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Spatial variation of seed rain in deciduous tropical forest

Variação espacial da chuva de sementes em floresta tropical decídua

Variación espacial de la lluvia de semillas en bosques tropicales caducifolios

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Abstract

Seed rain is an ecological process and its functional attributes are essential for maintaining the dynamics of natural regeneration. The objective of this research was to evaluate the spatial variation of the seed rain in a toposequence of a Seasonal Deciduous Forest defined by three elevations: (Base 512 m; Slope: 534 m and Top: 559 m). 15 collectors of 1 m² were installed at each elevation level. Data were collected monthly from September / 2017 to February / 2019. The seeds were classified according to the dispersion syndrome, habit and size. Non-Metric Multidimensional Scaling (NMDS) was used to verify the variation in species composition and distribution. We identified 20,217 propagules, belonging to 65 species and 30 families, in addition to 4 morphospecies, which represents 449 seeds / m². The families with the highest species richness were Fabaceae, Sapindaceae and Euphorbiaceae. Of the 65 species sampled, 71% were arboreal. Zoochoric species predominated (78%) and very small seeds corresponded to 53% of the sample. We demonstrate that, on a small spatial scale, the relief represents an important source of heterogeneity in the vegetation component, since the topographic gradient influenced the composition and distribution of the functional attributes of the seed rain.

Keywords: Altimetric dimension; Dispersion syndrome; Functional attributes; Heterogeneity; Topographic gradient.

Resumo

A chuva de sementes é um processo ecológico e seus atributos funcionais são essenciais para a manutenção da dinâmica de regeneração natural. O objetivo desta pesquisa foi avaliar a variação espacial da chuva de sementes em uma toposseqüência de uma Floresta Estacional Decidual definida por três cotas altitudinais: (Base 512 m; Declive: 534 m e Topo: 559 m). Foram instalados 15 coletores de 1 m² em cada nível de elevação. Os dados foram coletados mensalmente de setembro / 2017 a fevereiro / 2019. As sementes foram classificadas de acordo com a síndrome de dispersão, hábito e tamanho. Escalonamento Multidimensional Não Métrico (NMDS) foi utilizado para verificar a variação na composição e distribuição das espécies. Identificamos 20.217 propágulos, pertencentes a 65 espécies e 30 famílias, além de 4 morfoespecies, o que representa 449 sementes / m². As famílias com maior riqueza de espécies foram Fabaceae, Sapindaceae e Euphorbiaceae. Das 65 espécies amostradas, 71% eram arbóreas. Espécies zoocóricas predominaram (78%) e sementes muito pequenas corresponderam a 53% da amostra. Demonstramos que, em pequena escala espacial, o relevo representa importante fonte de heterogeneidade do componente vegetacional, uma vez que o gradiente topográfico influenciou na composição e distribuição dos atributos funcionais da chuva de sementes.

Palavras-chave: Dimensões altimétricas; Síndrome de dispersão; Atributos funcionais; Heterogeneidade; Gradiente topográfico.

Resumen

La lluvia de semillas es un proceso ecológico y sus atributos funcionales son fundamentales para mantener la dinámica de la regeneración natural. El objetivo de esta investigación fue evaluar la variación espacial de la lluvia de semillas en una secuencia superior de un Bosque Deciduo Estacional definido por tres elevaciones: (Base 512 m; Desnivel: 534 my Top: 559 m). Se instalaron 15 colectores de 1 m² en cada nivel de elevación. Los datos se recolectaron mensualmente desde septiembre / 2017 hasta febrero / 2019. Las semillas se clasificaron según el síndrome de dispersión, hábito y tamaño. Se utilizó la escala multidimensional no métrica (NMDS) para verificar la variación en la composición y distribución de las especies.

Se identificaron 20,217 propágulos, pertenecientes a 65 especies y 30 familias, además de 4 morfoespecies, lo que representa 449 semillas / m². Las familias con mayor riqueza de especies fueron Fabaceae, Sapindaceae y Euphorbiaceae. De las 65 especies muestreadas, el 71% eran arbóreas. Predominaron las especies zoochóricas (78%) y las semillas muy pequeñas correspondieron al 53% de la muestra. Demostramos que, a pequeña escala espacial, el relieve representa una fuente importante de heterogeneidad del componente vegetal, ya que el gradiente topográfico influyó en la composición y distribución de los atributos funcionales de la lluvia de semillas.

Palabras clave: Dimensiones altimétricas; Síndrome de dispersión; Atributos funcionales; Heterogeneidad; Gradiente topográfico.

1. Introduction

Forests cover 31 percent of the global land area but are not equally distributed around the globe. (FAO & UNEP, 2020). The most representative phytophysiognomies are the Coniferous Forests, Temperate Forests, Evergreen Forest, Deciduous Forests, Tropical and Subtropical Forests (Reich & Frelich, 2002). Deciduous Tropical Forests, also known as Dry Forests and Seasonal Deciduous Forests, (hereafter called SDFs), occur in ice-free areas, where the mean annual temperature is 17 °C, and the mean annual precipitation is less than 1600 mm, with less than 100 mm of rainfall over five months. The SDFs are usually a transition zone between semi-desert regions and/or savannas with humid forests (Murphy & Lugo, 1986). Leaf loss in these forests can exceed 50% of the vegetation cover, which may rise up to 100% of trees and shrubs defoliation during the drought (IBGE, 2012; Pereira et al., 2011).

