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Fruit dispersal syndromes in animal disseminated plants at Tinigua National Park, Colombia

Síndromes de dispersión en plantas dispersadas por animales en el Parque Nacional Tinigua, Colombia

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ABSTRACT

Fruit dispersal syndromes (groups of plants with similar fruit morphology, presumably adapted to dispersal by a particular set of vectors) have been described in a variety of tropical localities. In some cases the presence of different syndromes in each locality suggests independent evolution of fruit traits in response to selective pressures imposed by the particular animal community in each place. However, it is still unclear how general are fruit syndromes, and this is important to understand the evolution of mutualistic relationships. We compiled morphological information from about 500 fleshy fruited species at a lowland Neotropical forest in Tinigua National Park, Colombia, in an effort to test for the existence of fruit dispersal syndromes. We found that about two thirds of the plant genera analyzed could be classified in two different fruit types (large, protected, dull colored fruits, versus small, unprotected, bright colored fruits). These two syndromes correspond to the mammal and bird dispersal syndromes originally described at Cocha Cashu Biological Station, Peru. Two years of field observations on several fruiting plants revealed close associations between these fruit syndromes and the presumed animal dispersal vector. Our results support the idea that fruit dispersal syndromes are more general in Neotropical forests than previously inferred. However, we caution that similar syndromes found at Cocha Cashu and Tinigua may be a consequence of the floristic resemblance of both regions, and may not necessarily imply an independent case for the evolution of mammal and bird dispersal syndromes. Therefore, additional studies of fruit syndromes and biogeographical analyses would be necessary to assess how general are dispersal syndromes in the Neotropics.

Key words: fruit syndromes, fruit morphology, Neotropical forests, convergent evolution, frugivory.

RESUMEN

Los síndromes de dispersión de frutos han sido descritos para diferentes bosques tropicales. En algunos casos la presencia de diferentes síndromes de dispersión sugiere la evolución independiente de características morfológicas de los frutos como respuesta a presiones de selección particulares. Sin embargo, hasta el momento hay evidencias contrastantes sobre qué tan generales son estos síndromes. Este estudio reúne la información morfológica de aproximadamente 500 especies de plantas con frutos carnosos, en el Parque Nacional Tinigua, Colombia, en un esfuerzo por encontrar síndromes de dispersión de semillas. Alrededor de dos tercios de los géneros de plantas analizados se pueden agrupar en dos categorías: (frutos grandes, con protección y colores opacos; y frutos pequeños, sin protección y de colores llamativos), que corresponden a los síndromes de dispersión por mamíferos y aves descritos por Janson (1983) en Cocha Cashu, Perú. Nuestros resultados apoyan la idea que los síndromes de dispersión endozoocórica son más generalizados de lo que se había planteado anteriormente. Consideramos que la similitud en los resultados obtenidos en este estudio y en el Perú no necesariamente implica evolución independiente de los síndromes de dispersión, porque las floras de estos lugares son bastante similares. Por lo tanto, más estudios de este tipo son necesarios para entender mejor qué tan generales son los síndromes de dispersión en bosques Neotropicales.

Palabras clave: síndromes de dispersión, morfología de frutos, bosques Neotropicales, evolución convergente, frugivoría.

INTRODUCTION

The process of seed dispersal by frugivores is a common interaction in almost every ecosystem and involves a large number of animal and plant species (Ridley 1930, Pijl 1972). For example, Neotropical rainforests animals disperse seeds of 50 % to 90 % of the plant species (Gentry 1988, Chapman 1995, Voss & Emmons 1996). The close ecological relationships that exist among some plant and animal species suggest that they have been subject to mutual selective pressures in the past (Janzen 1983). However, no specialized relationships, as required for species-to-species coevolution (Thompson 1994), have been convincingly documented in seed dispersal systems (Witmer & Cheke 1991).

Recent studies suggest that there are constraints on the evolution of fruit morphology (Howe 1984, Herrera 1985, 1986, Wheelwright 1988), and that dispersal systems have evolved mainly by diffuse coevolutionary processes (Janson 1983, Janzen 1983, Herrera 1985). First of all, different selective forces may act in every stage of a plant's life cycle (Schupp 1995) and this complex web of potential forces may limit co-evolutionary trends between plants and frugivores. Furthermore, other studies have shown that fruit shape could be associated with phylogenetic inertia and developmental constraints (Jordano 1995). Finally, some authors emphasize low heritability for the evolution of fruit traits (i.e., Obeso 1993). Consequently, diffuse coevolution is now considered as the main process affecting seed dispersal systems. This type of evolution might have produced different dispersal syndromes or associated morphological traits that could have evolved independently as adaptations for a particular seed disperser agent (Pijl 1972, Janson 1983).

Dispersal syndromes have been defined for groups of plant species with similar seed dispersal strategies, and the most general strategies involve completely different dispersal agents (Ridley 1930, Pijl 1972). For example, in a Peruvian rainforest, Janson (1983) found associations among three morphological fruit characters: size, color, and protection. Two-thirds of the fruits had one of two character complexes matching the morphological characteristics of mammals and birds. In particular, large, dull colored fruits (orange, yellow, brown or green) with a husk, were associated with primate dispersal, while small, bright colored fruits (red, black, white, blue, purple, or with mixed colors), without a husk, seemed suitable for bird dispersal. However, the generality of these two dispersal syndromes for tropical forests remains to be demonstrated.

Gauthier-Hion et al. (1984) found one syndrome for bird and primate fruits in an African forest and a second syndrome for seed dispersal by other mammal species. Fruits dispersed by birds and primates were associated with no pre-dispersal predation; yellow, orange, red or violet colors; less than 50 g, and succulent arils with soft or no protection. In contrast, fruits dispersed by ungulates, rodents, and elephants had pre-dispersal predation; green or brown colors; more than 50 g; fibrous or dry pulp and strong protection. Although, their results differ from Janson's, they support the idea of a syndrome generated by interaction with frugivores that do not occur in the Neotropics. Fisher & Chapman (1993) compiled data on fruit dispersal syndromes from five different tropical sites and found few fruit character associations (i.e., between color and protection). They also found that the flora of New Guinea has a good representation of large, protected fruits, which elsewhere have been associated with primate dispersal, despite the lack of evidence of primate occupation of the island in the past. It is known that the largest fruits in New Guinea are consumed by cassowaries, hornbills, and flying foxes[1], but without knowledge of their dispersal efficiency, it is difficult to predict which fruit syndromes might have evolved in the island and to validate New Guinea's data as evidence of uncoupled diffuse coevolutionary paths. Interestingly, in a different region with a reduced number of seed dispersers, a particular mistletoe species in the Loranthaceae (a family characterized by colorful fruits dispersed by birds) has green fruits and is exclusively dispersed by a marsupial (Amico & Aizen 2000). This study again suggests that different fruit syndromes might evolve in response to particular dispersal agents.

