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Variation in plant-animal interactions along an elevational gradient of moist forest in a semiarid area of Brazil

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ABSTRACT

Pollination and dispersal are critical ecological processes that directly affect the reproductive success of plants and are important for understanding the structure of plant communities. We compiled data on pollination and dispersal syndromes of 406 plant species distributed among different elevations in Área de Proteção Ambiental da Serra de Baturité (APASB) in northeastern Brazil. We aim to determine how the dispersal and pollination of the flora in the mountainous rainforest of APASB are affected by climate, relief and growth form. We hypothesized that plant community is comprised of different ecological groups based on biotic and abiotic syndromes. Melittophily was the most common (57%) pollination syndrome followed by non-specialized and ornithophily (7%). We found that 64% of species exhibited zoochory, 19% exhibited anemochory and 17% exhibited autochory. Pollination syndromes differed significantly only between types of growth form. Dispersal syndromes differed between topology, growth form and elevation. Six ecological groups were formed based on the interaction between dispersal-pollination and growth form, with predominantly zoochory in woody and anemochory in non-woody plants. Water availability may be the principal factor responsible for variation among dispersal syndromes. The proportion of ruderal species in the non-woody component explains the differences in syndromes between growth forms.

Keywords: altitude, humidity, melittophily, plant community, topology, water availability, zoochory

Introduction

Pollination and dispersal are critical ecological processes that directly affect the reproductive success of plants (Wunderlee 1997; Machado & Lopes 2004). The genetic diversity of plants is influenced by pollinators and dispersers that promote gene flow (Nason *et al.* 1997). Pollination and dispersal are current evidence of the evolutionary processes that led to the persistence of different populations of angiosperms in tropical forests (Behling *et al.* 2000; Auler *et al.* 2004).

In this sense, biotic pollinators represent important agents in tropical forests, as they are responsible for about

94% of all pollen flow (Ollerton *et al.* 2011). Pollination by vertebrates (mainly chiropterophily and ornithophily) corresponds to approximately 15% of the species of tropical forests plant community (Bawa 1990; Ollerton *et al.* 2011). Wind pollination is uncommon in tropical moist forests (Bawa 1990). It is more common to find plants pollinated by wind in areas with lower plant diversity and more open vegetation, such as savannas, or with seasonal deciduousness (Regal 1982; Tetetla-Rangel *et al.* 2013).

On the other hand, tropical vegetation has a great abundance of zoochoric species, followed by anemochoric and autochoric species (Howe & Smallwood 1982; Pijl 1982). Normally, zoochory predominates in the forests of humid climates or in forests that have weak seasonality

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(Howe & Smallwood 1982; Gentry 1983) such as forests located on humid mountains. Anemochory predominates in vegetation types associated with dry climates or with strong seasonality (Howe & Smallwood 1982; Tetetla-Rangel *et al.* 2013).

Therefore, there is a non-random spatial distribution of pollination and dispersal syndromes, with both vertical stratification and differentiation occurring in relation to habitat (Smith 1973; Roth 1987). Since the differentiated structure of vegetation results in stratification of food resources and microclimate, the animal community is also stratified, so that each stratum of vegetation has its characteristic pollinators (Smith 1973; Almeida-Neto *et al.* 2008).

Thus, we assume that plant species can form ecological groups, which are distributed differently according to environmental conditions. This study aims to determine how dispersal and pollination syndromes of the flora in the mountainous rainforest Serra de Baturité, Ceará State, are affected by the micro-climate, the relief and the growth form (woody or non-woody), which may help us understand the distribution of species in these enclaves of moist forest. We hypothesize that: (1) pollination and dispersal syndromes are clearly influenced by temperature and rainfall, (2) elevational variation and stratification of vegetation can influence syndrome distribution, and (3) the plant community is comprised of different ecological groups based on biotic and abiotic syndromes.