In the Americas, the SDFs occurs in a wide area that extends from the Caribbean to the eastern part of the Andes, with an extension of approximately 520 thousand km², distributed between North and Central America (39%), South America (52 %) and Caribbean islands (9%). Mexico has the largest amount of SDFs (38%), followed by Bolivia (25%), Brazil (17%), Colombia (6.5%), and Venezuela (6.2%) respectively (Murphy & Lugo, 1986; Portillo -Quintero & Sánchez-Azofeifa, 2010).

In Brazil, the SDFs are disconnected, mainly in the central and northeastern regions (Salis et al., 2004; Sevilha et al., 2004), with the largest areas located in the so-called “Arco do Pleistoceno”, an extensive area of forests that range from the Caatinga, in the northeast of Brazil, to the southwest through the Cerrado and reach the dry plains of Bolivia and Paraguay, in the Chaco (Oliveira-Filho et al., 2006). In the South, it occurs between the Mixed Rainforest (Araucaria Forest) and the Campos Sulinos (Pampas), in an area of subtropical climate (IBGE, 2012). It is estimated that the SDFs occupies 4% to 6% of the Brazilian territory (Espírito-Santo et al., 2008). The Bodoquena plateau region, in Mato Grosso do Sul is one of the last and largest remnants of this phytophysiognomy in Brazil that is still relatively well-preserved (Pott & Pott, 2003; Salzo & Matos, 2013). Mato Grosso do Sul also has SDFs in some stretches of floodplains by the Paraguay River, in its alluvial formation (IBGE, 2012).

The SDFs are conditioned to regions with climatic seasonality (Pennington et al., 2006), occurring as forest disjunctions among other forest and/or savanna types, with arboreal strata formed by predominantly deciduous species (Veloso et al., 1991). They are called Dry Forest or Limestone Forest, in reference to the local climatic conditions or lithology. The variations found in the structure of dry tropical forest fragments can be attributed to the characteristics of the substrate, position, landform, location in relation to other savannahs, fire history, and land use. The influence of environmental factors, such as altitude, topography and soil types, on the composition and dynamics of forests is well known for tropical rainforests (Charles-Dominique, 1995; Franklin et al., 2012; Homeier et al., 2010; Xia et al., 2016). However, there is still a lack of understanding on the association of the Seasonal Deciduous Forests structure and dynamics with some abiotic components, such as topography for instance (Arruda et al., 2013). Studies on the SDFs in Brazil focus mainly on structural aspects of the vegetation, which include several quantitative inventories and physiognomic-floristic descriptions (Felfili et al., 2007; Ivanauskas & Rodrigues, 2000; Nascimento et al., 2004; Pedralli, 1997; Silva & Scariot, 2003; Scariot et al., 2005).

Seed rain is an important tool that allows information about species composition, availability and seed diversity (Piña-Rodrigues & Aoki, 2014). Since dispersion is characterized as a dynamic and fundamental transport for the reproduction of plant species, as it provides a favorable location for seed germination, away from the mother plant (Howe, 1993; Gomes, 2018). Seed production and dispersion are important functional attriutes for the maintenance of plant populations, influencing the spatial distribution of species and the composition of the plant community, in addition to affecting gene flow within and between populations and enabling the colonization of new sites and habitat restoration (Bacles et al., 2006; Howe & Smallwood, 1982; Kroiss & Hillers-Lambers, 2015; Mateo et al., 2016; McConkey et al., 2012; Merritt et al., 2010; Reid et al., 2015; Vellend, 2010).

The propagule size influences the dispersion and establishment of plants and can become especially important in the face of climate change, as current habitats begin to change (Walck et al., 2011; Westoby et al., 1992). There is evidence that factors such as climate and soil pH can influence seed size (Tautenhahn et al., 2008), in addition to solar radiation (Foster & Janson, 1985; Frenne et al., 2011).

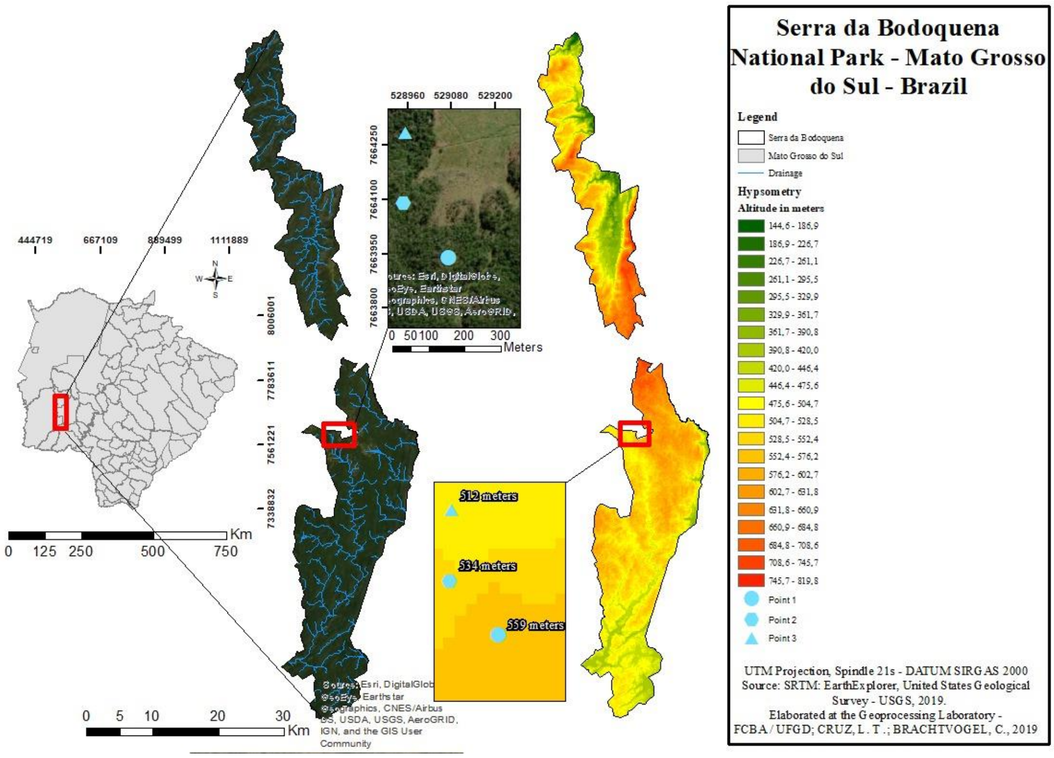
The goal of this research was to evaluate the spatial variation of the seed rain in a toposequence of a SDF, to answer the following questions: is there variation in the seed rain in relation to the position occupied in this toposequence? What environmental factors influence this variation, if any? Are the dispersion syndromes and the propagules size related to the patterns detected?

