Reproductive characteristics and functional diversity in plant congregation along a chronosequence in Atlantic Forest

Características reprodutivas e diversidade funcional na assembléia de plantas ao longo de uma cronesequência em Floresta Atlântica

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ABSTRACT

The association of reproductive characteristics of the species with the patterns of abundance in tropical forests at different stages of succession provides a fundamental knowledge for understanding the forest regeneration processes. This work aimed to describe the floral reproductive characteristics to determine the pollination systems and functional diversity in a chronosequence (5, 16, 24.30 years old of regeneration) and a mature forest in the state of Pernambuco Atlantic forest. It was verified how pollination syndromes are distributed among the different regeneration ages. Our hypothesis is that functional diversity of pollination syndromes is influenced by the age of regeneration. The surveys were conducted in a total of 150 plots. A total of 109 species and 1,945 individuals (40 families and 81 genera) were recorded. In general the distribution of reproductive characteristics was different between the young forest and the mature forest. There were trends of increase of the proportion of some reproductive characteristics towards mature forest. The predominant pollination syndrome along the chronological sequence was the melittophily. The results did not corroborate the hypothesis that the functional diversity of pollination syndromes is influenced by the age of forest regeneration.

Keywords: Floral biology; floral morphology; natural regeneration; pollination syndrome; young forests

RESUMO

A associação das características reprodutivas das espécies com os padrões de abundância em florestas tropicais em diferentes estádios de sucessão fornece um conhecimento fundamental para a compreensão dos processos de regeneração da floresta. Este trabalho teve como objetivo descrever as características reprodutivas florais para determinar os sistemas de polinização e a diversidade funcional em uma cronesequência (5, 16, 24,30 anos de regeneração) e uma floresta madura na floresta atlântica de Pernambuco. Foi verificado como as síndromes de polinização são distribuídas entre as diferentes idades de regeneração. Nossa hipótese é que a diversidade funcional das síndromes de polinização é influenciada pela idade da regeneração. As pesquisas foram realizadas em um total de 150 parcelas. Um total de 109 espécies e 1.945 indivíduos (40 famílias e 81 gêneros) foram registrados. Em geral, a distribuição das características reprodutivas foi diferente entre floresta jovem e floresta madura. Houve tendências de aumento da proporção de algumas características reprodutivas em direção à floresta madura. A síndrome de polinização predominante ao longo da cronesequência foi a melitófila. Os resultados não corroboraram a hipótese de que a diversidade funcional da polinização de síndromes é influenciada pela idade da regeneração da floresta.

Palavras-chave: Biologia floral; Florestas jovens;Regeneração natural;Síndromes de polinização.

INTRODUCTION

Forest regeneration is a process of secondary succession at the community and ecosystem level over an area that was previously covered by forest (WIRTH et al., 2009). In the process of secondary succession there is a progression of stages during which forests have a gradual enrichment of species

and an increase in structural and functional complexity (CHAZDON, 2012; GUARIGUATA; OSTERTAG, 2001; TABARELLI; MANTOVANI, 1999). As the regeneration develops and diversifies, the availability of resources increases attracting a wide variety of small and large animals, which become regular visitors or residents in these forests (CHAZDON, 2012).

The association between the patterns of abundance of plant species in tropical forests at different stages of succession and their reproductive characteristics provides a fundamental knowledge for understanding the regeneration process and the essential roles that animals play, for example: at pollinating (MAGNAGO et al, 2014; QUESADA et al, 2009).

Floral signs are important for attracting animal visitors. These signs relate especially in how visitors perceive the flowers and involve features such as size, floral type, color and odor release (GRINDELAND et al., 2005; ROSSI, 2014). The shape and size are floral characteristics that have been used in community-level studies for revealing important implications, not only in plant-pollinator relation, but also for influencing the reproductive success of the plant (BARBOSA, 1997). The floral morphology can either exclude visitors or attract potential pollinators by the interdependent relationship between the size of the flowers and pollinators by the occurrence of different types of floral rewards (MACHADO; LOPES, 2002). Some empirical data show that changes in pollinator communities during succession are driven by the structure and vegetation diversity (ALBRECHT; RIESEN; SHMID, 2010; DEVOTO et al., 2012.).