Fruit syndromes have been analyzed using a variety of methods (i.e., Knight & Siegfried 1983, Dowsett-Lemaire 1986), which is an additional problem to assess how widespread are they. For example, Fisher & Chapman (1993), excluded fruits with mixed colors from their analyses and these methodological differences might explain some contrasts found

[1] MACK A & D WRIGHT (2002) The frugivore community and the fruiting plant flora in a New Guinea rainforest. Tropical Forest: Past, Present, Future: 69pp. Annual Meeting of the Association for Tropical Biology, Panamá City, Panamá.

when comparing fruit syndromes among tropical sites.

The main purpose of this work was to assess dispersal syndromes in the flora of Tinigua National Park, Colombia. Furthermore, we wanted to verify whether fruits classified in a particular morphological syndrome were actually visited preferentially by the same group of seed dispersers predicted to be associated with the syndrome. Although our results documented two main dispersal syndromes coincident with Janson (1983), we suggest that further studies are necessary to evaluate the general occurrence of these dispersal syndromes in Neotropical forests.

MATERIAL AND METHODS

Study area

This study was conducted at the CIEM (Centro de Investigaciones Ecológicas Macarena), a tropical rain forest in the northwestern Amazon, between the eastern Andes and Sierra de la Macarena, in the Departamento del Meta, Colombia. The CIEM is located on the right margin of Río Duda (2º 40' N, 74º 10' W; 350-400 m of altitude) about 13 km before it reaches the Río Guayabero, and it is part of Parque Nacional Tinigua (Stevenson et al. 1994). Mean annual temperature is around 26 ºC, and is relatively constant throughout the year. Precipitation varies between 2,600-2,800 mm annually, with a dry season between December and March and a rainy season between April and November; peak rainfall occurs in June and July (Kimura et al. 1995, Stevenson 2002). There are six basic vegetation types: mature terra firme forest, open canopy terra firme forest, two types of lowland seasonally flooded forest, secondary forest and riparian forest (Hirabuki 1990, Stevenson 2002).

A total of 445 bird species have been recorded at CIEM (Cadena et al. 2000). Many are frugivorous or eat fruits as part of their diet. Curassows, toucans, trogons, parrots, tanagers, manakins, woodpeckers, thrushes and other birds eat fruit regularly. There are seven primate species at the study site: Ateles belzebuth, Lagothrix lagothricha, Allouata seniculus, Cebus apella, Saimiri sciureus, Callicebus cupreus and Aotus brumbacki (see Stevenson 2002). All of them eat fruits as part of their diets. There are several other fruit-eating mammals at the CIEM including tayras (Eira barbara), tapirs (Tapirus terrestris) and some of the 34 bat species reported at the site (Rojas 1997).

Field protocols

We classified fleshy fruits into bird and mammal-dispersed classes following Janson (1983). We selected the plants collected at the CIEM (Stevenson et al. 2000, Stevenson unpublished data) that have fleshy fruits, or can potentially offer a food source to frugivores. Morphological information was taken mainly from the fruit guide of the study site (Stevenson et al. 2000). We made additional fruit measurements in the field during the study period (November 1999-July 2001), and used information from a guide to the fruits of Guyana (Roosmalen 1985). For each plant species with fleshy fruits we recorded its fruit size, color, and protection. Fruit size was either small or large. Fruit size was considered as the smaller dimension between its width and length. Large fruits are those that have a larger dimension than the average fruit size of all the plant species in this study. For capsular fruits, because the capsule is not manipulated by frugivores, we only considered the size of the seeds and fleshy pulp.

We considered the following color categories: red, white, black, blue/purple, green, yellow, brown, orange and mixed colors. A mixed color fruit has at least two different colors when ripe, including its supporting structures. The third morphological character was the presence or absence of protection. Protected fruits were those that presented a distinct hard, non-nutritious layer as a barrier to feeding. Fruits with a soft, flexible skin covering at least 10 % of the external fruit dimension were also considered protected. Otherwise fruits were considered unprotected.

Some studies of the evolution seed dispersal and fruit morphology often focused on the species level, without considering its consequences (see Fischer & Chapman 1993). This may overestimate the number of evolutionary events that led from an ancestral to a derived character (Lord et al. 1995), because phylogenetically related species are not independent unities (Harvey & Pagel 1991). In our study, we used genera as the taxonomic unit to determine the existence of associations between fruit characters (Janson 1983, 1992). We distinguished monomorphic genera (those with only one combination of fruit characters) from polymorphic ones. Each monomorphic genus was considered a basic morphological unit (BMU), and each set of species within a polymorphic genus sharing the same fruit characters was also considered a BMU.

For monomorphic genera, we calculated the percentage of protected genera in each fruit color category. We tested heterogeneity and subset homogeneity (Sokal & Rohlf 1995) to group different color fruits according to their percentage of protection. Afterwards, we tested heterogeneity within each of the subgroups or types obtained. Polymorphic genera were assigned to color groups derived from monomorphic genera analysis. A χ^2 test was used to determine association between fruit color and protection.

Color categories were the following: type A, low percentage of protection and bright colors (white, red, blue, black and mixed colors), and type B, high percentage of protected genera and dull colors (orange, green, yellow and brown). We used a Kolmogorov-Smirnov test to assess differences in fruit size between type A (n = 300) and type B (n = 191) fruits. We performed this test at the species level, because fruit size varies considerably between polymorphic and monomorphic genera.

All genera were classified dichotomously by size, color and protection which yielded eight possible combinations. We used a G-test of independence (Sokal & Rohlf 1995) to determine associations among fruit traits.

For the BMU having character complexes associated with fruit dispersal by mammals (large, type B color and protected) or birds (small, type A color and unprotected) (Pijl 1972, Janson 1983), we obtained information on visits by frugivores. This information was gathered from previous studies at the CIEM, especially for primates and birds (see Stevenson et al. 2000 and references therein). Observations on more than 75 plant species for more than 3,438 h were carried out to corroborate whether species with a particular syndrome were actually visited by the predicted seed dispersal vector. These observations were conducted mostly between 06:00 and 10:00 h and between 15:00 and 18:00, from a point of good visibility on the ground. Seed removal by nocturnal animals was checked only indirectly (using fruit traps) for a smaller set of plant species (n = 5).

