

Mapping Dipterocarp Seed Dispersal Under Natural and Experimental Conditions In Maliau Basin

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Abstract: In this study we sought to both observe and model Dipterocarp seed dispersal during a mast fruiting event in Maliau Basin in Sabah, Malaysia. In choosing genera with differing numbers of fruit 'wings' (*Dryobalanops* spp, 5; *Parashorea* spp, 3) we sought to answer the question of whether or not their morphological variability entailed a divergence in dispersal distances. To do this we first observed the seed shadow of each tree under natural conditions by recording the number and distance of seeds along transects originating from the parent tree. Following this we collected 20 intact seeds from each tree genus and performed 200 experimental seed drops from a 5m platform, measuring the distance traveled by each seed. We then extrapolated the experimental data and compared it to the observed data for each tree. We found that there were no significant differences in seed shadow around any of the trees under natural conditions but that there was a significant difference in distance traveled under experimental conditions between the two genera. When we extrapolated the experimental data we found that the *Parashorea* model was a very poor fit for the observed data, but that the *Dryobalanops* model fit the observed data relatively well. Though there may have been complicating errors in our methods, our results seem to indicate that there is at least one unaccounted for equalizing factor that causes a convergence of dispersal distances under natural conditions.

Introduction: Mast fruiting events, approximately two week long periods during which a very great number of trees with gravity, wind and animal dispersed seeds all bear fruit simultaneously over vast stretches of forest (historically large fractions of the island of Borneo), have become quite rare due to a combination of factors, including the fragmentation of the forest and recent irregularities in ENSO cycles. While they historically occur approximately every six or seven years, such an event had not been observed for over a decade in Maliau Basin, the largest stretch of contiguous, virgin lowland rain forest left in the Malaysian state of Sabah. During this project we were lucky enough to be in Maliau Basin during one of the rare mast fruiting events. To take advantage of the coincidence, we decided to focus our project on the fruiting of the forest's most dominant family of trees, Dipterocarpaceae. The family is tremendously diverse, both in terms of number of species and in morphologic variation. How so many closely related trees species are able to coexist in one environment without competitive excluding one another is quite perplexing and perhaps could provide evidence for Hubbell's Neutral Theory of ecology. As a way of addressing these topics, we choose to study one of the most salient differences between the Dipterocarp genera (during the mast at least), their seed morphologies. By studying how their seed dispersal patterns vary with morphology, we will hopefully be able to determine some of the functional differences between the genera, differences that could potentially suggest a means of niche separation. On the other hand, a conserved dispersal distance across genera may suggest an optimal dispersal distance

This project will consist of two components; first we will conduct a set of observations to determine how the natural distribution of seeds (seed shadow) varies between two genera, *Dryobalanops* and *Parashorea* spp. These two genera were selected because they have large variation in seed morphology, where *Dryobalanops* spp has a larger seed husk, and five shorter but wider wings, while *Parashorea* spp had a smaller seed husk, three full size and two very small wings. We will then model the dispersal of the two genera experimental under controlled conditions. By comparing the experimental and observed data we will be able to determine the accuracy of our model, but more importantly be able to begin postulating what (if any) environmental factors play an important role in Dipterocarp seed dispersal.

For the observational study component of the project we hypothesize that there will be a

significant difference in the dispersal distance between the two genera but not within replicate plots of each species. Furthermore we hypothesize that there will be uniformity in the distribution of seeds toward each cardinal direction (e.g. the seed shadow will not be biased towards the south side of a tree), regardless of species. Secondly, we hypothesize that the ideal model based on experimental drop data will show that a significant difference in dispersal pattern exists between the genera. Lastly, we hypothesize that a linear extrapolation of the drop data will create an accurate model of the natural distribution.

Methods: In order to map the seed dispersal, we first identified four trees, two each of two different dipterocarp species (*Parashorea sp.*, and *Dryobalanops sp.*). For each tree, we laid four twenty meter transects radially away from the tree at 70°, 160°, 250° and 340° with respect to North. We then recorded the position of every seed of that species that the transect intersected. Using this data, we calculated the median distance along each transect and then averaged these values to get a rough average dispersal distance for the tree. We also used a clinometer to determine the height of each tree. Next, we collected 50-100 seed samples from each species and dropped them from different heights, mapping the dispersal. We then used this data to extrapolate the mean dispersal distance if the seeds had been dropped from canopy height. Finally, we used a Wilcox Rank Sum test to determine whether there was any significant difference first between the different directions for a given tree; second, between the two different species in both the natural and experimental settings; and finally, between the experimental and the natural setting data for each species (the R script we used is shown in Appendix 1).

