

Fruit Dispersal Syndrome Characterization of a Lowland Bornean Rainforest Masting Event

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Abstract

During the stay at Maliau Basin in the Malaysian state of Sabah a mast fruiting event occurred. This study attempts to categorize the various dispersal syndromes exhibited by the fruit found in the forest during that time. A wide variety of fruit traits were analyzed with the intention of subdividing the larger dispersal categories. A clear clustering of characters around four dispersal syndromes was found, with sub-clustering also evident. Some families and genera displayed radically different dispersal syndromes, showing a high degree of syndrome plasticity within a phylogenetic lineage. In most cases, plants from a wide variety of lineages converged on similar fruit morphologies, creating the syndromes. Observational evidence suggested that the dispersal syndrome utilized was related to the canopy layer height on which the fruit hung or fell to.

Introduction

The rainforests of Southeast Asia are globally unique, not because they are dominated by a single family (the Dipterocarpaceae), but because that family is exerting a controlling force on the flora and fauna to a degree found nowhere else. The entire family fruits in synchrony once every 5 to 7 years. This event is possibly triggered by “El Niño” southern oscillation events (Primack and Corlett 2005). Many other rainforest plants coordinate their fruit falls with the dipterocarps and what results is a mast fruiting (C.O. Webb, personal communication). Our time in Maliau happened to occur during the fruit fall of a masting event, which had not occurred for the past eleven years. This allowed for the collection and characterization of many fruits that are only seen during these events.

According to the Jansen-Connell hypothesis (citations), it is beneficial for a tree to distribute its progeny over a wide area to avoid high local seed predation, inbreeding, competition and disease. Seeds, in most cases, are incapable of transporting themselves through the force of the parent plant and must rely on energy provided by outside sources such as animals, wind, and water in most cases. Plants have evolved to either provide animals dispersal incentives or utilize non-biotic sources by investing energy in their fruit and seed morphology.

In the tropical rainforests there exists an environment with many layers and many biotic and non-biotic factors to harness for dispersal. These dispersal factors require different fruit morphologies to be harnessed. Janson (1983) found that the morphologies of much of the fruit in a tropical rainforest in Peru could be broken down into two types: one adapted to dispersal for birds and another for mammals. In this study I attempted to cover a broader range of dispersal types to include wind and cache dispersal (through stores of rodents and squirrels), and analyzed more fruit characters in the hope of sub-dividing the larger dispersal categories such as wind, cache, bird and mammal into more specialized dispersal syndromes. The central aim of this study was to discover which fruit characters determine dispersal syndromes and what causes them to be subdivided.

Hypotheses

By analyzing fruit characters using cluster analyses, dispersal syndromes will cluster together.

Distinct sub-clusters will occur within the larger clusters of dispersal syndromes.

Fruit morphologies will be related to the crown height.

Methods

The study was conducted from August 17th to 24th, 2007 in the Maliau Basin Conservation Area in Sabah, Malaysian Borneo. All available ripe fruit was collected by walking along the forest floor around and within the conservation area. Other methods such as climbing, tree shaking and stick throwing were used to secure fruit still on the tree. In all, fruit from 48 species was collected. Characters were recorded for a suite of numerical and factorial measurements such as fruit and seed size, presence of a husk and skin color (See Table 1). The character data were analyzed using cluster analyses with the *daisy*, and *hclust* tools within the R statistical analysis package.

Ecological data was gathered in daily morning sessions by observing animals feeding on the fruit. Also, any fruit seen moving by any other means was noted. Finally, the forest strata (upper, middle, lower, ground) of the fruit was noted when found.

Results and Discussion

A cluster dendrogram was produced as a result of analysis with the R software program (Fig. 1). The dendrogram shows clear clustering and sub-clustering of fruits which shared similar sets of traits. The traits which seemed to characterize the clusters the most were fruit size, presence or absence of a hard husk, fleshiness, and presence or absence of wings. Three main clusters emerged as shown in green, other colors and browns as branches on the dendrogram. The brown cluster is defined by the fruits all having a brown color and being dry (non-fleshy). The colored (non-green) cluster is defined by the fruits being colorful and fleshy, whereas the green group (durians) may be separated out mainly by size of fruit and seeds.

Seven distinct sub-clusters (individual color blocks in Fig.1) emerged from the three broader clusters. These sub-clusters are within the brown and colored clusters. The colored group split into one group with large, fleshy and partly (37.5%) sweet fruits (Fig. 1, orange block), one with small, unsweet (0%) flesh and few seeds (red block) and another group with small fruits and many seeds (blue block). The characters exemplified by the brown cluster are very different from the colored ones in that they lack flesh and color. Fruits belong to two distinct groups within this larger cluster. The two outer sub-clusters all have wings (an extended and flattened piece of tissue) attached to the seed, whereas the middle cluster lacks wings and has a hard outer shell (husk). All these traits are typical of fruit with abiotic primary dispersal agents.

