

Diversity and structure of the understory of two forest ecotones in Maranhão and the influence of the urban environment

Catherine Rios Santos (✉ catherineriosantos@gmail.com)

Universidade Federal de Minas Gerais

Melissa Oda-Souza

Universidade Estadual do Piauí

Eduardo Bezerra Almeida

Universidade Federal do Maranhão (UFMA)

Carmen Sílvia Zickel

Universidade Federal Rural de Pernambuco

Research Article

Keywords: transition areas, Cerrado, Amazonian forest, phytosociology, urbanization

Posted Date: January 19th, 2023

DOI: <https://doi.org/10.21203/rs.3.rs-2464511/v1>

License: © ⓘ This work is licensed under a Creative Commons Attribution 4.0 International License. [Read Full License](#)

Additional Declarations: No competing interests reported.

Version of Record: A version of this preprint was published at Urban Ecosystems on November 4th, 2023. See the published version at <https://doi.org/10.1007/s11252-023-01449-2>.

Abstract

Forest ecotones are floristically rich but anthropogenic disturbances can differentiate their vegetation structure. This study evaluated the understory diversity of urban and nonurban forests in Maranhão. It tested the hypotheses that the understory of the nonurban forest has greater diversity and richness and that the spatial distribution of these variables in the understory of the urban forest has weak spatial dependence. The study was conducted in the municipalities of São Luís (urban area) and São José de Ribamar (nonurban area). Thirty plots (25m²) were demarcated and the woody individuals up to 2 m tall were measured. All phytosociological parameters were calculated. The differences in richness, density, and diversity were analyzed between the areas with the Mann-Whitney test, non-metric multidimensional scaling, and Hutcheson t-test. To visualize the variation in richness and diversity of the vegetation, ordinary kriging was used. There was a difference in the floristic composition and density of each species in the two areas; the richness and diversity were significantly greater in the nonurban area. The species with the highest IVs were *Faramea nitida*, *Myrcia amazonica*, and *Ephedranthus pisocarpus* in the nonurban forest and *Protium heptaphyllum*, *Randia armata*, and *Moquilea tomentosa* in the urban forest. Both understories had high diversity compared to other Amazonian regions. However, weak spatial dependence was found in the urban area, suggesting high anthropogenic interference in the environment. It is noteworthy that the areas represent a parcel of original ecotone vegetation in Maranhão and effective actions are needed to restore and conserve its diversity.

Introduction

The global loss of biodiversity is increasing due to urban expansion and deforestation that significantly reduce original forest cover, mainly in Amazonian areas (Martins and Oliveira 2011). Currently, many territories do not have core forest areas outside of legally protected land (Silva Junior et al. 2020). This is alarming because it demonstrates the vulnerability of forest environments that are not delimited as conservation units, as occurs in Amazonian-Cerrado transition areas in Maranhão. Despite the high diversity of organisms, the lack of collections and losses from disorderly agricultural growth have resulted in little interest in conservation politics conserving these areas (Maciel et al. 2016; Santos 2022).

Urbanization has also been highlighted as another factor that threatens the biodiversity in Amazonian-Cerrado transition areas, which structurally influences forest fragments. Further, urbanization alters migration and dispersal patterns, reduces the habitat and resources of species, and increases the vulnerability of species to environmental stochasticity due to edge and isolation effects (Sonnier et al. 2020).

Additionally, urban centers have high heterogeneity due to different forms of management, resulting in new types of habitats in their vegetated areas. This environmental complexity promotes colonization of new species tolerant to stress, which enables urban forests to have high plant richness (Ranta 2021). Thus, studies aimed at analyzing plant diversity in urban environments are necessary, as there is no consensus on the effects of urbanization on plant diversity (Lippe and Kowarik 2021).

Forested areas in urban centers have a diversity and composition of species that are responsible for maintaining ecological systems and ecosystem services of cities. Among these services, the flow of pollinators and dispersers, air filtration, and the reduction of heat islands and noise pollution are notable (Lv et al. 2019). Forest fragments in transition/ecotone areas and under anthropogenic disturbance have a floristic diversity that represents adjacent domains and, consequently, it is important to conserve these fragments (Pinheiro and Monteiro 2008).

Thus, studies about plant diversity and richness of urban forests are allies of can contribute to conservation, since they serve as are diagnostic tools and that provide information used to avoid extreme cases of deforestation and fragmentation.. Since urban forests have high discontinuity of the spatial dependence of species, they lose the original condition of the forest matrix (Rios et al. 2020).

Native understory plants are vulnerable to the effects of urbanization because it is difficult for them to regenerate in highly urbanized environments (Huang et al. 2012). The present study tested the following hypotheses: 1) the understory of the urban forest ecotone has lower floristic richness and diversity compared to the nonurban forest; 2) the spatial distribution of the richness and diversity of the understory in the urban forest ecotone has weak spatial dependence, while the variability of the richness and diversity in the nonurban forest has strong spatial dependence that is common in balanced forests.

Materials And Methods

Study area

The study was conducted in two open ombrophilous forest fragments in two transition areas on Maranhão Island, in Maranhão State, Brazil (IBGE 2021). The climate in the fragments is Aw, according to the classification by Köppen (Alvares 2013), with two well-defined seasons, a rainy season from January to June and a dry season from July to December. The annual rainfall varies from 1,250 to 2,000 mm and the temperature ranges from 26° C to 33°C, with an average of 28° C (INMET 2019).

The first fragment is Sítio Santa Eulália (02°31'04"S, 44°16'30"W) in the municipality of São Luís, MA (Fig. 1), which has forest influenced by urbanization and mangroves (IBGE 2021). In 1990, the vegetation was cleared, and the area was subdivided and of the streets paved. Subsequently, the housing construction project in the area was abandoned (Sousa 2018). In 2012, an asphalt expressway was built that links the center of the city of São Luís to outer neighborhoods, which further fragmented Sítio Santa Eulália that currently has approximately 167 ha of vegetation (Silva et al. 2022). Therefore, this site was considered an urban area because it is surrounded by residential, commercial and industrial buildings, and roads and highways, which result in anthropogenic impacts (Guerra et al. 2017).

The second fragment is Sítio Aguahy (02°38'47"S, 44°09'05"W) in the municipality of São José de Ribamar, MA, which comprises 400 ha of vegetation with species that occur in Amazonian, Cerrado, restinga, and mangrove forests. It is in the rural zone of the municipality (Fig. 1). Sítio Aguahy is on the property of

the Companhia Farmacêutica Quercegen Agronegócios Ltda. and is 16 km from the urban zone in the municipality of São José de Ribamar. It is considered a nonurban area (rural) for having surrounding vegetation at different stages of succession (Guerra et al. 2017).

Data Collection

For the sampling, in each area 30 plots (25m²) were randomly demarcated. These were 10 m apart and 30 m from the edge (Rigueira et al. 2012). For this work to be restricted to the woody stratum, the height and diameter of only young woody canopy and shrub individuals up to 2 m tall were measured (Santos et al. 2018). For this, a more comprehensive sampling criterium was adopted, where all individuals at ground height with a minimum diameter of 1 cm were measured with a caliper, which is equivalent to individuals with a circumference greater than 3 cm, as described by Gomes et al. (2009).

All the plants measured were collected, and herbarium specimens of the collected material were made following the methodology in Peixoto and Maia (2013). The species were identified using specialized literature (Ribeiro et al. 1999; Alves et al. 2013; Gonçalves and Lorenzi 2011), consulting with specialists, and comparing the material with images of exsiccatae on the Re flora (Flora do Brasil 2020) and *Specieslink* virtual herbaria and collections in the Maranhão Herbarium (MAR) at the Universidade Federal do Maranhão. When plants could not be identified to the species level, morphospecies were used. The angiosperms were listed following the APG IV (2016) classification system. The spelling of the species and author names, as well as the growth habit, were verified using the Flora do Brasil 2020 database.

Data analysis

With the data obtained, the following parameters were analyzed: density (absolute and relative), frequency (absolute and relative), importance value (IV), cover value (CV), Shannon index (H'), and Pielou index (J'). These were all calculated using FITOPAC 2.1.

The hypsometric distribution of the community was evaluated using histograms constructed with the height data of the species recorded. The diametric distribution of the community was evaluated using histograms constructed with the data of the individual samples, in which diameter classes were established with an amplitude of 1 cm.

To verify the difference in the average richness of species among the 30 plots in each area, the non-parametric Mann-Witney test was used. All the variables were submitted to a Shapiro-Wilk test (W test) to test the normality. The diversities of the areas were transformed into effective numbers, based on Hill's first three numbers, $q = 0$ (species richness), $q = 1$ (Shannon's diversity) and $q = 2$ (Simpson's diversity), to compare the diversity profiles (Chao et al. 2014). To verify if there were statistical differences in the Shannon-Weaver diversity indices between the areas, Hutcheson's t-test was used (Zar 1999).

To confirm if a difference exists in the density of the floristic composition between the areas, nonmetric multidimensional scaling (NMDS) was used with the density data of each species per plot of both areas; a Bray-Curtis similarity matrix was generated (Santos et al. 2007). To test if a statistical difference existed between the urban and nonurban environments, an ANOSIM test was conducted using the Vegan package (Warton et al. 2012). All the analyses were made using R Studio version 1.3.1.

To analyze the spatial distribution and spatial dependence of the richness and diversity of the understory species in the fragments, the total number of plants and total number of species were recorded for each sample. The richness (S) and diversity (H') variables were calculated per sample using the vegan package (Oksanen et al. 2020) in the software R (R Core Team 2022). The H' and S values were associated to the coordinates of each sample unit to analyze the geostatistics.

An exploratory descriptive analysis was conducted to observe the behavior of the data. To test the normality hypothesis, Box-Cox transformations were used (Box and Cox 1964). This analysis directly depends on the λ parameter that is the transformation coefficient of the data. In practice, for a data set a confidence interval is obtained for λ that, if it includes the value one, indicates that the transformation of data is not necessary. This transformation has been used in forest studies (Oda-Souza et al. 2010) and discussed in the context of geostatistic modeling (Christensen et al. 2001).

A semivariogram (Matheron 1963) was used to represent the level of dependence between variable values and their geographic locations:

$$\hat{\gamma}(u) = \frac{1}{2N(u)} \sum_{a=1}^{N(u)} (z(x_a) - z(x_a + u))^2$$

where $\hat{\gamma}(u)$ is the semivariance estimated for each distance or distance class u , $N(u)$ is the number of pairs of points separated by u , and $z(x_a)$ and $z(x_a + u)$ are the variable values on point x_a and $x_a + u$, respectively.

To obtain the set of parameters, the Matérn correlation function was adjusted (Diggle and Ribeiro Jr. 2007) with $k = 0.5, 1.0$ and 2.0 , where the first case corresponds to the exponential model.