Results: We found that there was no significant difference between the distribution of seeds along each transect of a given tree, which at least to some extent justifies our pooling the data for each tree. Next, we found that there was no significant difference between any of the trees in their natural environment, but when we dropped the seeds from our 5m platform, we found a significant difference between the distance traveled by *Parashorea* and the *Dryobalanops* seeds. These results are summarized by histograms in Figure 1. Finally, in our last test, we found that there was a significant difference between the model projection and the actual *Parashorea* dispersal, but no significant difference between the model projection and the actual *Dryobalanops*. All T-test results are summarized in Appendix 2.

Discussion: At the outset of this project we put forth two pairs of hypotheses about the nature of *Dryobalanops* and *Parashorea* primary fruit dispersal as well as our ability to model it experimentally. Beginning with our first pair of hypotheses, we found each to be half correct. Firstly we found no significant differences between replicates of each species, but we also found no significant differences in the distribution of dispersal distances between species either. In contradiction to the second hypothesis we found no directional patterning of seed dispersal for each tree, but did find that lack of patterning to be uniform across all the trees we observed. This result was particularly surprising given that all four trees studied were inside a small shallow valley cut by the Maliau River, which would lead one to believe that strong wind episodes would largely come along one main axis.

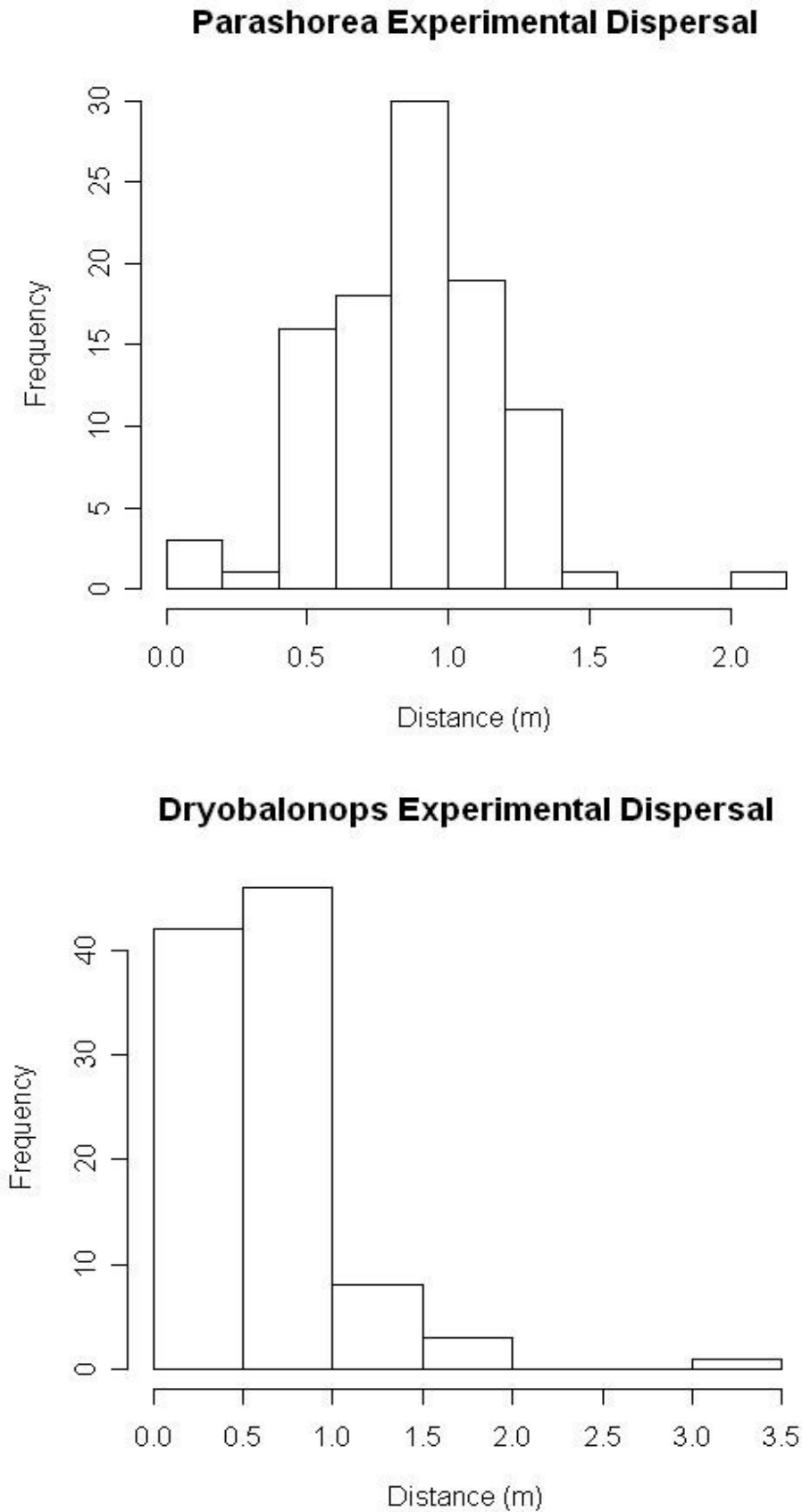
The results for our second pair of hypotheses were quite interesting in light of the initial results. We found that unlike the seed shadows for the trees in natural conditions, the experimental seed drops supported our hypothesis, showing a highly significant difference between the 'dispersal' distance of three-winged *Parashorea* fruit and the five-winged *Dryobalanops* fruit. When we extrapolated the experimental data to compare the model to the observational data, we unexpectedly found that our hypothesis was again half accurate; while the *Dryobalanops* model data was significantly different from the observed data, the modeled *Parashorea* data was not significantly different, and for both replicates had a strikingly similar distribution.

