

Affects of Seed Density and the Occurrence of Multiple Masting Species on Terrestrial Predation of *Parashorea* and *Quercus* Fruits

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Abstract:

One of the most unique and mysterious facets of the Bornean rainforests are the cycles of mast fruiting observed regionally on an average of every seven to ten years. While many theories seeking to explicate the mechanism responsible for such a system have been proposed, none have been proven due largely to the difficulty of studying the event. In the forests of the Maliau basin Sabah, the mast fruiting has grown to include a wide range of species, two of the more prevalent being *Quercus* and the Dipterocarps. By studying predation rates in *Quercus* and *Parashorea* of mixed density and proportion we hoped to study the affects of the enormous fruit density and diversity on individual seed predation. Our study yielded no statistically significant results, however, one interesting trend was noted between the mortality rates of *Parashorea* and *Quercus* in mixed plots suggesting that an increase in absolute diversity may contribute to the survival rate of individual seeds (Webb 1997).

Introduction:

Mast fruiting is believed to have originated from the coordination of the Dipterocarpaceae to the fruiting cycles of the original masting species, the oaks (Ashton, Givenish: 1988). This shift from a single masting group to a highly diverse array of masting species introduced a previously unknown abundance of fruits, causing an increase in fruit density which has interesting implications for predation rates and overall seedling survival. Janson and Connel***describe a scenario where fruit density has a great impact on survival, the lone species concept, which states that the farther a fruit falls from its parent tree (placing it in a less dense conspecific fruit population), the greater its chance of survival. It stands to reason then, that greater phylogenetic diversity contained in a dispersal area should enhance seedling survival. This effect can be linked to two parameters: absolute density, which is the number of same-species seeds in a given area, or relative density, which is the number of any species of seeds in a given area (Webb 1997). In this study, the effects of the lone species concept and absolute density are assessed by experimentally exploring the effects of increased species participation (representing increased phylogenetic diversity) and different dispersal densities (representing absolute density) in masting events on seed survival. We focused on differing densities of *Parashorea* fruits alongside differing densities of *Quercus* fruits in order to test the effects of multiple fruit-types on survival. We hypothesized that a lower fruit density would correlate with lower mortality rates as a result of less predation and that the presence of other fruit types (in this case *Quercus* fruits) would lower the mortality rate of *Parashorea* fruit.

Methods:

Parashorea and acorn fruits were gathered from the secondary forests and inspected for signs of previous herbivory. Only mature, viable fruits lacking any previous signs of predation were used. Following the collection, random samples of 1x1 meter plots of primary forests were censused in order to establish the average density of *Parashorea* seeds within multiple replicates. Based on this data we established a set number of seeds for high and low density plots, each consisting of varying proportions of *Parashorea* and *Quercus* seeds totaling twenty or six seeds respectively.

Six replicates were established, each containing a total of eight one by one meter plots. Of these plots, four represented high density seed dispersal areas and four represented low density areas. High density plots contained one plot with each of the following proportions: 20 *Parashorea* (P), 15 P and 5 *Quercus* (Q), 10 P and 10 Q, 5 P and 15 Q. Low density plots contained one plot with each of the following proportions: 6 P, 4 P and 2 Q, 3 P and 3 Q, 2 P and 4 Q. All plots were placed about ten meters off of the entrance path to the secondary forest. On the fourth day of the experiment, the plots were inspected, and the numbers of predated and surviving seeds from each genus were recorded.

Using the statistical platform R, we analyzed our data with ANOVA, correlation, and binomial tests.

Results:

Plots were monitored throughout the course of the project. On the fourth day, we recorded overall predation rates, including both insect bore holes and missing seeds, which were presumably carried off (Figure 1). Statistical analysis in R, utilizing binomial analysis, ANOVA, and tests for correlation, showed no significant difference in predation due to either density or the presence of a second seed species. No significant difference was found between high and low density plots of *Parashorea* or *Quercus*, whether the two species were analyzed separately or in conjunction. There was also no significant correlation between the predation rates on one species and the proportion of second-species seeds present. However, although it was not significant, an interesting trend was observed for an inverse relationship between *Quercus* and *Parashorea* mortalities.

Total Percentage Predated:	
High Density Total	23.96
<i>Parashorea</i>	24.94
<i>Quercus</i>	18.39
Low Density Total	18.78
<i>Parashorea</i>	12.15
<i>Quercus</i>	21.52

Figure 1: The total percentage of predation observed in high and low density plots. *Quercus* and *Parashorea* densities are shown separately and congruently. To see the numbers for each individual plot please see the appendix.

