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Research Article

Tree species composition, breeding systems, and pollination and dispersal syndromes in three forest successional stages in a tropical dry forest in Mesoamerica

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Abstract

Tropical dry forests (TDF) in Mesoamerica are highly endangered by the expansion of human activities (e.g., agriculture and cattle ranching). In contrast, TDF in Costa Rica have experienced outstanding restoration due to changes in economic and conservation policies. Currently TDF landscapes in Costa Rica are a mosaic of different successional stages. Tree breeding systems and pollination and dispersal syndromes are key elements for understanding restoration processes in TDFs. In this study we describe and compare tree species composition and diversity in three TDF successional stages (early, intermediate and late) in Guanacaste, Costa Rica. We describe for the first time tree species breeding systems and pollination and dispersal syndromes for the largest and most significant TDF remnant in Mesoamerica. We set up nine plots, three per successional stage, and we measured and identified 1,072 trees from 96 species. Species richness and diversity indices were higher for the intermediate stage. Monoecy was the most common breeding system, as in other tropical life zones. Insects were the dominant pollinators, facilitated by the trees' small inflorescences. Wind was found to be not only the next most influential pollinator, mainly in open and disturbed early forests, but also it was also a good seed dispersal agent. As TDF age increases so does the relevancy of birds and mammals as dispersers; the late stage therefore has more tree species with adaptations to these dispersers.

Key words: Santa Rosa National Park; Costa Rica; monoecy; dioecy; species richness

Resumen

Los bosques secos tropicales (BST) están altamente amenazados en Mesoamérica debido a actividades humanas (agricultura y ganadería). Sin embargo, Costa Rica ha experimentado un importante proceso de restauración del BST como consecuencia de cambios en economías y políticas de conservación. Actualmente la cobertura forestal es un mosaico de estadíos sucesionales. Los sistemas reproductivos de las especies de árboles, sus síndromes de polinización y dispersión de semillas y cómo estos síndromes son afectados por condiciones ambientales y, son importantes elementos para entender los procesos de restauración del BST. En este estudio describimos y comparamos la composición y diversidad de especies de árboles en tres estadios sucesionales del BST en Guanacaste, Costa Rica. También describimos por primera vez los sistemas reproductivos y síndromes de polinización y dispersión para las especies de árboles presentes en el más importante remanente BST en Mesoamérica. Instalamos nueve parcelas en tres estadios sucesionales (temprano, intermedio y tardío, tres parcelas por estadio) y medimos e identificamos 1,072 árboles pertenecientes a 96 especies. La riqueza y diversidad de especies fue mayor para el estadio intermedio. El sistema de reproducción monoica fue el más común, siguiendo el patrón general para zonas de vida tropicales. La mayoría de especies de árboles son polinizadas por insectos, y los árboles poseen inflorescencias pequeñas. El viento es un importante polinizador, y dispersor de semillas, y este síndrome es más común en bosques tempranos y perturbados. Las aves y mamíferos aumentan su importancia como dispersores conforme los BSTs maduran, por lo tanto el estadío tardío posee más especies de árboles con adaptaciones para estos agentes dispersores.

Palabras clave: Parque Nacional Santa Rosa; Costa Rica; monoico; dioico; riqueza de especies

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Introduction

Among the most threatened ecosystems worldwide are the tropical dry forests (TDFs) [1-8]. In the Neotropics, particularly in Mesoamerica, TDFs are heavily utilized and perturbed by anthropogenic activities, primarily by agriculture expansion, tourism, and an increase in human settlements [9-11]. However, in some countries such as Costa Rica, TDFs are experiencing a significant comeback due to changes in socio-economic conditions [12-15]. Consequently, the TDFs in Costa Rica are a mosaic of secondary forests with varying ages and fragment sizes [1, 11, 16-18]. Currently, the vertical structure of Costa Rica's TDF is composed of deciduous and semi-deciduous trees with heights between 5 to 15 m [18, 20], organized mainly in two strata: understory and canopy [18]. The understory has more evergreen species, adapted to low light conditions during the wet season, than the canopy layer [18-20].

The species diversity and composition of TDF successional stages are influenced and driven by natural and anthropogenic disturbances [21, 22]. Forest fires and the secondary effects of tropical storms (i.e. strong winds, extreme rainfalls) allow the opening of canopy gaps, interrupting the natural forest succession. This disruption is described by the Intermediate Disturbance Hypothesis (IDH) [23-25], which argues that any ecological community in equilibrium is affected by disturbances that enhance species diversity by allowing for species colonization and establishment [26].

Species presence or absence in a particular habitat can be determined by different factors (e.g. abiotic and biotic) [27]. In the case of plants, their mobility and location in the landscape is determined by seed dispersal strategies. For this reason, plants have adaptations that optimize seed dispersal by abiotic factors such as wind and water, or biotic dispersers such as fauna (e.g., fleshy colored fruits, seeds with food reward) [28], although there is debate about ripe-colored fruits as a strategic defence against pests and as an attractor of dispersers [28]. However, even when the seeds succeed at colonizing a site, seed germination and seedling success require other favorable conditions (e.g. soil humidity, light exposure or shade, amount of rain, and less competition with conspecifics and heterospecifics) [29, 30]. Plant reproduction is also important [30] and is related to pollinators and seed dispersers [31]. The variety of seed dispersal and pollination syndromes range from very generalist (e.g., wind, water, gravity) to very specific (e.g., particular species of fauna) [32]. The success of each strategy is variable, but specialization depends highly on other organisms, which means that the pollinator or disperser can be absent or specific to a particular habitat. The presence or absence of pollinators and dispersers can be affected by anthropogenic activities such as deforestation and forest fragmentation [33], by unusual climatic conditions, or by specific habitat characteristics such as seasonal flooding or drought conditions. [33].

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Studies on the ecology and dynamics of plant species for TDFs are mainly focused on a few particular species [34-36], but at the community level differences in breeding systems, pollination, and seed dispersal syndromes in TDFs are not well understood or studied [34]. Type and frequency of breeding systems (e.g. monoecy and dioecy) have been studied mainly in the Neotropical rainforest, but there are few such studies for TDF [37-39]. The sexual systems (e.g. monoecy and dioecy), pollination syndromes, and the characteristics of flowers and fruits can influence the forest dynamics and successional processes [38, 40]. Therefore, plant pollination and seed dispersal strategies can determine the plant community composition in a particular site [41]. Furthermore, plant community can also influence the presence or absence of pollinators and seed dispersers, as well as the presence and abundance of certain plant species and breeding systems. Additionally, vegetation cover, related to different forest successional stages, can affect pollinators' and dispersers' presence, abundance, and composition [42, 43].