Through direct observation, the dispersal strategy of the dipterocarp fruits becomes clear. When the ripe seeds are on the tree and the wind picks up, the seeds detach and begin to spin much like a helicopter. I have personally seen these seeds carried over 100 meters over an open area. The fruits with a hard husk seem to not have any primary dispersers, as they all fall under the parent tree. Once they have fallen, rodents and squirrels gather large quantities and bury them for later consumption. Often they are forgotten and germinate where planted. This is an example of cache dispersal.

The green cluster is made up of three species of durian (*Durio*), two green and one yellow. As stated earlier, all three mapped far away from the other clusters. Despite this they most likely belong to

the syndromes exhibited by the colored cluster. The green durian is commercially eaten by a mammal (*Homo sapiens*) and displays many characters befitting a mammal fruit, such as its odor, seed texture, thick husk, spines, sweetness and large size. No one is exactly sure what disperses durian because everything seen eating it either does not touch the seeds or destroys them through chewing. It seems likely that elephants may be able to disperse the seeds because of their habit of eating durian whole (albeit after chewing). A simple experiment could be performed where an elephant is fed a number of durians, after which the feces could be examined for viable seeds.

The yellow durian (Figure 1, 30) was less similar than the other two green species of durian. It is not cultivated and looks superficially similar to the green durian in that it has a husk, spines and is large in size. The remaining characters differ from that of the green durian in that it displays a red, chalky flesh that is not sweet after dehiscing on the tree and does not smell. These characters are indicative of a bird dispersal syndrome and may be dispersed by horn-bills. Discussions with local guides revealed that the horn-bills do swallow the seeds.

These trait clusters represent different adaptive solutions to the problems associated with germinating near the parent tree. All are geared towards the dissemination of the seeds to a place where conditions are more favorable for seed growth but, as the wide array of trait clusters show, the techniques vary greatly. The morphology of the fruit is indicative of the technique the plant uses to disperse its seeds. Janson (1983) related the size, color and husk presence of neotropical fruit to the size, vision and jaw form of the birds and mammals which feed on them. He found that there was a tight link between all of these factors which revealed separate bird and mammal adapted dispersal syndromes (a clustering of certain fruit traits to suit the abilities of the disperser). The orange cluster in Fig. 1 of large, fleshy, sometimes sweet fruits fits the mammal (specifically primate) dispersal syndrome, while the red and blue clusters fit the bird dispersal syndrome.

The genus *Durio* is an interesting example of syndrome plasticity. Some members of the genus seem to employ mammals as dispersers and some seem to use birds. Another case is found within the family *Dipterocarpaceae*. This family usually has a highly conserved dispersal strategy through the use of wings to harness the wind but two members analyzed mapped into the cache dispersal cluster. The wings were much reduced and the seed coat formed a hard husk. These fruits demonstrate that the selective pressure of the disperser is more important than the phylogenetic lineage to which the plant belongs.

Many non-related fruits share a similar morphology. For example, from the 48 types of fruit sampled, less than half a dozen distinct trait clusters appeared. Although two fruits picked up from the forest floor may look similar, they more likely than not come from very different plant lineages. For example, the bird dispersed fruits in the red and blue clusters comprise at least seven different families of plants, but all look similar. These clusters are an excellent example of convergent evolution across multiple families and orders to a set of characters that allows these seeds to be propagated.

The dispersal agents of wind, mammals, birds, and rodents are not evenly distributed throughout the layers of the forest height profile. Primates are mainly found in the mid and upper layers of the canopy, rodents on the forest floor, different birds inhabit different canopy levels and wind exists mainly at the top of the canopy. Many fruit falls to forest floor, which is isolated from wind and animals that are completely arboreal, of which there are many. What this does is allow the fruit to gain access to ground foraging birds and mammals who do not climb trees, as well as all of the lower level tree dwellers. To effectively harness these dispersal agents the plants must produce and drop (or retain) fruit in the right place.

Although the exact height at which the mature fruit occurs was not noted for each species, informal observations done during the study may provide some insights as to whether the canopy level the fruit occupies influences the type of fruit produced. On one fruit collecting trip through the "nature trail", about 30 different species of fruit were collected from understory trees. The vast majority of these fruits were within the red and blue clusters of Fig. 1, the bird dispersed fruits. The convergence of

so many different understory tree species upon small, tasteless, bright fruit seems to reflect the fact that birds are common throughout the understory layer while mammals, wind and rodents are not.