Discussion:

Despite the fact that our statistical tests did not show any significant relationship between absolute density, presence of a second species, and seed predation, an inverse correlation between *Quercus* and *Parashorea* survival was observed in a plot of this data (Figure 2). Although not significant, this implies a relationship in support of our original hypothesis regarding the effects of multiple fruiting species on seed predation, namely, that an increase in species diversity may provide some level of protection for individual seeds. One possible mechanism for this relationship involves the satiation of predators by the availability of a multitude of different fruits (Asthon and Givenish, 1988). In this case, the presence of multiple species (*Quercus* and *Parashorea*) would provide more seeds than the local predator population would be able to consume, thus, as predation rates rise for one species, the other is spared. If this is the case, then predator satiation may also be a factor upholding the lone species hypothesis; having a diversity of fruit trees surrounding a seed dispersal area, as opposed to a dispersal area surrounded by conspecific trees, would provide a buffer, reducing the lone species' predation. Exploring this implied inverse effect of mortality between varying seed species would provide an interesting topic for further research.

Although lacking statistically significant results, the data collected for this experiment may still contribute to a study of longer duration seeking to answer similar questions. Over a longer period of time broader and more diverse populations of fruits could be tested giving rise to a wider range of predators. A longer time period would also take into account any behavioral patterns affecting seed predation. We also believe that a change in our study methods might have greatly altered our results. For example, it is probable that each of the eight replicate plots placed at each site may have been too close to one another, thus nullifying any possible density affects by lumping each starting seed population into six large plots of equal density. The data from this project opens the door to a multitude of interesting questions for future long-term research regarding absolute density, seed mortality by predation, and the phenomena that is mast fruiting.

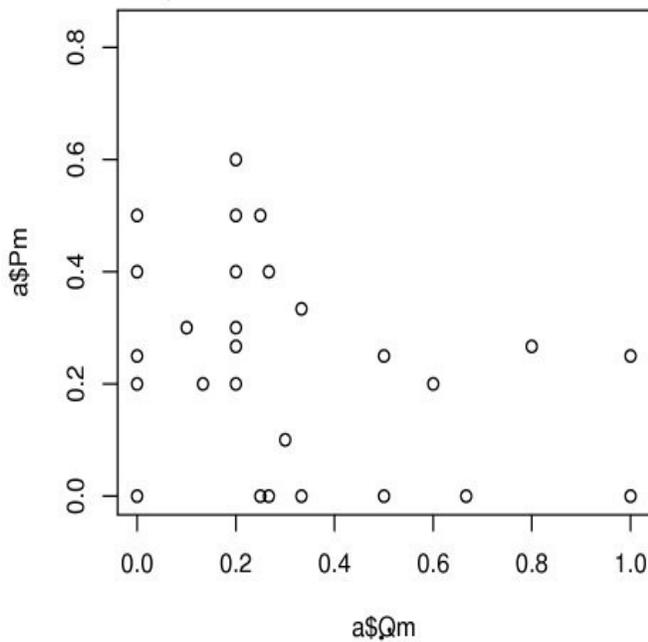


Figure 2:

This plot represents the rate of *Parashorea* mortality (a\$Pm) on the y-axis as a function of *Quercus* mortality (a\$Qm) on the x-axis.

References:

1. Ashton, P.S., Givenish, T.L., Appanah, S. (1988), 'Staggered Flowering in the Dipterocarpaceae: New Insights into Floral Induction and the Evolution of Mast Fruiting in the Aseasonal Tropics' *The American Naturalist* 132(1), 44-66.
2. Curran, L., , C. O. Webb, C.O. (2000), 'Experimental Tests of the Spatiotemporal Scale of Seed Predation in Mast-Fruiting Dipterocarpaceae' *Ecological Monographs* 70(1), 129-148.
3. Webb , C.O. (1997), 'Seedling Ecology and Tree diversity in a Bornean Rain Forest' *Phdthesis Dartmouth College*.
4. Rversion 2.5.1 (2007-06-27(. Copyright(C)2007 The R Foundatoin for Statistical Computing. ISBN 3-900051-07-0.
5. Jansen, Connel (199?) *Lone Species Concept* note, although we allude to Jansen, Connel in our paper, we were unable to find the paper with which we could properly reference them.