Materials and methods

Study area

The study took place in the mountainous rainforest of the protected area of Serra de Baturité (Área de Proteção Ambiental da Serra de Baturité; APASB) located in north-eastern Brazil. This forest, known regionally as *brejo de altitude*, are surrounded by woody savanna (caatinga) (Silva & Casteletti 2003), and have more amiable conditions (e.g., soil moisture, air temperature, dense vegetation cover) than the surrounding semiarid regions.

The APASB covers an area of 32,690 ha between the geographical coordinates of 4° 08' and 4° 27' S and 38° 50' to 30° 05' W. The local climate is Aw, hot and semi humid, according to the Köppen-Geiger classification (Peel *et al.* 2007), with average temperatures between 20.8° C and 26.5° C and rainfall between 1085 and 1711 mm.year⁻¹. The soil classes vary between Argisols, Inceptisols and Entisols (Araújo *et al.* 2007) and the elevation reaches up to 1200m.

Data sampling

We compiled diversity data from the floristic surveys of Araújo *et al.* (2007). These authors investigated the composition of the flora of six areas of different elevational zones

(400-600m, 600-800m and higher than 800m on leeward and windward side) of the Serra de Baturité. We made nomenclature corrections and checked the validity of species names and author abbreviations used in the surveys based on the usual botany databases (*Lista de Espécies da Flora do Brasil*, Flora Brasiliensis online, Royal Botanical Garden - Kew, Missouri Botanical Garden - MBOT and specialized literature).

We explored the literature for each species, or closely related species, and conducted field trips for two years in order to confirm pollination syndromes. The pollination syndromes were classified according Faegri & Pijl (1979) and Bullock (1994) as: anemophily (wind), cantharophily (beetles), phalenophily (moths), sphingophily (hawk-moths), melittophily (bees), myiophily (flies), ornitophily (birds), psychophily (butterflies), chiropterophily (bats), ambiphily (two pollinators) and generalist. The use of pollination syndromes has been controversial and the subject of much discussion in the literature (Ollerton *et al.* 2009). However, a recent and important survey supports the syndrome concept, indicating that convergent floral evolution is driven by adaptation to the most effective pollinator group (Rosas-Guerrero *et al.* 2014). Others discuss the methodological cautions that should be taken when using pollination syndromes (Ollerton *et al.* 2015).

The classification of dispersal syndromes followed Pijl (1982), where the species were classified into three groups: anemochoric, zoochoric and autochory. Growth form was classified into: tree, shrub, subshrub, herb, liana, epiphytic and mistletoe (Cain & Castro 1959; Whittaker 1975). These were subsequently grouped into woody (tree, shrub, subshrub and lianas) and non-woody (herb, epiphytic and mistletoes), in order to analyze the distribution of syndromes separately for each growth type (woody and non-woody) for the windward and leeward environments and for the different elevations.

Climate data were compiled from a number of databases and are available from the WorldClim program (Hijmans *et al.* 2005). Bioclimatic variables were obtained at a 1-km spatial resolution. The databases used to produce these climate metrics came from the Global Historical Climatology Network (GHCN). We obtained data for temperature (maximum, mean and minimum), rainfall, air humidity, soil humidity, altitude and topology.

Statistical analysis

We tested for correlation between all pairs of climatic and positional variables used in this study using the Spearman rank coefficient to avoid using variables with autocorrelation and high VIF (variance inflation factor). Accordingly, we excluded mean temperature, air humidity and topology (Tab. 1).

We tested differences in the proportions of dispersal and pollination syndromes for the types of growth forms



Table 1. Abiotic characteristics of each area analyzed in APASB, Ceará. L = leeward, W = windward.