Therefore, in the early successional stages there is a dominance of generalist species (e.g. pollinated by various small insects) (CHAZDON et al. 2003; OPLER et al, 1980; RAMIREZ, 2004). In the final stages, where there is greater floristic and structural complexity, the proportion of specialization species for floral characteristics (e.g. pollinated by bats, hawkmoths and other mammals) increases, as well as the availability of resources (KOCH; SAHLI, 2013; PARRISH; BAZZAZ, 1979). In general, there is a pollination syndrome accumulation tendency along the succession (Chazdon et al. 2003; RAMIREZ, 2004; DEVOTO et al, 2012). Opler et al. (1980), for example, by studying the secondary succession in the rainforest of Costa Rica noted that along the succession there was an increase in the number of pollination syndromes; whereas in the early stage species pollinated by the wind, small butterflies, small and medium bees were recorded, and with the successional advance, three other syndromes were recorded (cantarophily, chiropterophily and ornithophily), with different proportions according to the successional stage.

Recently pollination syndromes approaches have been analyzed from the functional point of view (GIRÃO et al, 2007; LOPES et al, 2009), which becomes even more interesting when combining this information with the successional communities. The functional diversity quantifies a range of functional features within the community, allowing to evaluate how characteristics are distributed within the functional space (MAGNAGO et al, 2014; VILLÉGER; MASON; MOUILLOT, 2008).

This paper aims to describe the floral reproductive characteristics to determine the pollination systems and functional diversity in a chronosequence (5, 16, 24, 30 years after the abandonment of sugarcane cultivation) and a mature forest in the Atlantic Forest of Pernambuco State, checking how pollination syndromes are distributed among the different ages of the forest. The hypothesis of the present study is that the functional diversity of the pollination syndromes increases with the regeneration of the forest age.

METHODS AND MATERIALS

Field of study and selection of areas

Weekly collections in four young fragments were carried out (5, 16, 24, 30 years of regeneration) and one in a mature forest (over 60 years) belonging to Usina São José (USJ), located in the North Forest Zone of Pernambuco, in a Dense Ombrophilous Forest area (IBGE, 2012). The property covers 270 square kilometers, where there are 202 patches of native vegetation (Atlantic Forest), 96 areas of young forest and 106 remnants of mature forest (TRINITY et. al., 2008).

The local climate is of the '(hot and humid) kind, with an average annual temperature of 24.9 ° C, average rainfall of 1687 mm (Pernambuco Meteorological Laboratory - LAMEPE / ITEP). The geological formation is the Barreiras Group of the Plio-Pleistocene age, with predominantly sandy soils and heavily undulated relief (CPRH, 2003).

Young forests of 16 and 24 years were selected by Nascimento et. al. (2014) from aerial photographs from the 60s, 70s, 80s and satellite images from 2005. In addition, two more areas were defined with an abandonment time of 5 and 30 years using aerial photographs; the images mentioned above and interviews with former residents. For comparison, an area of mature forest studied by Smith (2010) was selected. It is important to note that the mature forest is one where we could not detect if there was human intervention in the previous 60 years, relying on available photographs and satellite images, and interviews with residents,.

Data collection

Survey of arboreal individuals and reproductive characteristics of arboreal species

The survey was conducted on a total of 150 plots (equivalent to 1.5 ha), distributed in four young forests with different regeneration ages (5 (20 ha), 16 (388 ha), 24 (306 ha) and 30 (101 ha)) and in a mature forest (357 ha). In each forest, 30 permanent plots of 10 × 10 m to 10 m away from each other were installed, for sampling of arboreal individuals with stem diameter at the breast height (DBH)> 5 cm, measured at 1.30 m above the ground.

The sampled species were identified with the help of experts and comparisons with collections deposited in the Herbarium Sergio Tavares (HST) and Dárdano de Andrade Lima (IPA). The dried specimens were deposited in the Herbarium Professor Vasconcelos Sobrinho (PEUFR). The species list was prepared in accordance with family and occurrence of locations. Classification of Angiosperm families followed the recommendations of APG III (2009).