The characteristics of the remaining TDF fragments (size, shape and conservation status), underline the importance of its successional dynamics. Thus, it is not only critical to evaluate tree species composition in the TDF successional stages (early, intermediate, and late), but also it is important to understand how breeding systems, and pollination and seed dispersal syndromes vary across these successional stages, and whether these factors can restrict or potentiate the presence of some plant species to a particular successional stage.

In this study we describe and compare the breeding systems, pollination and seed dispersal syndromes of tree species in three TDF successional stages in Guanacaste, Costa Rica. The comparisons are based on the species composition, diversity and differences among successional stages, the main objective being to determine which reproductive traits influence the TDF restoration process.

Methods

Study Area

The study area is located in the Santa Rosa National Park (SRNP), on the North-Western coast of Costa Rica (10°48'53" N, 85°36'54" W). This conservation area protects one of the largest dry forest remnants in Mesoamerica (Fig. 1). The climate has a dry season of six months (December-May) and a highly variable annual precipitation that ranges from 915 mm yr^{-1} to 2,558 mm yr^{-1} (Fig. 2) [4].

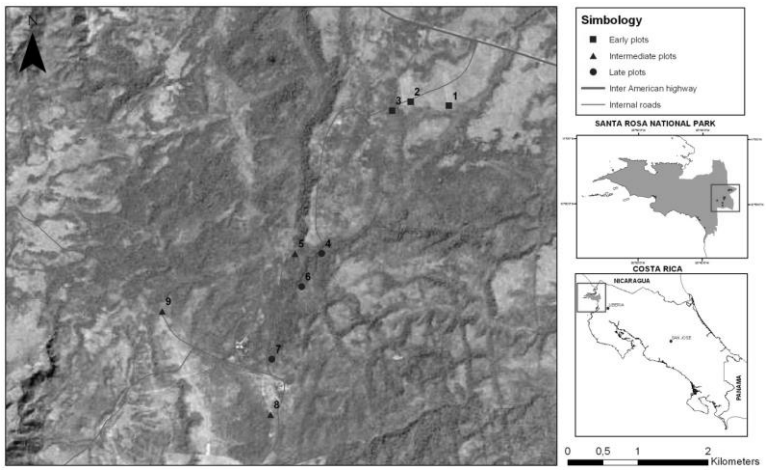


Fig. 1. Santa Rosa National Park map showing locations of the nine plots in the three TDFs successional stages, Guanacaste, Costa Rica.

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The current land cover is a mixture of forest successional stages and pasture areas, as the SRNP was created from an old Spanish Hacienda (i.e., cattle ranching farm) [10, 11, 18]. In addition, most of the current TDF at SRNP is under intensive fire control, which in turn creates a very heterogeneous forest with a high diversity of habitats and biotic communities [44].

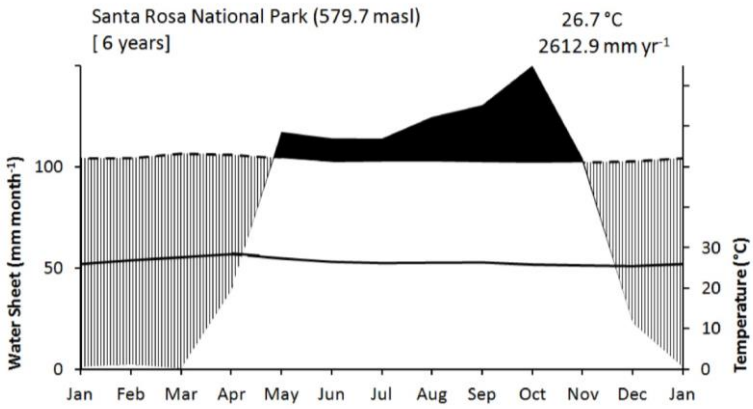


Fig. 2. Climate diagram for Santa Rosa National Park based on 6 years of meteorological data (2006-2011). It shows the monthly variation of wettest months (black solid area), evapo-transpirated water (white solid area), and water deficit (vertical lined area) defined by the potential evapotranspiration (dotted line) and temperature (solid line).

Data collection

Forest successional stages were selected based in their structure and composition according to Kalacska et al. [18]. They describe the forest succession in SRNP in terms of forest structure: tree height, number of canopy layers, tree light tolerance, and plant types, using forest age as a descriptive characteristic of the forest development and not as a deterministic factor. The categories of estimated forest ages in 2007 for these stages according to Kalacska et al. [18] are 21 years old (early stage), 32 y.o. (intermediate stage), and 90 y.o. or older (late stage) (Fig. 3).



Fig. 3. Forest successional stages a) early, b) intermediate, c) late, dry season, Santa Rosa National Park, Guanacaste, Costa Rica.

According to protocols described by Alvarez et al. [45], nine permanent plots of 1,000 m^2 (50 x 20 m, three per successional stage) were established. The selection of forest patches was performed previously by Kalacska et al. [18], who evaluated TDF in SRNP and determined its random spatial distribution. The distance between plots ranged from 400 to 1,000 m. In each plot, we measured and identified all trees with diameters at breast height (DBH, i.e., 1.3 m) larger than 5 cm.

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We classified each tree species within the plots according to its breeding system (e.g. monoecious or dioecious), pollination, and seed dispersal syndromes. Breeding systems, pollination, and seed dispersal syndromes were determined for each species, and we supported our findings with literature review, scientific articles and species monographs. We had advice from plant parataxonomists of SRNP, and we also checked in the field for some of the tree species pollination syndromes that are not well determined. Monoecious plants have male and female flowers on the same individual (tree), including perfect flowers. Dioecious plants have flowers of one sex, male or female on different individuals [46]. We established the categories for pollination and seed dispersal syndromes according to Chazdon et al. [47].For pollination we established: entomophily (insects, including the Orders Coleoptera, Hymenoptera, Hemiptera, Diptera and other); lepidopterophily (Order Lepidoptera, moths, hawkmoths, and butterflies); anemophily (wind); chiropterophily (bats); and ornithophily (birds). Since some species can have more than one pollination system, we categorized them by the most important for each of the species observed [48]. We then classified trees according to the following seed dispersal syndromes: anemochory (wind); autochory (ballistic); barochory (gravity); chiropterochory (bats); mastochory (mammals other than bats); ornithochory (birds); and saurochory (reptiles). We also determined tree species richness, species diversity, composition, and abundances for each successional stage.