Altitude/Side	Temperature max (°C)	Temperature min (°C)	Rainfall (mm)	Soil humidity (%)	Altitude (m)
400 – 600m L	27.625	19.142	1085.763	0.054	460
600 – 800m L	25.742	17.500	1158.710	0.056	714
>800m L	25.301	17.223	1511.543	0.055	826
400 – 600m W	25.442	17.292	1221.860	0.071	473
600 – 800m W	27.517	19.167	1558.710	0.064	759
>800m W	25.150	16.992	1711.543	0.090	824

and different elevations with the tests of independence chi-square and partitioned chi-square (Zar 1996). Tests were performed using the statistical package Statistica 9.0.

To verify the formation of ecological groups in the plant community (association between dispersal and pollination syndromes), we used the number of species per pollination syndrome as the response variable and dispersal syndrome as the explanatory variable in a principal component analysis (PCA) for each component (woody and non-woody) of the vegetation with PC-Ord 6.0 statistical package (McCune & Mefford 2011).

Results

We compiled data for 406 woody and non-woody species (Tab. S1 in supplementary material). Melittophily was the most frequent pollination syndrome (57%), followed by ornithophily and unspecialized or generalist pollination (7%), and anemophily and phalenophily (5%). The other syndromes occurred at lower frequencies: myiophily (4%), cantharophily and chiropterophily (3%), and sphingophily and psychophily (2%). For some species, we suggested ambiphily (the occurrence of two pollinators) (4%).

Myiophily and unspecialized pollination were distributed evenly among the different types of habits, as was melittophily. Most syndromes were observed among woody vegetation, particularly trees. However, psychophily was more common among shrubs (Tab. 2), which occupy the forest understory.

The most frequent dispersal syndrome was zoochory (64%), followed by anemochory (19%) and autochory (17%). Zoochory was more frequently observed in trees, shrubs and herbs (Tab. 2). On the other hand, anemochory occurred in all habits, but had a higher prevalence in the upper stratum of the vegetation, with its greatest frequency being among lianas and epiphytic herbs (Tab. 2).

The lower and leeward areas had a more severe climate, with extreme maximum and minimum temperatures, low rainfall and low levels of soil humidity, when compared to higher and windward areas, which had a milder climate (Tab. 1). We detected significant correlations between

zoochory ($r_s = 0.88$) and anemochory ($r_s = -0.77$) and soil humidity and found a negative correlation between elevation and the relative frequency of autochoric species ($r_s = -0.94$). On the other hand, there were no correlations between any type of syndrome and temperature. Furthermore, for pollination, our analyses showed an increase in melittophily at sites with higher rainfall (Tab. 3).

Variation in topology did not influence the distribution of pollination syndromes ($\chi^2 = 0.72094$ df = 3, $p = 0.8745$); the syndromes were similar between the windward and leeward slopes, with a dominance of melittophily (Fig. 1). There was a significant difference in pollination syndromes between woody and non-woody plants ($\chi^2 = 44,941$ df = 3, $p < 0.0001$). Melittophily was dominant in woody species (61%), while other syndromes were more common among non-woody vegetation (63%), with ornithophily being the most frequently observed (23%) followed by anemophily (15%); no species had the generalist pollination syndrome (Fig. 1).

Pollination syndromes were similarly distributed among elevations (400-600m/600-800m: $\chi^2 = 3.5703$ df = 3, $p = 0.32089$; 400-600m/>800m: $\chi^2 = 3.1061$ df = 3, $p = 0.37964$; 600-800m/>800m: $\chi^2 = 0.7118$ df = 3, $p = 0.87089$).

The distribution of dispersal syndromes was significantly different between the windward and leeward sides ($\chi^2 = 5.9692$ df = 2, $P < 0.05$), with a smaller proportion of zoochorous species on the leeward side and a consequent increase in biotic syndromes on the windward side (Fig. 2). There was also a significant difference in dispersal syndromes between woody and non-woody species ($\chi^2 = 34.333$, $p < 0.0001$, df = 2). Among woody species, zoochory was dominant (67%) compared to abiotic syndromes. Among non-woody species, abiotic syndromes prevailed with anemochoric species being the most frequent (45%), although the frequency of autochory is reduced (Fig. 2).

