10
	Maximum	8.03	0.07	0.88	3.25
	CV%	12.60	7.61	1.06	3.72

The spatial distribution of species in the urban, peri-urban, and rural forest fragments showed different patterns (Figure 7). Species in the urban forest fragment generally exhibited an aggregated distribution up to 50.0 m distance, transitioning to a random distribution at greater distances. We observed a similar pattern in the peri-urban forest fragment, but for a distance of up to 30.0 m. The spatial distribution pattern for the rural forest fragment was completely random.

The spatial distribution patterns among the studied areas also show distinctions when considering specific species (Figure 8). The species *C. dinissi* presented one of the highest importance values in the peri-urban and rural forest fragments, exhibiting an aggregated pattern between 20.0 and 40.0 m of distance in the peri-urban fragment and a completely random pattern in the rural forest fragment. The species *G. klotzschiana* had high importance values in the urban and peri-urban areas, and showed aggregated spatial distribution patterns in both types of forest fragments, up to distances of 70.0 m for the urban forest fragment and up to 55.0 m for the peri-urban fragment. Finally, the species *P. rigida* had among the highest importance values in the urban and peri-urban areas, presenting aggregated spatial distribution patterns up to 45.0 m of distance in the urban forest fragment and completely random in the peri-urban forest fragment.

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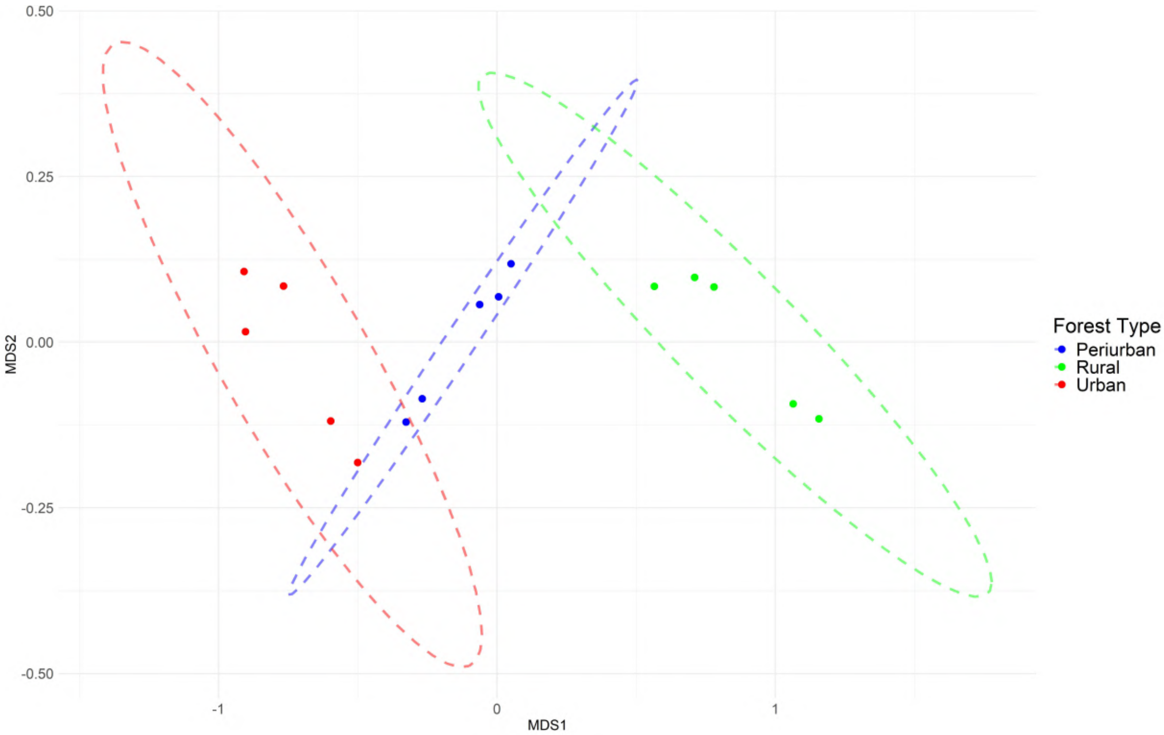