Data analysis

We estimated tree species diversity for each successional stage using Shannon diversity index (H') [49, 50], and we then compared this index among successional stages with two sample T-tests [51]. We performed a Jaccard's coefficient of similarity (J) and cluster analysis based on plot species composition for the successional stages [52]. We also performed a Morisita Index (Cλ) and a cluster analysis based on plot species composition and abundance [53]. Both indexes have been used widely to compare tree species composition among forest stages [52, 54, 55]. Finally, we performed Chi-squares tests to compare breeding systems among successional stages.

Results

Species Composition and Diversity

We measured a total of 1,104 trees in the nine successional plots. These trees were classified in 96 species, and grouped in 41 families (Appendix 1). Tree species richness was highest in the intermediate successional stage (72 species), followed by the late (61 species), and then early (32 species) stages (Appendix 1). Some endangered species such as Cocobolo (*Dalbergia retusa*) and Spanish cedar (*Cedrela odorata*), and species with high risk of extinction like Mahogany (*Swietenia macrophylla*) [56, 57], were found in all three TDF successional stages with a low abundance (e.g. *Swietenia macrophylla* individuals percentage per stage: early: 0.3%, intermediate 0.9%, and late 0.2%). The early forest stage is dominated by species well adapted to open habitats like Silk cotton tree (*Cochlospermum vitifolium*), Madero negro (*Gliricidia sepium*) and Yayo (*Rehdera trinervis*) (Appendix 1) [44, 58]. These are also sun-loving species (heliophytes) that have anemochory and autochory dispersal syndromes. Molenillo (*Luehea candida*) and Guácimo (*Guazuma ulmifolia*) are the dominant species of the intermediate stage, and these are old tall trees that remain in forest patches. Mexican jumping bean (*Sebastiana pavoniana*) and Cancerina (*Semialarium mexicanum*) are shade tolerant species that prevail in the late stage.

In the early successional stage, there was a total of 20 families, the intermediate stage 35 families, and the late stage 36 families (Appendix 1). Tree species from the Fabaceae family were present in all the successional stages (Table 1) with abundances between 15-21% of the total individuals registered in each stage (early: 20.4%, intermediate: 18.5%, and late: 15.9%); however, this family is more dominant in the early and intermediate stages. Some families were highly dominant in only one particular successional stage: Verbenaceae (29.5%) and Cochlospermaceae (18.2%) in early stage and

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Euphorbiaceae (20%) in the late stage (Table 1). Some families were only present or at least more common in some stages, for example Burseraceae in late stage; Tiliaceae, Flacourtiaceae, Sterculiaceae and Boraginaceae in the intermediate stage (Table 1).

Table 1. Tree families with a percent of composition greater than 5% in three tropical dry forest successional stages in Santa Rosa National Park, Guanacaste, Costa Rica.

Stage	Family	No of species	% Composition
Early	Verbenaceae	2	29,5
	Fabaceae	7	20,4
	Cochlospermaceae	1	18,2
	Hippocrateaceae	1	5,3
	Malphigiaceae	1	5,3
Intermediate	Fabaceae	12	18
	Tiliaceae	4	9
	Rubiaceae	4	9
	Meliaceae	6	8
	Flacourtiaceae	4	7
	Bignoniaceae	5	6
	Sterculiaceae	2	6
	Boraginaceae	2	6
Late	Euphorbiaceae	5	20,0
	Rubiaceae	6	14,5
	Hippocrateaceae	1	11,6
	Fabaceae	8	10,8
	Bignoniaceae	4	6,8
	Burseraceae	3	5,7

The intermediate stage is the most diverse (H' = 3.89), while the early and late stages account for H' values of 1.90 and 3.31 respectively. The diversity indices showed differences among the three stages (late vs. intermediate, T= 7.93, df= 784, p< 0.0001; late vs. early, T= 12.99, df= 609, p< 0.0001; intermediate vs. early, T= 19.30, df= 471, p<0.0001). Of 96 species in total, 17 species were common to all successional stages, while four species were exclusive to the early stage, 22 to the intermediate stage, and eight to the late stage (Appendix 1). Species similarity among successional stages was low, and we determined 26% of species similarity between the early and the intermediate stages, 33% between the early and the late stages, and 44% between intermediate and late stages. Based on Jaccard's similarity, we determined two major groups from a cluster analysis. One group allocates the three early stages plots with an intermediate plot (I3) and a late plot (L2), and the second groups two intermediate and two late stage plots (Fig. 4). The first group is based on the presence of four common species among the plots Yayo (*Rehdera trinervis*), Silk cotton tree (*Cochlospermum vitifolium*), Cancerina (*Semialarium mexicanum*), and Nance (*Byrsonima crassifolia*) showing a dominance of pioneer species. The second group is based on the presence of shade intolerant species like Molenillo (*Luehea candida*), Guácimo (*Guazuma ulmifolia*), and Madroño negro (*Guettarda macrosperma*) (Appendix 1). Most trees of these species are old trees that remain when forests become old.

The cluster based on Morisita Index showed also two main groups (Fig. 5). Plot similarities were very low, but two early plots (E1 and E2) had a high similarity (>0.8) due to the high abundance of Yayo (*Rehdera trinervis*) (35% of the total trees) and Silk cotton tree (*Cochlospermum vitifolium*) (25% of the total trees) (Appendix 1). The plot with the lowest species similarity is a late stage of succession (L1), due to the high dominance of Mexican jumping bean (*Sebastiana pavoniana*) (32% of the total trees) and Quina (*Exostema mexicanum*) (12%) (Appendix 1).