Selecting the best performing models was done based on the smallest square sum of residues (SQR) and Akaike information criterion (AIC). The ratio dependency spatial (RD%) was calculated as the ratio between the nugget effect (Co) and sill (Co + C), expressed as a percentage. Values above 75% indicate weak spatial dependence, those between 25 and 75% indicate moderate spatial dependence, and those up to 25% indicate strong spatial dependence (Cambardella et al. 1994).

To illustrate the variation in richness and diversity of the vegetation, after adjusting and selecting the spatial modes, ordinary kriging was used (Isaaks and Srivastava 1989). The geostatistical analyses were made using the geoR package (Ribeiro Jr et al. 2020).

Results

In total, 11,246 individuals were collected in the 60 plots sampled, and 158 species were identified that were distributed in the following way: nonurban area (Sítio Aguahy), 5,748 individuals, 100 species, of which 64% are exclusive to this habitat; and urban area (Sítio Santa Eulália), 5,498 individuals, 58 species, of which 37.9% are exclusive to this habitat. In the nonurban area, there were 100 species, 67 genera and 34 families, and in the urban area there were 58 species, 44 genera and 25 families (Table 1).

Table 1

List of understory species in urban and non-urban areas and their respective phytosociological parameters. UR = Urban Forest; NUR = Nonurban Forest; N = Number of Individuals; RD = Relative Density; RF = Relative Frequency; ADo = Absolute Dominance; IV = Importance Value. Tree; Shr = shrub; Lia = liana; Pal = palm tree; Sub = subshrub. AM = Amazon; CA = Caatinga; CE = Cerrado; AF = Atlantic Forest; PA = Pampas; PT = Pantanal.

Species	Families	Habits	Domains	Forests	N	RD	RF	ADo	IV (%)	N	RD	RF	ADo	IV (%)
<i>Abarema cochleata</i> (Willd.) Barneby	Fabaceae	Tree	AM	UR	1	0,02	0,18	0	0,07	-	-	-	-	-
<i>Actinostemon conceptionis</i> (Chodat & Hassl.) Hochr.	Fabaceae	Sub	CE, AF	NUR	-	-	-	-	-	39	0,68	1,09	0,01	0,72
<i>Adenocalymma</i> sp.	Bignoniaceae	Lia	-	NUR	-	-	-	-	-	206	3,59	2,54	0,05	2,83
<i>Agonandra brasiliensis</i> Miers ex Benth. & Hook. F.	Opiliaceae	Tree	AM, CA, CE, AF, PT	UR	32	0,58	1,45	0,02	0,72	-	-	-	-	-
<i>Amasonia arborea</i> Kunth	Lamiaceae	Sub	AM, CE	UR, NUR	3	0,05	0,55	0	0,20	25	0,44	1,21	0	0,61
<i>Anemopaegma parkeri</i> Sprague	Bignoniaceae	Lia	AM, CE	UR, NUR	172	3,13	2,55	0,63	3,57	291	5,07	3,62	0,05	3,59
<i>Anaxagorea</i> sp.	Annonaceae	Tree	-	NUR	-	-	-	-	-	33	0,57	0,85	0,01	0,66
<i>Astrocaryum vulgare</i> Mart.	Arecaceae	Pal	AM, CE	UR, NUR	30	0,55	1,45	0,42	1,79	17	0,3	1,09	0,03	0,85
<i>Attalea speciosa</i> Mart. ex Spreng.	Arecaceae	Pal	AM, CE	UR, NUR	25	0,45	0,91	0,12	0,77	20	0,35	1,69	0,03	1,19
<i>Bauhinia dubia</i> G. Don	Fabaceae	Sub	AM, CE	UR, NUR	99	1,8	3,27	0,51	3,06	86	1,5	2,54	0,03	1,81
<i>Bowdichia virgilioides</i> Kunth	Fabaceae	Shr	AM, CA, CE, AF, PT	NUR	-	-	-	-	-	4	0,07	0,36	0	0,14
<i>Calophyllum brasiliense</i> Cambess.	Calophyllaceae	Tree	AM, CA, CE, AF	NUR	-	-	-	-	-	62	1,08	1,09	0,02	0,95
<i>Calycolpus goetheanus</i> (Mart. ex DC.) O. Berg	Myrtaceae	Tree	AM, CE	UR, NUR	145	2,64	2,18	0,49	2,94	55	0,96	0,85	0,05	1,36
<i>Campomanesia aromatica</i> (Aubl.) Griseb.	Myrtaceae	Tree	AM, CA, AF	UR, NUR	29	0,53	2	0,19	1,37	17	0,3	0,24	0	0,22
<i>Casearia javitensis</i> Kunth	Salicaceae	Shr, Tree	AM, CA, CE, AF	UR, NUR	55	1	2,91	0,16	1,74	1	0,02	0,12	0	0,05
<i>Chiococca nitida</i> Benth.	Rubiaceae	Shr, Sub	AM, AF	NUR	-	-	-	-	-	10	0,17	0,72	0	0,31
<i>Chloroleucon</i> sp.	Fabaceae	Shr, Tree	-	UR	3	0,05	0,36	0,04	0,24	-	-	-	-	-
<i>Cissus erosa</i> Rich	Vitaceae	Shr, Lia	AM, CA, CE, AF, PT	UR	2	0,04	0,36	0	0,13	-	-	-	-	-
<i>Coccoloba latifolia</i> Lam.	Polygonaceae	Shr, Tree	AM, CA, CE, AF	NUR	-	-	-	-	-	1	0,02	0,12	0	0,05
<i>Connarus favosus</i> Planch.	Connaraceae	Shr	AM, CA	UR, NUR	5	0,09	0,36	0,02	0,19	84	1,46	2,66	0,01	1,53
<i>Cordia</i> aff. <i>nodosa</i> Lam.	Boraginaceae	Shr	AM, AF	NUR	-	-	-	-	-	115	2	2,42	0,03	1,98
<i>Cordia myrciifolia</i> (K.Schum.) C. H. Perss. & Delprete	Rubiaceae	Shr	AM, CA, CE, AF	NUR	-	-	-	-	-	148	2,58	1,33	0,03	1,83
<i>Croton cajucara</i> Benth.	Euphorbiaceae	Shr	AM	NUR	-	-	-	-	-	1	0,02	0,12	0	0,06

Species	Families	Habits	Domains	Forests	N	RD	RF	ADo	IV (%)	N	RD	RF	ADo	IV (%)
<i>Cupania diphylla</i> Vahl	Sapindaceae	Tree	AM, CE	UR, NUR	25	0,45	1,27	0	0,58	49	0,85	1,09	0,01	0,77
<i>Cynophalla flexuosa</i> (L.) J.Presl	Capparaceae	Shr	AM, CA, CE, AF, PT	UR	2	0,04	0,36	0	0,13	-	-	-	-	-
<i>Dalbergia</i> cff. <i>cearensis</i> Ducke	Fabaceae	Tree	CA	NUR	-	-	-	-	-	44	0,77	1,33	0,01	0,85
<i>Dipteryx alata</i> Vogel	Fabaceae	Tree	CE	NUR	-	-	-	-	-	62	1,08	2,05	0,05	1,76
<i>Duguetia echinophora</i> R. E. Fr.	Annonaceae	Tree	AM, CE	UR, NUR	172	3,13	1,82	0,13	2,00	39	0,68	0,24	0,01	0,39
<i>Dulacia candida</i> (Poepp.) Kuntze	Olacaceae	Shr, Tree	AM	NUR	-	-	-	-	-	2	0,03	0,24	0	0,11
<i>Dulacia guianensis</i> (Engl.) Kuntze	Olacaceae	Shr, Tree	AM, CE	NUR	-	-	-	-	-	21	0,37	0,6	0,11	2,01
<i>Ephedranthus pisocarpus</i> R. E. Fr.	Annonaceae	Tree	AM, CA	UR, NUR	259	4,71	1,64	0,03	2,21	452	7,87	3,5	0,04	4,38
<i>Erythroxylum passerinum</i> Mart.	Erythroxylaceae	Shr, Tree	AF	NUR	-	-	-	-	-	47	0,82	0,97	0,01	0,75
<i>Erythroxylum</i> sp.	Erythroxylaceae	Shr, Tree	-	NUR	-	-	-	-	-	134	2,33	2,05	0,03	1,88
<i>Eschweilera ovata</i> (Cambess.) Mart. ex Miers	Lecythidaceae	Tree	AM, AF	UR	134	2,44	2,91	0,93	4,29	-	-	-	-	-
<i>Eugenia biflora</i> (L.) DC.	Myrtaceae	Shr, Tree	AM, CA, CE	UR, NUR	274	4,98	4,91	0,44	4,49	64	1,11	1,45	0,01	1,01
<i>Eugenia caducibracteata</i> Mazine	Myrtaceae	Tree	AM	NUR	-	-	-	-	-	68	1,18	1,33	0,18	3,59
<i>Eugenia densiracemosa</i> Mazine & Faria	Myrtaceae	Shr, Tree	AM, CE	NUR	-	-	-	-	-	221	3,85	1,21	0,02	2,04
<i>Eugenia flavescens</i> DC.	Myrtaceae	Shr, Tree	AM, CA, CE, AF	NUR	-	-	-	-	-	49	0,85	1,21	0	0,74
<i>Eugenia protenta</i> McVaugh	Myrtaceae	Tree	AM	UR	42	0,76	2	0,53	2,35	-	-	-	-	-
<i>Eugenia puniceifolia</i> (Kunth) DC.	Myrtaceae	Shr, Sub	AM, CA, CE, AF, PT	UR, NUR	4	0,07	0,55	0,19	0,73	72	1,25	0,85	0,03	1,20
<i>Eugenia stictopetala</i> Mart. ex DC.	Myrtaceae	Shr, Tree	AM, CA, CE, AF	UR, NUR	73	1,33	3,09	0,06	1,63	80	1,39	1,69	0,02	1,40
<i>Faramea bracteata</i> Benth.	Rubiaceae	Shr	AM, CE	NUR	-	-	-	-	-	31	0,54	0,6	0,01	0,55
<i>Faramea nitida</i> Benth.	Rubiaceae	Shr	AM, CA, CE, AF	UR, NUR	17	0,31	1,09	0,05	0,60	549	9,56	3,5	0,33	9,39
<i>Guapira opposita</i> (Vell.) Reitz	Nyctaginaceae	-	-	UR	13	0,24	1,27	0	0,51	-	-	-	-	-
<i>Guapira</i> sp.	Nyctaginaceae	Shr, Tree	AM, CA, CE, AF	NUR	-	-	-	-	-	2	0,03	0,24	0	0,16
<i>Guazuma ulmifolia</i> Lam.	Malvaceae	Tree	AM, CA, CE, AF, PA, PT	NUR	-	-	-	-	-	9	0,16	0,36	0	0,18
<i>Helicteres pentandra</i> L.	Malvaceae	Shr, Tree	AM, CE	NUR	-	-	-	-	-	3	0,05	0,36	0	0,15
<i>Himatanthus articulatus</i> (Vahl) Woodson	Apocynaceae	Tree	AM, CE	NUR	-	-	-	-	-	53	0,92	0,97	0,01	0,80