All species recorded in the survey were distributed in two main classes of reproductive characteristics: floral biology and sexual system. 1.Floral Biology - 1. Inconspicuous (≤ 4 mm); 2. Small (≤ 10 mm); 3. Medium (> 10 ≤ 20 mm); 4. Large (> 20 ≤30 mm); e 5. Very Large (> 30 mm). Resources - 1. Nectar; 2. Oil; 3. Pollen; 4. Nectar/ Pollen; 5. Others (resin, foral tissues and undetermined). Foral Type Size - 1. Flag; 2. Brush; 3. Inconspicuous; 4. Disc; 5. Tube; 6. Others (Bell, câmera, gullet). Anthesis Period - 1. Nocturnal; 2. Diurnal. 2.Sexual System - 1. Dioicy (including all subtypes); 2. Hermaphrodite (Including hermaphrodite heterostyly); e 3. Monoecy (Including all subtypes).

From this information the pollination syndromes according to Faegri and Van Der Pijl (1979) was inferred. The information was based on field observations, comprehensive floras review, published data and specimens' survey in the Herbarium UFP (UFPE) and PEUFR (UFRPE).

For each portion of the fragments studied, the proportion of species and individuals within the 28 categories that compose the three main classes of reproductive characteristics was calculated.

Data analysis

The variation in the proportion of species and individuals at different ages for reproductive traits was analyzed using one-way ANOVA, followed by the Tukey post-hoc test. In order to stabilize the variance, the data were converted into percentages arcsine $\sqrt{x} / 100$.

For the evaluation of the reproductive characteristics distribution in different ages the non-metric multidimensional scaling was conducted (NMDS), with ordinations of all 150 plots using the Gower similarity matrix (coefficient) of reproductive traits composition (KREBS, 1989).

For the verification of the hypothesis, a grid with species represented in lines and functional traits (pollination syndromes) in the columns was built. For this, the binary distance was used (PAVOINE et al., 2009) because the data were qualitative. FD index was calculated, which is similar to PD (PHYLOGENETIC DIVERSITY FAITH, 1992), since both are based on the phylogenetic and functional dendrograms arms' length summation, respectively. Thus, the functions "ses.mpd" and "ses.mntd" of the "Picante" packet (KEMBEL et al., 2010), are used to calculate PD (were also used to calculate the FD).

RESULTS AND DISCUSSION

Reproductive characteristics of arboreal species

A total of 109 species and 1,945 individuals (40 families and 81 genera) were recorded in the 150 sampled plots. Of the 109 species studied, 70 were collected and observed in the field and the rest were analyzed through bibliographic references. Species and individuals with diurnal flower

anthesis, hermaphrodites and those that show nectar as the main resource for pollinators occurred in greater proportion in all studied forests (Tables 1 and 2).

The Atlantic Forest of São José at different ages (5, 16, 24 and 30 years after the abandonment of sugarcane and mature forest) is characterized by species with predominantly diurnal flowers, of inconspicuous size, hermaphrodites and species that provide nectar as the main attractive feature to pollinators. However, these forests do not have the same pattern, as some reproductive characteristics change with the different regeneration ages. The differences between the forests were more evident in terms of the proportion of species (forests differed by 57.14%) than in terms of individuals (52.38%) among the reproductive characteristics.

As for the sexual system, in all the analyzed fragments, hermaphroditism was more frequent with a significant difference between the ages for species and individuals (Tables 1 and 2). As for the dioecious sexual system, there was an increase in the proportion of species and individuals towards mature forest (Tables 1 and 2). The predominance of hermaphroditism at all ages of the chronosequence, was also described by Rossi (2014) when studying a chronosequence ranging from 2-80 years after the abandonment of agricultural crops in areas of dense ombrophylous forest in Paraná. A similar pattern was reported by Chazdon et al. (2003), when they studied different tropical forests in northeastern Costa Rica. In Atlantic Forest fragments in the Northeast, hermaphrodite systems occurred in greater proportion in young forests than in preserved forests (GIRÃO et al., 2007; LOPES et al., 2009). The increase in the proportion of dioecy along the chronosequence in the present study shows that

Table 1 - Percentage of arboreal species (mean ± standard deviation) per reproductive traits in forests of different ages and mature forest at São José's Plant, Igarassu, PE, Brazil. Young forests (FJ 5 = five years, FJ 16 = 16, 24 = FJ 24, FJ 30 = 30 years) and mature forest (FM); N = number of species recorded.