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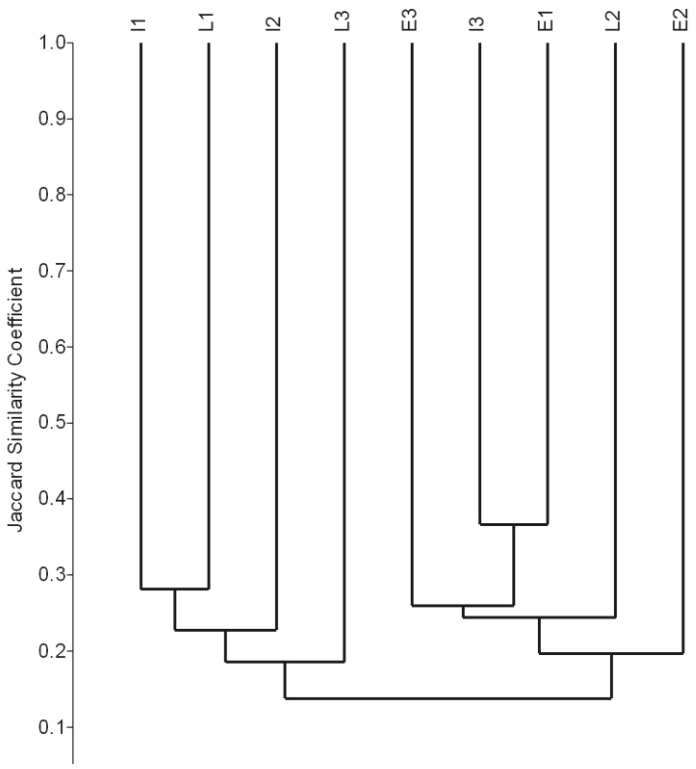


Fig. 4. Cluster analysis for Jaccard Similarity Coefficient based on plot species composition in the Early (E1, E2, E3), Intermediate (I1, I2, I3), and Late (L1, L2, L3) successional stages of Tropical Dry Forests in Santa Rosa National Park, Guanacaste, Costa Rica.

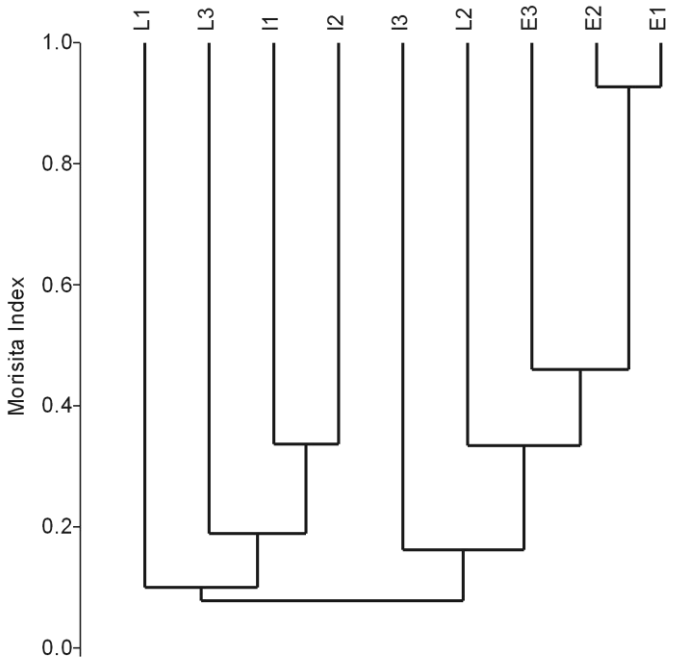


Fig. 5. Morisita Index cluster analysis based on plot species composition in the Early (E1, E2, E3), Intermediate (I1, I2, I3), and Late (L1, L2, L3) successional stages of Tropical Dry Forests in Santa Rosa National Park, Guanacaste, Costa Rica.

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Breeding systems, pollination and dispersal syndromes

Monoecy was the most common breeding system in terms of total number of individuals or total number of species (X^2= 920.41, df= 1, p<0.0001; X^2_{yates} = 135.91, df= 1, p<0.0001, respectively), while the dioecy system was present only in a few individuals and species in all stages (Table 2). We determined five different pollination syndromes in the three TDF successional stages at SRNP (entomophily, lepidopterophily, anemophily, chiropterophily, and ornithophily). Entomophily was the most frequent syndrome either by number of individuals or number of species, followed by lepidopterophily in all the successional stages (Table 3). Anemophily was important in number of trees pollinated, but only few species are pollinated by wind (Table 3). Chiropterophily and ornithophily were important syndromes for some trees, but only few species rely on them. Some tree species are generalistic and depend on more than a single pollinator (Appendix 1). Seven different dispersal syndromes were observed in all the TDF successional stages, wind and birds being the most important agents in number of individuals and number of species dispersed (Table 4). Mastochory is also a very important syndrome in terms of number of species dispersed for all the successional stages, and bats are important for some particular species such as Gumbo-limbo (*Bursera simaruba*), Nance (*Byrsonima crassifolia*), Ojoche (*Brosimum alicastrum*), and Jagua (*Genipa americana*). There are some tree species, Madero negro (*Gliricidia sepium*), Spanish cedar (*Cedrela odorata*), *Bernardia nicaraguensis*, and Casco de venado (*Bauhinia ungulata*) that do not depend on animals for seed dispersal (e.g. autochory and barochory) (Appendix 1).

Table 2. Tree species richness and breeding systems observed in three tropical dry forests (TDFs) successional stages in Santa Rosa National Park, Guanacaste, Costa Rica-

	Early		Intermediate		Late	
Breeding System	**#species**	**#individuals**	**#species**	**#individuals**	**#species**	**#individuals**
Monoecy	30	307	69	290	57	419
Dioecy	2	11	3	17	4	15
TOTAL	**33**	**318**	**72**	**307**	**61**	**434**

Table 3. Pollination syndrome by tree individuals and species observed in three tropical dry forest successional stages in Santa Rosa National Park, Guanacaste, Costa Rica.

	EARLY		INTERMEDIATE		LATE	
Pollination Syndrome	**#species**	**#individuals**	**#species**	**#individuals**	**#species**	**#individuals**
Entomophily	24	292	55	227	46	370
Lepidopterophily	10	25	17	109	17	133
Anemophily	4	20	7	45	6	24
Chiropterophily	3	6	2	11	4	8
Ornithophily	0	0	1	1	2	4

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Table 4. Seed dispersal syndrome by tree individuals and species observed in three tropical dry forest stages in Santa Rosa, National Park, Guanacaste, Costa Rica.