Appendix:

Plot Number	Starting # of <i>Quercus</i>	Starting # of <i>Parashorea</i>	Ending number of <i>Quercus</i>	Ending # of <i>Parashorea</i>	Site
P1	0	20	0	15	1
P2	0	20	0	13	2
P3	0	20	0	15	3
P4	0	20	0	16	4
P5	0	20	0	16	5
P6	0	20	0	16	6
P7	5	15	4	11	1
P8	5	15	2	12	2
P9	5	15	5	12	3
P10	5	15	4	12	4
P11	5	15	1	11	5
P12	5	15	4	11	6
P13	10	10	8	5	1
P14	10	10	10	6	2
P15	10	10	8	6	3
P16	10	10	7	9	4
P17	10	10	9	7	5
P18	10	10	8	7	6
P19	15	5	11	5	1
P20	15	5	10	5	2
P21	15	5	11	3	3
P22	15	5	11	5	4
P23	15	5	12	2	5
P24	15	5	13	4	6
P25	0	6	0	6	1
P26	0	6	0	5	2
P27	0	6	0	5	3
P28	0	6	0	5	4
P29	0	6	0	5	5
P30	0	6	0	1	6
P31	2	4	2	2	1
P32	2	4	2	3	2
P33	2	4	0	4	3
P34	2	4	2	3	4
P35	2	4	1	3	5
P36	2	4	0	3	6
P37	3	3	3	3	1
P38	3	3	1	3	2
P39	3	3	1	3	3
P40	3	3	2	2	4
P41	3	3	1	3	5
P42	3	3	2	3	6
P43	4	2	4	2	1
P44	4	2	4	2	2
P45	4	2	4	2	3
P46	4	2	3	1	4
P47	4	2	2	2	5
P48	4	2	3	2	6

Figure 3: The numbers of *Parashorea* and *Quercus* seeds by replicate plot at the start of the experiment and the numbers of surviving seeds after four days.

```
>a<-read.table("Rtable.csv" , sep="\t" , header=TRUE , row.names=1)
> a<-read.table("Rtable.csv" , sep="\t" , header=TRUE , row.names=1)
```

```

3 2 6
> a$Site <- as.factor(a$Site)
> a$tot = a$Qs + a$Ps
> a
2 6 6
> a$Qm=(a$Qs-a$Qe)/a$Qs
> a$Pm=(a$Ps-a$Pe)/a$Ps
> a
6 0.2500000 0.0000000
> a$Dn=as.factor(a$tot)
> plot(a$Qs, a$Qm)
> plot(a$Ps,a$Pm)
> cor.test(a$Ps,a$Pm)

```

Pearson's product-moment correlation

```

data: a$Ps and a$Pm
t = 1.6626, df = 46, p-value = 0.1032
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
-0.04938598 0.48913462
sample estimates:
cor
0.2380897

```

```
> cor.test(a$Qs,a$Qm)
```

Pearson's product-moment correlation

```

data: a$Qs and a$Qm
t = -1.3266, df = 34, p-value = 0.1935
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
-0.5129831 0.1150898
sample estimates:
cor
-0.2218338

```

```
> aov(a$Qm~a$Qs+a$Dn)
```

Call:

```
aov(formula = a$Qm ~ a$Qs + a$Dn)
```

Terms:

	a\$Qs	a\$Dn	Residuals
Sum of Squares	0.1359189	0.0000034	2.6260838
Deg. of Freedom	1	1	33

```

Residual standard error: 0.2820963
Estimated effects may be unbalanced

```

```

12 observations deleted due to missingness
> summary(aov(a$Qm~a$Qs+a$Dn))
      Df Sum Sq Mean Sq F value Pr(>F)
a$Qs   1 0.13592  0.13592   1.708 0.2003
a$Dn   1 3.448e-06 3.448e-06 4.333e-05 0.9948
Residuals 33 2.62608  0.07958

```

```

12 observations deleted due to missingness
> glm(a$Qm~a$Dn, family=binomial, weights=a$Qs)

```

```

Call: glm(formula = a$Qm ~ a$Dn, family = binomial, weights = a$Qs)

```

```

Coefficients:
(Intercept)  a$Dn20
-0.7777      -0.4119

```

```

Degrees of Freedom: 35 Total (i.e. Null); 34 Residual
(12 observations deleted due to missingness)

```

```

Null Deviance:      54.29
Residual Deviance: 52.87  AIC: 110
> summary(glm(a$Qm~a$Dn, family=binomial, weights=a$Qs))

```

```

Call:
glm(formula = a$Qm ~ a$Dn, family = binomial, weights = a$Qs)

```

```

Deviance Residuals:
    Min       1Q   Median       3Q      Max
-2.3052 -1.1261 -0.1794  0.5995  2.6776

```

```

Coefficients:
      Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.77777    0.2930  -2.654 0.00795 **
a$Dn20      -0.4119    0.3419  -1.205 0.22835
---
Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

```

```

(Dispersion parameter for binomial family taken to be 1)

```

```

Null deviance: 54.286 on 35 degrees of freedom
Residual deviance: 52.871 on 34 degrees of freedom
(12 observations deleted due to missingness)
AIC: 109.97

```

```

Number of Fisher Scoring iterations: 4

```

```

> summary(glm(a$Pm~a$Dn, family=binomial, weights=a$Ps))