Tabela 1 - Porcentagem de espécies arbóreas (Média ± desvio-padrão) por características reprodutivas em florestas de diferentes idades e floresta madura na Usina São José, Igarassu, PE, Brasil. Florestas jovens (FJ 5 = cinco anos, FJ 16 = 16 anos, FJ 24 = 24 anos, FJ 30 = 30 anos) e Floresta madura (FM); N= número de espécies registradas.

Reproductive Characteristics (% indivíduals)	FJ 5 Mean±SD	FJ 16 Mean±SD	FJ 24 Mean±SD	FJ 30 Mean±SD	FM Mean±SD	P
Sexual System (N=88)						
Hermaphrodite	66,66±36,19ab	76,17±20,42a	65,21±17,58ab	61,17±15,95ab	55,39±15,37b	0,011
Diecious	15,84±32,48	19,67±33,06	19,38±31,50	25,99±25,99	34,31±36,14	0,191
Monoecious	17,50±36,02	4,16±14,14	15,41±32,64	17,18±29,92	10,30±19,01	0,304
Floral Type (N=87)						
Brush	11,40±27,18	10,05±14,48	5,30±10,85	5,43±11,90	5,0±12,77	0,438
Flag	42,00±38,00a	18,90±21,84b	19,20±16,54b	8,20±8,79b	15,2±21,42b	< 0,0001
Disc	5,00±13,54c	22,95±20,99b	16,48±15,10bc	16,07±17,23bc	38,21±28,63a	< 0,0001
Inconspicuous	17,00±31,71	7,40±14,52	7,80±11,95	9,80±17,10	24,00±8,33	0,075
Pipe	8,9±17,48b	12,50±14,30ab	18,70±14,15ab	21,80±20,01a	22,15±20,90a	0,01
Others	15,7±31,13b	28,20±19,51a	32,52±32,03a	38,70±34,19a	17,20±31,31b	0,016
Anthesis (N=45)						
Diurnal	68,33±38,85ab	68,94±20,31ab	61,53±19,39b	73,51±20,38ab	80,30±20,38a	0, 05
Nocturnal	31,67±36,85ab	31,06±20,31ab	38,47±19,39a	26,49±20,38ab	19,70±20,38b	0,05
Floral Size (N=83)						
Inconspicuous	25,00±30,31ab	24,78±15,76a	36,57±18,85ab	43,07±20,13b	24,19±22,84ab	0,002
Small	25,16±16,51	25,45±13,53	27,24±13,33	25,05±12,84	31,36±17,30	0,828
Medium	35,50±16,63	40,61±12,52	28,52±18,12	21,73±18,12	28,86±18,60	0,069
Large	7,20±16,51	6,20±13,53	4,48±13,33	5,00±12,84	8,03±17,30	0,885
Very Large	6,64±16,63	2,96±12,52	3,19±12,65	5,15±18,12	7,56±18,60	0,809
Resources (N=59)						
Nectar	13,22±21,11ab	32,72±31,25a	31,45±30,34ab	30,24±28,01ab	31,92±27,24b	0,041
Pollen	25,40±14,66a	19,62±11,32ab	7,77±4,49b	9,29±5,36b	13,44±7,76ab	0,014
Nectar/Pollen	30,16±37,36ab	16,83±18,48a	41,27±28,74b	32,85±20,55ab	37,55±28,97b	0,012
Oil	18,55±22,50a	12,94±12,69ab	9,11±13,23ab	9,20±13,75ab	7,25±11,38b	0,043
Others	12,67±23,40	17,89±12,49	10,40±15,27	18,42±19,95	9,84±16,01	0,182

Different letters indicates statistical differences by Tukey test (P <0.05) and same letters indicate not statistically different from each other.