Figure 5. Diversity similarity among the groups of urban, peri-urban, and rural forest fragments using NMDS analysis, altGower dissimilarity method (solution reached with 20 runs, stress = 0.002), Anosim with 999 permutations (R^2 = 0.92, p-value = 0.001)

Figura 5. Similaridade da diversidade entre os grupos de fragmentos florestais urbanos, periurbanos e rurais utilizando a análise NMDS, método de dissimilaridade altGower (solução alcançada com 20 execuções, stress = 0,002), Anosim com 999 permutações (R^2 = 0,92, p-value = 0,001)

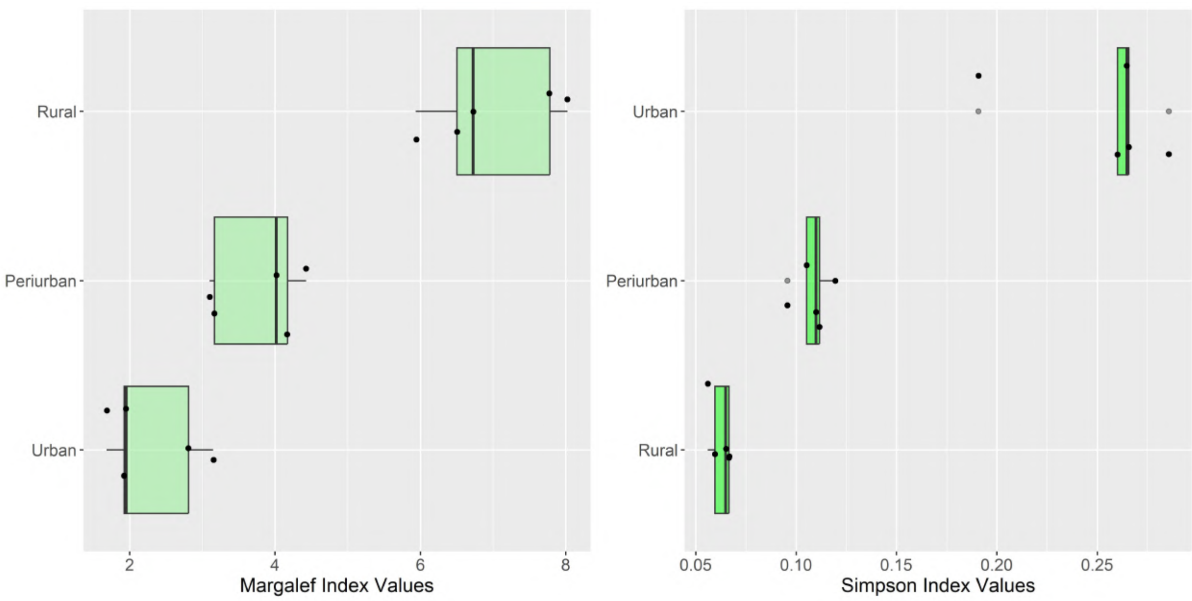

Figure 6. Range of variation and distinction among the forest fragments regarding the assessed diversity indices

Figura 6. Amplitude de variação e distinção entre os fragmentos florestais quanto aos índices de diversidade avaliados