RESULTS

We examined 491 plant species, corresponding to 80 % of the fleshy-fruited plants found at the study site. Fruit characters are described in Appendix 1. We found an association between fruit protection and color (Fig. 1). We found heterogeneity in the percentage of protected monomorphic genera (n = 197) in each color category ($\chi^2_{(8)}$ = 51.5, P < 0.001), but subgroups within each type were homogeneous [type A: ($\chi^2_{(4)}$ = 4.30, P > 0.05; type B: $\chi^2_{(3)}$ =3.93, P > 0.05)]. Type A and type B color fruits showed differences in the proportion of protected genera (G_H = 49.4, P < 0.001). Because of the small number of polymorphic genera, we grouped them in type A and type B colors. Fifteen out of the 40 polymorphic genera were grouped in one color category. Of the remaining 25 polymorphic genera, 23 varied in color and two in protection. No genus varied in both traits. From the 23 polymorphic genera, five out of eight protected BMUs are of type B color and 22 out of the 53 unprotected BMUs are of type B color, yielding no statistical association ($\chi^2_{(1)}$ = 0.53, P > 0.05). In the two genera that vary in protection, one of two protected BMU are type B color ($\chi^2_{(1)}$ = 0, P > 0.05) and have no significant association between color and protection.

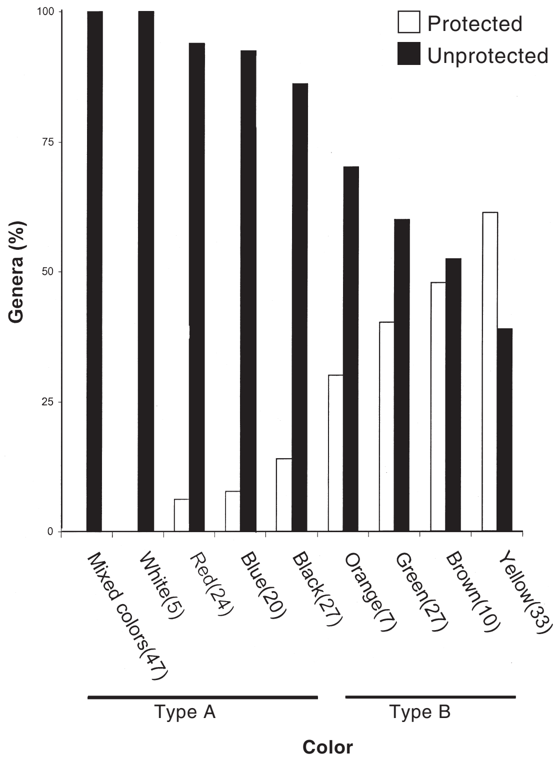

Fig. 1: Percentage of protected and unprotected fruits iby different color categories in the flora of Parque Nacional Tinigua, Colombia. The number of monomorphic genera is shown in parenthesis.

Porcentaje de frutos protegidos y sin protección en las diferentes categorías de color, en la flora del Parque Nacional Tinigua, Colombia. Los números en paréntesis corresponden al número de géneros monomórficos.

We found differences in the size distribution between type A and type B fruits (Kolmogorov-Smirnov test D = 0.507, n = 491, $P < 0.001$) (Fig. 2). Average fruit size was 17.3 mm (range 1-200 mm, n = 491). Average size of type A fruits was 11.4 mm on average (n = 300), with 87 % of them smaller than the average size of all the fruits analyzed, while type B were 27.2 mm on average (n = 191) and 62 % were larger than the overall average. Almost 65 % of all BMUs (n = 299) analyzed here belonged either to large, type B and protected or small, type A and unprotected fruits (Table 1). These two character complexes corresponded closely to the fruit morphology of primates and bird dispersal syndromes (Pijl 1972, Janson 1983). The hypothesis of independence between fruit traits was rejected for the three fruit traits considered in this study ($G_{(4)} = 165.5$, $P < 0.001$) and for each combination any two characters: color and protection ($G_{(1)} = 53.4$, $P < 0.001$); color and size ($G_{(1)} = 70.1$, $P < 0.001$); size and protection ($G_{(1)} = 80.6$, $P < 0.001$).

Out of 299 BMUs, 193 have fruit character complexes associated with either bird (n = 150) or primate dispersal (n = 43). We observed birds (excluding parrots) eating fruits of 84 BMUs; 76 of them corresponding to type A fruits. Primates were observed eating 83 BMUs; 53 of them corresponding to type B fruits. There was a significant association between the type of disperser (bird or primate) and fruit morphology (Aves: $\chi^2_{(1)} = 7.2$, $P < 0.05$; Primates: $\chi^2_{(1)} = 8.4$, $P < 0.05$).