Table 2 – Percentage of arboreal individuals (mean ± standard deviation) per reproductive traits in forests of different ages and mature forest at São José, Igarassu, PE, Brazil. Young forests (FJ 5 = five years, FJ 16 = 16, 24 = FJ 24, FJ 30 = 30 years) and mature forest (FM); N = number of registered individuals.

Tabela 2 - Porcentagem de indivíduos arbóreos (Média ± desvio-padrão) por características reprodutivas em florestas de diferentes idades e floresta madura na Usina São José, Igarassu, PE, Brasil. Florestas jovens (FJ 5 = cinco anos, FJ 16 = 16 anos, FJ 24 = 24 anos, FJ 30 = 30 anos) e Floresta madura (FM); N= número de indivíduos registrados.

Reproductive Characteristics (% indivíduals)	FJ 5 Mean±SD	FJ 16 Mean±SD	FJ 24 Mean±SD	FJ 30 Mean±SD	FM Mean±SD	P
Sexual System (N=1746)						
Hermaphrodite	64,05±36,71b	82,97±17,23a	62,50±23,89b	56,07±20,18b	57,67±15,82b	< 0.0001
Diecious	25,88±39,34ab	10,30±20,92b	24,94±30,82ab	33,84±36,94[a]	36,09±35,50a	0,026
Monoecious	10,07±28,62	8,73±19,20	12,56±22,56	10,09±19,74	6,24±19,06	0,865
Type Floral (N=1667)						
Brush	8,16±21,67	7,90±13,88	7,20±14,47	8,40±8,68	7,30±18,05	0,998
Flag	32,70±42,03	23,50±20,03	23,60±21,08	20,20±24,50	23,80±30,15	0,561
Disc	5,94±17,17b	18,56±19,02c	13,85±17,93bc	10,28±8,00bc	40,72±24,89a	< 0.0001
Inconspicuous	38,2±45,30ab	26,80±27,07ab	41,00±39,00ab	42,60±41,53[a]	15,10±23,93b	0,024
Pipe	6,30±17,37	2,70±10,93	10,30±16,51	8,52±8,93	7,90±19,32	0,389
Others	8,70±19,67b	20,50±19,51a	4,05±12,84b	10,00±8,08ab	5,18±13,00b	< 0.0001
Anthesis (N=1246)						
Diurnal	77,99±33,49ab	71,98±23,80ab	64,98±22,82b	67,37±29,69b	88,30±12,00a	0, 004
Nocturnal	22,01±33,49ab	28,02±23,80ab	35,02±22,82ab	32,63±29,69[a]	11,70±12,00b	0,004
Floral Size (N=1928)						
Inconspicuous	58,92±35,40	60,16±33,57	54,18±22,27	54,77±22,85	52,03±18,34	0,772
Small	10,21±20,89	12,00±29,48	17,03±20,44	20,42±29,60	23,80±32,53	0,224
Medium	14,33±30,40	16,24±30,40	14,79±27,92	19,26±27,92	18,24±29,28	0,953
Large	12,11±26,33	7,66±20,11	8,71±8,53	3,72±8,53	3,33±9,42	0,298
Very Large	4,43±14,73	2,89±6,28	5,29±12,94	1,83±5,24	2,60±9,55	0,707
Resources (N=1245)						
Nectar	31,26±34,32	29,78±31,31	36,67±27,72	32,08±34,72	27,56±28,80	0,855
Pollen	17,15±31,42[a]	14,78±15,24a	5,23±13,95b	6,04±16,63b	17,56±20,45a	0,042
Nectar/Pollen	13,26±25,02b	16,45±20,74b	43,67±29,71a	49,03±29,08[a]	25,73±29,83b	< 0.0001
Oil	26,93±31,73[a]	6,06±9,66b	9,80±20,04b	4,14±16,50b	15,13±21,22ab	0,0004
Others	11,40±23,72b	32,93±35,64a	4,63±13,71b	8,71±14,55b	14,02±13,78b	0,023

Different letters indicates statistical differences by the Tukey test (P <0.05) and the same letter indicates no statistical difference from each other

species with more specialized sexual systems tend to occur at higher proportions in the later stages, a trend also observed by Chazdon et al. (2003). Quesada et al. (2009) reported that dioecy is absent or occurs in a lower proportion in the initial stages of regeneration than in mature forest. According to Spencer and Barrett (1998) this is due to the fact that the dioecy is common in arboreal species.