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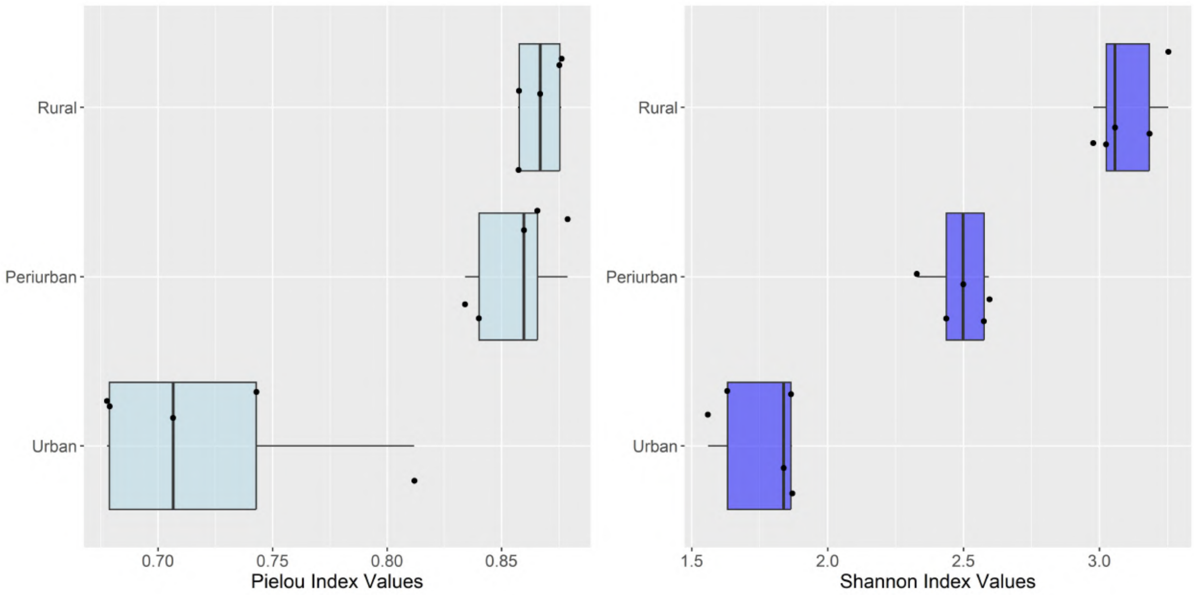

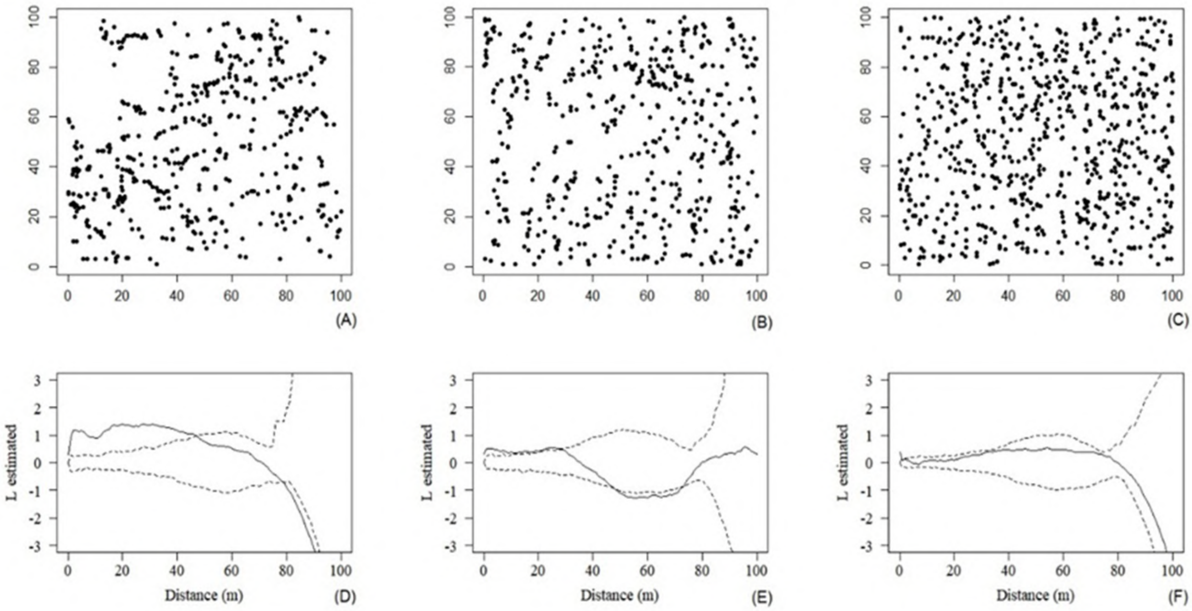

Figure 7. Spatial distribution of trees for the Urban (A), Peri-urban (B), and Rural area (C), and the results for the Ripley's K function for species in the Urban (D), Peri-urban (E), and Rural area (F). The confidence envelopes (99%) for the Montecarlo Method for Complete Spatial Randomness (CAE) simulations are represented by the dashed lines. The solid lines demonstrate the fit by Ripley's K Function