Species	Families	Habits	Domains	Forests	N	RD	RF	ADo	IV (%)	N	RD	RF	ADo	IV (%)
<i>Himatanthus drasticus</i> (Mart.) Plumel	Apocynaceae	Tree	AM, CA, CE	UR	2	0,04	0,36	0,13	0,49	-	-	-	-	-
<i>Hirtella racemosa</i> Lam.	Chrysobalanaceae	Shr, Tree	AM, CA, CE, AF	UR, NUR	38	0,69	2,18	0,01	0,97	22	0,38	0,72	0,01	0,50
<i>Hymenaea courbaril</i> L.	Fabaceae	Tree	AM, CA, CE, AF, PT	NUR	-	-	-	-	-	13	0,23	0,85	0	0,43
<i>Hymenaea parvifolia</i> Huber	Fabaceae	Tree	AM	UR, NUR	15	0,27	0,91	0	0,41	49	0,85	1,69	0,02	1,08
<i>Hymenopus reticulatus</i> (Prance) Sothers & Prance	Chrysobalanaceae	Tree	AM	NUR	-	-	-	-	-	2	0,03	0,12	0	0,08
Indeterminada 1	-	-	-	UR	5	0,09	0,91	0	0,33	-	-	-	-	-
Indeterminada 2	-	-	-	UR	1	0,02	0,18	0	0,07	-	-	-	-	-
Indeterminada 3	-	-	-	NUR	-	-	-	-	-	1	0,02	0,12	0	0,05
Indeterminada 4	-	-	-	NUR	-	-	-	-	-	8	0,14	0,36	0	0,17
Indeterminada 5	-	-	-	NUR	-	-	-	-	-	8	0,14	0,48	0,01	0,29
Indeterminada 6	-	-	-	NUR	-	-	-	-	-	67	1,17	0,6	0	0,63
Indeterminada 7	-	-	-	NUR	-	-	-	-	-	23	0,4	0,36	0,01	0,34
Indeterminada 8	-	-	-	UR, NUR	3	0,05	0,55	0	0,21	98	1,71	1,69	0,02	1,41
Indeterminada 9	-	-	-	NUR	-	-	-	-	-	2	0,03	0,12	0	0,05
Indeterminada 10	-	-	-	UR, NUR	8	0,15	0,36	0	0,18	7	0,12	0,36	0	0,19
<i>Inga alba</i> (Sw.) Willd.	Fabaceae	Tree	AM, CE	NUR	-	-	-	-	-	9	0,16	0,48	0	0,28
<i>Inga</i> sp.1	Fabaceae	-	-	NUR	-	-	-	-	-	6	0,1	0,24	0	0,13
<i>Inga</i> sp.2	Fabaceae	-	-	NUR	-	-	-	-	-	74	1,29	1,81	0,03	1,44
<i>Justicia</i> sp.	Acanthaceae	-	-	NUR	-	-	-	-	-	1	0,02	0,12	0	0,05
<i>Kielmeyra</i> sp.	Calophyllaceae	-	-	NUR	-	-	-	-	-	21	0,37	0,85	0,01	0,51
<i>Lecythis lurida</i> (Miers) S. A. Mori	Lecythidaceae	Tree	AM, AF	UR, NUR	1	0,02	0,12	0	0,05	1	0,02	0,12	0	0,05
<i>Luehea</i> sp.	Malvaceae	-	-	NUR	-	-	-	-	-	3	0,05	0,24	0	0,12
<i>Maclura tinctoria</i> (L.) D. Don ex Steud.	Moraceae	Shr, Tree	AM, CA, CE, AF, PA, PT	UR	1	0,02	0,18	0	0,07	-	-	-	-	-
<i>Mandevilla hirsuta</i> (A. Rich.) K. Schum.	Apocynaceae	Lia	AM, CA, CE, AF	UR	436	7,93	2	0,09	3,54	-	-	-	-	-
<i>Mangifera indica</i> L.	Anacardiaceae	Tree	-	UR, NUR	13	0,24	0,18	0	0,14	308	5,36	3,02	0,04	3,40
<i>Manilkara bidentata</i> (A.DC.) A.Chev.	Sapotaceae	Shr, Tree	AM, CE	NUR	-	-	-	-	-	65	1,13	1,57	0,02	1,27
<i>Matayba guianensis</i> Aubl.	Sapindaceae	Shr, Tree	AM, CE, AF, PT	UR	46	0,84	2,55	0,14	1,52	-	-	-	-	-
<i>Miconia ciliata</i> (Rich.) DC.	Melastomataceae	-	-	NUR	-	-	-	-	-	2	0,03	0,12	0	0,05
<i>Moquilea tomentosa</i> Benth.	Chrysobalanaceae	Tree	AF	UR, NUR	141	2,56	3,45	1,74	6,68	43	0,75	0,97	0,01	0,75
Morfoespécie 1	Bignoniaceae	-	-	NUR	-	-	-	-	-	2	0,03	0,24	0	0,10
Morfoespécie 2	Bignoniaceae	-	-	NUR	-	-	-	-	-	13	0,23	0,36	0	0,24

Species	Families	Habits	Domains	Forests	N	RD	RF	ADo	IV (%)	N	RD	RF	ADo	IV (%)
Morfoespécie 3	Bignoniaceae	-	-	NUR	-	-	-	-	-	2	0,03	0,12	0	0,06
Morfoespécie 4	Euphorbiaceae	-	-	NUR	-	-	-	-	-	3	0,05	0,12	0	0,06
Morfoespécie 5	Malvaceae	-	-	UR	3	0,05	0,36	0	0,14	-	-	-	-	-
Morfoespécie 6	Moraceae	-	-	UR	10	0,18	0,55	0	0,25	-	-	-	-	-
Morfoespécie 7	Rutaceae	-	-	UR	4	0,07	0,73	0	0,27	-	-	-	-	-
Morfoespécie 8	Polygonaceae	-	-	NUR	-	-	-	-	-	10	0,17	0,24	0	0,15
<i>Mouriri guianensis</i> Aubl.	Melastomataceae	Shr, Tree	AM, CA, CE, AF, PT	NUR	-	-	-	-	-	73	1,27	1,21	0,02	1,13
<i>Myrcia amazonica</i> DC.	Myrtaceae	Shr, Tree	AM, CE, AF	UR, NUR	40	0,73	1,64	0,08	1,01	261	4,54	2,54	0,44	8,93
<i>Myrcia cuprea</i> (O.Berg) Kiaersk.	Myrtaceae	Shr, Tree	AM	UR	97	1,76	3,09	0,31	2,44	-	-	-	-	-
<i>Myrcia guianensis</i> (Aubl.) DC.	Myrtaceae	Shr, Tree, Sub	AM, CA, CE, AF, PT	UR	3	0,05	0,36	0,01	0,17	-	-	-	-	-
<i>Myrcia selloi</i> (Spreng.) N. Silveira	Myrtaceae	Shr, Tree	CE, AF, PA	UR	54	0,98	3,09	0,16	1,79	-	-	-	-	-
<i>Myrcia splendens</i> (Sw.) DC.	Myrtaceae	Tree	AM, CA, CE, AF, PT	UR, NUR	94	1,71	2	0,03	1,32	2	0,03	0,24	0	0,09
<i>Myrcia tomentosa</i> (Aubl.) DC.	Myrtaceae	Shr, Tree	AM, CA, CE, AF	NUR	-	-	-	-	-	57	0,99	0,24	0,01	0,55
<i>Myrciaria floribunda</i> (H. West ex Willd.) O. Berg	Myrtaceae	Tree	AM, CA, CE, AF	NUR	-	-	-	-	-	2	0,03	0,24	0	0,11
<i>Myrciaria tenella</i> (DC.) O. Berg	Myrtaceae	Tree	AM, CA, CE, AF	UR, NUR	46	0,84	2,36	0,31	1,90	67	1,17	1,45	0,02	1,16
<i>Nectandra</i> sp.	Lauraceae	-	-	NUR	-	-	-	-	-	9	0,16	0,72	0	0,34
<i>Ocotea glomerata</i> (Nees) Mez	Lauraceae	Tree	AM, CA, CE, AF	UR, NUR	16	0,29	1,27	0,03	0,59	211	3,67	2,9	0,07	3,19
<i>Ouratea castaneifolia</i> (DC.) Engl.	Ochnaceae	Tree	AM, CA, CE, AF	NUR	-	-	-	-	-	30	0,52	1,09	0	0,59
<i>Ouratea hexasperma</i> (A.St.-Hil.) Baill.	Ochnaceae	Tree	CE	UR, NUR	127	2,31	4,18	0,37	3,15	14	0,24	0,48	0	0,27
<i>Ouratea</i> sp.	Ochnaceae	-	-	UR, NUR	391	7,11	4,36	0,19	4,34	189	3,29	2,54	0,02	2,23
<i>Palicourea colorata</i> (Willd. ex Roem. & Schult.) Delprete & J. H. Kirkbr.	Rubiaceae	Shr	AM, CA, CE, AF	NUR	-	-	-	-	-	19	0,33	0,36	0	0,25
<i>Palicourea hoffmannseggiana</i> (Schult.) Borhidi	Rubiaceae	Shr	AM, CA, CE, AF, PA, PT	NUR	-	-	-	-	-	73	1,27	0,85	0,02	0,97
<i>Palicourea</i> sp.	Rubiaceae	-	-	NUR	-	-	-	-	-	3	0,05	0,24	0	0,10
<i>Paullinia</i> sp.	Sapindaceae	-	-	UR, NUR	12	0,22	1,45	0	0,57	115	2	1,69	0,02	1,46
<i>Pilocarpus microphyllus</i> Stapf ex Wardlew.	Rutaceae	Tree	AM, CA	NUR	-	-	-	-	-	140	2,44	1,81	0,03	1,85
<i>Piper tuberculatum</i> Jacq.	Piperaceae	Shr	AM, CA, CE, AF, PA, PT	NUR	-	-	-	-	-	7	0,12	0,36	0	0,21
<i>Plenotoma orientalis</i> Sandwith	Bignoniaceae	Lia	AM, CE	NUR	-	-	-	-	-	68	1,18	1,57	0,01	1,01