2. Methods

2.1 Study area

The study was carried out in Serra da Bodoquena National Park under the authorization number 56258-3 at the Chico Mendes Institute for Biodiversity Conservation (ICMBIO). The park is a protected area created in 2000, which covers parts of the municipalities of Bonito, Bodoquena, Jardim and Porto Murtinho, in Mato Grosso do Sul (21°08'02”; 20°38'26” S; 56°48'31”; 56°44'28” O) and has an area of over 77.000 hectares and altitudes among 450m and 800 m (ICMBIO, 2013) (Figure 1).

Figure 1. Location of the study area, Serra da Bodoquena National Park, MS.

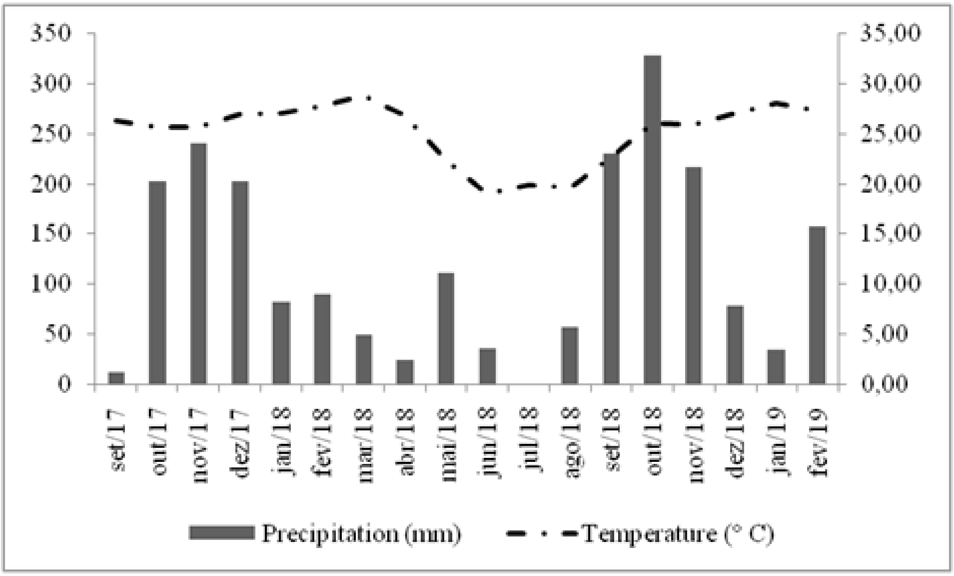


Sourse: Research authors (2019)

The area is basically composed of limestone rocks from the Bocaina Formation, Grupo Corumbá, which favors the formation of different types of cavities, such as caves, sinks and resurgences (Sallun-Filho & Karmann, 2007). The climate is humid tropical with dry winter (Aw), according to the Köppen classification, with hot and rainy season between October and April and dry season between May and September, with annual precipitation between 800 and 1800 mm, an annual average of 1400 mm, and average annual temperature of 22 ºC, with a predominance of the Polar Atlantic Air Mass over the Continental Tropical Air Mass (IBGE, 2005; Mariani, 2001; Farias de Souza et al., 2004).

During the research period, rainfall ranged from 0.2 mm in July 2018 to 329 mm in October 2018, while the minimum temperature was 19°C in June 2018 and the maximum was 28.8 °C in March 2018 (data from the National Meteorological Institute - INMET/Jardim-MS) (Figure 2). The predominant vegetation is Seasonal Semideciduous Forest and Seasonal Deciduous Forest. The savanna fragments occupy flat areas, while forest fragments occupy rocky outcrops and margins of watercourses (ICMBIO, 2013).

Figure 2. Meteorological data (precipitation and temperature) between September 2017 and February 2019.



Source: Inmet / Semagro / Agraer / Cemtec-MS.

2.2 Experimental design

We established three sample areas along a toposequence, in the Seasonal Deciduous Forest, at the base of the toposequence (512 m), at the intermediate portion (slope 534 m) and at the top (559 m), each with different characteristics in terms of soil depth, litter thickness and moisture. In each area, 15 collectors with 1 m² each were randomly installed, made out of fine mesh screen, smaller than 1 mm, suspended one meter from the ground the collectors were installed in the beginning of August 2017, with the collections carried out every 30 days and completed in February 2019, and the collected material was properly packed in plastic bags and taken for drying and sorting at the Environmental Restoration Laboratory of the Federal University of Grande Dourados. Fruits and seeds were separated from the rest of the material, dried in an oven, or placed in 70% alcohol. Seeds were identified by specialists, specialized literature, and/or comparison with the material available in the herbarium collection of the Federal University of Grande Dourados. The scientific names were obtained in the Flora do Brasil database (Flora do Brasil, 2020). The identified species and/or morphospecies were classified according to life form (Whittaker, 1975) and dispersion syndrome (Van Der Pijl, 1982), being further categorized into five size classes according to Tabarelli & Peres (2002) and Melo et al., (2006) as it follows: 1: very small (<1 to 3 mm) 2:

small (3.1 to 6 mm); 3: medium (6.1 to 15 mm); 4: large (15.1 to 30 mm) and 5: very large (> 30 mm). Seed density was estimated according to Ellenberg & Mueller-Dombois (1974).