Before drawing or speculating on any meaningful conclusions from these results, we

unfortunately have to qualify them for at least a few different reasons. Firstly there were several factors that were difficult or impossible to control for when comparing all four of the subject trees. Perhaps the two most important of these factors were that we had no system for measuring and/or controlling for the height of the trees (which were emergents) above the rest of the canopy and also that our *Parashorea* specimens were on one side of the river, in undisturbed forest while the *Dryobalanops* both were only found on the other side of the river, which though supposedly left as a river buffer, may have been logged in the recent past. We also faced a serious methodological error, in that we measured the distribution of seeds along transects rather than within set wedges fanning out from the tree. Thus the observed distributions of seeds within the trees' seed shadows were biased towards seeds closest to the trees. This is quite problematic when we compared the observed data with the experimental data, which was not biased towards closer drops (though it was biased towards healthy seeds).

While controlling for some of these factors may have made our results more powerful for drawing conclusions, they still provide material for unforeseen conclusions and additional speculation about some of the factors governing dispersal of the two genera. As with any model, ours tried to simplify a complex situation into the smallest number of explanatory variables, for us just height of drop and seed morphology. The fact that this worked for *Dryobalanops* is quite interesting, given that it does not take into account two additional variables that at least anecdotally seems important: the wind conditions at the point when the seed breaks off the tree and the presence of other vegetation along the seeds descent path towards the ground. Anecdotally it seemed that the majority of the seeds were broken free from their parent tree during episodes of high wind and could travel great distances before hitting the canopy and falling to the ground with much less lateral movement due to other vegetation and vastly decreased wind. Our experimental drops on the other hand were conducted under still wind conditions in open air. What makes this situation even more interesting is the fact that the *Parashorea* model failed miserably to predict the trees' dispersal distributions, greatly overestimating the median dispersal distance. This fact (combined with our experimental results showing that under open air, still wind conditions the seeds have very different dispersal distributions) strongly suggests that there was some equalizing factor or alternatively a set of factors that differentially affected the two genera. Though it is speculative, it at least makes a nice story to suggest that the latter is the case, and that the two anecdotal factors mentioned above are the missing elements for our dispersal models, particularly as they tend to balance each other out (making the *Dryobalanops* model accurate) but potentially having a differential impact on the two genera (stronger winds could have had an exaggerated affect on the dispersal of one seed morphology compared to the other).

Figure 1: Experimental Data ($W = 7512$, $p\text{-value} = 8.402e-10$)