All the fruits with a hard husk, including the green durians, were found on the forest floor. This is the realm of seed hoarding (and potentially dispersing) rodents, and larger ground mammals which may disperse durian. The yellow durian remains high up on the tree when ripe and dehisces, which makes the fruit much more accessible to animals lacking hands. Personal observations of hornbills were always of them in or flying to tall trees, and on more than one occasion they were observed in a yellow durian tree. Many upper canopy and emergent trees have winged or fluffy seeds. This can be viewed as a response to the greater degree of airflow above the canopy that can be harnessed for moving seeds. Almost all of the dipterocarps collected, which are largely emergents, have winged seeds to harness the force provided by the wind.

The fruit dendrogram (Fig. 1) is a snapshot of an event that happens very rarely. Fruit is on the ground for only a few weeks each masting period, and the last was eleven years ago. Most of the time the forests of Sundaland are a “fruit desert” (Primack and Corlett 2005). It would be interesting to see what a types of fruit are produced during the non-masting period and to study how the animals cope with the lack of fruit. Figs, fruiting year-round and eaten by birds and mammals alike, must surely play a large role during these times. Another interesting comparison could be made with the community level fruit output of New Guinea, which lacks primates but is mostly Asian floristically.

Acknowledgments

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References

Primack, R.B. and Corlett, R.T. (2005) *Tropical Rainforests: An Ecological and Biogeographical Comparison*, Blackwell