Evaluating the floral types in chronosequence there was a trend of increase in species of floral tube type (Table 1). The increase of floral tube type in the chronosequence indicates an increase of flowers with less accessible resources and more specialized, as observed by Lopes et al. (2009), who have compared interior areas of mature forest with areas of young forests. Similarly, Girão et al. (2007) found lower proportions of floral tube type species in fragmented areas compared to inland areas of the forest. In contrast, Rossi (2014) observed no difference in the proportion of tube type flowers in the chronosequence. This increase in the proportion of species with flowers with more specialized floral morphology is an advantage for the plant as it results in a higher efficiency in pollination and promotes loyalty of pollinators, with a consequent increase in pollen flow (JOHNSON; STEINER, 2000) and discourages or prevents the access of floral resources by others (robbers or inefficient pollinators) than the most efficient pollination agents (AIGNER 2004).

Regarding anthesis it was noted that although all the forests along the chronosequence have been dominated by species with diurnal anthesis, those with nocturnal anthesis were more frequent in the forest of 24 years of regeneration. About floral size, there was an increasing trend in the proportion of small flowers toward the mature forest (Tables 1 and 2). In young forests of age 16 and 24 years, the highest proportions of species with nocturnal anthesis occurred, pollinated by bats and / or hawkmoths,

such as *Inga cayennesis, I.ingoides, Himatanthus phagedaenicus* and *Paypayrola blanchetiana*. These species pollinated by nocturnal animals usually have flowers with white, greenish or pale colors, twilight opening nocturnal, issuing sweetish odors and nectar production (BAWA, 1990; FAEGRI; VAN DER PIJL 1980).

The most abundant resource was nectar / pollen, with an upward trend in the proportion of species that had this feature along the chronosequence (Table 1). However, in terms of individuals, in spite of the difference in proportions between forests, no pattern was found (Table 2). In a large part of the forests analyzed here, the nectar was the resource that predominated, with higher proportions in mature forest, as expected, since most pollinators groups are nectar consumers (ENDRESS, 1994). In general, nectar is the most common feature in Brazilian ecosystems, followed by pollen (GIRÃO et al., 2007; MACHADO; LOPES, 2004; OLIVEIRA; GIBBS, 2000; OLIVEIRA et al, 2009; TAVARES, 2011).

The increase in the floral tube type flowers in chronosequence in the present study indicates an addition of flowers with less accessible resources and more specialized, as observed by Lopes et al. (2009) who have compared the interior areas of mature forest with areas of young forests. Similarly, Girão et al. (2007) found lower proportions of species of floral tube type in fragmented areas compared to inland areas of the forest. In contrast, Rossi (2014) observed no difference in the proportion of flowers of the tube type along the chronosequence. This increase in the proportion of species with flowers with more specialized floral morphology is an advantage for the plant as it results in a higher efficiency in pollination and promotes loyalty of pollinators, with a consequent increase in pollen flow (JOHNSON; STEINER, 2000) and discourages or prevents access to floral resources by other animals (robbers or inefficient pollination) than the more efficient pollination agents (AIGNER, 2004).

In short, the forest of early chronosequence (5 years) was dominated by species and individuals having reproductive characteristics as hermaphroditism, type flag flowers, diurnal, medium size and species that offer nectar and pollen as resources. Young forests with more advanced ages (24 and 30) showed some similar characteristics such as diurnal anthesis, hermaphrodite flowers, flowers with inconspicuous sizes, with "other" floral type, with nectar and pollen the most abundant resource. In mature forest, the assembly was dominated by trees with reproductive characteristics as floral disc, small size and higher proportion of dioecy.