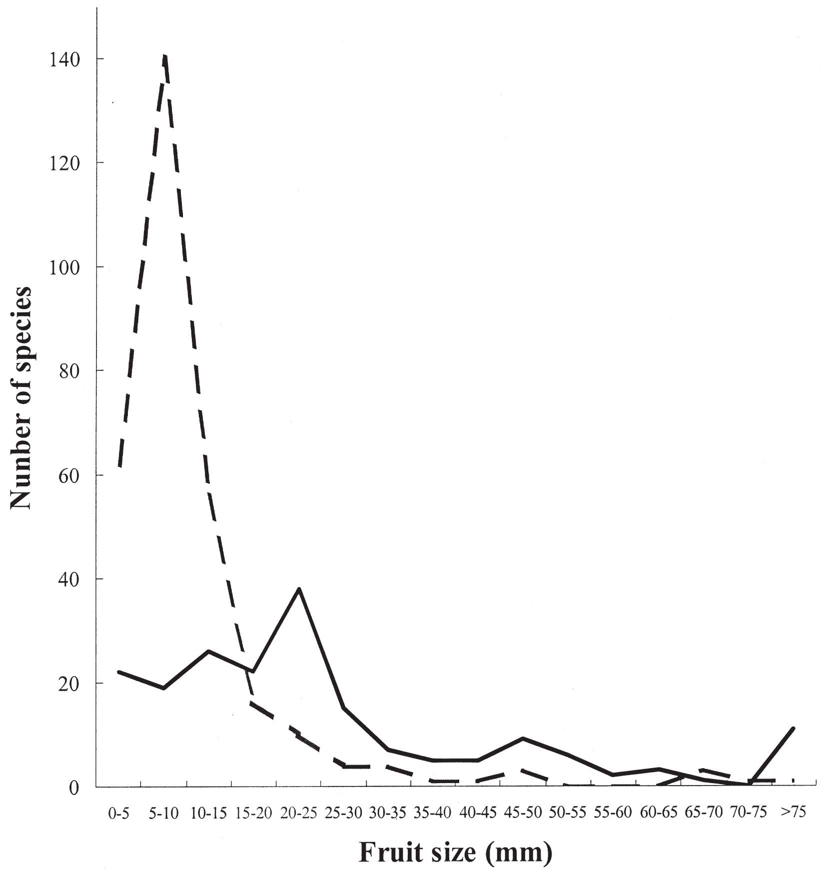

Fig. 2: Fruit size distribution for type A (non-protected and with bright colors) and type B fruits (protected and with dull colors) at Tinigua National Park. The dashed line represents type A fruits and the continuous line represents type B fruits.

Distribución del tamaño de los frutos de tipo A (sin protección y con colores vistosos) y tipo B (protegidos y con colores opacos) en el Parque Tinigua. La línea punteada corresponde a los frutos de tipo A, mientras que la línea continua corresponde a los frutos de tipo B.

TABLE 1

Distribution of BMUs (morphological basic units) into eight possible combinations of three fruit characters (fruit size, color, and protection) for animal dispersed plants at Tinigua National Park, Colombia. Type A and type B colors described in the text. Numbers in parenthesis are expected values assuming independence of characters.

Distribución de BMUs (unidades morfológicas básicas) en las ocho posibles combinaciones de tres caracteres morfológicos de los frutos (tamaño, color y grado de protección), para las plantas dispersadas por animales en el Parque Tinigua, Colombia. Los números en paréntesis corresponden a los valores esperados asumiendo independencia entre los caracteres

Size	Type A color		Type B color	
	Protected	Unprotected	Protected	Unprotected
> 17.3 mm	7 (12.5)	22 (49.7)	43 (7.8)	29 (31.0)
< 17.3 mm	5 (24.4)	150 (97.4)	5 (15.3)	38 (60.4)

DISCUSSION

The main result of this study at Tinigua is that fruit traits such as color, size, and protection are associated with the previously described bird and mammal dispersal syndromes (Ridley 1930, Pijl 1972, Janson 1983). Further, this relationship partly agrees with the use of fruits by the corresponding frugivore vectors. We found that very few bird species (some parrots, curassows, corvids and icterids) consume fruits with the primate dispersal syndrome as the size and protection of these fruits acts as a barrier to access its pulp and seeds. Nevertheless, monkeys frequently consumed fruits with the bird syndrome, and for no plant species did we find good evidence of relying on only one frugivores species for its fruit removal and dispersal. The complex web of interactions between frugivores and plants, including interactions between phylogenetically unrelated taxa do not fit the models of species-to-species coevolutionary process (Thompson 1994). Therefore, diffuse coevolution seems the most likely path for the evolution of these systems, although other non-evolutionary fortuitous events may also have a place. For example, under certain circumstances plant-frugivore interactions can be ecologically strong in spite of the lack of evolutionary history. In particular, the artificial introduction of plant species to new habitats has revealed that local frugivores are able to consume fruits never seen before, resulting in strong plant-animal interactions without evolutionary history (Herrera 1985). Thus, in the absence of a fossil record that could confirm strong interactions in the past, we are limited to describing the products of evolution and speculating about their potential origins.

Reciprocal evolution between birds and type A fruits seem to be more difficult than that between primates and type B fruits. Because of morphological constraints, many birds in Neotropical rainforests are unable to eat fruits that are either large or have a husk (Wheelwright 1985, Peres & Roosmalen 2002). Only few guilds (i.e., parrots, crows, and icterids) have the ability to manipulate fruits with their feet, breaking up the fruit’s husk rather than swallowing the whole fruit. Thus, if the seeds are more efficiently dispersed by primates than by birds, it is likely that plants could evolve husks to limit bird access to the fruit pulp. On the other hand, primates do not have morphological limitations to exploit the majority of fruits in the forest and this seems to be the reason why they exploit both type A fruits and type B fruits. Therefore, even if primates are not very efficient dispersers compared to birds, it would be difficult for plants to evolve morphological adaptations to limit the access of primates. It is possible that plants have used other means to deter fruit consumption by primates, such as chemical composition of fruits. For example, it is known that some families (i.e., Solanaceae) that are predominantly dispersed by bats and birds contain high quantities of secondary compounds in the pulp (Chipollini & Levey 1997b). One of the hypotheses to explain the presence of these compounds in the pulp of fruits is the selection of particular seed dispersal agents (Chipollini & Levey 1997a), and we believe that the inclusion of nutritional analyses could reveal additional fruit dispersal syndromes.

The results about the association of fruit character complexes with particular groups of frugivores, are very similar to those reported by Janson (1983) in the Peruvian rainforest at Cocha Cashu. Both studies found associations between the size, color and presence or absence of protection. At Tinigua and Cocha Cashu, respectively, 65 % and 66 % of the fleshy fruits analyzed are either small, type A colors without a husk; or large, type B colors with a husk. Further, at both sites associations were found between the fruit character complexes and the dispersal agents. Primates and birds tend to consume preferentially those fruits assigned to their particular dispersal syndromes (Pijl 1972, Janson 1983). These results suggest that the primate and bird dispersal syndromes are more general in Neotropical communities than previously inferred (see Fisher & Chapman 1993). However, one possible explanation for this finding could be the similarity in plant and animal assemblages between sites. At least 37 % of the plant species present at Tinigua occur also at Cocha Cashu and this was the second highest percentage of similarity among 18 Neotropical localities compared with the Tinigua flora (Stevenson & Castellanos unpublished data). Animal composition is also very similar, especially birds and mammals. For example, frugivores represent a significant proportion of animal biomass, and primates, tapirs, and peccaries are the most important components at both sites (Terborgh 1983, Stevenson 1996, 2002). The avifauna is also very similar between these sites and the frugivore guild makes up a considerable fraction of avian biomass (Terborgh et al. 1990, Cadena et al. 2000), especially represented by few families such as curassows, tinamous, toucans, trogons and others. This suggests that a great proportion of the avian biomass, at both sites, have fruits as an important item of their diets. Other families of avian frugivores are diverse at these sites, like tanagers and manakins (Terborgh et al. 1990, Cadena et al. 2000). These results confirm the general similarities reported previously for the fauna and flora of western Amazonian forests (Gentry 1988, Voss & Emmons 1996). In summary, at this point it is difficult to argue that the presence of primate and bird dispersal syndromes at both sites was either the result of similar evolutionary histories or of independent evolution driven by similar dispersers. For two Neotropical sites included in Fisher & Chapman's (1993) study, only one showed a significant association of fruit characters corresponding to dispersal syndromes, therefore more studies of this type for a variety of vegetation types could help to clarify whether bird and primate dispersal syndromes are of general occurrence in Neotropical forests.