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Figures

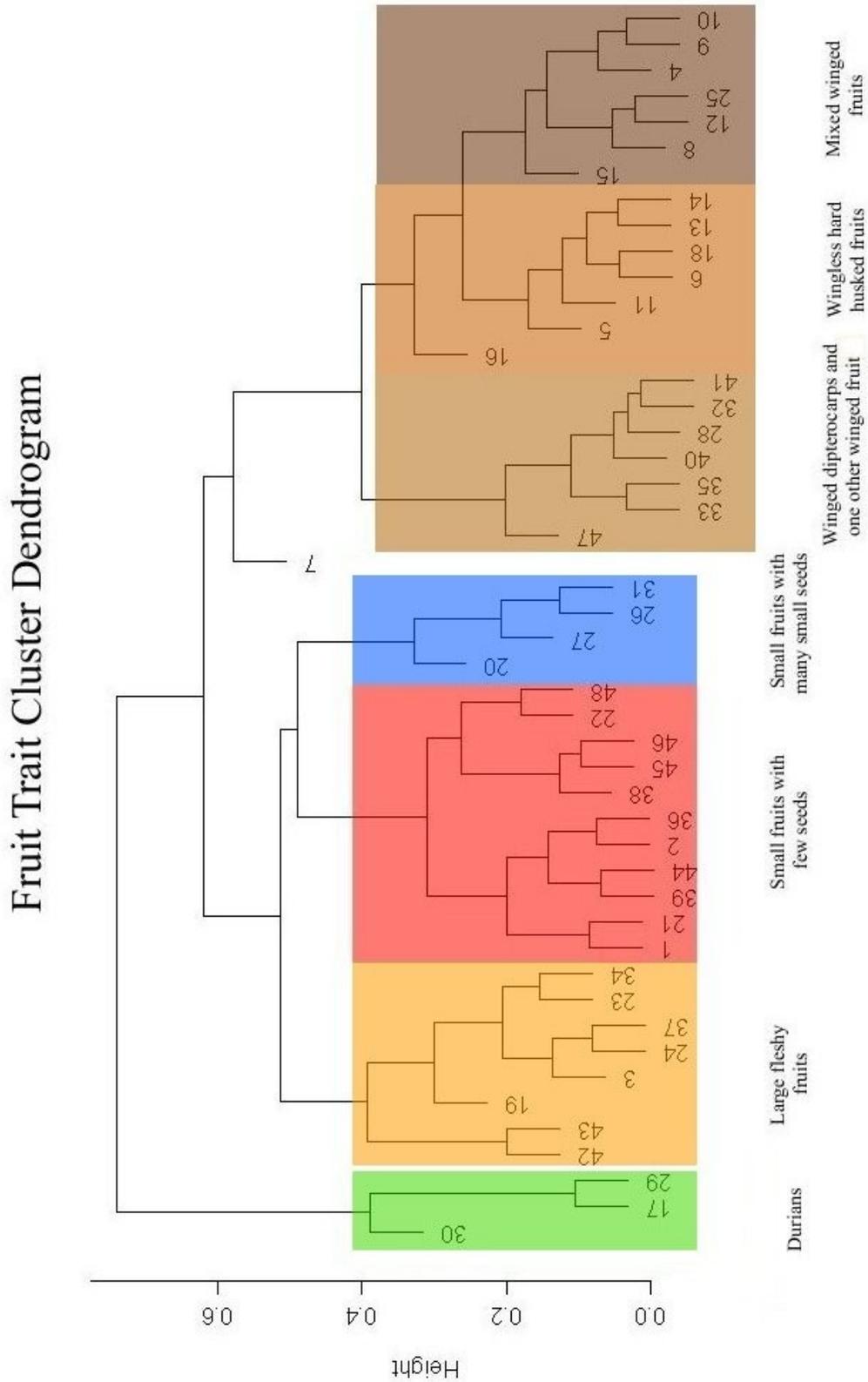


Figure 1: Dendrogram of 48 fruits found in Maliau Basin using 17 characters.

Fruit	Species	Family	Dry vs. fleshy	Fruit length (mm)	Fruit width (mm)	Skin Color	Total weight (g)	Hard husk surrounding seed?	Flesh color
1		Connaraceae	Fleshy	27		8 Red	1.9 No		Orange
2	<i>Baccauria</i>	Euphorbiaceae	Fleshy	13		12 Red	2 No		Blue
3	<i>Luvunga</i>	Rutaceae	Fleshy	32		17 Yellow	4 No		Clear
4	<i>Parashorea</i>	Dipterocarpaceae	Dry	78		80 Brown	1 No		N/A
5	<i>Eusideroxylon</i>		Dry	85		49 Brown	74.7 Yes		N/A
6	<i>Vatica</i>	Dipterocarpaceae	Dry	55		43 Brown	22.8 Yes		N/A
7	<i>Gynostoma</i>	Casauraceae	Dry	35		35 Brown	7.2 No		N/A
8		Fabaceae	Dry	74		25 Brown	0.2 No		N/A
9	<i>Parashorea</i>	Dipterocarpaceae	Dry	120		84 Brown	6.2 No		N/A
10	<i>Parishia</i>	Anacardiaceae	Dry	100		75 Brown	1 No		N/A
11	<i>Shorea</i>	Dipterocarpaceae	Dry	114		57 Brown	0.7 Yes		N/A
12	<i>Combretum</i>	Combretaceae	Dry	25		24 Brown	0.2 No		N/A
13		Dipterocarpaceae	Dry	15		16 Brown	1.4 Yes		N/A
14	<i>Trigobalanus verif</i>	Fagaceae	Dry	13		12 Brown	0.3 Yes		N/A
15	<i>Koompassia</i>	Fabaceae	Dry	92		26 Brown	0.4 No		N/A
16	<i>Castanopsis</i>	Fagaceae	Dry	15		17 Brown	0.5 Yes		N/A
17	<i>Durio</i>	Malvaceae	Fleshy	145		115 Green	734 Yes		White
18	<i>Lithocarpus</i>	Fagaceae	Dry	27		45 Brown	21.8 Yes		N/A
19	<i>Nephilium</i>	Sapindaceae	Fleshy	49		40 Red	20 No		Clear
20	<i>Cidemia hirta</i>	Melastomataceae	Fleshy	11		8 Blue	0.2 No		N/A
21	<i>Aporosa</i>	Euphorbiaceae	Fleshy	16		17 Yellow-orange	2 No		Orange
22		Curcubitaceae	Fleshy	79		35 Red	27.1 No		White
23			Fleshy	33		26 Red	4.6 No		No
24			Fleshy	25		14 Yellow	2.2 No		Clear
25			Dry	12		35 Brown	0.01 No		N/A
26	<i>Ficus</i>	Moraceae	Fleshy	13		12 Red	0.7 No		White
27		Rubiaceae	Fleshy	6		6 Yellow	0.1 No		White
28		Dipterocarpaceae	Dry	84		75 Brown	2.8 No		Brown
29	<i>Durio</i>	Malvaceae	Fleshy	155		135 Green	1015 Yes		White
30	<i>Durio</i>	Malvaceae	Fleshy	113		115 Yellow	408 Yes		Red
31	<i>Ficus</i>	Moraceae	Fleshy	17		12 Red	1.1 No		White
32			Dry	83		44 Brown	0.4 No		Brown
33			Dry	63		30 Brown	0.3 No		Brown
34			Fleshy	6		5 Red	0.2 No		Clear
35	<i>Shorea</i>	Dipterocarpaceae	Dry	82		49 Brown	3.6 No		Brown
36	<i>Baccauria</i>	Euphorbiaceae	Fleshy	20		25 Red	2.7 No		Blue
37	<i>Aglia</i>	Meliaceae	Fleshy	20		21 Yellow	4.2 No		Clear
38	<i>Eugenia</i>		Fleshy	10		9 Purple	0.5 No		White
39		Conneraceae	Fleshy	18		10 Red	1.2 No		White
40		Dipterocarpaceae	Dry	90		47 Brown	2.9 No		Brown
41		Dipterocarpaceae	Dry	92		60 Brown	1.6 No		Brown
42	<i>Hausfieldia</i>		Fleshy	34		28 Yellow	17.3 No		Yellow
43	<i>Irvingiz</i>		Fleshy	52		40 Yellow	43.8 No		Yellow
44		Vitaceae	Fleshy	20		12 Red	0.7 No		White
45			Fleshy	30		13 Red	4 No		White
46			Fleshy	11		7 Red	0.4 No		White
47			Dry	16		9 Brown	0.6 Yes		Brown
48	<i>Baccauria</i>	Euphorbiaceae	Fleshy	33		28 Green	14.2 No		White