Species	Families	Habits	Domains	Forests	N	RD	RF	ADo	IV (%)	N	RD	RF	ADo	IV (%)
<i>Protium heptaphyllum</i> (Aubl.) Marchand	Burseraceae	Shr, Tree	AM, CA, CE, AF	UR, NUR	1187	21,59	5,45	2,2	14,94	89	1,55	2,54	0,01	1,49
<i>Pseudima frutescens</i> (Aubl.) Radlk	Sapindaceae	Shr, Tree	AM, AF	UR, NUR	288	5,24	2,91	0,2	3,26	21	0,37	0,97	0,01	0,58
<i>Quiina</i> sp.	Quiinaceae	Shr	-	NUR	-	-	-	-	-	28	0,49	0,85	0,03	0,89
<i>Randia armata</i> (Sw.) DC.	Rubiaceae	Shr, Tree	AM, CA, CE, AF	UR, NUR	362	6,58	4,73	1,25	7,14	31	0,54	1,57	0,01	0,81
<i>Rinorea flavescens</i> (Aubl.) Kuntze	Violaceae	Tree	AM	NUR	-	-	-	-	-	9	0,16	0,36	0	0,19
<i>Rourea induta</i> Planch.	Connaraceae	Shr, Tree	CE	UR, NUR	419	7,62	5,45	0,1	4,62	16	0,28	1,33	0	0,55
<i>Serjania salzmanniana</i> Schlttdl.	Sapindaceae	Lia	AM, CE, AF	NUR	-	-	-	-	-	2	0,03	0,24	0	0,09
<i>Simarouba</i> sp.	Simaroubaceae	-	-	NUR	-	-	-	-	-	31	0,54	0,85	0,01	0,62
<i>Swartzia arumateuana</i> (R. S. Cowan) Torke & Mansano	Fabaceae	Tree	AM	NUR	-	-	-	-	-	13	0,23	0,48	0	0,28
<i>Syagrus cocoides</i> Mart.	Arecaceae	Pal	AM, CE	NUR	-	-	-	-	-	8	0,14	0,72	0,04	0,85
<i>Tabebuia</i> sp.	Bignoniaceae	Tree	-	UR, NUR	4	0,07	0,55	0,05	0,33	7	0,12	0,36	0	0,17
<i>Tabernaemontana flavicans</i> Willd. ex Roem. & Schult.	Apocynaceae	Shr	AM, CE, AF	NUR	-	-	-	-	-	10	0,17	0,24	0	0,14
<i>Tocoyena brasiliensis</i> Mart.	Rubiaceae	Shr, Tree	AM, CA, CE, AF	UR	3	0,05	0,36	0	0,14	-	-	-	-	-
<i>Trema</i> sp.	Cannabaceae	Shr, Tree	-	UR	10	0,18	1,45	0,01	0,57	-	-	-	-	-
<i>Vismia guianensis</i> (Aubl.) Choisy	Hypericaceae	Shr, Tree	AM, CA, CE, AF	UR, NUR	2	0,04	0,18	0	0,07	6	0,1	0,24	0	0,12
<i>Xylopia sericea</i> A. St.-Hil.	Annonaceae	Shr, Tree	AM, CE, AF	NUR	-	-	-	-	-	4	0,07	0,12	0	0,07

For the nonurban forest, the families with the highest importance value (IV) were Lauraceae (17%), Myrtaceae (14.8%), Rubiaceae (10.3%), Bignoniaceae (6.25%), and Annonaceae (5%). For the urban forest, the families with the highest IV were Burseraceae (15.8%), Myrtaceae (15.7%), Lecythidaceae (8.5%), Rubiaceae (8.3%), and Chrysobalanaceae (7.9%).

The species with the highest IV in the nonurban forest were *Faramea nitida*, *Myrcia amazonica*, *Ephedranthus pisocarpus*, *Anemopaegma parkeri*, *Eugenia caducibracteata*, *Mangifera indica*, *Ocotea glomerata*, *Adenocalymma* sp., *Ouratea* sp., *Eugenia densiracemosa*, *Dulacia guianensis*, *Cordia* aff. *nodosa*, *Erythroxylum* sp., and *Pilocarpus microphyllus*, representing 51.1% of the IV. The species with the highest IV in the urban forest were *Protium heptaphyllum*, *Randia armata*, *Moquilea tomentosa*, *Rourea induta*, *Eugenia biflora*, *Ouratea* sp., *Eschweilera ovata*, and *Anemopaegma parkeri*. Together, these species accounted for 50% of the importance value, demonstrating that a set of few species dominates the area.

In the nonurban forest, the average height of the individuals sampled was 38 cm. In the urban forest, the average height was 28 cm, and the stratum was less dense. For the hypsometric distribution, the classes with the greatest number of individuals in both areas were the lowest value (2–22 cm and 22–42 cm), concentrating the young individuals of the canopy species (Fig. 2). *Myrciaria tenella* and *Syagrus cocoides* reached the tallest height (2 m) in the nonurban area. The tallest species in the urban area were *Protium heptaphyllum* and *Randia armata*, which both reached 1.9 m.

For the two areas, the diametric distribution curve was unimodal, with the lower diameter classes (0.1–1; 1.1–2; 2.1–3 cm) concentrating most of the individuals, which highlights that few individuals were recorded in the next diameter classes (Fig. 3). In the nonurban forest, the species that had the largest diameters were *Myrcia amazonica* (18.9 cm) and *Eugenia caducibracteata* (8.5 cm). In the urban forest, *Randia armata* (16 cm) had the largest diameter.

Of the species recorded in the nonurban area, there were 38 trees, 15 shrubs, 3 subshrubs, 2 lianas, and 3 palms. For the urban area, there were 30 tree species, 16 shrubs, 2 subshrubs, 3 lianas, and 2 palms. The individuals that were not identified or classified with a growth habit in the field were not included in this count.

The average richness of species in the nonurban area ($M_d = 23.5$) was significantly greater ($p < 0.05$) than that in the urban area ($M_d = 17.5$). In the nonurban area, the richness varied between 11 and 48 species per plot, while in the urban area the richness was 9 to 36 species per plot. The diversity in the nonurban area was significantly greater ($t = -33.731$; $p < 0.05$) than the diversity in the urban area (Fig. 4). The equability of the nonurban area ($J' = 0.827$) showed more heterogeneity than that of the urban area ($J' = 0.741$).

There is a difference in the floristic composition and density of each species in the two areas (urban and nonurban), and there is a consistent formation of two distinct groups: one with the urban area plots, but with a lower degree of aggregation, since there is space between the plots in the center and those near the fragment edge (Fig. 5a); and another group that includes plots in the nonurban area that is more aggregated (Fig. 5b). The stress level was near zero (0.16), indicating reliable spatial ordination of the data.

The number of species (S) varied from 11 to 50 and the Shannon-Wiener diversity index (H') was from 1.71 to 3.27 in the nonurban fragment (NUR), while in the urban fragment (UR) S varied from 9 to 38 and H' from 0.77 to 2.89 (Table 2). The closeness of the average and median values was verified for the S and H' variables in the NUR and UR fragments and all the confidence intervals of the parameter estimates of the Box-Cox transformations included the value one. These results express the symmetry of the distributions. The coefficient of variation changed from 13 to 36%. The lowest measure of dispersion around the average was for H' in the NUR fragment, which was 13.53%. The CV% values for S in the NUR and UR fragments were close to each other, 37.30 and 36.21, respectively.

Table 2
Descriptive statistics of understory richness (S) and diversity (H') in nonurban (NUR) and urban (UR) forest fragments and on Ilha do Maranhão, state of Maranhão, Brazil.

Forest Fragment	Variable	Minimum	Maximum	Average	Median	SD	CV(%)	Box-cox
NUR	S	11,00	50,00	28,63	25,00	10,68	37,30	$-0,75 < \lambda < 1,20$
	H'	1,71	3,27	2,66	2,70	0,36	13,53	$-0,45 < \lambda < 4,27$
UR	S	9,00	38,00	19,00	17,50	6,88	36,21	$-1,06 < \lambda < 1,12$
	H'	0,77	2,89	2,03	2,11	0,46	22,66	$0,87 < \lambda < 3,70$

SD, standard deviation; CV(%), coefficient of variation

The Matérn model with $k = 2.0$ was selected to describe the spatial distribution, since it had the best fit, with the lowest SQR and AIC, according to the semivariographic analysis (Fig. 6) and the adjusted parameters (Table 3). The absence or weak spatial dependence for the variable H' in the UR fragment can be seen in the semivariograms (Fig. 6d).

Table 3
Semivariographic parameters of understory richness and diversity (H') in urban (UR) and nonurban (NUR) forest fragments on Ilha do Maranhão, state of Maranhão, Brazil.

Forest Fragment	Variable	SQR	AIC	Co	C	A	GDE%
NUR	S	133189,04	234,20	95,46	50,71	17,69	65,30
	H'	0,32	31,46	0,07	0,07	4,94	50,00
UR	S	60602,19	207,82	17,11	37,74	10,80	31,20
	H'	1,48	46,40	0,22	0,00	100,00	100,00

SQR, square sum of residues; AIC, Akaike information criterion; Co, nugget effect; C, structured variation; A, range and RD%, ratio dependency spatial

According to the estimated parameters and RD%, the S and H' variables in the NUR and the S variable in the UR had moderate spatial dependencies. The H' variable in the UR had weak spatial dependence, as confirmed by the semivariogram.

The kriging map (Fig. 7) for the NUR fragment shows that the regions with the largest S values are in the lower part of the fragments. For the H' variable, the largest values of diversity occur in the upper and middle part of the area. In the UR fragment, the largest S values are in the center of the area and the lowest H' values are concentrated on the edges of the area; the H' values are homogeneously distributed, justifying the weak spatial dependence.

Discussion

The results reveal that the density and diversity of species decreases with an increase in urbanization. Despite the elevated diversity index for the urban forest fragment, based on the results the understory cannot recover its diversity over time because it has weak spatial dependence. This demonstrates that the understory community is as negatively impacted by urbanization as the canopy.

The differences in the understory diversity can be related to environmental disturbances caused mainly by urbanization, since the species in the understory are more sensitive to changes associated to soil use and this affects those growing to the canopy (Pennington et al. 2021). This difference in diversity can also be related to the size of the study areas, since continuously forested areas have more heterogeneity of habitats and more microhabitats (Lima et al. 2015).

The diversity and equability values for the nonurban forest ecotone were above the range of values recorded in studies of the understory in Amazonia, which had $H' = 3.16$ and $J' = 0.62$ (Oliveira and Amaral 2005) and $H' = 3.09$ and $J' = 0.76$ (Narducci et al. 2020). These elevated diversity values, in addition to

indicating ecological stability of the forest (Bordin et al. 2019), corroborate the characteristics of the nonurban forest, which is a transition area and has more diversity due to the exchange of species (Maracahipes et al. 2015; Franoso et al. 2016).

The lower equability found in the urban area can be influenced by the predominance of species tolerant to conditions resulting from urbanization, increasing the density of these few species in the community (Braga and Jardim 2019). In these areas, where there is a high degree of anthropogenic disturbance, the species tolerant to stress are favored, demonstrating that urbanization can positively or negatively affect different taxa (Ranta and Viljanen 2011).

Therefore, the reduced richness and diversity in the understory of the urban area reflects how the environmental condition can affect transition forests (Morandi et al. 2015), influencing the predominance of species tolerant to environmental changes and increasing the density of these few species in the community (Braga and Jardim 2019).

In the urban forest, the tallest species were the most representative in the understory structure, showing they are well established in the area. This corroborates studies by Mendes et al. (2013) that showed that the individuals were distributed in all height classes. The height distribution in the nonurban forest indicates that the shrub, subshrub, and liana species are adapted to the understory conditions, in which the recruitment of young individuals of canopy trees is continuous (Meira Neto and Martins 2003).