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APPENDIX 1

Animal dispersed plant species in Tinigua National Park, that were included in the analyses of dispersal syndromes. The columns show the morphological traits for each plant species. Fruit size refers to the largest dimension of the fruit (width or length)

Listado de las especies de plantas del Parque Nacional Tinigua que fueron incluidas en el análisis de síndromes de dispersión de frutos. Las columnas muestran los caracteres morfológicos de cada especie. El tamaño de los frutos hace referencia a la dimensión mas grande (entre largo y ancho del fruto)

Species	Fruit size (mm)	Color	Protection
Gnetum nodiflorum	27.5	Red	No
Anthurium clavigerum	4	Blue/purple	No
Anthurium eminens	7.5	Blue/purple	No
Anthurium fendleri	5	Blue/purple	No
Anthurium kunthii	5	Blue/purple	No
Anthurium cf. superbum	5	Blue/purple	No
Anthurium gracile	3	Red	No
Caladium bicolor	3	Yellow	No
Dieffenbachia longispatha	6.5	Red	No
Dieffenbachia cf. parlatoii	6.5	Red	No
Dracontium sp.	6	Orange	No
Monstera adansonii	12.5	White	No
Monstera dilacerata	12.5	White	No
Monstera lechleriana	5.5	White	No
Monstera gracilis	6	Yellow	No
Philodendron sp.	3	Yellow	No
Philodendron divaricatum	3.5	Yellow	No
Philodendron ernestii	2.3	Yellow	No
Philodendron fragrantissimum	5.5	Red	No
Philodendron cf cuneatum	2.5	White	No
Spathiphyllum cannaefolium	15.6	Green	No
Syngonium podophyllum	30	Yellow	Yes
Syngonium yurimaguense	34	Yellow	Yes
Aiphanes aculeata	22.5	Red	No
Attalea insignis	50	Brown	No
Astrocaryum chambira	47.5	Yellow	No
Bactris corossilla	20.5	Blue/purple	No
Bactris macana	24	Red	No
Bactris maraja	17.5	Black	No
Euterpe precatoria	11.5	Black	No
Geonoma macrostachya	8	Black	No
Geonoma interrupta	5	Black	No
Iriartea deltoidea	34	Mixed	No
Oenocarpus bataua	45	Mixed	No
Oenocarpus mapora	11.5	Mixed	No
Socratea exorrhiza	22.5	Mixed	No
Syagrus sancona	24	Orange	No
Aechmea rubiginosa	24	Yellow	Yes
Araeococcus flagellifolius	10	Mixed	No
Dichorisandra cf. aequatorialis	6	Mixed	No
Dichorisandra hexandra	6	Mixed	No
Dichorisandra villosula	12	Blue/purple	No
Tradescantia zanonia	4	Blue/purple	No
Costus guianensis	20	Mixed	No
Costus scaber	17.5	Mixed	No
Costus spiralis	17.5	Mixed	No
Dimerocostus strobilaceus	11.5	Brown	No
Asplundia moritziana	15	Green	Yes
Carludovica palmata	9	Red	No
Cyclanthus bipartitus		Green	No
Xiphidium caeruleum	4	Red	No
Heliconia episcopalis	8	Mixed	No
Heliconia hirsuta	10	Mixed	No
Heliconia latispatha	10	Mixed	No
Heliconia marginata	10	Mixed	No
Heliconia rostrata	8.5	Mixed	No
Heliconia spathocircinata	9	Mixed	No

Species	Fruit size (mm)	Color	Protection
Heliconia stricta	15	Mixed	No
Eucharis ulei	10	Mixed	No
Calathea inocephala	9	Mixed	No
Pleiostachya pruinosa	8.5	Mixed	No
Smilax aequatorialis	16	Orange	No
Phenakospermum guyanense	70	Red	No
Renealmia breviscapa	6	Mixed	No
Renealmia cernua	7	Mixed	No
Antrocaryon amazonica	26	Yellow	No
Spondias mombin	25	Yellow	No
Spondias venulosa	25	Yellow	No
Tapirira guianensis	7.5	Yellow	No
Annona sp.	55	Yellow	No
Duguetia quitarensis	115	Red	Yes
Guatteria punctata	5.5	Blue/purple	No
Malmea sp.	14	Blue/purple	Yes
Oxandra mediocris	7.5	Blue/purple	No
Rollinia edulis	50	Green	Yes
Ruizodendron ovale	17.5	Black	No
Unonopsis cf. guatterioides	14	Green	No
Xylopia amazonica	8	Red	No
Pacouria guianensis	140	Yellow	Yes
Stemmadenia grandiflora	14	Mixed	No
Tabernaemontana heterophylla	12	Mixed	No
Tabernaemontana sananho	15	Mixed	No
Dendropanax caucanus	10	Black	No
Schefflera morototoni	7.5	Black	No
Sciadodendron excelsum	8.5	Black	No
Bixa urucurana	18	Mixed	No
Pachira orinocensis	25	Green	No
Quararibea cf. wittii	22.5	Orange	No
Cordia bicolor	8.5	Green	No
Cordia bifurcata	4	Red	No
Cordia nodosa	11	White	No
Cordia cf ripicola	14	Black	No
Tournefortia foetidissima	6	White	No
Bursera inversa	8.5	Blue/purple	No
Crepidospermum goudotianum	5	Red	No
Crepidospermum rhoifolium	11	Orange	No
Dacryodes sp.	19	Black	No
Protium aracouchini	8.5	Mixed	No
Protium crenatum	11	Mixed	No
Protium glabrescens	10	Mixed	No
Protium robustum	17	Mixed	No
Protium sagotianum	22	Mixed	No
Trattinnickia rhoifolia	8.5	Black	No
Epiphyllum phyllanthus	35	Red	No
Hylocereus polyrhizus	75	Red	No
Pereskia aculeata	26.5	Yellow	No
Pereskia bleo	45	Yellow	No
Disocactus sp.	6	White	No
Rhipsalis baccifera	5	White	No
Dialium guianense	6.5	Brown	Yes
Hymenaea courbaril	60	Brown	Yes
Hymenaea oblongifolia	25.5	Brown	Yes
Capparis detonsa	20	Green	No
Capparis frondosa	11	Blue/purple	No
Crateva tapia	62.5	Yellow	Yes
Carica cf. goudotianum	40	Orange	Yes
Jacaratia digitata	45	Orange	No
Cecropia engleriana	10	Green	No
Cecropia ficifolia	10	Green	No
Cecropia membranacea	9.5	Green	No
Cecropia sciadophylla	15	Yellow	No
Coussapoa asperifolia	14	Red	No
Coussapoa orthoneura	7	Red	No
Coussapoa villosa	23	Mixed	No
Pourouma bicolor	11.5	Blue/purple	Yes