	EARLY		INTERMEDIATE		LATE	
Dispersal Syndrome	**#species**	**#individuals**	**#species**	**#individuals**	**#species**	**#individuals**
Anemochory	12	184	21	100	19	159
Mastochory	12	30	21	97	24	126
Ornithochory	11	43	38	135	25	136
Autochory	4	62	5	23	6	26
Chiropterochory	3	19	5	21	4	29
Barochory	2	4	2	8	1	1
Saurochory	1	1	4	24	3	13

Discussion

Species composition

Species richness and diversity of the TDFs evaluated in this study are consistent with the Intermediate Disturbance Hypothesis (IDH) [59], the intermediate stage being the most diverse and with the highest species richness. According to this hypothesis, intermediate successional stages at the SRNP have in general a level of recovery that is a transition in structure, physiognomy, microhabitats, and microclimates between young and old-growth forests [59]. This transition makes the intermediate stage viable and suitable for tree species that reside in both young open habitats and old-growth forests. However, the intermediate stage shares more species with the late stage than with the early stage, suggesting that the transition characteristics of the intermediate successional stage facilitate a higher colonization and establishment of species more adapted to older successional stages. Pioneer tree species were mostly found in the early stage; these species are fast- growing and well-adapted to disturbed habitats with full sunlight exposure [44, 60].

Not surprisingly in our study, heliophitic plant families were dominant in the early successional stage (e.g. Verbenaceae, Cochlospermaceae and Fabaceae). The late successional stage has a more shaded understory and forest floor, and more humid soils (pers. obs.), which promote tree species germination and growth. This may explain why some species are restricted to this stage, Huevos de caballo (*Stemmadenia obovata*), Mexican jumping bean (*Sebastiana pavoniana*), Quebracho (*Lysiloma divaricatum*), Canelo (*Ocotea veraguensis*), and Quina (*Exostema mexicanum*). Low abundances of valuable timber species, Ron ron (*Astronium graveolens*), Cocobolo (*Dalbergia retusa*), Spanish cedar (*Cedrela odorata*), and Mahogany (*Swietenia macrophylla*) are related to past selective pressure from logging [56-58, 61, 62]. Some important dry forest pioneer species like Cocobolo (*D. retusa*) and Ron ron (*A. graveolens*), both wind-dispersed species, were absent from the early stage, which may be due to the absence of close mother trees [63, 64]. The low species similarity among successional stages shows that the stages are very different in tree species composition, suggesting that the plots evaluated for each forest successional can have a particular history of species colonization and establishment (Fig. 4). This is also supported by the cluster analysis based on species composition and

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species abundances (Fig. 5). We think this is a combination of species habits (e.g. heliophytic, shade-tolerant) and high abundance of some particular species due to their dispersal syndromes in the successional plots. Two heliophytic wind-dispersed trees showed a high dominance in two early plots (E1 and E2), which had the highest species similarity. In contrast, one late successional stage plot with the lowest species similarity is dominated by two shade-tolerant species that have anemochory, Quina (*Exostema mexicanum*) and possibly autochory Mexican jumping bean (*Sebastiana mexicanum*, unknown dispersal syndrome) [65].

Breeding systems

Monoecy is the most common breeding system observed in this study in terms of number of individuals and number of species. Monoecy is a basal evolutionary plant characteristic of flowering plants, and about 80% of the flowering tree species worldwide are monoecious [65]. Monoecy is present in tree species with small flowers and not dependant on specific pollinators, while specific reliable pollinators are needed only for dioecious species to succeed [67, 68]. Even though dioecious plants are in relatively lower numbers, their out-crossing is much more effective than out-crossing of monoecious plants [46, 69]. Dioecy also avoids self-pollination and autonomous reproduction, and increases genetic variability in unpredictable environments [46, 70, 71]. However, self-pollination can be important for monoecious tree species in TDF, particularly when conspecifics are few and/or far away from each other [71]. Some scientific investigations have found that the ratio between monoecy:dioecy is 3:1 (20-25% of the trees are dioecious) for TDFs [72, 73], but surprisingly, in our study only 4% of the trees are dioecious, indicatingthat in the dry forests of SRNP trees are rarely dependant on specific pollinators, but rely mainly on generalist pollinators (e.g.,insects and wind). This is supported by our findings for both pollination and dispersal syndromes, where the high frequency of strong winds allows tree species take advantage of this particular climatic condition.

Pollination syndromes

Entomophily is one of the most common and important pollination syndromes in several biomes throughout the Neotropics [34, 74-79]. Our results for SRNP confirm this pattern, which is also reported for dry forests in Brazil [34]. Most of the tree species observed in our study have small inflorescences that seem to be adapted to pollination by small visitors such as insects. In addition, SRNP has an enormous insect diversity of about 13,000 species with the potential to visit flowers and pollinate them. High insect diversity can define plant species composition in habitats, being important seed predators and primary pollinators, and therefore determining the presence/absence and abundance of plant species in habitats [80].

Wind pollination (anemophily) can be an important pollination agent in early forests (open and disturbed) where pollinators may be scarce due to increased distance from less disturbed forests. We have observed few wind-pollinated tree species in the early stage, but one species was highly dominant there, Yayo (*Rehdera trinervis*) (Appendix 1). Also, wind does not prevent insects completely from visiting flowers; however, evaluating the success of these visits was not part of this study.

In our study, chiropterophily was a frequent syndrome in some tree species like Guapinol (*Hymenaea courbaril*) and Palanco (*Sapranthus palanga*), but again, most of tree species surveyed in this study have small inflorescences that are more adapted for insect pollination. These particular species are highly dependent on chiropterophily due to their floral structures [81, 82]. Ornithophily is less common in TDF than in forests at higher elevations (e.g. mid and high) with higher amounts of mist and humidity [83].

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Dispersal syndromes

Wind is a very important dispersal agent, mainly in the early stage, where the majority of tree species have dry fruits (e.g. legumes, siliques, achenes, samaras, capsules) (pers. obs.). Plants with seeds and fruits adapted to wind-dispersal are less dependant on the presence of a specific disperser. This is very advantageous in SRNP, because the fruiting period of the majority of species takes place in the dry season, during which trade winds in SRNP are dominant and strong [44].