The areas above 800m were significantly different from other elevations (1-2: $\chi^2 = 0.50054$, df = 2, $p = 0.77859$; 1-3: $\chi^2 = 18.113$, df = 2, $p < 0.0001$; 2-3: $\chi^2 = 15.701$, df = 2, $p < 0.0004$). The elevations of 400-600m and 600-800m showed a similar distribution of dispersal syndromes, with a greater proportion of animal dispersed species (Fig. 2).



Table 2. Number and percentage of pollination and dispersal syndromes per growth forms in APASB, Ceará.

SYNDROMES	WOODY			NON WOODY			
	Tree	Shrub	Subshrub	Herb	Epiphytic	Liana	Mistletoe
POLLINATION							
Melittophily	159(39.2%)	36(8.9%)	3(0.7%)	16(3.9%)	8(2%)	10(2.5%)	0
Unspecialized	2(0.5%)	4(1%)	3(0.7%)	7(1.7%)	8(2%)	3(0.7%)	0
Phalenophily	24(5.9%)	3(0.7%)	0	0	0	0	0
Myiophily	6(1.5%)	4(1%)	1(0.2%)	6(1.5%)	0	1(0.2%)	4(1%)
Ornitophily	15(3.7%)	2(0.5%)	0	2(0.5%)	0	1(0.2%)	0
Anemophily	11(2.7%)	3(0.7%)	0	1(0.2%)	1(0.2%)	0	0
Chiropterophily	5(1.2%)	4(1%)	0	1(0.2%)	0	0	0
Ambiphily	6(1.5%)	2(0.5%)	0	5(1.2%)	1(0.2%)	0	0
Cantharophily	6(1.5%)	4(1%)	0	0	1(0.2%)	0	0
Sphingophily	7(1.7%)	1(0.2%)	0	0	1(0.2%)	0	0
Psychophily	1(0.2%)	5(1.2%)	1(0.2%)	1(0.2%)	1(0.2%)	0	0
Indeterminate	5(1.2%)	1(0.2%)	1(0.2%)	1(0.2%)	0	1(0.2%)	0
DISPERSION							
Anemochory	32(7.9%)	4(1%)	3(0.7%)	12(3%)	17(4.2%)	7(1.7%)	0
Autochory	35(8.6%)	19(4.7%)	4(1%)	8(2%)	0	5(1.2%)	0
Zoochory	180(44.3%)	46(11.3%)	2(0.5%)	20(4.9%)	4(1%)	4(1%)	4(1%)

Table 3. Spearman rank correlations of dispersal and pollination variables of plant communities and the respective climatic and geographical variables.

Variables	Zoochory	Anemochory	Autochory	Melittophily
Temperature max	-0.60NS	0.37NS	0.77NS	-0.48NS
Temperature min	-0.37NS	0.29NS	0.60NS	-0.25NS
Rainfall	0.94***	-0.60NS	-0.82*	0.83*
Soil humidity	0.88**	-0.77**	-0.37NS	0.65NS
Altitude	0.54NS	-0.20NS	-0.94***	0.65NS

NS, non-significant; *P < 0.05; **P < 0.01; ***P < 0.001.