Figura 7. Distribuição especial das árvores no fragmento urbano (A), periurbano (B) e rural (C), e os resultados da função K de Ripley para as espécies no fragmento urbano (D), periurbano (E) e rural (F). Os envelopes de confiança (99%) pelas simulações do Método Montecarlo para a Completa Aleatoriedade Espacial (CAE) estão representados pelas linhas. As linhas contínuas demonstram o ajuste pela Função K de Ripley

4. DISCUSSION

The species with the highest importance values (IV) for the forest fragment in the urban area (*Parapiptadenia rigida*, *Gymnanthes klotzschiana*, and *Bauhinia forficata*) are adapted to the local

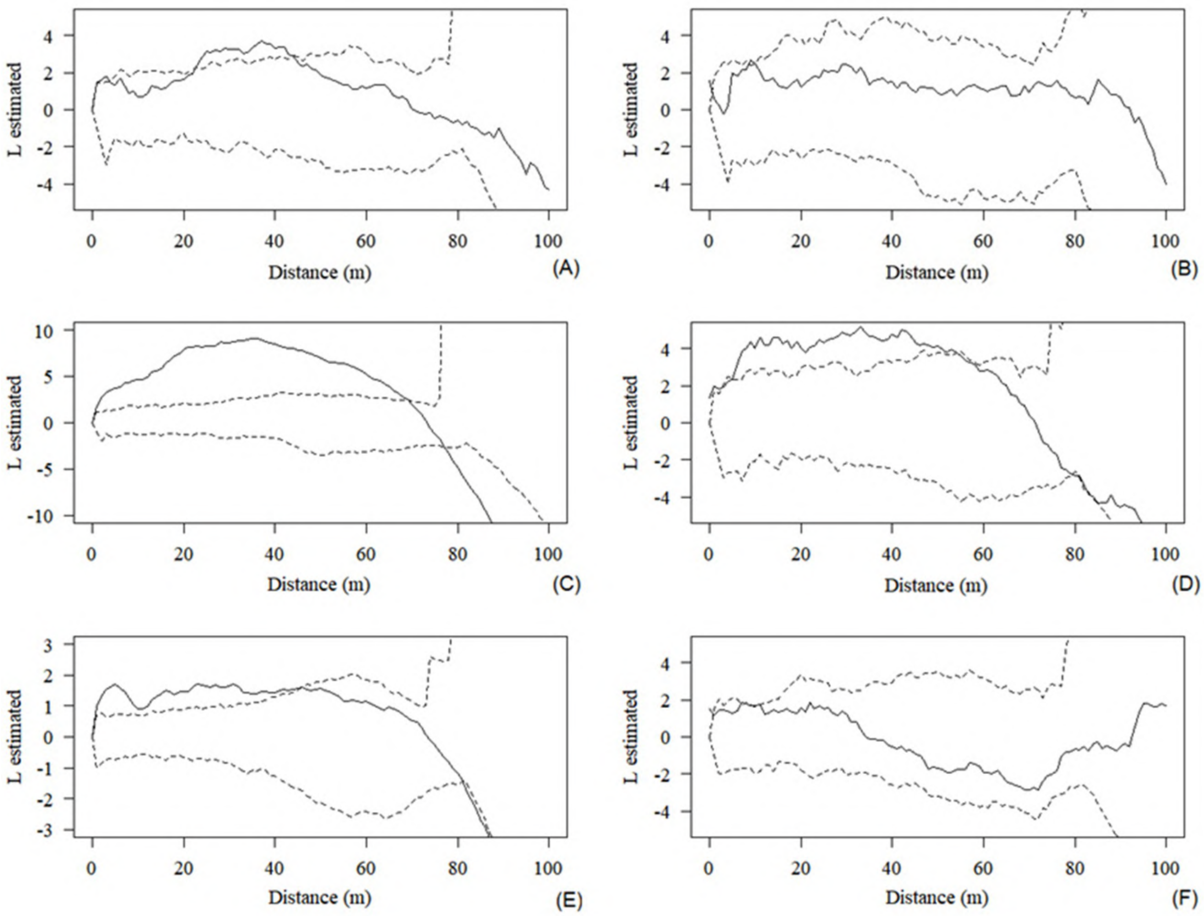

Figure 8. Spatial distribution by the Ripley's K function for C. dinissi in the Peri-urban area (A) and Rural forest fragment (B); for G. klotzschiana in the Urban (C) and Peri-urban forest fragment(D); for P. rigida in the Urban (E) and Peri-urban forest fragment (F). The confidence envelopes (99%) for the Montecarlo Method for Complete Spatial Randomness (CAE) simulations are represented by the dashed lines. The solid lines demonstrate the fit by Ripley's K Function

Figura 8. Distribuição especial pela função K de Ripley para C. dinissi fragmento periurbano (A) e Rural (B); para G. klotzschiana no fragmento urbano (C) e periurbano (D); para P. rigida no fragmento urbano (E) e periurbano (F). Os envelopes de confiança (99%) pelas simulações do Método Montecarlo para a Completa Aleatoriedade Espacial (CAE) estão representados pelas linhas. As linhas contínuas demonstram o ajuste pela Função K de Ripley

edaphoclimatic conditions (Scipioni et al., 2012; Meyer et al., 2012; Callegaro et al., 2017) and the high IV is also related to the seed dispersal syndrome, which is autochoric for all three species (Carvalho, 2003; Severiano, 2015; Kieras et al., 2018), and anemochoric for *P. rigida* (Carvalho, 2003; Severiano, 2015). The fully urbanized surroundings in an area surrounded by streets and buildings with varying degrees of soil impermeability, with or without the presence of plants in garden landscaping, restrict seed dispersion within the fragment, except for the group of species comprising the regenerating layer favored by zoochoric dispersion.