Many species in the tropics, including TDF, are either entirely or partially dependant on birds and mammals for seed dispersal [84-87]. Fleshy fruits and dry indehiscent fruits are important food sources for birds (171 species of birds present in SRNP) and mammals such as monkeys, agoutis and other rodents, white-tailed deer, peccaries, and others. However, the forest structure of the early successional stage (e.g. open short canopy) is not suitable for monkeys, though White-Faced capuchin monkeys (*Cebus capucinus*) in SRNP may visit early stages to feed on fruit of Acacia trees (*Vachellia collinsii*), which are highly dominant in early stages [88]. The absence of closed canopy can also limit bird visits, lengthening time for tree species colonization and establishment in early stages of the forest. On the other hand, seed dispersal by animals helps seeds travel, colonize and establish farther away from their parent trees, which reduces mortality by predation, pathogens, and intraspecific competition associated with parents' proximity [89]. Autochory (ballistic) and barochory (gravity) are other important seed dispersal strategies in trees that do not depend on any disperser [86], such as those producing dry fruits, specifically dehiscent fruits like legumes and siliques . Even when we identified a few tree species with these dispersal traits, these were very abundant mainly in the early successional stage, Guácimo de monte (*Helicteres baruensis*), Casco de venado (*Bauhinia ungulate*), and Madero negro (*Gliricidia sepium*) (Appendix 1). Barochory in SNRP TDF is currently demonstrated by species with large heavy fruits, which used to be dispersed by extinct megafauna [90].

Implications for Conservation

Our study describes the floristic composition of three successional stages of the dry forest of SRNP in Costa Rica. This is one of the most significant and largest remnants of dry forest in Mesoamerica. Tree species in this region are not only related to abiotic factors such as soil humidity and canopy shade, but also to biotic factors such as seed dispersers and proximity to seed mother trees, as well as other biophysical soil properties [91]. Many tree species common to Costa Rican TDF are missing from the early stage, and consequently species composition is different from intermediate and late stages. We found that many tree species are restricted to the late stage, and some of them are very rare in Costa Rican dry forests in general.

This study describes for the first time breeding systems and pollination and dispersal syndromes for a large number of tropical dry forest tree species through a succession. This knowledge is critical in terms of conservation because it gives an idea on what species colonize a perturbed place, and how long it takes for some other to colonize and establish in older forests. We observed a transition in species composition across a dry forest succession, showing how species are replaced when the forest becomes older. In terms of pollination and dispersal agents this study shows how syndromes vary across the dry forest succession and how some specific syndromes are restricted to certain forest age. Insects are important to consider in this TDF remnant due to their relevance as key pollinators for TDFs. SRNP dry forest fosters a high insect diversity that promotes pollination of many tree species. This information is crucial on how natural restoration occurs in a dry forest, but also critical for restoration efforts of this highly endangered ecosystem in other countries in the Mesoamerican region.

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Appendix 1. Tree species observed in numbers and percentages, including diameter at breast height (DBH), their breeding system, and pollination and seed dispersal syndrome in three tropical dry forest stages in Santa Rosa National Park, Guanacaste, Costa Rica.