2.3 Statistical analysis

The sample ordering was obtained by the Non-Metric Multidimensional Scaling (NMDS), based on the Bray-Curtis dissimilarity matrix using the Vegan package (Oksanen et al., 2018) of the statistical software R, version 3.5.1 (R Core Team, 2018). From species relative abundance, dispersion syndrome, and seed size we obtained the variation in species composition across environmental gradients. We used the Multivariate Analysis of Variance - MANOVA, according to Friedrich et al., (2016).

3. Results

65 species were sampled over 18 months, belonging to 30 families, in addition to four morphospecies. The most representative families were Fabaceae, Euphorbiaceae and Sapindaceae, while the species with the highest number of seeds were Myrsine umbellata (6.489 seeds), Terminalia mameluco (2.381 seeds), Erythroxylum sp. (1.884 seeds) and Cybianthus detergens (1.648 seeds), which represents 38% of the total We registered 20.217 seeds (449 seeds / m²), with 13.820 seeds at the base (68%), 3.898 on the slope (19%) and 2.499 at the top (13%) (Table 1).

Table 1. List of the seed rain species in the three altimetric levels of the toposequence (base, slope and top), located in the Serra da Bodoquena MS National Park, 2017 / 2019.

Family	Species	Habits	S.D	Nº propagules			Size
				Base	Slope	Top	
Anacardiaceae	*Myracrodruon urundeuva* Allemão	Tre	Ane			138	VS
Apocynaceae	*Forsteronia pubescens* A.DC.	Lia	Ane	43	14		A
Asteraceae	*Lessingianthus scabrifoliatus* (Hieron.) H.Rob.	Bus	Ane			10	VS
Bignoneaceae	*Callichlamys latifolia* (Rich.) K.Schum.	Lia	Ane	1			L
	Fridericia florida (DC.) L.G.Lohmann	Lia	Ane		5		L
	Handroanthus heptaphyllus. (Vell.) Mattos.	Tre	Ane	99	96	24	L
	Tanaecium neobrasiliense L.G.Lohmann	Lia	Ane			6	A
Cannabaceae	*Celtis iguanaea* (Jacq.) Sarg.	Tre	Zoo	40	53	10	S
Celastraceae	*Hippocratea volubilis* L.	Her	Ane	14	3		VL

Combretaceae	*Terminalia mameluco*. Pickel.	Tre	Ane	2296	51	34	VL
Dioscoreaceae	*Dioscorea multiflora* Mart. ex Griseb.	Lia	Ane	13	3		L
Erythroxylaceae	*Erythroxylum* sp.	Tre	Zoo		1882	2	S
Euphorbiaceae	*Adelia membranifolia* (Müll.Arg.) Chodat & Hassl.	Tre	Aut		1	11	A
	Croton floribundus Spreng.	Tre	Zoo	20	2	1	S
	Euphorbiaceae 1.				1		VS
	Manihot sp.	Bus	Zoo		4		A
	Sebastiania brasiliensis Spreng.	Tre	Zoo	7	6	32	S
	Sapium glandulosum. (L.) Morong.	Tre	Zoo		10		S
Fabaceae	*Anadenanthera colubrina* (Vell.) Brenan	Tre	Ane	5	7	5	L
	Guibourtia hymenifolia (Moric.) J. Leonard	Tre	Zoo	2	6	4	A
	Inga sp.	Tre	Zoo	93			A
	Parapiptadenia rigida (Benth.) Brenan	Tre	Zoo	276	40	107	A
	Pterogyne nitens Tul.	Tre	Ane	21	2	11	VL
	Pilocarpus pennatifolius Lem.	Tre	Aut		6	4	A
	Senegalia polyphylla. (DC.) Britton & Rose	Tre	Aut	6	3		A
	Sclerolobium sp.	Tre	Aut		4		L
Lauraceae	Lauraceae 1.			236			S
	Nectandra megapotamica (Spreng.) Mez.	Tre	Zoo	1	1		A
Lecythidaceae	*Cariniana legalis* (Mart.) Kuntze	Tre	Ane	112	1		VL
Malpighiaceae	*Diplopterys pubipetala* (A.Juss.) W.R.Anderson & C.C.Davis	Tre	Ane			2	VL
	Mascagnia cordifolia (A. Juss.) Griseb.	Lia	Ane	14			L
Malvaceae	*Ceiba pubiflora* (A.St.-Hil.) K.Schum.	Tre	Ane	10			S
	Guazuma ulmifolia Lam.	Tre	Zoo	180			VS
	Helicteres lhotzkyana (Schott & Endl.) K.Schum.	Tre	Aut			1	VS
	Heliocarpus sp.	Tre	Aut	3	22		VS
Meliaceae	*Guarea guidonia* (L.) Sleumer	Tre	Zoo	5	1		S
	Trichilia catigua A.Juss.	Tre	Zoo		544	4	A
	Trichilia clausseni C.DC.	Tre	Zoo		1		A
	Trichilia pallida Sw.	Tre	Zoo			6	S
Menispermaceae	*Disciphania ernstii* Eichler	Lia	Zoo	193	2	123	A
Moraceae	*Ficus* sp.	Tre	Zoo		67		VS
	Maclura tinctoria (L.) D.Don ex Steud.	Tre	Zoo	140			VS
Myrtaceae	*Calyptranthes* sp.	Tre	Zoo		6		S
	Eugenia sp.	Tre	Zoo	4			A
	Eugenia florida DC.	Tre	Zoo	306			S
	Myrtaceae 1.	Tre	Zoo		2	3	S
	Psidium sp.	Tre	Zoo	1	4		VS
Nyctaginaceae	*Guapira opposita* (Vell.) Reitz	Tre	Zoo	2	1	74	A
Phyllanthaceae	*Margaritaria nobilis* L.f.	Tre	Zoo	39	72	5	S
Poaceae	*Olyra ciliatifolia* Raddi	Her	Zoo			47	VS
Primulaceae	*Cybianthus detergens*. Mart.	Bus	Zoo	1522	117	9	VS
	Myrsine umbellata Mart.	Tre	Zoo	5932	141	416	VS
Rhamnaceae	*Sageretia elegans* (Kunth) Brongn.	Lia	Zoo	108			S
Rubiaceae	*Randia ferox* (Cham. & Schltdl.) DC.	Tre	Zoo	5	2	34	S
Rutaceae	*Balfourodendron riedelianum* (Engl.) Engl.	Tre	Ane	1	1	12	L