Species	Fruit size (mm)	Color	Protection
Pourouma minor	14	Blue/purple	No
Pourouma mollis triloba	11.5	Blue/purple	Yes
Pourouma petiolulata	11.5	Blue/purple	Yes
Maytenus macrocarpa	10	Mixed	No
Hirtella americana	11.5	Black	No
Licania cf. arborea	20	Green	No
Licania kunthiana	9.5	White	No
Licania subarachnophylla	27.5	Brown	No
Chrysochlamys aff membranacea	4	Mixed	No
Clusia grandiflora	9	Mixed	No
Clusia nigrolineata	6	Mixed	No
Clusia palmicida	6	Mixed	No
Clusia renggeroides	5	Mixed	No
Clusiella sp.	5	Mixed	No
Garcinia macrophylla	50	Yellow	Yes
Garcinia madruno	32.5	Yellow	Yes
Buchenavia capitata	10.5	Yellow	No
Cnestidium rufescens	6	Mixed	No
Connarus punctatus	10	Mixed	No
Rourea glabra	4	Mixed	No
Maripa cf. axilliflora	18	Yellow	Yes
Maripa peruviana	14	Yellow	Yes
Calycophysum cf. pedunculatum	65	Orange	Yes
Cayaponia capitata	50	Red	Yes
Cayaponia ophtalmica	25	Red	No
Cayaponia cf. ruizii	24	Blue/purple	No
Cayaponia granatensis	19	Blue/purple	No
Gurania eriantha	20.8	Green	Yes
Gurania cf. macrantha	20.8	Green	Yes
Gurania pedata	20.8	Green	Yes
Gurania rizantha	20.8	Green	Yes
Melothria dulcis	30	Yellow	Yes
Psiguria triphylla	25	Green	Yes
Sicydium diffusum	7	Black	No
Dichapetalum spruceanum	15	Black	No
Tapura acreana	10	Green	No
Davilla nitida	5	Red	No
Davilla rugosa	5	Blue/purple	No
Doliocarpus multiflorus	9	Blue/purple	No
Tetracera willdenowiana	3	Mixed	No
Diospyros artanthifolia	30	Yellow	Yes
Muntingia calabura	12.5	Red	No
Sloanea guianensis	8	Red	No
Alchornea glandulosa	8.5	Red	No
Caryodendron orinocense	45	Green	No
Drypetes amazonica	10.5	Green	No
Hyeronima alchorneoides	4.5	Blue/purple	No
Hyeronima oblonga	3.5	Blue/purple	No
Margaritaria nobilis	4	Blue/purple	No
Omphalea diandra	90	Green	Yes
Pera arborea	5	Mixed	No
Pera benensis	5	Mixed	No
Plukenetia polyadenia	19	Green	Yes
Sapium glandulosum	6	Mixed	No
Apium laurifolium	5	Mixed	No
Sapium marmieri	6	Mixed	No
Andira inermis	50	Green	No
Dipteryx micrantha	29.5	Yellow	No
Swartzia arborescens	20	Green	Yes
Swartzia cardiosperma	13	Green	Yes
Swartzia leptopetala	16	Green	Yes
Swartzia trianae	22	Green	Yes
Casearia aculeata	3	Red	No
Laetia corymbulosa	7	Mixed	No
Laetia procera	4	Mixed	No
Lindackeria paludosa	8	Mixed	No
Mayna odorata	20	Yellow	Yes
Drymonia serrulata	12	Mixed	No

Species	Fruit size (mm)	Color	Protection
Salacia macrantha	37.5	Yellow	Yes
Tontelea attenuata	20	Yellow	Yes
Tontelea sp.	20	Yellow	Yes
Aniba hostmanniana	12.5	Mixed	No
Endlicheria krukovii	19	Mixed	No
Endlicheria sericea	17.5	Mixed	No
Nectandra membranacea	12	Green	No
Ocotea sp.	7	Mixed	No
Ocotea cernua	7.5	Mixed	No
Ocotea longifolia	7	Mixed	No
Ocotea oblonga	14.5	Mixed	No
Ocotea tomentosa	8	Green	No
Ocotea cf. amazonica	10	Green	No
Ocotea floribunda	12.5	Black	No
Rhodostemonodaphne kunthiana	15	Mixed	No
Rhodostemonodaphne synandra	15	Mixed	No
Couroupita guianensis	200	Brown	Yes
Eschweilera andina	80	Brown	No
Grias peruviana	55	Brown	No
Gustavia hexapetala	47.5	Orange	Yes
Gustavia poeppigiana	50	Green	Yes
Strychnos schultesiana	90	Yellow	Yes
Phthirusa retrofelxa	5	Red	No
Psittacanthus cucullaris	11.5	Red	No
Struthanthus orbicularis	3.5	Blue/purple	No
Adenaria floribunda	3	Blue/purple	No
Byrsonima crispa	9.5	Yellow	No
Byrsonima cf. japurensis	9.5	Yellow	No
Marcgravia macrophylla	10	Mixed	No
Norantea guianensis	9	Mixed	No
Souroubea sympetala	10	Mixed	No
Bellucia grossularioides	15	Green	No
Bellucia pentamera	35	Green	No
Blakea rosea	10	Black	No
Clidemia hirta	8.5	Blue/purple	No
Clidemia inobsepta	4	Blue/purple	No
Clidemia octona	9.5	Blue/purple	No
Clidemia septuplinervia	10	Blue/purple	No
Clidemia sp.	13.5	Blue/purple	No
Henriettella fissanthera	4	Green	No
Henriettella sylvestris	5	Green	No
Leandra longicoma	5	Blue/purple	No
Loreya strigosa	11.5	Green	No
Miconia cf. affinis	5.5	Blue/purple	No
Miconia elata	4	Blue/purple	No
Miconia napoana	8.5	Blue/purple	No
Miconia ampla	7.5	Yellow	No
Miconia argyrophylla	4.5	Black	No
Miconia cf. prasina	4	Black	No
Miconia ternatifolia	3	Black	No
Miconia dolichorryncha	3.5	Black	No
Miconia erioclada	7	Black	No
Miconia nervosa	7	Mixed	No
Miconia trinervia	4	Mixed	No
Guarea guidonia	11	Mixed	No
Guarea kunthiana	8	Mixed	No
Trichilia martiana	8	Mixed	No
Trichilia maynasiana	8	Mixed	No
Trichilia micrantha	10	Mixed	No
Trichilia pallida	7	Mixed	No
Trichilia cf. verrucosa	15	Mixed	No
Trichilia pleeana	7	Mixed	No
Trichilia tuberculata	9	Mixed	No
Mendoncia lindavii	13.5	Blue/purple	No
Mendoncia odorata	13.5	Blue/purple	No
Abuta grandifolia	12	Yellow	Yes
Abuta aff grandifolia	12	Yellow	Yes
Cissampelos cf. tropaeolifolia	5	Red	No