Appendix 1: R Script

```
# call in data

data1=read.table("proj3_data.csv", sep="\t", header=T)
data1
x=data1$X70
y=data1$X160
z=data1$X250

#left out last transect because we had to truncate it

wilcox.test(x,y,paired=FALSE,alternative="two.sided")
wilcox.test(x,z,paired=FALSE,alternative="two.sided")
wilcox.test(y,z,paired=FALSE,alternative="two.sided")

data2=read.table("proj3_data2.csv", sep="\t", header=T)
data2
a=data2$X70
b=data2$X160
c=data2$X340

# left out truncated data

wilcox.test(a,b,paired=FALSE,alternative="two.sided")
wilcox.test(a,c,paired=FALSE,alternative="two.sided")
wilcox.test(b,c,paired=FALSE,alternative="two.sided")

data3=read.table("proj3_data3.csv", sep="\t", header=T)
data3
d=data3$X70
e=data3$X160
f=data3$X250
g=data3$X340

wilcox.test(d,e,paired=FALSE,alternative="two.sided")
wilcox.test(d,f,paired=FALSE,alternative="two.sided")
wilcox.test(d,g,paired=FALSE,alternative="two.sided")
wilcox.test(e,f,paired=FALSE,alternative="two.sided")
wilcox.test(e,g,paired=FALSE,alternative="two.sided")
wilcox.test(f,g,paired=FALSE,alternative="two.sided")

data4=read.table("proj3_data4.csv", sep="\t", header=T)
data4
h=data4$X70
i=data4$X160
j=data4$X250
k=data4$X340

wilcox.test(h,i,paired=FALSE,alternative="two.sided")
wilcox.test(h,j,paired=FALSE,alternative="two.sided")
wilcox.test(h,k,paired=FALSE,alternative="two.sided")
wilcox.test(i,j,paired=FALSE,alternative="two.sided")
wilcox.test(i,k,paired=FALSE,alternative="two.sided")
wilcox.test(j,k,paired=FALSE,alternative="two.sided")

#since none of the results had a significant p-value, we know that
#it is safe to pool all of the data for each tree
```

```

data=read.table("proj3_finaldata.csv",sep="\t",header=T)
data
l=data$Para1..48m.
m=data$Para2..47m.
n=data$Dryo1..49m.
p=data$Dryo2..64m.

wilcox.test(l,m,paired=FALSE,alternative="two.sided")
wilcox.test(l,n,paired=FALSE,alternative="two.sided")
wilcox.test(l,p,paired=FALSE,alternative="two.sided")
wilcox.test(m,n,paired=FALSE,alternative="two.sided")
wilcox.test(m,p,paired=FALSE,alternative="two.sided")
wilcox.test(n,p,paired=FALSE,alternative="two.sided")

drop=read.table("proj3_combdrop.csv",sep="\t",header=T)
drop
wilcox.test(drop$Para.drop,drop$Dryo.drop,paired=FALSE,alternative="two.sided")

jpeg(file="dryo.jpg",width=500)
hist(drop$Dryo.drop,breaks=10, main="Dryobalonops Experimental Dispersal",
xlab="Distance (m)")
dev.off()

jpeg(file="para.jpg",width=500)
hist(drop$Para.drop,breaks=10, main="Parashorea Experimental Dispersal",
xlab="Distance (m)")
dev.off()

finaldata=read.table("proj3_combdrop.csv",sep="\t",header=T)
finaldata

q=finaldata$ModelPara1..48m.
s=finaldata$ModelDryo1..49m.
r=finaldata$ModelPara2..47m.
t=finaldata$ModelDryo2..64m.

wilcox.test(l,q,paired=FALSE,alternative="two.sided")
wilcox.test(m,r,paired=FALSE,alternative="two.sided")
wilcox.test(n,s,paired=FALSE,alternative="two.sided")
wilcox.test(p,t,paired=FALSE,alternative="two.sided")

```

Appendix 2: Wilcoxon Test Results

Tests Between Natural Trees:

Parashorea 1 and Parashorea 2
W = 7549.5, p-value = 0.2234
alternative hypothesis: true mu is not equal to 0

Parashorea 1 and Dryobalonops 1
W = 6211, p-value = 0.7772
alternative hypothesis: true mu is not equal to 0

Parashorea 1 and Dryobalonops 2
W = 4764.5, p-value = 0.5691
alternative hypothesis: true mu is not equal to 0

Parashorea 2 and Dryobalonops 1
W = 8158.5, p-value = 0.349
alternative hypothesis: true mu is not equal to 0

Parashorea 2 and Dryobalonops 2
W = 6258, p-value = 0.08464
alternative hypothesis: true mu is not equal to 0

Dryobalonops 1 and Dryobalonops 2
W = 5897.5, p-value = 0.3838
alternative hypothesis: true mu is not equal to 0

Test Between Two Models:

data: drop\$Para.drop and drop\$Dryo.drop
W = 7512, p-value = 8.402e-10
alternative hypothesis: true mu is not equal to 0

Tests Between Models and Actual Trees:

Parashorea 1
W = 3655.5, p-value = 0.002029
alternative hypothesis: true mu is not equal to 0

Parashorea 2
W = 4897, p-value = 5.422e-05
alternative hypothesis: true mu is not equal to 0

Dryobalonops 1
W = 6570.5, p-value = 0.4429
alternative hypothesis: true mu is not equal to 0

Dryobalonops 2
W = 4767, p-value = 0.4234
alternative hypothesis: true mu is not equal to 0