	Zanthoxylum sp.	Tre	Zoo	2	5	814	VS
Sapindaceae	*Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl.	Tre	Zoo	74	211	90	S
	Averrhoidium paraguaiense Radlk.	Tre	Zoo	1	297	37	A
	Cardiospermum grandiflorum. Sw.	Lia	Zoo	179	36		A
	Cupania castaneaefolia Mart.	Tre	Zoo	3		3	S
	Serjania caracasana (Jacq.) Willd.	Lia	Ane	658	131	382	L
	Sapindaceae 1.			26			S
Sapotaceae	*Chrysophyllum gonocarpum*. (Mart. & Eichler ex Miq.) Engl.	Tre	Zoo		12		A
Vitaceae	Cissus *erosa* Rich.	Lia	Zoo	1051		14	VS
Vochysiaceae	*Vochysia* sp.	Tre	Ane	4	15	6	A
	Undetermined 1			23	2	16	S
	Undetermined 2			45	3		S
	Undetermined 3			4			A
	Undetermined 4				2	2	VS

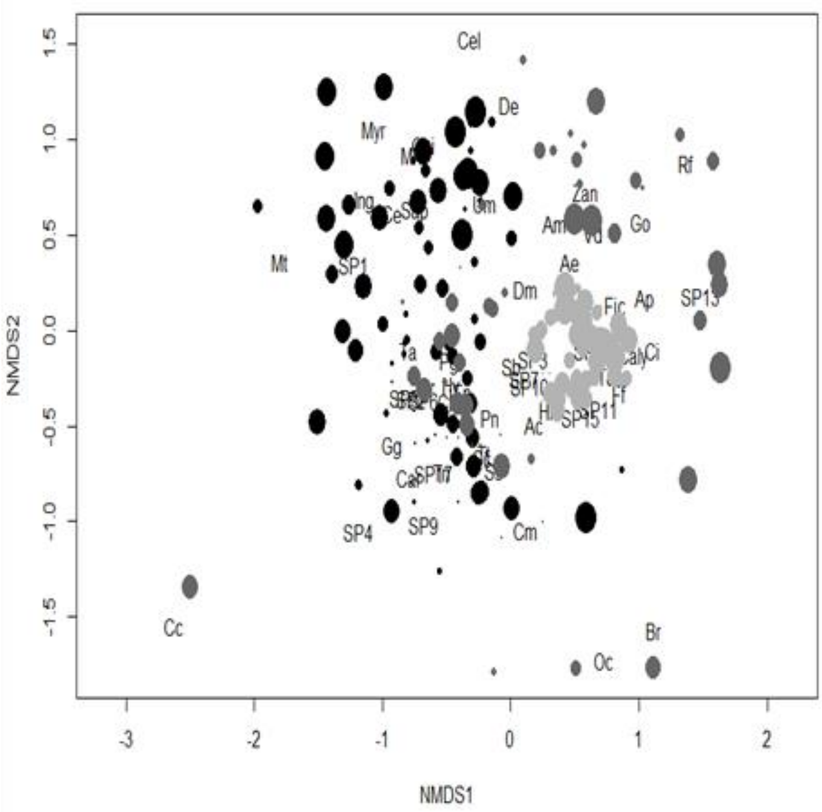
Legend: S.D-Dispersion syndrome;
Lia-liana; Tre-Tree; Bus-Bush; Her-herbaceous; Ane-anemochorous; Zoo-zoochoric; Aut-autochorous;
Size: VS-very small; A-average; L-large; VL-very larg

Source: Research authors (2019).