Species	Fruit size (mm)	Color	Protection
Disciphania ernstii	2.1	Blue/purple	No
Odontocarya tripetala	9	Yellow	No
Odontocarya mallosperma	9	Yellow	No
Sciadotenia ramiflora	7.5	Green	No
Sciadotenia toxifera	17.5	Green	No
Abarema jupunba	6	Mixed	No
Enterolobium cyclocarpum	35	Black	Yes
Enterolobium schomburgkii	17.5	Black	No
Inga cf acreana	24	Green	Yes
Inga acuminata	27.5	Green	Yes
Inga alba	12.5	Green	Yes
Inga cylindrica	25	Green	Yes
Inga brachyrhachys	12.5	Green	Yes
Inga heterophylla	17.5	Green	Yes
Inga densiflora	12.5	Green	Yes
Inga edulis	11.2	Green	Yes
Inga gracilior	19	Green	Yes
Inga leiocalycina	22.5	Green	Yes
Inga macrophylla	30	Green	Yes
Inga sapindoides	22.5	Green	Yes
Inga umbellifera	20.5	Green	Yes
Inga marginata	12.5	Green	Yes
Inga stenoptera	25	Green	Yes
Inga tenuistipula	28.5	Green	Yes
Inga acrocephala	40	Green	Yes
Inga thibaudiana	23	Green	Yes
Inga vera	12.5	Green	Yes
Inga vismiifolia	70	Green	Yes
Parkia multijuga	70	Black	Yes
Samanea saman	16.5	Black	Yes
Stryphnodendron guianense	9.5	Black	Yes
Siparuna cf asperula	3	Red	No
Siparuna gilgiana	3	Red	No
Siparuna cervicornis	3	Blue/purple	No
Siparuna cuspidata	3	Blue/purple	No
Batocarpus amazonicus	40	Yellow	No
Batocarpus orinocensis	50	Green	Yes
Brosimum alicastrum	20.5	Yellow	No
Brosimum guianense	16.5	Red	No
Brosimum aff. lactescens	15	Blue/purple	No
Brosimum lactescens	15	Orange	No
Brosimum utile	16	Green	No
Castilla ulei	30	Yellow	Yes
Clarisia biflora	23	Green	No
Clarisia racemosa	14.5	Red	No
Dorstenia contrajerva	25	Green	No
Ficus americana	9	Red	No
Ficus andicola	6	Red	No
Ficus donnell-smithii	8	Red	No
Ficus guianensis	6.5	Red	No
Ficus pertusa	6	Red	No
Ficus sphenophylla	6.5	Red	No
Ficus trigona	9.5	Red	No
Ficus gomelleira	17	Green	No
Ficus insipida	31.5	Green	Yes
Ficus maxima	32.5	Green	No
Ficus membranacea	22.5	Green	No
Ficus nymphaeifolia	23	Green	No
Ficus obtusifolia	24	Green	No
Ficus paraensis	16	Green	No
Ficus schultesii	25	Green	No
Ficus trigonata comp maximiliana	25	Green	No
Ficus trigonata comp trigonata	27.5	Green	No
Ficus usiacurina	20	Green	No
Ficus yoponensis	15	Green	No
Ficus sp. 2126	19	Green	No
Helicostylis tomentosa	25	Yellow	No
Maquira calophylla	22.5	Yellow	Yes

Species	Fruit size (mm)	Color	Protection
Perebea mollis	24	Yellow	No
Perebea xanthochyma	4.5	Red	No
Pseudolmedia laevigata	7.5	Red	No
Pseudolmedia laevis	8	Red	No
Pseudolmedia obliqua	14	Yellow	No
Sorocea briquetii	6.5	Blue/purple	No
Sorocea steinbachii	10	Blue/purple	No
Trophis racemosa	7	Red	No
Iryanthera juruensis	13	Mixed	No
Iryanthera leavis	19	Mixed	No
Virola calophylla	11	Mixed	No
Virola cf. cariniata	12	Mixed	No
Virola cf elongata	10	Mixed	No
Virola flexuosa	12	Mixed	No
Virola multinervia	12	Mixed	No
Virola peruviana	13	Mixed	No
Virola sebifera	10	Mixed	No
Ardisia panurensis	4	Blue/purple	No
Ardisia pellucida	6.5	Blue/purple	No
Stylogyne turbacensis	8	Mixed	No
Campomanesia speciosa	30	Brown	Yes
Eugenia biflora	6	Blue/purple	No
Eugenia florida	12.5	Red	No
Eugenia nesiotica	24.5	Red	No
Eugenia stipitata	45	Yellow	No
Eugenia lambertiana	8.5	Yellow	No
Guapira cf cuspidata	10	Red	No
Guapira olfersiana	8.5	Black	No
Neea laxa	8	Mixed	No
Neea cf divaricata	6.5	Blue/purple	No
Neea verticillata	10.5	Black	No
Ouratea cf polyantha	6	Mixed	No
Ouratea weberbaueri	7.5	Mixed	No
Heisteria acuminata	7	Mixed	No
Heisteria nitida	11	Mixed	No
Passiflora ambigua	55	Yellow	Yes
Passiflora cf. micropetala	21	Black	Yes
Passiflora vitifolia	55	Green	Yes
Phytolacca rivinoides	4	Mixed	No
Trichostigma octandrum	6.5	Mixed	No
Peperomia laxiflora	1	Green	No
Peperomia magnoliifolia	5	Green	No
Peperomia rotundifolia	1	Green	No
Peperomia serpens	1	Green	No
Piper aduncum	5	Green	No
Piper aequale	5	Green	No
Piper arboreum	5	Green	No
Piper cf. avellanum	4	Green	No
Piper cumanense	3	White	No
Piper demeraranum	7	Breen	No
Piper fresnoense	4	Breen	No
Piper hispidum	5	Breen	No
Piper laevigatum	3	Breen	No
Piper peltata	5	Breen	No
Piper phytolaccaefolium	4	Green	No
Coccoloba densifrons	13.5	Black	No
Coccoloba coronata	7.5	Blue/purple	No
Coccoloba mollis	11.5	Blue/purple	No
Coccoloba cf. parimensis	7.5	Blue/purple	No
Quiina macrophylla	7.5	Red	No
Prunus myrtifolia	10.2	Blue/purple	No
Alibertia cf hadrantha	30	Black	No
Bertiera guianensis	4.5	Black	No
Duroia hirsuta	25	Yellow	Yes
Genipa americana	80	Brown	Yes
Genipa cf. williamsii	60	Brown	Yes
Geophila cordifolia	4	Red	No
Geophila repens	5	Red	No