For the diametric distribution, the concentration of individuals with low diameter values indicates that the group of understory species in the present study is represented mostly by young individuals, and canopy trees are naturally regenerating in both areas (Machado 2017). The diametric and hypsometric distribution pattern found indicate that the regeneration process in the plant community is continuous. This confirms the resilient characteristic of transition areas because, despite the differences in the structure of the forests, the understory of the urban area manages to maintain good fruit production and continuous recruitment (Elias et al. 2013).

In both areas, the shrub habit is predominant. Shrubs are characterized as residents of the understory for being in this stratum for their entire life cycle, and their mortality rates and recruitment are essential to maintain the dynamic equilibrium of a mature understory (Porto 2008; Colmanetti et al. 2015).

In both forest fragments, only a few species were highly dense and dominant in the understory, while others were represented by few individuals in the areas (Table 1). In the nonurban forest, the pattern of species with a low density is similar to that found in Amazonian vegetation (Oliveira and Amaral 2005). The dominance of a few species in the urban forest understory can be related to changes in environmental conditions, such as more available light, microclimate changes and heterogenous distribution of soil nutrients, which results in the population growth of plants tolerant to disturbed environments and a decrease in other species (Tabarelli et al. 2012; Santana et al. 2020).

The families with the highest IV in the nonurban forest (Annonaceae, Bignoniaceae, and Lauraceae) and urban forest (Burseraceae, Chrysobalanaceae, Lecythidaceae) are also mentioned in studies conducted in the Amazonian understory (Cond e and Tonini 2013; Carim et al. 2015; Andrade et al. 2017). This could be due to the greater influence of Amazonian vegetation on the Maranh o fragments (Costa and Almeida Jr. 2020).

The species with the highest IV in the nonurban forest (*F. nitida*, *M. amaz nica*, and *E. piscocarpus*) contributed to the shade, recruitment (Krause 2008; Santos and Alves 2012), and maintenance of ecological interactions in the forest, such as attracting larger dispersers, for example, mammals (Gressler et al. 2006). For the urban area, the species with the highest IV (*P. heptaphyllum*, *R. armata*, and *R. induta*) are characteristic of regenerating environments and develop in areas with a lot of light, which aggregates individuals and increases their density (Silva et al. 2012; Paulus 2005; Diniz and Franceschinelli 2014).

Among the differences in the floristic and structural composition of the two areas, the dominance of *P. heptaphyllum* in the understory is notable. Generally, in urban areas the high degree of anthropogenic disturbance can favor pioneer species and species tolerant to impacts. This differs from balanced forests, where shade-tolerant species at a more advanced stage of ecological succession are maintained (Tabarelli et al. 2012).

Both understory areas had high diversity compared to other Amazonian regions. However, the weak spatial dependence in the urban area found by kriging suggests elevated anthropogenic interference, since the distribution of diversity in urban understory, for the most part, does not depend on biotic and abiotic factors found in the environment (Rios et al. 2020).

The edges of urban forests are surrounded by asphalt and buildings that absorb light, increase the temperature and decrease humidity in the forest interior, which impedes the development of mature species and favors the establishment of anthropogenic and ruderal species (Rigueira et al. 2012). Although in the present work the size of the border was delimited, the successional stage, age, and size of the fragment influence the intensity and range of the edge effect, making it difficult to standardize of the border in forest environments (Hamberg et al. 2009).

Therefore, the distribution of diversity in the urban area can be related the edge of the fragment, which favors a higher density of anthropogenic species. This is the case for *Mandevilla hirsuta* that was represented by 396 individuals in the plots near the edge (88% of the total density of this species in the area). This species is frequently found in disturbed environments (Naranjo et al. 2011). On the other hand, *Himatanthus drasticus* only occurred in one plot. Although, this species is very common in other urban fragments in Maranh o (Almeida Jr. et al. 2021) and areas of urban Cerrado in the Northeast Region, where its density increases after environmental disturbances (Moro et al. 2011).

It is worth noting that the low spatial dependence found could recover, which highlights the urgent need for management and restoration projects in the area. The anthropogenic influence in urban fragments reduces plant diversity, mainly along edges, and in extreme cases this leads to the loss of the forest matrix condition due to the discontinuity of the spatial dependence of the species (Oliveira et al. 2020).

It is further suggested that the variation in the slope in the nonurban area (NUR) seems to be responsible for variations in the richness of the understory, since the kriging map shows a concentration of the S variable in plots in flatter areas of the fragment. This indicates an "equilibrated" forest because the spatial

structure of the understory is formed by biotic and abiotic interactions (Cesare and Ferreira 2013). This spatial conformation is also found in different Amazonian Forest matrices and can be attributed to factors such as topography and pluviosity (Zuleta et al. 2020).

It can be concluded that the present study found structural and floristic differences between the urban and nonurban areas. The nonurban area has higher richness and diversity indices, as well as species with the highest IV that are representatives of Amazonian vegetation. The structural patterns indicate the dominance of a few species in the urban area, with hypsometric and diametric distributions typical of regenerating environments. Allied to these data, the kriging showed weak spatial dependence for the richness of the urban understory, reinforcing the urgent need for restoration and conservation actions in the fragment. Finally, due to deforestation and fragmentation of the forests in Maranhão, the forest remnants analyzed have replaced and lost species; despite this, they still represent records of original vegetation, and effective and emergency actions are needed to restore and conserve the richness and diversity in them.

Declarations

Funding: The authors would like to thank the FAPEMA (Fundação de Amparo à Pesquisa e Desenvolvimento Científico do Maranhão). Coordenação de Aperfeiçoamento de Pessoal de Nível Superior - CAPES (finance code 001). Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq, and receipt of Master Studentship grant of first author (grant n° 132505/2020-7).

Competing Interests: The authors have no relevant financial or non-financial interests to disclose.

Author contributions: Catherine Rios Santos, Eduardo Bezerra de Almeida Jr. and Carmen Sílvia Zickel conceived of the research idea; Catherine Rios Santos collected data; Melissa Oda- Souza performed statistical analyses and created figures; Catherine Rios Santos, Eduardo Bezerra de Almeida Jr. and Carmen Sílvia Zickel wrote the paper; all authors discussed results and commented on manuscript.

Availability of data and material: The datasets generated during and/or analysed during the current study are available from the corresponding author on request.

Conflict of interest: The authors declare that they have no conflict of interest.

Ethical approval: Not applicable.

Consent to participate: Not applicable.

Consent for publication: Not applicable.

References

1. Almeida Junior EB, Amorim IFF, Pires CS, Souza HL, Rabelo TO, Santos SM, Amorim GS, Rêgo MMC (2021) Estudo florístico no Parque Estadual do Sítio do Rangedor, um fragmento florestal urbano em São Luís, Maranhão. *Brasil Biodiversidade* 20:133–156
2. Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Koppens climate classification map for Brazil. *Meteorologische Zeitschrift, Alemanha. Meteorol.* 22:711–728
3. Alves MCJL, Lima PB, Lima LF, Zickel CS (2013) Descrição morfológica para identificação das plântulas de nove espécies lenhosas de uma floresta de restinga. *Biota Neotrop* 13:374–383
4. Andrade RT, Pansini S, Sampaio AF, Ribeiro MS, Cabral GS, Manzatto AG (2017) Fitossociologia de uma floresta de terra firme na Amazônia Sul-Occidental, Rondônia, Brasil. *Biota Amazônia.* 7:36–43
5. APG IV (2016) An update of the Angiosperm Phylogeny Group classification for the orders and families of flowering plants: APG IV. *J Linn Soc Bot* 181:1–20
6. Bordin KM, Ferreira LD, Rosina A, Malacarne M, Zanotelli P, Adami SF, Vendruscolo GS (2019) Community structure and tree diversity in a subtropical forest in southern Brazil. *Biota Neotrop* 19:2–11 FapUNIFESP (SciELO). <http://dx.doi.org/10.1590/1676-0611-bn-2018-0606>
7. Box GEP, Cox DR (1964) An Analysis of Transformations. *J Roy Stat Soc* 26(2):211–252
8. Braga EO, Jardim MAG (2019) Florística estrutura e formas de vida do estrato inferior de uma floresta ombrófila densa aluvial, Pará. *Brasil Cienc Florest* 29:1048–1059 Universidad Federal de Santa Maria. <http://dx.doi.org/10.5902/1980509821834>
9. Cambardella CA et al (1994) Field-scale variability of soil properties in Central Iowa soils. *Soil Sci Soc Am J* 58:1501–1511
10. Carim MJV, Guimarães JRS, Tostes LCL, Takiyama LR, Wittmann F (2015) Composition, structure and floristic diversity in dense rain forest in the Eastern Amazon, Amapá. *Brazil Acta Sci Biol Sci.* 37:419. Universidade Estadual de Maringá <http://dx.doi.org/10.4025/actasciobiolsci.v37i4.27536>
11. Chao A et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. *Ecol Monogr* 84:45–67
12. Christensen OF, Diggle PJ, Ribeiro JRPJ (2001) Analysing positive-valued spatial data: the transformed gaussian model. *geoENV – Geostatistics for Environmental Applications.* Ed., Kluwer, Amsterdam, pp 287–298
13. Colmanetti MAA, Shirasuna RT, Barbosa LM (2015) Flora vascular não arbórea de um reflorestamento implantado com espécies nativas. *Hoehnea* 42:725–735
14. Condé TM, Tonini H (2013) Fitossociologia de uma Floresta Ombrófila Densa na Amazônia Setentrional, Roraima, Brasil. *Acta Amazon* 43:247–260