The species with the highest IV in the peri-urban forest fragment (*Parapiptadenia rigida*, *Cinnamodendron dinisii*, and *Allophylus edulis*) are commonly found in forest remnants of the Mixed Ombrophilous Forest located in diversified environments, with different geological, geomorphological, and pedological conditions along the three plateaus of Paraná State (Cordeiro et al., 2011). The dispersal strategies of these species (anemochoric and autochoric) similarly influence the localized and abundant occurrence (Carvalho, 2003; Seneme et al., 2006; Severiano, 2015), even for the species with zoochoric dispersal syndrome (*Allophylus edulis*), which is typically found in the forest understory (Carvalho, 2003).

As a transitional environment with a larger total area than the urban fragment, the peri-urban forest is more connected in the landscape and tends to show less anthropogenic impact. It is one of the factors which enables better species dispersion through wind and fauna (Dubois & Cheptou, 2017), thereby justifying the higher number of trees compared to the urban forest. A more intense edge effect, like in the urban forest fragment, can also cause changes in species composition and community structure, affecting ecological process and species biodiversity (Harper et al., 2005).

The three species with the highest IVs in the rural forest fragment (*Araucaria angustifolia*, *Nectandra grandiflora*, and *Ilex paraguariensis*) exhibit zoochoric seed dispersal and are key species in more advanced successional stages (Carvalho, 2003; Felitto et al., 2017). The high incidence of zoochoric species in a forest provides benefits for both animals and plants, since animals are essential for seed dispersal and regeneration of other areas (Silva et al., 2012). Furthermore, zoochoric dispersal is a characteristic of environments in more advanced successional stages where trophic networks are better established (Moro & Lima, 2012).