At the top there were seven exclusive species (Myracrodruon urundeuva, Lessingianthus scabrifoliatus, Diplopterys pubipetala, Olyra ciliatifolia, Tanaecium neobrasiliense, Helicteres lhotzkyana, Trichilia pallida), on the slope, there were ten (Fridericia florida, Euphorbiaceae 1, Manihot sp., Sebastiania brasiliensis, Sclerolobium sp., Trichilia clausseni, Ficus sp., Calyptranthes sp., Chrysophyllum gonocarpum, undetermined 4) and ate the base 13 (Callichlamys latifolia, Parapiptadenia rigida, Lauraceae 1, Mascagnia cordifolia, Inga sp., Guazuma ulmifolia, Ceiba pubiflora, Maclura tinctoria, Eugenia sp., Eugenia florida, Sageretia elegans, Sapindaceae 1 and undetermined 3). Most species (21) were shared between the sampling areas, as follows: Handroanthus heptaphyllus, Celtis iguanaea, Terminalia mameluco, Croton floribundus, Sebastiania brasiliensis, Anadenanthera colubrina, Guibourtia hymenifolia, Parapiptadenia rigida, Pterogyne nitens, Disciphania nysia, Disciphania ernia, Disciphaia Margaritaria nobilis, Cybianthus detergens, Myrsine umbellata, Randia ferox, Balfourodendron riedelianum, Zanthoxylum sp., Allophylus edulis, Paraguayan Averrhoidium, Serjania caracasana, Vochysia sp and undetermined 1 (Table 1).

The greatest number of seeds was found at the end of the dry season and beginning of the rainy season, with the period of highest production between November and February, with peaks in November and December and the lowest production in April and July. The seed rain was seasonal, varying among the elevation levels. Figure 3 shows the variation in the composition and abundance of the plant species sampled in relation to the different altimetric levels and the collection periods, showing differences between the sampled areas (Pillai = Locations - 0.54478; gl 2 and 4; p <2.2 and -16 - Months = 0.48851; gl 17 and 34; p = 065e-10).

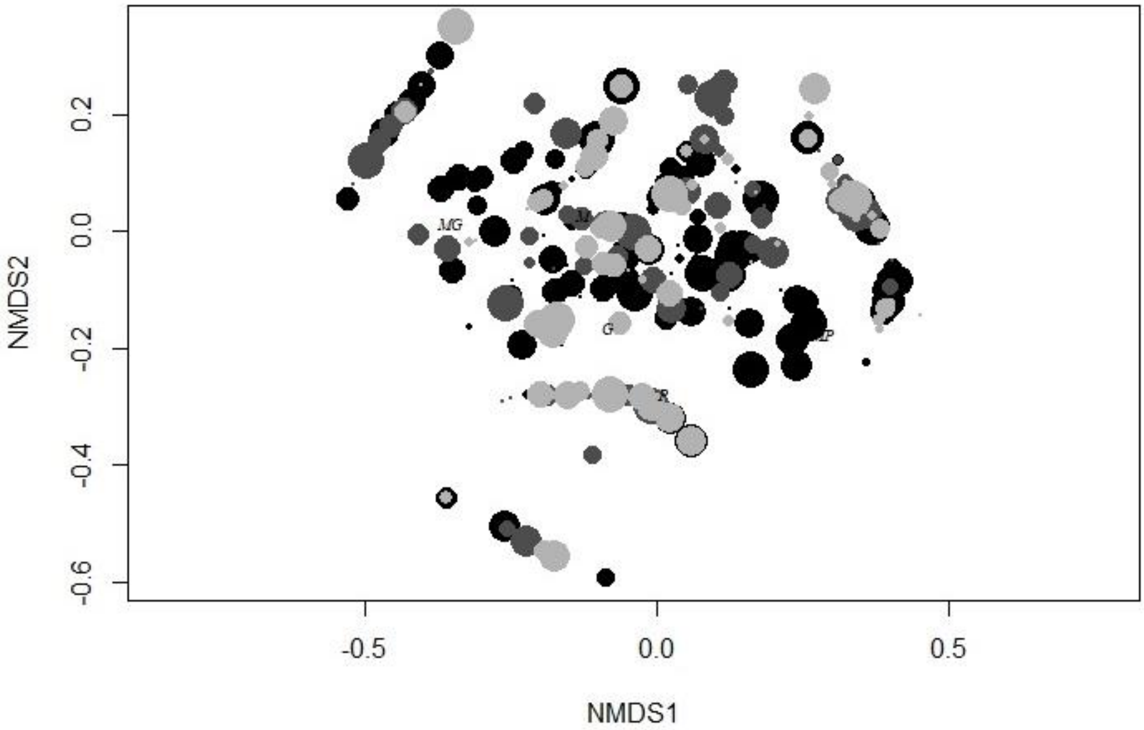
Figure 3. NMDS ordering of species composition at sampling sites.



Subtitle: Circle sizes represent the collection months from 1 to 18; the colors represent the gradient: black - base, light gray - top and dark gray - slope. The contribution of each species is given by the position in the graph: the further away from the “0.0” coordinates, the greater the contribution of the species to differentiate the samples. Source: Research authors (2019).

Figure 4 shows the NMDS ranking in relation to the variation in seed size (stress = 0.13, with 98% of the total variance being recovered in the Bray-Curtis distance matrix); altimetric quotas and months of collection explained the variation in seed size distribution (Pillai = Locations 0.03296; gl 1 and 365; p 0.002207; Months = 0.32819; gl 17 and 732; p = 8,165e-14), reinforcing the differences between the sampled areas and between the months of fieldwork.

Figure 4. NMDS ordering of seed size at sampling sites.