15. Costa LBS (2020) Checklist da flora fanerogâmica e mapeamento das áreas de fragmentos florestais urbanos em São Luís, Maranhão, Rev. Equador (UFPI). 9:26–39 Almeida JR, EB
16. Diggle PJ, Ribeiro JR, PJ (2007) Model Based Geostatistics. Springer, New York
17. Diniz VSS, Franceschinelli EV (2014) Estrutura populacional e brotamento de três espécies nativas do cerrado em diferentes regimes de queimadas. Rev Biol Trop 11:107–115
18. Elias F et al (2013) Resiliência de um cerradão submetido a perturbações intermediárias na transição Cerrado-Amazônia. Biotemas 26:49–61. <https://doi.org/10.5007/2175-7925.2013v26n3p49>
19. Françoço RD, Haidar RF, Machado R (2016) Tree species of South America central savanna: endemism, marginal areas and the relationship with other biomes. Acta Bot Bras 30:78–86. <https://doi.org/10.1590/0102-33062015abb0244>
20. Gomes JS, Silva ACBL, Rodal MJN, Silva HCH (2009) Estrutura do sub-bosque lenhoso em ambientes de borda e interior de dois fragmentos de Floresta Atlântica em Igarassu, Pernambuco. Brasil Rodriguésia 60:293–310
21. Gonçalves EG, Lorenzi H (2011) Morfologia Vegetal: organografia e dicionário ilustrado de morfologia das plantas vasculares, 2 edn. Instituto Plantarum de Estudos da Flora, São Paulo
22. Gressler E, Pizo MA, Morellato LPC (2006) Polinização e dispersão de sementes em Myrtaceae do Brasil. Rev Bras Bot 29:509–530
23. Guerra TNF, Araujo EL, Sampaio EVSB, Ferraz EMN (2017) Urban or rural areas: which types of surrounding land use induce stronger edge effects on the functional traits of tropical forests plants? Appl Veg Sci 20:538–548
24. Huang L et al (2013) Effect of urbanization on the structure and functional traits of remnant subtropical evergreen broad-leaved forests in South China. Environ Monit Assess 185:5003–5018. DOI: 10.1007/s10661-012-2921-5
25. IBGE, Instituto Brasileiro de Geografia e Estatística (2016) Manual técnico da vegetação brasileira. Fundação do Instituto Brasileiro de Geografia e Estatística. 275p
26. IBGE, Instituto Brasileiro de Geografia e Estatística (2021) Banco de informações ambientais. [online] <https://bdiweb.ibge.gov.br/#/home>
27. INMET – Instituto Nacional de Meteorologia (2019) (Acessado em: 08/01/2022). [online] www.inmet.gov.br
28. Isaaks EH, Srivastava RM (1989) An introduction to Applied geostatistics. Oxford University, New York
29. Lima RAF, Rando JG, Barreto KD (2015) Composição e diversidade no Cerrado do leste de Mato Grosso do Sul. Brasil Revista Árvore 39:9–24
30. LV, Hailiang et al. Efeitos da razão perímetro-área da intensidade da urbanização nas características da floresta, padrões da paisagem e suas associações na cidade de Harbin, nordeste da China, 1–55
31. Machado S (2017) Projeção da Estrutura Diamétrica de Grupos Ecológicos em uma Floresta Ombrófila Mista. Floresta e Ambient 24:2–10
32. Maciel EA, Oliveira-Filho AT, Eisenlohr PV (2016) Prioritizing rare tree species of the Cerrado-Amazon ecotone: warnings and insights emerging from a comprehensive transitional zone of south america. Natureza & Conservação 14:74–82. <http://dx.doi.org/10.1016/j.ncon.2016.10.002>
33. Maracahipes SL et al (2015) Diversity, floristic composition, and structure of the woody vegetation of the Cerrado in the Cerrado–Amazon transition zone in Mato Grosso. Brazil Rev Bras Bot 38:877–887
34. Matheron G (1963) Principles of geostatistics. Economic Geol Lanc 58:1246–1266
35. Meira Neto JAA, Martins FR (2003) Estrutura do sub-bosque herbáceo-arbustivo da mata da silvicultura, uma floresta estacional semidecidual no município de Viçosa-MG. Revista Árvore 27:459–471 FapUNIFESP (SciELO). <http://dx.doi.org/10.1590/s0100-67622003000400006>
36. Mendes FS, Jardim FSC, Carvalho JOP, Souza DV, Araujo CB, Oliveira MG, Leal ES (2013) Dinâmica da estrutura da vegetação do sub-bosque sob influência da exploração em uma floresta de terra firme no município de Moju – PA. Cienc Florest 23:377–389
37. Morandi OS et al (2015) Vegetation Succession in the Cerrado–Amazonian Forest Transition Zone Of Mato Grosso State, Brazil. Edinb J Bot 73:83–93. <http://dx.doi.org/10.1017/s096042861500027x>
38. Narducci T, Silva Y, Gazel JA, Brienza Junior S (2020) Regeneração natural do sub-bosque em plantios de Taxi-branco (*Tachigali vulgaris* L.F. Gomes da Silva & H.C. Lima) sob diferentes espaçamentos na Amazônia Brasileira. Biota Amazônia 10:16–21
39. Oksanen J et al (2020) vegan: Community Ecology Package. R package version 2.5-7. <https://CRAN.R-project.org/package=vegan>. Accessed 26 June 2021
40. Oliveira AN, Amaral LL (2005) Aspectos florísticos, fitossociológicos e ecológicos de um sub-bosque de terra firme na Amazônia Central. Acta Amazon 35:1–16
41. Oliveira RG, Pelissari A, Cysneiros V, Machado S (2021) Dependência e padrões espaciais da diversidade arbórea e grupos sucessionais em um remanescente urbano de Floresta Ombrófila Mista. Adv Forestry Sci 7(4):1223–1230
42. Paulus RI (2005) Caracterização morfológica e métodos para superação de dormência de sementes de *Randia armata*. De Candolle SW.). Universidade Federal de Pelotas, 37 edn. Mestrado) - Curso de Agronomia, Dissertação
43. Pennington DN, Hansel JR, Gorchov DL (2021) Urbanização e comunidades lenhosas de mata ciliar: Diversidade, composição e estrutura em uma paisagem metropolitana, 143: 1–28
44. Pinheiro MHO, Monteiro R (2008) Florística de uma Floresta Estacional Semidecidual, localizada em ecótono savânico-florestal, no município de Bauru, SP, Brasil. Acta Bot Bras 22:1085–1094
45. Porto ML (2008) *Comunidades Vegetais e Fitossociologia*: fundamentos para avaliação e manejos de ecossistemas. UFRGS. p240
46. Ranta P (2021) Plantas vasculares ao longo de um gradiente urbano-rural na cidade, p. 1–40

47. Ranta P, Viljanen V (2011) Plantas vasculares ao longo de um gradiente urbano-rural na cidade de Tampere, Finlândia. *Urban Ecosyst* 14:361–376. <https://doi.org/10.1007/s11252-011-0164-9>
48. Ribeiro JELS et al (1999) Flora da Reserva Ducke. INPA, Manaus, p 816
49. Ribeiro Júnior PJ, Diggle PJ, Schlather M, Bivand R, Ripley B (2020) *geoR: Analysis of Geostatistical Data*. R package version 1.8-1. <https://CRAN.R-project.org/package=geoR>. Accessed 02 May 2021
50. Rigueira DMG et al (2012) Influência da distância da borda e do adensamento foliar sobre a abundância de plantas pioneiras em um fragmento de floresta tropical submontana na Estação Ecológica de Wenceslau Guimarães (Bahia, Brasil). *Acta Bot Bras* 26:197–202
51. Santana JP, Rocha PA, Silva Oliveira EV, Prata APN, Ribeiro AS (2020) Phytosociology of the shrub-arboreal stratum of the ibura national forest, northeastern Brazil: Are 35 years sufficient to promote the regeneration of a forest fragment? *Neotrop. Biol Conserv* 15:89–106. <https://doi.org/10.3897/neotropical.15.e49114>
52. Santos CR (2022) Diversidade e estrutura do sub-bosque de florestas ecotonais urbanas e não urbanas no Maranhão. Universidade Federal Rural de Pernambuco, Recife, p 63
53. Santos LR, Ferreira JL, Silva C (2018) Florística e fitossociologia de um Sub-bosque Urbano em Rio Branco-AC, Brasil. *Biota Amazônia* 8:28–33
54. Santos MMA, Calvacanti DV, Silva JMC, Tabarelli M (2007) Biogeographical relationships among tropical forests in north-eastern Brazil. *J Biogeogr* 34:437–446
55. Santos SO, Alves M (2012) Flora da Usina São José, Igarassu, Pernambuco: Lauraceae. *Rodriguésia*.63:689–703
56. Silva ECG, Santos CR, Arouche MMB, Almeida Junior EB (2022) Florística em um fragmento urbano (Unidade de Conservação), Sítio Santa Eulália, São Luís, Maranhão. *Heringeriana* 16. Doi:10.17648/heringeriana.v16i1.917976
57. Silva Junior WR, Ferreira AWC, Ilkiu-Borges AL, Fernandes RS (2020) Ferns and lycophytes of remnants in Amazônia Maranhense, Brazil. *Biota Neotrop* 20:1–14
58. Silva PSD, Leal IR, Wirth R, Tabarelli M (2012) Spatial Distribution and Fruiting Phenology of *Protium heptaphyllum* (Burseraceae) Determine the Design of the Underground Foraging System of *Atta sexdens* L. (Hymenoptera: formicidae *Neotrop. Entomol* 41:257–262. <http://dx.doi.org/10.1007/s13744-012-0052-x>
59. Silva-Junior V, Souza DG, Queiroz RT, Souza LGR, Ribeiro SEM, Santos BA (2018) Landscape urbanization threatens plant phylogenetic diversity in the Brazilian Atlantic Forest. *Urban Ecosyst* 21:625–634. DOI: <http://dx.doi.org/10.1007/s11252-018-0745-y>
60. Sonnier G, Johnson SE, Waller DM (2020) Fragmentation reduces the importance of niche-based factors relative to dispersal traits in structuring temperate forest understories. *J Veg Sci* 31:75–83. <https://doi.org/10.1111/jvs.12824>
61. Sousa PR (2018) Análise de áreas degradadas por processos erosivos no baixo curso da bacia hidrográfica do Rio Anil, Ilha do Maranhão. São Luís: Universidade Estadual do Maranhão, 161p, Dissertação. Mestrado) - Curso de Geografia
62. Tabarelli M, Peres CA, Melo FPL (2012) The ‘few winners and many losers’ paradigm revisited: emerging prospects for tropical forest biodiversity. *Biodivers Conserv* 155:136–140
63. Warton DI, Wright TW, Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. *Methods in Ecology and Evolution* 3:89–101
64. Zar JH (1999) *Biostatistical analysis*, 4th edn. Prentice Hall, Upper Saddle River
65. Zuleta D, Russo SE, Barona A et al (2020) Importance of topography for tree species habitat distributions in a terra firme forest in the Colombian Amazon. *Plant Soil* 450:133–149. <https://doi.org/10.1007/s11104-018-3878-0>