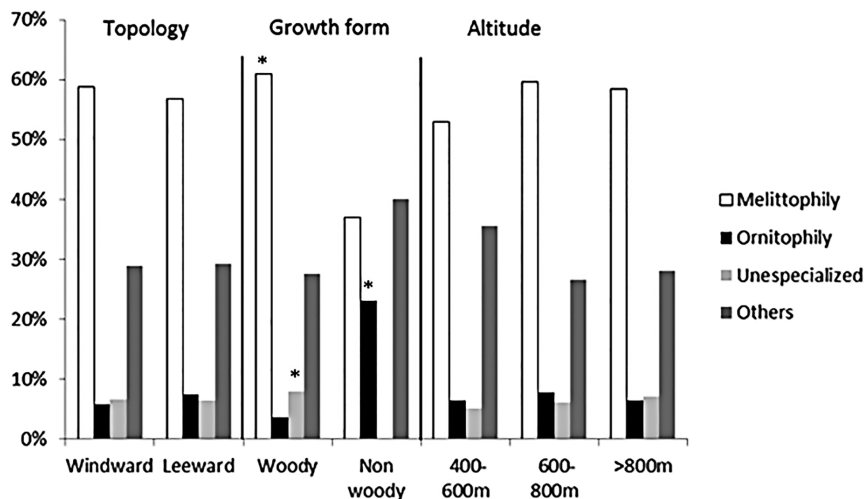


Figure 1. Percentage of pollination syndromes in relation to topology (windward and leeward), growth form (woody and non-woody) and altitude (400-600m, 600-800m, above 800m). The category “other” includes anemophily, phalenophily, myiophily, ambiphily, cantharophily, chiropterophily, sphingophily, psychophily and indeterminate. * Chi-square significant (p < 0,05).



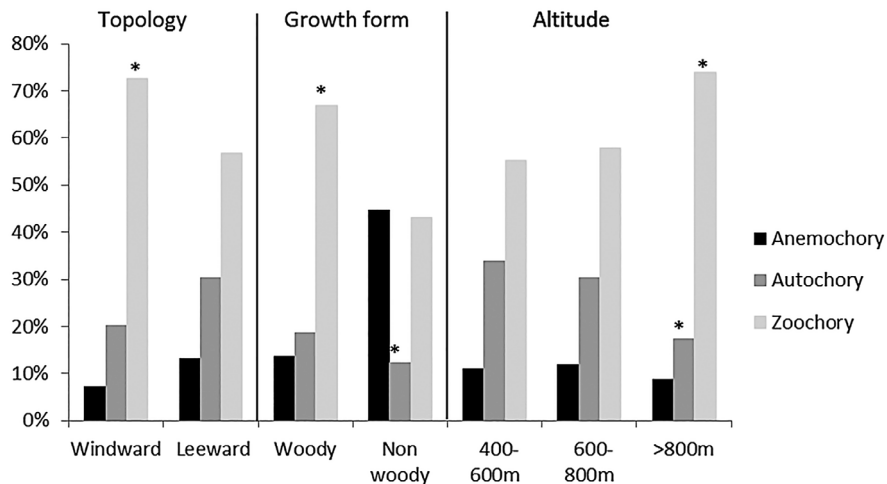


Figure 2. Percentage of dispersal syndromes according to topology (windward and leeward), growth form (woody and non-woody) and altitude (400-600m, 600-800m above 800m). * Chi-square significant ($p < 0,05$).

On the other hand, the areas above 800m may have a flora that is widely dispersed by animals (depending on whether the animals are still present there or not), with a consequent reduction of abiotic syndromes when compared to lower elevations (Fig. 2).

Dispersal syndromes were grouped by three principal components, which explained 28.42% of the variance in the data for woody plants (Fig. 3) and 23.67% of the variance in the data for non-woody plants (Fig. 4). Three specific ecological groups were formed in each case (Tab. 4). There were seven myophilous and phalenophilous species that were distributed equally among the groups. None of the woody species exhibited a generalist pollination syndrome.