Species	Fruit size (mm)	Color	Protection
Geophila macropoda	10	Black	No
Gonzalagunia cornifolia	6	White	No
Guettarda aromatica	11	Black	No
Hamelia axillaris	7.5	Black	No
Isertia leavis	8.5	Green	No
Posoqueria longiflora	35	Yellow	Yes
Psychotria bahiensis	7.5	Blue/purple	No
Psychotria bracteocardia	5	Blue/purple	No
Psychotria caerulea	8.5	Blue/purple	No
Psychotria casiquiaria	4.5	Blue/purple	No
Psychotria deflexa	9	Blue/purple	No
Psychotria herzogii	10	Blue/purple	No
Psychotria racemosa	4.5	Black	No
Psychotria psychotriifolia	7.5	Red	No
Psychotria muscosa	5	Red	No
Psychotria tenuifolia	6	Red	No
Psychotria viridis	6	Red	No
Psychotria poeppigiana	7	Mixed	No
Randia hondensis	20.5	Yellow	Yes
Rudgea cornifolia	7.5	White	No
Sabicea villosa	8	Blue/purple	No
Cupania cinerea	8	Mixed	No
Cupania cf. latifolia	8	Mixed	No
Cupania pallida	9	Mixed	No
Cupania scrobiculata	6	Mixed	No
Paullinia alata	8	Mixed	No
Paullinia bracteosa	8	Mixed	No
Paullinia faginea	7	Mixed	No
Paullinia grandifolia	10	Mixed	No
Paullinia hispida	7	Mixed	No
Paullinia obovata	9	Mixed	No
Paullinia rugosa	8	Mixed	No
Paullinia serjaniifolia	6	Mixed	No
Paullinia sp.	9	Mixed	No
Talisia intermedia	22	Yellow	Yes
Talisia cf. nervosa	20	Red	Yes
Vouarana guianensis	10	Mixed	No
Chrysophyllum argenteum	22	Green	No
Chrysophyllum cf lucentifolium	45	Yellow	No
Chrysophyllum sp.	27.5	Yellow	No
Chrysophyllum parvulum	10	Blue/purple	No
Pouteria caimito	25	Yellow	Yes
Pouteria cuspidata	22.5	Yellow	Yes
Pouteria lucuma	85	Yellow	No
Pouteria pariry	100	Yellow	No
Pouteria procera	37.5	Yellow	Yes
Pouteria reticulata	13.5	Blue/purple	Yes
Pouteria sp.	35	Brown	Yes
Sarcaulus brasiliensis	22.5	Yellow	Yes
Picramnia latifolia	5.5	Red	No
Simarouba amara	10	Black	No
Brunfelsia grandiflora	13.5	Green	No
Cestrum racemosum	4	Black	No
Cestrum sylvaticum	5	Black	No
Lycianthes cyathocalyx	6.5	Red	No
Lycianthes pauciflora	12.5	Red	No
Solanum cyathophorum	6.5	Black	No
olanum grandiflorum	47.5	Black	No
Solanum lepidotum	8.5	Black	No
Solanum pectinatum	48.2	Black	No
Solanum jamaicense	7.5	Red	No
Solanum cf. americanum		Red	No
Solanum cf. sessile	12	Red	No
Solanum sessiliflorum	31.6	Red	No
Solanum sp. 2125	11	Green	No
Witheringia solanaceae	7	Red	No
Guazuma ulmifolia	13	Black	No
Herrania nitida	50	Green	Yes

Species	Fruit size (mm)	Color	Protection
Sterculia apetala	15	Brown	No
Sterculia guapayensis	20	Brown	No
Sterculia colombiana	15	Mixed	No
Theobroma cacao	80	Yellow	Yes
Theobroma glaucum	80	Green	Yes
Theobroma subincanum	85	Brown	Yes
Clavija ornata	21.5	Yellow	Yes
Apeiba aspera	30	Black	Yes
Apeiba tibourbou	37.5	Black	Yes
Ampelocera edentula	18	Yellow	No
Celtis schippii	9	Black	No
Celtis iguanaeus	10	Yellow	No
Trema integerrima	3	Red	No
Trema micrantha	3	Red	Yes
Urera baccifera	3	Yellow	No
Urera caracasana	8.5	White	No
Aegiphila guianensis	4.5	Blue/purple	No
Aegiphila integrifolia	4.5	Blue/purple	No
Citharexylum spinosum	6.5	Black	No
Vitex compressa	20	Green	No
Vitex orinocensis	12.5	Blue/purple	No
Leonia crassa	52.5	Brown	Yes
Leonia glycycarpa	52.5	Brown	Yes
Phoradendron piperoides	4	Red	No
Cissus erosa	7	Blue/purple	No
Cissus microcarpa	11.5	Black	No
Cissus sicyoides	7.5	Black	No
	Average = 17.3		

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