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Family	Species	Breeding system	Pollination Syndrome	Seed dispersal Syndrome	Early			Intermediate			Late			Total	
					#individuals	%	DBH	#individuals	%	DBH	#individuals	%	DBH	#individuals	%
Anacardiaceae	*Astronium graveolens*	Dioecious	Entomophily	Anemochory				2	0,6	9,0	5	1,1	14,6	7	0,7
Anacardiaceae	*Spondias mombin*	Monoecious	Entomophily	Mastochory				7	2,2	35,0	1	0,2	38,9	8	0,7
Annonaceae	*Anona reticulata*	Monoecious	Entomophily	Mastochory/Barochory				4	1,3	17,2				4	0,4
Annonaceae	*Sapranthus palanga*	Monoecious	Chiropterophily	Mastochory/Ornithochory				7	2,2	15,0	2	0,5	18,2	9	0,8
Apocynaceae	*Forsteronia spicata*	Monoecious	Entomophily	Anemochory				1	0,3	6,7				1	0,1
Apocynaceae	*Stemmadenia obovata*	Monoecious	Lepidopterophily	Mastochory/Ornithochory				1	0,3	9,4	20	4,6	11,3	21	2,0
Bignoniaceae	*Crescentia cujete*	Monoecious	Lepidopterophily/Chiropterophily	Mastochory/Barochory	3	0,9	6,2				1	0,2	7,9	4	0,4
Bignoniaceae	*Tabebuia chrysantha*	Monoecious	Entomophily	Anemochory				1	0,3	7,3				1	0,1
Bignoniaceae	*Tabebuia ochracea*	Monoecious	Entomophily	Anemochory				3	1,0	9,8	14	3,2	9,2	17	1,6
Bignoniaceae	*Tabebuia rosea*	Monoecious	Entomophily	Anemochory				1	0,3	7,7				1	0,1
Bombacaceae	*Bombacopsis quinatum*	Monoecious	Lepidopterophily/Chiropterophily	Anemochory							1	0,2	71,2	1	0,1
Boraginaceae	*Cordia alliodora**	Monoecious	Lepidopterophily/Entomophily	Anemochory	1	0,3	23,0	7	2,2	14,9	1	0,2	10,5	9	0,8
Boraginaceae	*Cordia guanacastensis*	Monoecious	Lepidopterophily/Entomophily	Ornithochory	10	3,1	5,8							10	0,9
Boraginaceae	*Cordia panamensis*	Monoecious	Lepidopterophily/Entomophily	Ornithochory				12	3,8	10,3				12	1,1
Burseraceae	*Bursera graveolens*	Monoecious	Entomophily/Anemophily	Mastochory/Ornithochory	1	0,3	6,5				4	0,9	6,3	5	0,5
Burseraceae	*Bursera simarouba**	Monoecious/Dioecious	Entomophily	Ornithochory/Chiropterochory/Mastochory	1	0,3	7,5	1	0,3	10,2	21	4,8	25,6	23	2,1
Burseraceae	*Bursera tomentosa*	Monoecious	Entomophily	Ornithochory				1	0,3	5,9	1	0,2	28,1	2	0,2
Capparidaceae	*Capparis indica*	Monoecious	Lepidopterophily	Autochory/Ornithochory				2	0,6	19,0				2	0,2
Celastraceae	*Maytenus segoviarium*	Monoecious	Entomophily	Mastochory/Ornithochory							2	0,5	5,9	2	0,2
Chrysobalanaceae	*Hirtella racemosa*	Monoecious	Unknown	Ornithochory							1	0,2	5,6	1	0,1
Chrysobalanaceae	*Licania platypus*	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	10,7				1	0,1
Cochlospermaceae	*Cochlospermum vitifolium**	Monoecious	Entomophily	Anemochory	58	18,2	9,6	2	0,6	16,6	6	1,4	30,6	66	6,2
Dilleniaceae	*Curatella americana*	Monoecious	Entomophily	Unknown	3	0,9	9,5	1	0,3	7,0				4	0,4
Ebenaceae	*Diospyros salicifolia**	Monoecious	Entomophily	Mastochory	6	1,9	6,5	2	0,6	5,4	3	0,7	14,7	11	1,0
Erythroxylaceae	*Erythroxylum havanense*	Monoecious	Lepidopterophily/Entomophily	Ornithochory				1	0,3	6,4	1	0,2	8,1	2	0,2
Euphorbiaceae	*Bernardia nicaraguensis*	Dioecious	Anemophily	Autochory							2	0,5	5,2	2	0,2
Euphorbiaceae	*Euphorbia schlechtendalii*	Monoecious	Entomophily	Autochory	3	0,9	5,5				1	0,2	7,6	4	0,4
Euphorbiaceae	*Jatropha curcas*	Monoecious	Entomophily	Mastochory							8	1,8	11,3	8	0,7
Euphorbiaceae	*Margaritaria nobilis*	Monoecious	Entomophily	Autochory/Ornithochory				1	0,3	12,9				1	0,1
Euphorbiaceae	*Sapium glandulosum*	Monoecious	Entomophily	Autochory/Mastochory							1	0,2	42,4	1	0,1
Euphorbiaceae	*Sebastiana pavoniana*	Monoecious	Entomophily	Unknown				1	0,3	6,7	79	18,0	10,1	80	7,5
Fabaceae	*Acosmium panamense**	Monoecious	Entomophily	Anemochory	2	0,6	8,0	3	1,0	21,5	1	0,2	32,3	6	0,6
Fabaceae	*Ateleia herbert-smithii*	Dioecious	Anemophily	Anemochory	1	0,3	6,2	4	1,3	11,3				5	0,5
Fabaceae	*Bauhinia ungulata*	Monoecious	Chiropterophily	Barochory	1	0,3	5,3	4	1,3	15,5				5	0,5
Fabaceae	*Dalbergia retusa*	Monoecious	Entomophily	Anemochory	1	0,3	23,0				1	0,2	23,1	2	0,2
Fabaceae	*Gliricidia sepium**	Monoecious	Entomophily	Autochory	56	17,6	7,5	7	2,2	17,7	5	1,1	18,3	68	6,3
Fabaceae	*Hymenaea courbaril*	Monoecious	Chiropterophily	Mastochory							4	0,9	8,5	4	0,4
Fabaceae	*Lonchocarpus minimiflorus*	Monoecious	Entomophily	Anemochory				5	1,6	7,9	27	6,2	7,9	32	3,0
Fabaceae	*Lysiloma divaricatum*	Monoecious	Anemophily	Anemochory				2	0,6	44,1	8	1,8	25,2	10	0,9
Fabaceae	*Machaerium biovulatum**	Monoecious	Anemophily	Anemochory	3	0,9	22,7	2	0,6	7,3	2	0,5	10,1	7	0,7
Fabaceae	*Piptadenia flava*	Monoecious	Entomophily	Anemochory				10	3,2	10,1				10	0,9
Fabaceae	*Piscidia carthagenensis*	Monoecious	Entomophily	Anemochory				2	0,6	26,4	1	0,2	13,5	3	0,3
Fabaceae	*Prosopis juliflora*	Monoecious	Entomophily	Mastochory				14	4,4	6,9				14	1,3
Fabaceae	*Samanea saman*	Monoecious	Entomophily	Ornithochory/Mastochory				1	0,3	132,1				1	0,1
Fabaceae	*Vachellia collinsii*	Monoecious	Entomophily	Mastochory/Ornithochory	1	0,3	6,7	7	2,2	6,9				8	0,7
Fagaceae	*Quercus oleoides*	Monoecious	Anemophily	Mastochory	14	4,4	23,1				1	0,2	45,0	15	1,4
Flacourtiaceae	*Casearia arguta*	Monoecious	Lepidopterophily/Entomophily	Ornithochory	1	0,3	6,4	3	1,0	12,4				4	0,4
Flacourtiaceae	*Casearia corymbosa*	Monoecious	Lepidopterophily/Entomophily	Ornithochory				4	1,3	8,8				4	0,4
Flacourtiaceae	*Casearia nitida*	Monoecious	Lepidopterophily/Entomophily	Ornithochory				7	2,2	8,3				7	0,7
Flacourtiaceae	*Casearia sylvestris*	Monoecious	Lepidopterophily/Entomophily	Ornithochory/Autochory				10	3,2	7,1	11	2,5	5,4	21	2,0
Flacourtiaceae	*Zuelania guidonia*	Monoecious	Entomophily	Mastochory/Ornithochory							1	0,2	17,9	1	0,1