Fruit	Wings small(<20mm)	Wings large(>20mm)	Dehiscent on tree?	Sweet flesh?	Flesh bitter / sour	Skin spiny?	Seed length (mm)	Seed width (mm)	#seeds/fruit
1	1	0	0 Yes	No	No	No	20	9	1
2	0	0	0 Yes	No	Yes	No	10	8	1
3	0	0	0 No	Yes	No	No	21	9	1.5
4	0	0	5 No	N/A	N/A	No	10.5	9	1
5	0	0	0 No	N/A	N/A	No	63	34	1
6	0	0	0 No	N/A	N/A	No	32	17	1
7	20	0	0 Yes	N/A	N/A	Yes	5	4	20
8	0	0	0 No	N/A	N/A	No	1	1	1
9	2	2	3 No	N/A	N/A	No	2	2	1
10	2	2	3 No	N/A	N/A	No	10	9	1
11	2	2	3 No	N/A	N/A	No	10	7	1
12	4	4	0 No	N/A	N/A	No	11	4	1
13	5	5	0 No	N/A	N/A	No	11	13	1
14	0	0	0 No	N/A	N/A	No	3	3	1
15	0	0	1 No	No	N/A	No	27	10	1
16	0	0	0 No	No	N/A	Yes	2	2	1
17	0	0	0 No	Yes	No	Yes	35	23	20
18	0	0	0 No	N/A	N/A	No	13	23	1
19	0	0	0 No	Yes	No	Yes	25	14	1
20	0	0	0 No	N/A	N/A	No	0.1	0.1	75
21	0	0	0 Yes	No	No	No	10	8	3
22	0	0	0 Yes	No	Yes	No	10	8	31
23	0	0	0 No	No	No	No	25	11	1
24	0	0	0 No	No	No	No	23	11	1
25	5	5	0 No	N/A	N/A	No	5	3	1
26	0	0	0 No	Yes	No	No	0.1	0.1	75
27	0	0	0 No	No	No	No	0.1	0.1	60
28	2	2	3 No	No	No	No	22	15	1
29	0	0	0 No	Yes	No	Yes	36	19	17.5
30	0	0	0 Yes	No	No	Yes	33	17	12.5
31	0	0	0 No	Yes	No	No	0.01	0.01	75
32	2	2	3 No	No	No	No	12	11	1
33	2	2	0 No	No	No	No	10	7	1
34	0	0	3 No	No	No	No	5	4	1
35	2	2	0 No	No	No	No	17	12	1
36	0	0	0 Yes	No	No	No	11	8	3
37	0	0	0 No	No	No	No	13	13	1
38	0	0	0 No	No	Yes	No	8	6	1
39	0	0	0 Yes	No	Yes	No	10	5	1
40	0	0	5 No	No	No	No	18	15	1
41	2	2	3 No	No	No	No	13	12	1
42	0	0	0 No	No	Yes	No	23	12	1
43	0	0	0 No	Yes	No	No	45	32	1
44	0	0	0 Yes	No	No	No	11	7	1
45	0	0	0 No	No	Yes	No	25	10	1
46	0	0	0 No	No	No	No	9	6	1
47	0	0	0 No	No	No	No	9	5	1
48	0	0	0 Yes	No	Yes	No	15	9	1

Table 1: Character data of the 48 fruits analyzed.