There was a change in the occurrence of syndromes along the regeneration in relation to ornithophilous and anemophilous species. Only one ornithophilous species was found in the 16-year old forest. Anemophilous species were registered in young forests of 5, 24 and 30 years of age, being absent in the 16-year old young forest and mature forest. The remaining pollination syndromes occurred throughout the chronosequence, but in different proportions in ages. The mature forest had fewer syndromes than other forests. The pollination syndrome with greater representation was the melittophily, present throughout the chronosequence, both in number of species and individuals. Then came the pollination by several small insects and other insects (beetles, butterflies and flies).

For species with more specialized pollination (bats and hawkmoths), differences were found between forests, but with some standards. The species pollinated by hawkmoths were of higher proportions in the 24 and 30 years old forests. In terms of individuals, there was no significant difference between the different forests.

The forests of different ages had the predominance of melittophily with 40% of registered syndromes, a pattern also observed by Ramirez (2004) by studying different successional stages in rainforest of Venezuela. Bees are the main sponsors of plant breeding in tropical forests because they can use a big variety of resources of flowers and visit great diversity of flower types (BAWA, 1990; KIMMEL et al, 2009; MARTINS; BATTLE, 2007; RAMIREZ; BRITO 1992; SILVA et al, 2012; TAVARES, 2011).

Ramirez (2004), when studying pollination syndromes along the succession in tropical forest in the Central Plains of Venezuela, observed differences in frequency of pollination; where the intermediate stage vegetation had the highest proportions of species pollinated by bees, other insects and birds than at other ages. In the chronosequence studied in São José, the 24 years forest had higher proportions of sphingophilous and chiropterophilous species. Ramirez (2004) found higher proportions of chiropterophilous in mature forest species, differently from the present study. This difference can be explained by the fact that intermediate successional stages may contain the largest number of species, with pioneer and secondary species co-habiting the same area (TOWNSEND et al., 2010).

Different from expected, there was no increase of pollination syndromes along the chronosequence; the opposite reported by Opler et al. (1980) in a cronossequence in the rainforest of Costa Rica. It should be noted that in São José there was a small number of chiropterophilous, sphingophilous and ornithophilous species, which can be due to: 1) the area being drier than other forests already

studied in the region; 2) reflection of the state of conservation of these forests, because in vegetation conserved in more humid areas of the Atlantic Forest region pollination by these biotic vectors happens more frequently (GIRÃO et al., 2007; LOPES et al, 2009; MACHADO; LOPES, 2004).

Similarity and functional diversity of reproductive characteristics

The NMDS analysis applied to the reproductive characteristics of forests of 5, 16, 24 and 30 years and mature one, revealed the formation of two groups of species (Fig. 1A). The first group was composed of species of mature forest (FM) and young forest 16 (FJ 16) and the second group was formed by young species of forests 30 (FJ 30) and 24 years (FJ 24), isolating the five-year forest (FJ5). As regards the similarity of the characteristics in terms of individuals, there were also two groups: the first with young forests 16 and 30 and the second group formed by mature forest and 24 year old forest, as well isolating the five-year forest (Figure 1B). These standards were well supported by low levels of stress: 0.07 (species) and 0 (individuals) (Figs. 1A and 1B). The groups formed by young forests with older ages and mature forest and the isolation of the 5-year forest indicate that the forest in early stage showed a difference of reproductive characteristics, both at the level of species as of individuals. This can be explained by the fact that younger areas exhibited less arboreal species than other areas.