Figures

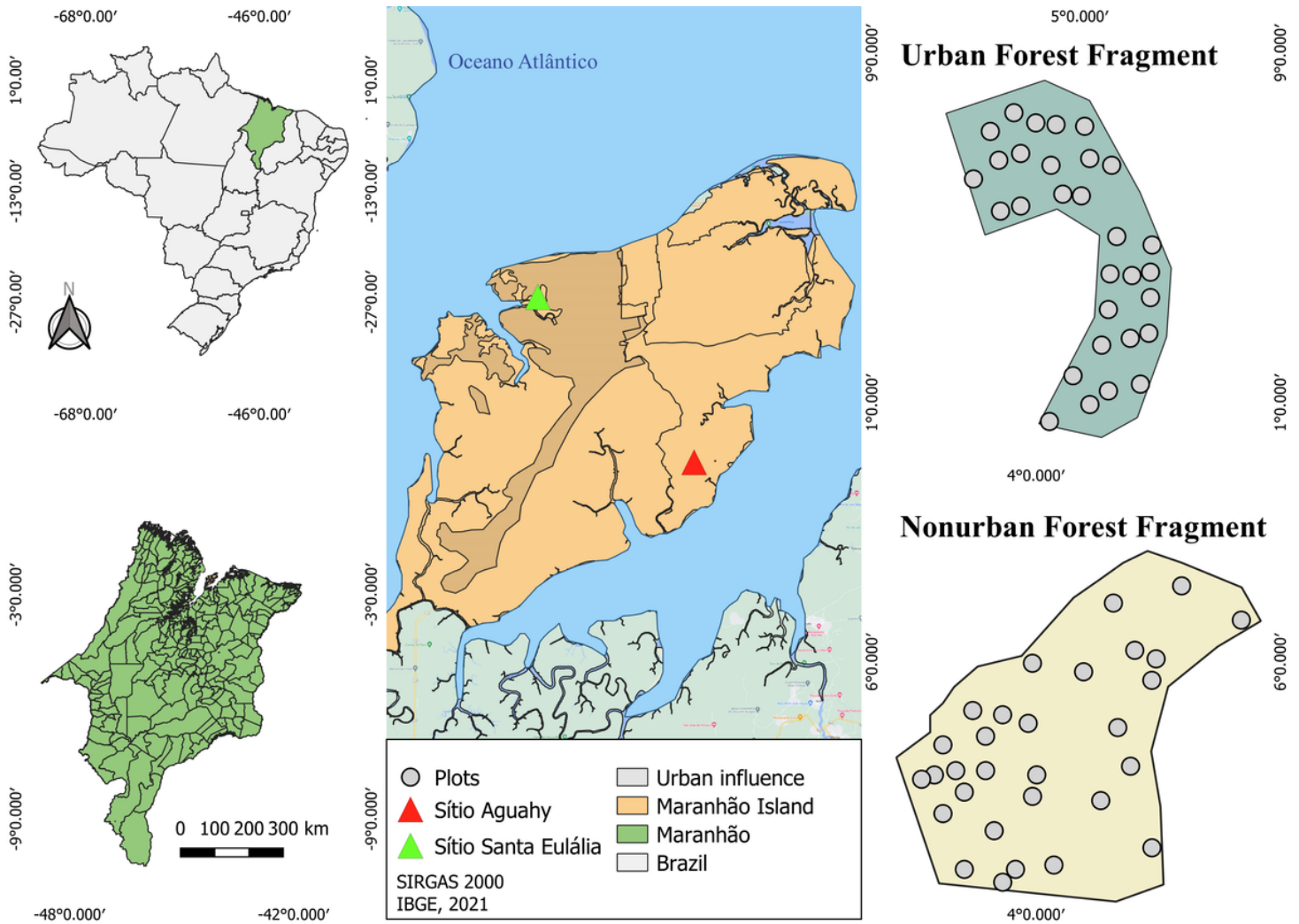


Figure 1
 Plots used for phytosociological sampling in urban and non-urban forest fragments on Maranhão Island, Maranhão, Brazil. In the box on the left above is the map of Brazil and below is the map of Maranhão. In the highlighted center is the Map of the Island of Maranhão with the urban area (green triangle) and nonurban area (red triangle). The box on the right shows the layout of the plots in the urban (above) and nonurban (below) fragments. Figure created in QGIS 3.22

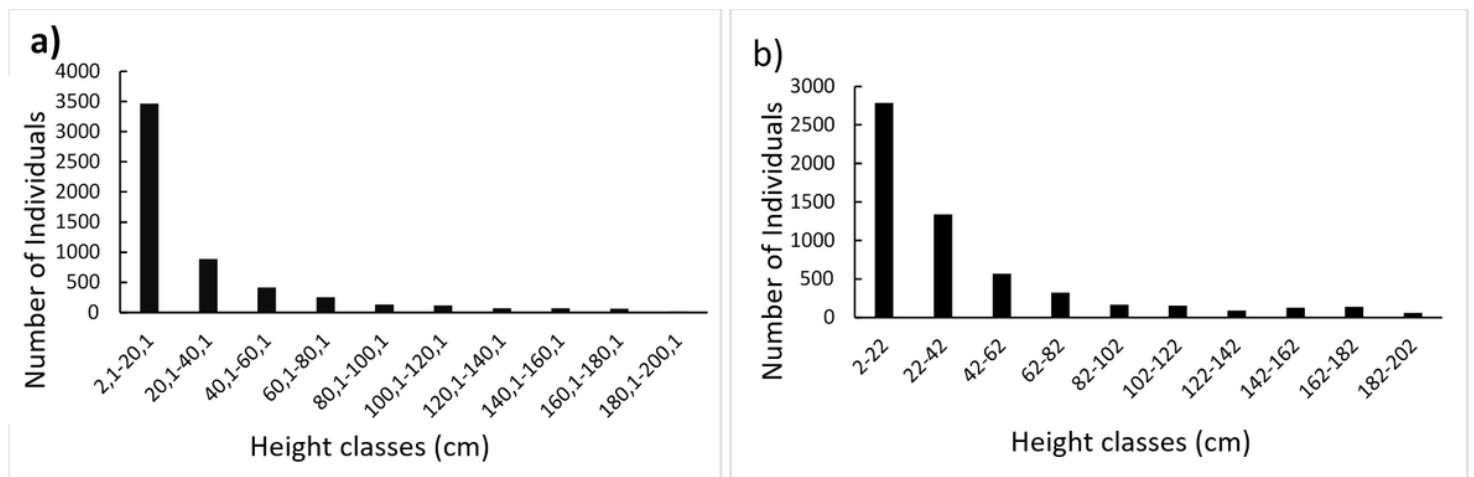


Figure 2
 Distribution of individuals by height classes of the species sampled in each area: a) urban area, Sítio Santa Eulália, São Luís, MA; b) nonurban area, Sítio Aguahy, São José de Ribamar, MA. Figure created in Excel 2016

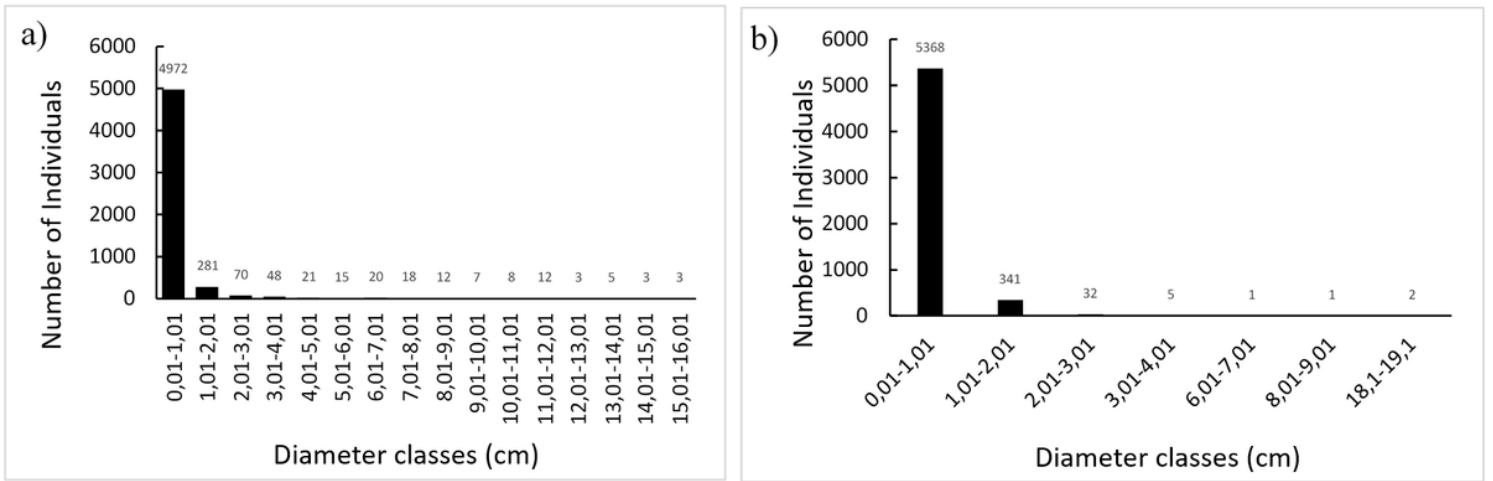


Figure 3
 Distribution of individuals by diameter classes of the species sampled in each area: a) urban area, Sítio Santa Eulália, São Luís, MA; b) nonurban area, Sítio Aguahy, São José de Ribamar, MA. Figure created in Excel 2016

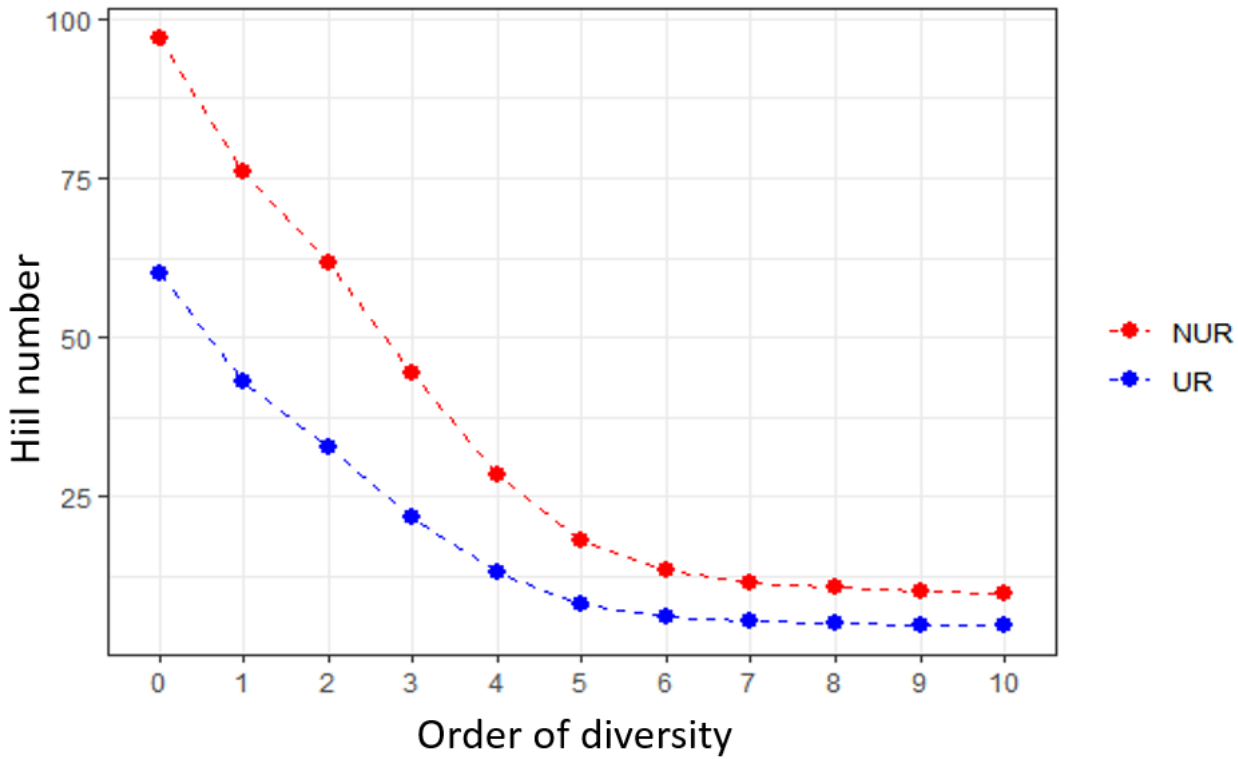


Figure 4
 Diversity profiles of urban and nonurban areas, showing the greatest diversity found in the non-urban environment, on Ilha do Maranhão, state of Maranhão, Brazil. Figure created in software R