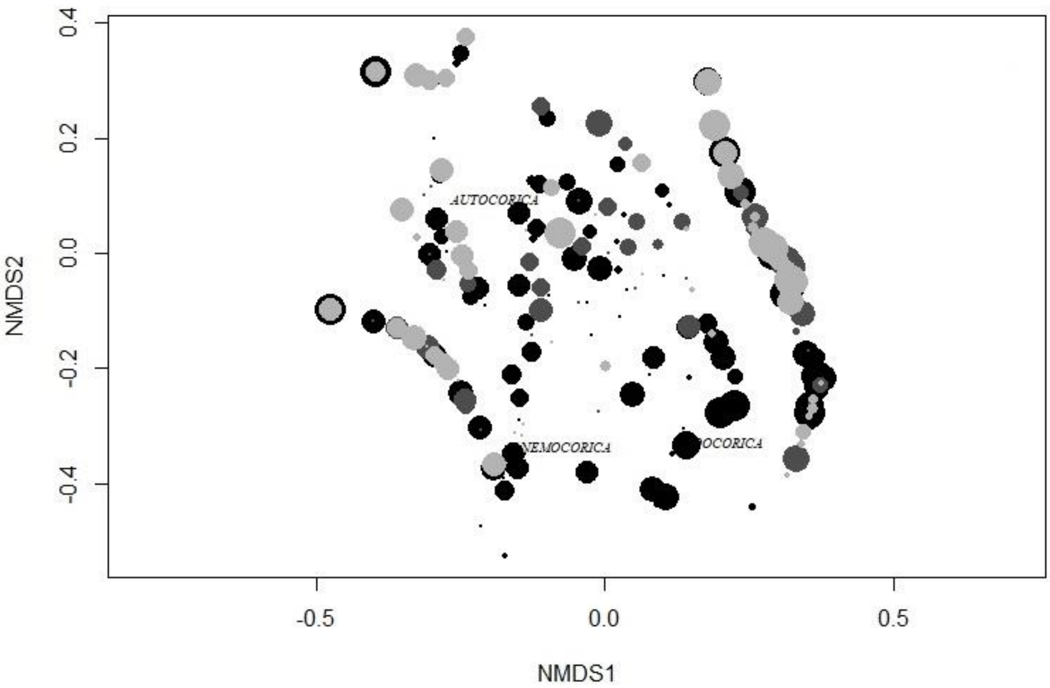
Subtitle: Circle sizes represent the collection months from 1 to 18; the colors represent the gradient: black - base, light gray - top and dark gray - slope. The contribution of each size is given by the position on the graph: the further away from the "0.0" coordinates, the greater the size contribution to differentiate the samples. Seed Sizes: PM: very small, P: Small; M: Average; G: Great; MG: Very big. Source: Research authors (2019)

Very small seeds showed greater variation in abundance between the elevation levels, with 83% at the base, 14% on the slope, and only 3% at the top. At the base, the majority of seeds were very small, which corresponded to 53% of the total (10.637 seeds), represented by 14 species. Small seeds represented 16% (3.312 seeds and 18 species), medium seeds 11% (2.163 seeds and 19 species), large seeds 7% (1.461 seeds and 9 species), and very large seeds 13% (2.547 seeds and 5 species) (see Table 1).

In relation to species habits, 76% (46 species) are arboreal, 9% (3) shrubby, 15% (11) lianas and (2) herbaceous. Tree species accounted for 74.9% of the total sampled seeds (15.155 seeds), while shrubs and lianas accounted for 8% (1.662) and 14.7% (2.976), respectively.

Zoochoric species predominated in the seed rain in the three altimetric levels, corresponding to 78% (15.546 seeds and 37 species), followed by anemochoric species, with 22% (4.031 seeds and 18 species) and autochorous (61 seeds and 6 species) (see Table 1). Figure 5 shows that the ordering of the variation in dispersion syndromes was related to the elevational quotas and fieldwork period. Ordering in two dimensions resulted in a stress = 0.13 and recovered 98% of the total variance in the matrix (Pillai = Locations 0.04510; gl 1 and 366; p 0.0002148; Months = 0.51756; gl 17 and 734; p <2.2e-16).

Figure 5. NMDS ordering of the dispersion syndrome at the sampling sites.



Subtitle: Circle sizes represent the collection months from 1 to 18; the colors represent the gradient: black - base, light gray - top and dark gray - slope. The contribution of each syndrome is given by the position on the graph: the further away from the 0,0 coordinates, the greater the contribution of the dispersion syndrome to differentiate the samples. Source: Research authors (2019)

4. Discussion

The number of species recorded in the seed rain was similar to that of Sccoti et al., (2011) in an SDF area in Rio Grande do Sul, while Battilani (2010), in the Planalto da Bodoquena registered 117 species in three years of sampling. Our results differed a bit from some floristic studies on the shrub-tree component carried out in that same region, however, they were carried out in areas with riverside forests (Baptista-Maria et al., 2009) or in ecotonous areas of forest formations (Zavala et al., 2017), that has greater richness than the SDFs. Nevertheless, the large number of propagules registered in this research shows the potential that the remaining SDFs have to support the restoration of degraded areas, aiming to maintain biodiversity, considering the different reproductive strategies of the species that compose this type of vegetation. In Deciduous Seasonal Forest, natural regeneration develops satisfactorily, presenting floristic composition and high diversity, with a clear increase in the dominance and density of some key species (Scipioni et al., 2009).

Fabaceae, which stood out as the most representative families in species richness, is considered a typical family of the Brazilian forests (Oliveira-Filho & Fontes, 2000; Oliveira et al., 2016), with great importance for environmental restoration due to the ability to fix nitrogen that several species have and, consequently, improvement of soil conditions. Therefore, its species are considered facilitators of ecological succession (Canosa et al., 2012). Sapindaceae is a very diverse family, especially in the North - Amazon Forest - and Southeast - Atlantic Forest regions of Brazil, with emphasis on the species of *Serjania*, the richest genus in Brazil (Somner et al., 2010). Composed almost exclusively by lianas, species of this genus play a role in environmental dynamics, forming true "biological corridors" in the forest canopy (Aschoff, 2012). Euphorbiaceae, which also stood out in this study, has fast growth as one of its main characteristics, participating in the initial stages of succession and contributing to the rapid plant densification in areas undergoing restoration (Amaral et al., 2013).