The functional diversity index was not influenced by the age of regeneration (Table 3). Thus, this study does not confirm the hypothesis that the functional diversity of pollination syndromes is influenced by the age of regeneration of forests. This pattern differs from those reported by Lopes et al. (2009) where the functional diversity was higher in forests conserved inside areas than in areas of young forests, although the diversity index they used was different. It is possible that the mature forest is also a regeneration area at a more advanced stage floristically although functionally similar to the others.
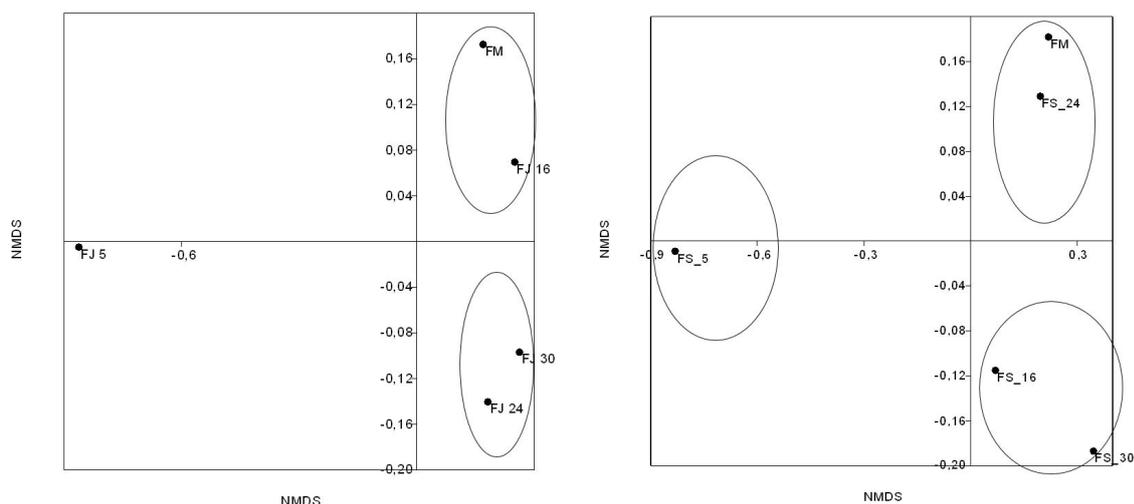

Figure 1 – Ordination by the Non-metric Multidimensional Scaling method (NMDS) of young forest and mature forest based on the similarity in reproductive characteristics in terms of (A) species and (B) individuals in São José, Igarassu, PE, Brazil. Young forests (FJ 5 = 5 years, FJ 16 = 16, 24 = FJ 24, FJ 30 = 30 years) and mature forest (FM).

Figura 1 - Ordenação pelo método do escalonamento multidimensional não métrico (NMDS) das florestas jovens e floresta madura com base na semelhança nas características reprodutivas em termos de (A) espécies e (B) indivíduos na Usina São José, Igarassu, PE, Brasil. Florestas jovens (FJ 5 = 5 anos, FJ 16 = 16 anos, FJ 24 = 24 anos, FJ 30 = 30 anos) e Floresta madura (FM).

Table 3 - Functional diversity (Z value) of pollination syndromes for areas with different ages along the chronosequence; young forests (FJ 5 = 5 years, FJ 16 = 16, 24 = FJ 24, FJ 30 = 30 years) and mature forest (FM). p values <0.05.

Tabela 3 - Diversidade funcional (Z valor) de síndromes de polinização para as áreas com diferentes idades ao longo da cronossequência. Florestas jovens (FJ 5 = 5 anos, FJ 16 = 16 anos, FJ 24 = 24 anos, FJ 30 = 30 anos) e Floresta madura (FM). Valores de p < 0,05.

	Area	Z value	P value
FD	FJ 05	0,79	0,75
	FJ 16	0,20	0,59
	FJ 24	0,18	0,58
	FJ 30	0,06	0,53
	FM	-0,69	0,26

CONCLUSION

The different ages differ in most reproductive traits (5, 16, 24, 30 years and mature forest). Overall, the biggest differences were between five years old forest and others. There were, towards mature forest, upward trends in the proportion of some reproductive characteristics such as flowers' tube-type, small flowers, dioecious sexual system and nectar/pollen production. The predominant pollination syndrome was melittophily along the chronosequence and more specialized syndromes were found in higher proportions in young forests of 24 and 30 years. There wasn't a trend towards a greater number of syndromes in the mature forest, as expected. But rather, it had the lowest number of syndromes. The results did not corroborate the hypothesis that the functional diversity of pollination syndromes is influenced by the age of forest regeneration.

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