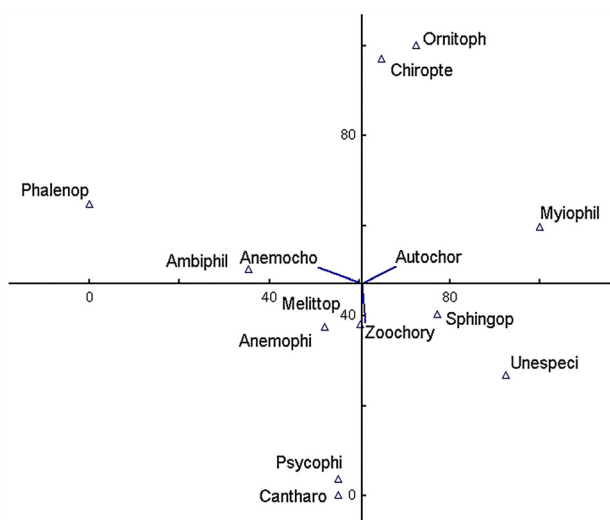


Figure 3. Three ecological groups formed by PCA linking pollination and dispersal syndromes of species of the woody component of the vegetation of APASB. The principal components explained 28.42% of the variance in the data.

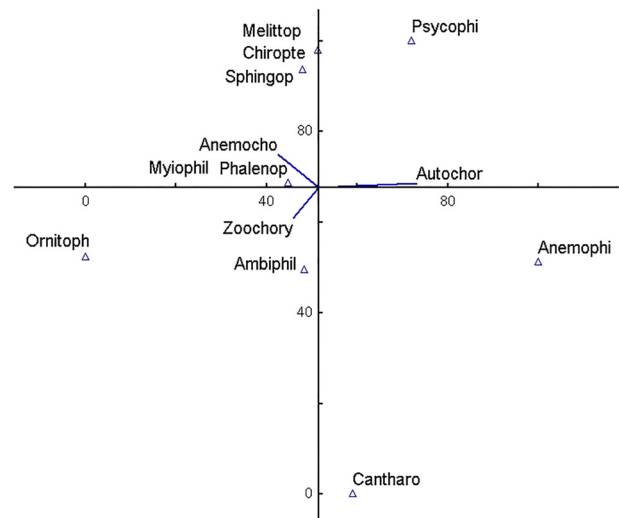


Figure 4. Three ecological groups formed by PCA linking pollination and dispersal syndromes of species of the non-woody component of the vegetation of APASB. The principal components explained 23.67% of the variance in the data.

Discussion

The influence of microclimate, relief and growth form

Elevation has just a slight effect on the range and proportions of pollination syndromes because pollinators have a range of resources available to them in all strata (Ollerton *et al.* 2006). On the other hand, due to the positive correlation between zoochory and rainfall and soil humidity, we hypothesize that humidity is the key factor affecting the proportion of zoochoric species. Similar



Table 4. The ecological groups formed by the pollination-dispersal interaction and some examples for each group.

Group	Number of species	Dispersal Syndrome	Pollination Syndrome	Examples
1	17	Autochory	Ornithophilous, chiropterophilous and myophilous	<i>Dicliptera ciliaris</i> Juss., <i>Lonchocarpus sericeus</i> (Poir.) Kunth, <i>Esenbeckia leiocarpa</i> Engl.
2	199	Zoochory	Sphingophilous, anemophilous, melittophilous, unspecialized, cantharophilous and psychophilous	<i>Thyrsodium spruceanum</i> Benth., <i>Ilex sapotifolia</i> Reissek, <i>Cereus jamacaru</i> DC.
3	14	Anemochory	Phalenophilous and ambiphilous	<i>Aspidosperma multiflorum</i> A. DC., <i>Coutarea hexandra</i> (Jacq.) K. Schum.
4	4	Autochory	Anemophilous and psychophilous	<i>Becquerelia cymosa</i> Brongn., <i>Cipura paludosa</i> Aubl.
5	18	Anemochory	Melittophilous, chiropterophilous and sphingophilous	<i>Commelina benghalensis</i> L., <i>Vriesea platynema</i> Gaudich., <i>Epidendrum nocturnum</i> Jacq.
6	6	Zoochory	Ornithophilous, ambiphilous, cantharophilous	<i>Peperomia circinnata</i> Link, <i>Costus spiralis</i> (Roscoe), <i>Anthurium gracile</i> (Rudge) Lindl.

results have been previously reported in the literature (e.g. Gentry 1982; Howe & Smallwood 1982; Tabarelli *et al.* 2003; Almeida-Neto *et al.* 2008).