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Family	Species	Breeding system	Pollination Syndrome	Seed dispersal Syndrome	Early			Intermediate			Late			Total	
					#individuals	%	DBH	#individuals	%	DBH	#individuals	%	DBH	#individuals	%
Hippocrateaceae	*Semialarium mexicanum**	Monoecious	Entomophily	Anemochory	17	5,3	6,0	8	2,5	12,8	53	12,1	9,1	78	7,3
Lauraceae	*Ocotea veraguensis*	Monoecious	Entomophily	Ornithochory				1	0,3	6,8	4	0,9	7,1	5	0,5
Malphigiaceae	*Bunchosia biocellata*	Dioecious	Entomophily	Mastochory/Ornithochory							3	0,7	18,6	3	0,3
Malphigiaceae	*Byrsonima crassifolia**	Monoecious	Entomophily	Ornithochory/Chiropterochory	17	5,3	9,0	11	3,5	17,1	1	0,2	25,7	29	2,7
Malvaceae	*Helicteres baruensis*	Monoecious	Chiropterophily	Autochory	2	0,6	6,8							2	0,2
Malvaceae	*Malvaviscus arboreus*	Monoecious	Ornithophily	Ornithochory				1	0,3	6,8				1	0,1
Melastomataceae	*Mouriri myrtilloides*	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	6,8	1	0,2	5,0	2	0,2
Meliaceae	*Cedrela odorata*	Monoecious	Entomophily	Autochory				4	1,3	38,7				4	0,4
Meliaceae	*Swietenia macrophylla**	Monoecious	Lepidopterophily/Entomophily	Anemochory	1	0,3	10,4	3	1,0	25,1	1	0,2	33,2	5	0,5
Meliaceae	*Trichilia glabra*	Monoecious	Entomophily	Ornithochory				3	1,0	19,7				3	0,3
Meliaceae	*Trichilia havanensis*	Monoecious	Entomophily	Ornithochory				1	0,3	11,2				1	0,1
Meliaceae	*Trichilia hirta*	Monoecious	Entomophily	Ornithochory				12	3,8	13,9				12	1,1
Meliaceae	*Trophis racemosa*	Monoecious	Anemophily	Ornithochory				4	1,3	18,8				4	0,4
Moraceae	*Brosimum alicastrum*	Monoecious	Anemophily	Mastochory/Ornithochory/Chiropterochory				6	1,9	8,2				6	0,6
Moraceae	*Ficus bullenei*	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	58,4				1	0,1
Moraceae	*Maclura tinctoria*	Dioecious	Anemophily	Ornithochory				9	2,9	21,7				9	0,8
Myrsinaceae	*Ardisia revoluta*	Monoecious	Entomophily	Ornithochory/Saurochory				1	0,3	5,3	5	1,1	9,2	6	0,6
Myrtaceae	*Eugenia hiraeifolia*	Monoecious	Entomophily	Ornithochory							2	0,5	10,0	2	0,2
Myrtaceae	*Eugenia oerstediana**	Monoecious	Entomophily	Ornithochory	1	0,3	6,2	1	0,3	6,5	8	1,8	7,4	10	0,9
Nyctaginaceae	*Pisonia aculeata**	Dioecious	Entomophily	Ornithochory	10	3,1	10,3	7	2,2	7,2	2	0,5	5,9	19	1,8
Ochnaceae	*Ouratea lucens*	Monoecious	Bees	Ornithochory							1	0,2	7,5	1	0,1
Opiliaceae	*Agonandra macrocarpa*	Monoecious	Unknown	Mastochory				1	0,3	68,4				1	0,1
Proteaceae	*Roupala complicata*	Monoecious	Entomophily	Anemochory							1	0,2	8,7	1	0,1
Rhamnaceae	*Karwinskia calderoni*	Monoecious	Entomophily	Chiropterochory				2	0,6	9,1	1	0,2	9,4	3	0,3
Rubiaceae	*Alibertia edulis*	Monoecious	Lepidopterophily	Mastochory				1	0,3	11,9	2	0,5	5,4	3	0,3
Rubiaceae	*Calycophyllum candidissimum*	Monoecious	Lepidopterophily	Anemochory				13	4,1	12,4	3	0,7	24,6	16	1,5
Rubiaceae	*Chomelia spinosa*	Monoecious	Lepidopterophily	Mastochory	1	0,3	7,9				3	0,7	6,5	4	0,4
Rubiaceae	*Exostema mexicanum*	Monoecious	Lepidopterophily/Entomophily	Ornithochory				4	1,3	12,2	28	6,4	11,2	32	3,0
Rubiaceae	*Genipa americana*	Dioecious	Lepidopterophily/Entomophily	Mastochory/Ornithochory/Chiropterochory/Autochory	1	0,3	11,4				6	1,4	10,5	7	0,7
Rubiaceae	*Guettarda macrosperma**	Monoecious	Lepidopterophily	Mastochory	1	0,3	5,9	12	3,8	18,9	24	5,5	13,6	37	3,5
Sapindaceea	*Allophylus occidentalis*	Monoecious	Entomophily	Ornithochory				1	0,3	11,3				1	0,1
Sapindaceea	*Thouinidium decandrum*	Monoecious	Entomophily	Anemochory				1	0,3	5,7	2	0,5	45,3	3	0,3
Sapotaceae	*Chrysophyllum brenesii*	Monoecious	Entomophily	Mastochory/Ornithochory				1	0,3	5,5	3	0,7	8,7	4	0,4
Sapotaceae	*Manilkara chicle*	Monoecious	Entomophily	Mastochory/Ornithochory				4	1,3	17,2	4	0,9	12,9	8	0,7
Simaroubaceae	*Simarouba glauca*	Monoecious	Entomophily	Mastochory/Ornithochory/Saurochory				4	1,3	5,7	1	0,2	6,3	5	0,5
Sterculiaceae	*Guazuma ulmifolia**	Monoecious	Anemophily	Mastochory/Saurochory	1	0,3	5,6	18	5,7	14,7	7	1,6	22,9	26	2,4
Sterculiaceae	*Sterculia apetala*	Monoecious	Entomophily	Mastochory/Ornithochory				2	0,6	12,7				2	0,2
Theopharastaceae	*Jacquinia nervosa*	Monoecious	Ornithophily	Mastochory/Ornithochory							3	0,7	10,3	3	0,3
Tiliaceae	*Apeiba tibourbou*	Monoecious	Entomophily	Mastochory				2	0,6	33,5				2	0,2
Tiliaceae	*Luehea candida**	Monoecious	Lepidopterophily/Entomophily	Anemochory	4	1,3	10,5	24	7,6	15,2	13	3,0	14,4	41	3,8
Tiliaceae	*Luehea speciosa**	Monoecious	Lepidopterophily/Entomophily	Anemochory	2	0,6	6,9	4	1,3	12,3	2	0,5	18,6	8	0,7
Tiliaceae	*Muntingia calabura*	Monoecious	Lepidopterophily	Ornithochory/Chiropterochory/Saurochory				1	0,3	8,2				1	0,1
Turneraceae	*Erblichia odorata*	Monoecious	Ornithophily	Ornithochory							1	0,2	5,7	1	0,1
Verbenaceae	*Lippia oxyphyllaria*	Monoecious	Entomophily	Anemochory	3	0,9	6,8							3	0,3
Verbenaceae	*Rehdera trinervis**	Monoecious	Entomophily	Anemochory	91	28,6	9,0	2	0,6	23,3	17	3,9	24,8	110	10,3
				Total	**318**	**100,0**		**315**	**100,0**		**439**	**100,0**		**1072**	**100,0**

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