The rare species observed in urban and peri-urban forest fragments, which are among the most abundant in the rural fragment, such as *Casearia sylvestris, Matayba elaeagnoides*, *Nectandra megapotamica*, and *Curitiba prismatica*, exhibit zoochoric dispersal (Carvalho, 2003; Iarmul et al., 2021). This serves as one of the indicators that these areas are in the process of evolving from an intermediate succession to a more advanced stage, increasing complexity and trophic networks (Moro & Lima, 2012). It is also important to state that urban forest fragmentation reduces the size and increases the isolation of plant populations, diminishes the supply of ecosystem services from pollinators, reduces disperser populations, or limits access to habitats (Bonte et al., 2011; Zambrano et al., 2020). In this regard, fragments with a larger total area and better landscape connectivity allow better dispersion and the occurrence of diversified species, justifying the higher number of families and species in the rural forest fragment.

The main invasive exotic species sampled (*Ligustrum lucidum* and *Hovenia dulcis*) have a zoochoric dispersal syndrome, which enhances seed dissemination and contamination of other forest remnants (Vigilato & Zampar, 2011). These two species are identified as the most aggressive in the Mixed Ombrophilous Forest ecosystem, leading to significant floristic changes by restricting the regeneration of native species through competition over the years (Lazzarin et al., 2015; Reis et al., 2021). These species are assigned as invasive species by the Land and Water Institute of Paraná and are commonly found in isolated forest remnants in the southern region of Brazil, which are under harsh conditions that characterize the urban ecosystem in cities (Cordeiro et al., 2011; Brun et al., 2017; Nunes et al., 2018). Biological invasion by exotic species in forest fragments has negative consequences for biodiversity and ecosystem functioning (Nunes et al., 2018), posing a significant environmental problem in urban green areas already impacted by anthropogenic actions and isolation that comes from landscape fragmentation (Reis et al., 2021). However, only one specimen of *Ligustrum lucidum* was found in the sampled regenerating layer in the urban forest fragment.

The forest succession stage differed among the studied areas, and the evaluated characteristics suggest that the rural forest fragment is in a late-successional stage. This result is attributed to the rural fragment's

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location in a National Forest conservation unit located on the border of an agricultural production farm, and so it is under a lower degree of anthropogenic intervention and potentially longer regeneration time, allowing for better forest development and establishment (Dubois & Cheptou, 2017). It should additionally be noted that succession stages correspond to a stochastic process influenced by frequent disturbances that promote continuous variation on vegetation at different scales, both spatial and temporal (Ribeiro et al., 2010).

The late-successional stage of forest regeneration is also supported by the assessed diversity characteristics. Diversity indices are fundamental tools for describing how diverse one environment is compared to another, as well as expressing the degree of development and interaction of species within the environment (Magurran, 2011; Kanieski et al., 2017). Despite the limited sampling of forest fragments (quantity of them), the observed trend from rural to urban environment is interesting, expected, and representative. Studies performed in different cities and ecosystems have pointed out these distinctions between the rural and urban environments due to anthropogenic pressure on urban forest remnants and to the characteristics of the environmental changes in the urban ecosystem (Nock et al., 2013; Newbold et al., 2015; Aronson et al., 2016).

However, the urban forest fragment demonstrates resilience to the environmental conditions of the urban ecosystem. The stability of the tree cover and the abundant natural regeneration across the three evaluated tree layers may indicate sustainable floristic composition and favorable conditions for progression toward a late-successional stage, provided the current state is maintained without human interference (Dey, 2014; Chazdon & Uriarte, 2016). This is a significant perspective due to the potential for providing ecosystem services, such as regulating the local microclimate, reduced surface runoff, carbon storage, shelter for fauna, and serving as a steppingstone for fauna species between more connected and preserved forest fragments towards the peri-urban and rural environment.