Intra and interspecific variations in seed production and dispersion syndromes influenced the spatial distribution of seeds during the fieldwork period. Such variations may be related to the species phenological and reproductive characteristics, as pointed out in other studies of seed rain for both individual and community levels (Araújo et al., 2004; Armesto et al., 2001; Au et al., 2006; Hampe et al., 2004; Masaki et al., 2007; Shen et al., 2007). Variations in the composition of seed rain among collectors and between altimetric levels were influenced by the occurrence of exclusive species of specific habitats and by variations of seed abundance through space. The species composition in the seed rain, in general, is related to the local plant community (Penhalber & Vani, 1997) but tends to be different between areas (Au et al., 2006; Pivello et al., 2006; Rother et al., 2009), between habitats (Martini & Santos, 2007), under trees with different forms of dispersion (Clark et al., 2004) and among seed collectors in the same stretch of the forest (Hardesty & Parker, 2002).

Such variations are related to several factors, such as environmental heterogeneity, floristic composition, phenological patterns of the local community, dispersal agent activities, and topographic gradients. The topographic gradient is an environmental variable that indirectly influences a series of other environmental factors closely related to the patterns of plant distribution in the Atlantic Forest (Eisenlohr et al., 2013; Meireles et al., 2008; Oliveira-Filho & Fontes, 2000; Oliveira et al., 2013; Pedroni et al., 2013). The results of this study confirm that for the SDFs, the topographic gradient is also important in determining functional patterns and affects the seed rain composition. The differences in richness and abundance of the seed rain between the elevation levels can be a consequence of several factors, such as soil conditions, topography and microclimate characteristics, that change along the elevational quotas (Ferreira-Júnior et al., 2007; Ferreira-Júnior et al., 2012; Jones et al., 2011; Klein, 1980 , 1984; Marangon et al., 2013; Veloso & Klein, 1959).

Wolf et al., (2012) observed that greater species richness is expected where topographic variations on a local scale result in greater availability of water in the soil. Some studies carried out in wetland and riverside areas have shown that some species are indicative of each portion of the slope (Borghi et al., 2004; Moro et al., 2001). Considering that several other studies report the influence of topography on the organization of plant species communities (Cardoso & Schiavini, 2002; Higuchi et al., 2012; Higuchi et al., 2013; Rodrigues et al., 2007), the occurrence of indicator species on the slope and top can be partially explained by the ecological requirements of these species, associated with distinct ecological niche. Along the altitudinal gradient studied, environmental variations were observed, which are associated with soil type, slope, humidity, and microclimate, as also registered by Oliveira-Filho et al., (1998), Thomas & Winner (2002) and Homeier et al., (2010), Webb & Peart (1999).

The large amount of small seeds recorded at the base of the slope is related to the presence of species associated with more humid areas, such as *Maclura tinctoria*, *Myrsine umbellata*, and *Cissus erosa*, that are typical of these environments. Generally, species that produce smaller seeds, under favorable environmental conditions, have a higher growth rate compared to larger-seed species. These species may also have the dispersal process optimized since the small size increases the number of seeds ingested by the dispersers (Graham et al., 1995; Larson et al., 2015; Moles & Westoby, 2006; Muller-Landau, 2010; Pereira et al., 2013). On the other hand, large seeds have a greater amount of stored resources, and thus are more likely to germinate (Pesendorfer et al., 2016), and also has a better ability to cope with adverse environmental conditions and competition when in seedling stage (Fenner & Thompson, 2005; Lebrija-Trejos et al., 2016). However, larger seeds are more susceptible to post-dispersal predation due to their greater nutritional value (Jansen et al., 2004).

The diversity in the propagules size is an interesting aspect in the evolution of the plants since it has already been demonstrated that the seed mass strongly influences other important characteristics, in addition to the shape and type of fruit dehiscence, implying in the geographic species distribution and interactions (Barroso et al., 1999). At the base of the slope, where more zoochorous individuals were recorded, there is greater proximity to a watercourse, where *Myrsine umbellata* is abundant, which has attractive fruits to the fauna and can bring other zoochoric diaspores, confirming the importance of biotic agents in the gene flow in forest formations. Junior et al., (2012) pointed out that the relationship between plants and frugivores is essential for the conservation and maintenance of ecosystems, and the proportion of zoochoric species recorded in this study follows the dispersion pattern described for tropical forests (Howe & Smallwood, 1982; Stefanello et al., 2010).

Anemochorous diaspores occurred in a smaller amount, being generally associated with pioneer species, in dry environments, and less frequent than zoochorous in tropical forests (Wilkander, 1984). Pioneer species play an important role in environmental restoration, as they assist in the forest regeneration, guaranteeing their resilience and facilitating the process of forest succession after natural or anthropic disturbances (Capellesso et al., 2015; Mantovani & Martins, 1988; Martins et al., 2012; Vieira & Scariot, 2006)

5. Conclusion

We demonstrated that, on a small spatial scale, the landform represents an important source of heterogeneity from the vegetational component, determined by the fact that the study area is located in a region formed by geologically complex land, with varied lithologies and a mosaic of phytophysiognomies shaped by the combination of topography, microclimate, and altitude.

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