In this sense, the windward side of the mountain has a higher proportion of animal dispersed species, probably due to the greater water availability. On the other hand, the drier conditions of the leeward side can explain the lower number of zoochorous species and a greater proportion of abiotic syndromes. Many authors have related open and drier vegetation to anemochorous and autochorous species (Opler *et al.* 1980; Roth 1987; Drezner *et al.* 2001; Griz & Machado 2001). Since the largest proportion of zoochorous species is found in the upper areas (above 800m), water availability may also regulate the distribution of syndromes by elevation.

Species dispersed by wind can also benefit from fragmented landscapes (Howe & Smallwood 1982; Almeida-Neto *et al.* 2008) or open environments, such as the lower areas of the Serra de Baturité, while for animal-dispersed species a fragmented environmental matrix often constitutes an insurmountable obstacle. The low occurrence of anemochory in tropical forests is explained by the wetter environment, which would prevent the dispersal of diaspores by wind (Negrelle 2002; Almeida-Neto *et al.* 2008).

On the other hand, zoochoric species are prevalent in all the habitats of a rainforest (Yamamoto *et al.* 2007). There is a predominance of zoochorous trees and shrubs in tropical forests (Roth 1987; Negrelle 2002; Tetetla-Rangel *et al.* 2013) and seasonal rainforests (Ortega 1986; Kinoshita *et al.* 2006). The uneven distribution of populations of different zoochoric species among several strata of the vegetation can cause a large displacement of frugivorous fauna throughout the year to search for food resources, thereby favoring a wide dispersal of seeds.

The presence of ruderal species in the non-woody component of vegetation indicates a higher proportion

of anemochory since these species have winged or hairy diaspores and occupy primarily open places (Janzen 1988; Tabarelli *et al.* 1999; Drezner *et al.* 2001; Almeida-Neto *et al.* 2008). The high incidence of anemochory in epiphytic herbs is due to the increased exposure of the seeds of these canopy species to the wind, increasing the chance of dispersion (Talora & Morellato 2000; Spina *et al.* 2001).

Ecological groups formed by pollination-dispersal interaction

Plant species with the same type of dispersal have particular characters, such as the period of flowering, fructification and pollen availability (Skov 2000), which enable the formation of groups that have a close relationship between the maintenance of specific pollinators and the dispersal abilities.

In this sense, anemochoric species (group 3) have a more specific distribution in the plant community, since woody plants with seeds dispersed by wind are usually in the upper strata of the forest, forming or emerging from the canopy (Howe & Smallwood 1982; Kinoshita *et al.* 2006). The effectiveness of the mechanism of dispersal by wind increases with the height of the tree (Nunes *et al.* 2003). On the other hand, group 5 consists of important species for the maintenance of non-woody component. Group 5 also has bees as effective pollinators, contributing to the genetic interchange and reproduction of these plants (Fenster *et al.* 2004). Groups 1 and 4 have specific pollinators of woody and non-woody autochoric species.

Zoochoric species (groups 2 and 6) produce fruits and seeds that provide food for vertebrates, thus the fauna associated with this resource contributes to the distribution of these species in the environment and influences the structure and diversity of plant species (Clark & Poulsen 2001; Tetetla-Rangel *et al.* 2013).



So the high biodiversity of zoochoric plants provides a variety of mechanisms that increase the supply of food for dispersers (Fenster *et al.* 2004).

The existence of ecological groups based on pollination and dispersal characters is important for understanding how plant-pollinator/disperser interactions can be influenced by abiotic factors. This knowledge is also required to comprehend the levels of the plant community by revealing differences that are difficult to detect with only floristic and phytosociological studies, due to the ample amount of species groups that comprise certain regions.

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