The decrease in diversity values along the rural-to-urban gradient characterized by the lowest diversity and highest dominance in urban areas may result from distinct ecological patterns. Diversity tends to be higher in preserved and connected forest fragments within the landscape (Araújo et al., 2022). Conversely, the higher likelihood of trees being the same species in urban fragments across different studied areas indicates greater dominance and lower species richness. Urban forest fragments are often described as homogenized (Lososová et al., 2012; Groffman et al., 2014), meaning that urban forests within the same ecosystem tend to be more similar in species composition compared to natural areas. This trend may be attributed to urbanization's impact on bird communities, which reduces seed dispersal diversity and negatively affects forest regeneration. Alternatively, urbanization may favor species with anemochorous dispersal, such as *P. rigida*, but also species more tolerant to environmental stress such as *O. puberula and B. forficata*.

Despite the isolated condition in the urban matrix characterized by lower species diversity values and greater floristic simplification, the urban forest fragment demonstrates resilience. The sampled regenerative capacity shows the diversified presence of forest species, particularly in the understory and primarily consisting of species with a zoochoric dispersal syndrome. This highlights the importance and presence of birds in the urban area, contributing to the regeneration process and forest perpetuation.

The aggregated distribution pattern for species in the urban forest fragment may indicate the presence of natural disturbance or disturbances derived from illegal interventions such as tree cutting. However, the species *G. klotzschiana*, one of the most abundant in the urban area, has an autochoric seed dispersal (Carvalho, 2003) and is rare inside dense primary forests, typically occurring in groups. This characteristic could also justify the observed aggregated pattern. On the other hand, the species *P. rigida*, abundantly present in the urban and peri-urban areas, is a pioneer species with an anemochoric dispersal syndrome, more frequently found in open and less dense forests with wide and expressive dispersion. This characteristic could justify the tendency towards the random spatial distribution pattern. A similar pattern is observed for the species *C. dinisii*, abundant in the peri-urban and rural areas. It is a pioneer species commonly found in the Mixed Ombrophilous Forest and is known to be very attractive to birds.

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5. CONCLUSION

This case study across the urban-to-rural gradient revealed notable differences among the three forest fragments concerning floristic composition, species diversity, and spatial distribution. The findings suggest that urban ecosystem conditions significantly influence species composition patterns. Furthermore, the adapted procedures proved to be reliable in reflecting the secondary forest succession stages, effectively addressing the subjectivity associated with Conama Resolution N° 2/1994.

The rural forest fragment is distinguished by more balanced ecological processes, such as species dispersal, diversity, and regeneration, and therefore serves as a model for understanding regional forest dynamics supported by landscape connectivity. In contrast, although the urban forest fragment is isolated and fully surrounded by urban structures, it exhibits notable resilience. It showcases distinct ecological processes related to species dispersal, diversity, and regeneration, with evidence suggesting progression toward a more complex forest succession stage.

The presence of invasive exotic species in the urban and peri-urban fragments underscores the challenges posed by urban ecosystems, while the persistence of key species associated with late-successional stages in all fragments suggests potential for ecological recovery and resilience. Spatial distribution patterns were also varied with urban and peri-urban fragments exhibiting aggregated distributions at shorter distances, reflecting localized ecological interactions. In contrast, the rural fragment showed more random distribution, indicative of a mature and balanced forest structure.

These findings emphasize the importance of tailored conservation strategies

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that consider the unique ecological contexts of each forest fragment. While urban and peri-urban forests face greater ecological constraints, their resilience and capacity for regeneration highlight their value in maintaining biodiversity and ecosystem services in human-dominated landscapes. By understanding and supporting these dynamics, stakeholders can enhance forest management practices, promote connectivity, and foster ecological restoration across the urban-to-rural gradient.

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AUTHOR CONTRIBUTIONS

Aguiar, J. T. de: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Writing – original draft; Cuchi, T.: Formal analysis, Investigation, Methodology, Software, Validation, Visualization, Writing – review and editing; Bobrowski R.: Conceptualization, Methodology, Software, Supervision, Validation, Visualization, Writing – review and editing.

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