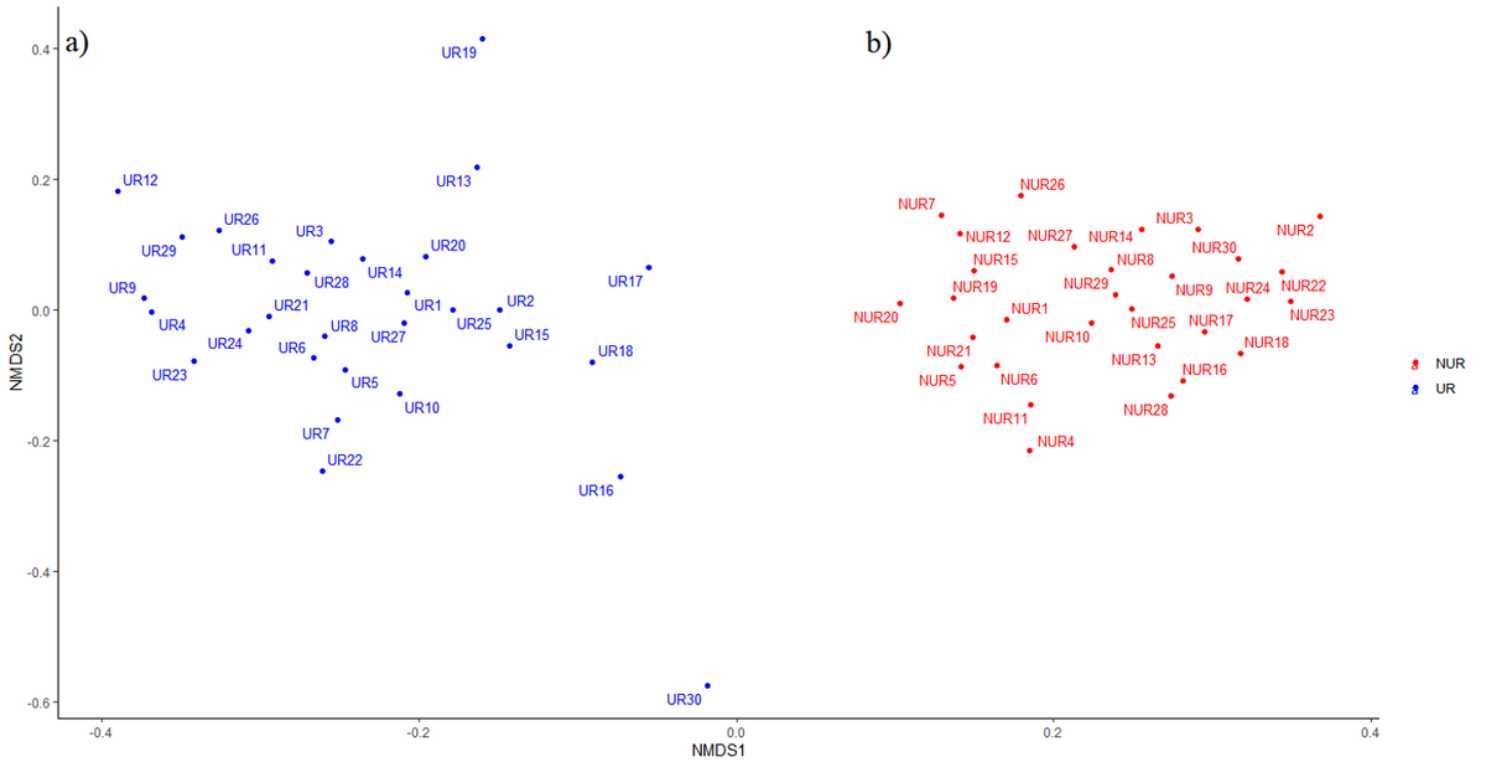


Figure 5
 NMDS showing the difference in floristic composition and density of each species occurring in urban (5a) and nonurban (5b) areas. Figure created in software R

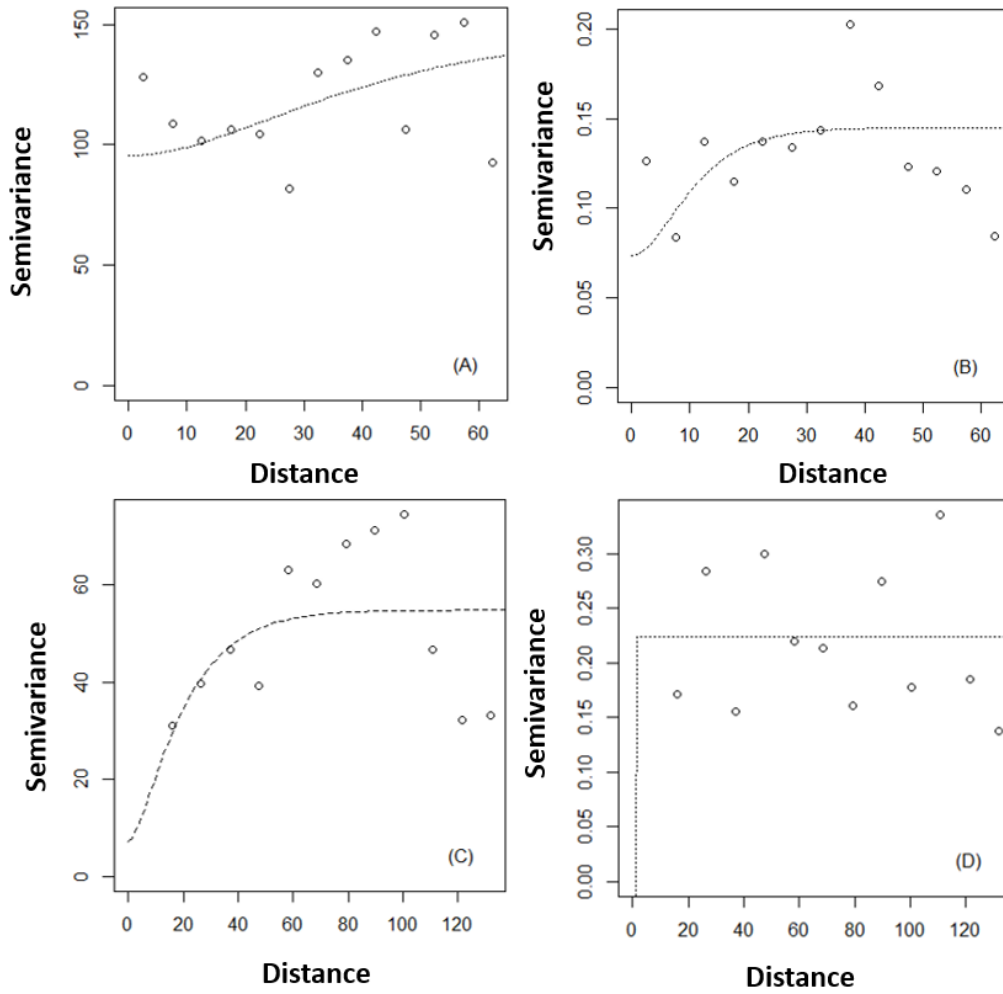


Figure 6
 Semivariogram: A = richness (S), B = diversity (H') of the understory in a nonurban fragment (NUR) and C = richness (S), D = diversity (H') of the understory in urban fragment (UR) on Ilha do Maranhão, state of Maranhão, Brazil. Figure created in software R

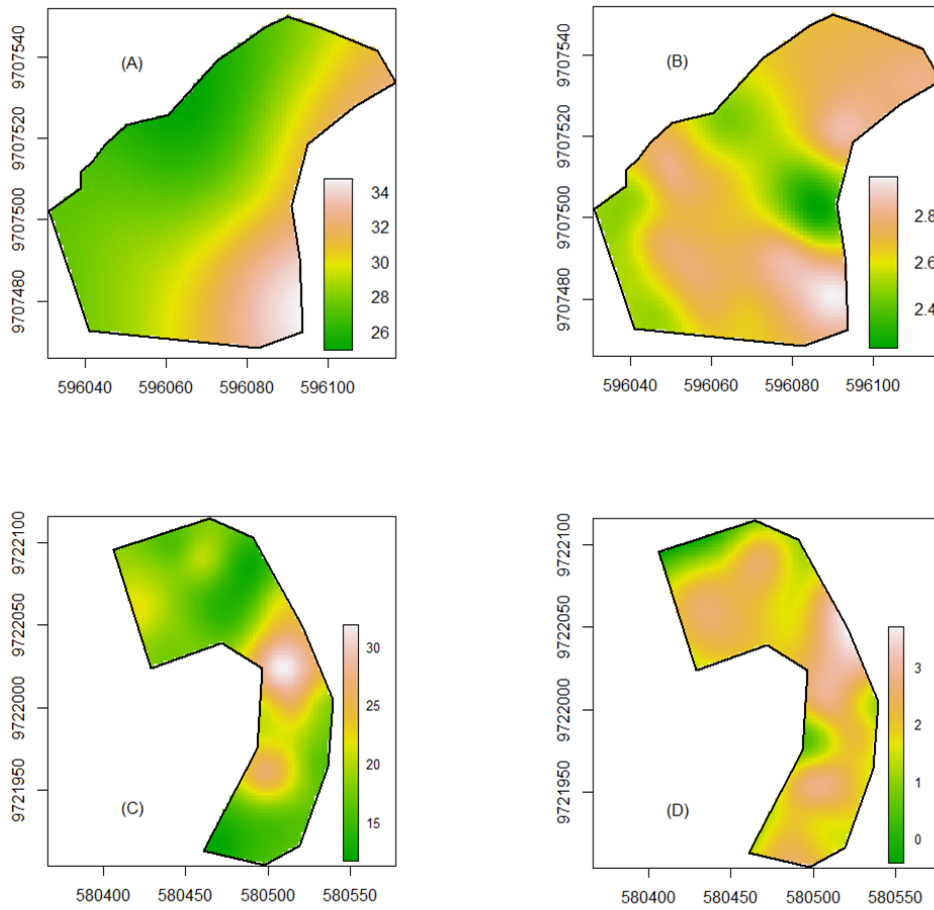


Figure 7
 Kriging maps: (A) richness (S), (B) diversity (H') of the understory in the nonurban patch (NUR) and (C) richness (S), (D) diversity (H') of the understory in an urban fragment (UR) on Ilha do Maranhão. Figure created in software R