```

```

Call:
glm(formula = a$Pm ~ a$Dn, family = binomial, weights = a$Ps)

```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7092	-0.9151	-0.1413	0.3090	3.4173

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.4572	0.2693	-5.411	6.26e-08 ***
a\$Dn20	0.3763	0.3002	1.253	0.21

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 52.943 on 47 degrees of freedom
Residual deviance: 51.299 on 46 degrees of freedom
AIC: 133.94

Number of Fisher Scoring iterations: 4

```
> summary(glm(a$Pm~a$Ps, family=binomial, weights=a$Ps))
```

Call:

```
glm(formula = a$Pm ~ a$Ps, family = binomial, weights = a$Ps)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7303	-0.9729	-0.3305	0.2667	3.1932

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.35035	0.27070	-4.988	6.09e-07 ***
a\$Ps	0.01491	0.01892	0.788	0.431

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 52.943 on 47 degrees of freedom
Residual deviance: 52.320 on 46 degrees of freedom
AIC: 134.96

Number of Fisher Scoring iterations: 4

```
> summary(glm(a$Qm~a$Qs, family=binomial, weights=a$Qs))
```

Call:

```
glm(formula = a$Qm ~ a$Qs, family = binomial, weights = a$Qs)
```

Deviance Residuals:

Min 1Q Median 3Q Max
-2.3878 -1.2008 -0.2116 0.6179 2.3687

Coefficients:

Estimate Std. Error z value Pr(>|z|)
(Intercept) -0.69218 0.32417 -2.135 0.0327 *
a\$Qs -0.04169 0.03105 -1.343 0.1794

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 54.286 on 35 degrees of freedom
Residual deviance: 52.478 on 34 degrees of freedom
(12 observations deleted due to missingness)
AIC: 109.58

Number of Fisher Scoring iterations: 4

> summary(glm(a\$Qm~a\$Ps, family=binomial, weights=a\$Qs))

Call:

glm(formula = a\$Qm ~ a\$Ps, family = binomial, weights = a\$Qs)

Deviance Residuals:

Min 1Q Median 3Q Max
-2.3931 -1.0860 -0.1338 0.6968 2.6166

Coefficients:

Estimate Std. Error z value Pr(>|z|)
(Intercept) -1.047755 0.302435 -3.464 0.000531 ***
a\$Ps -0.005619 0.037441 -0.150 0.880704

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 54.286 on 35 degrees of freedom
Residual deviance: 54.263 on 34 degrees of freedom
(12 observations deleted due to missingness)
AIC: 111.36

Number of Fisher Scoring iterations: 4

> summary(glm(a\$Pm~a\$Qs, family=binomial, weights=a\$Ps))

Call:

glm(formula = a\$Pm ~ a\$Qs, family = binomial, weights = a\$Ps)

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7636	-1.0420	-0.3228	0.2634	3.1435

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.21781	0.16205	-7.515	5.7e-14 ***
a\$Qs	0.01317	0.02515	0.523	0.601

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 52.943 on 47 degrees of freedom
Residual deviance: 52.672 on 46 degrees of freedom
AIC: 135.31

Number of Fisher Scoring iterations: 4

```
> summary(glm(a$Pm~a$Qs+a$Dn, family=binomial, weights=a$Ps))
```

Call:

```
glm(formula = a$Pm ~ a$Qs + a$Dn, family = binomial, weights = a$Ps)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7382	-0.9189	-0.1351	0.3014	3.4247

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.463755	0.272839	-5.365	8.1e-08 ***
a\$Qs	0.003899	0.026196	0.149	0.882
a\$Dn20	0.363253	0.312997	1.161	0.246

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 52.943 on 47 degrees of freedom
Residual deviance: 51.277 on 45 degrees of freedom
AIC: 135.92

Number of Fisher Scoring iterations: 4

```
> summary(glm(a$Qm~a$Ps+a$Dn, family=binomial, weights=a$Qs))
```

Call:

```
glm(formula = a$Qm ~ a$Ps + a$Dn, family = binomial, weights = a$Qs)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.3558	-1.1768	-0.2624	0.5855	2.4544

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.86663	0.32001	-2.708	0.00677 **
a\$Ps	0.03197	0.04618	0.692	0.48875
a\$Dn20	-0.59315	0.43397	-1.367	0.17169

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 54.286 on 35 degrees of freedom
Residual deviance: 52.396 on 33 degrees of freedom
(12 observations deleted due to missingness)
AIC: 111.50

Number of Fisher Scoring iterations: 4

```
> summary(glm(a$Qm~a$Ps+a$Qs, family=binomial, weights=a$Qs))
```

Call:

```
glm(formula = a$Qm ~ a$Ps + a$Qs, family = binomial, weights = a$Qs)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-2.3558	-1.1768	-0.2624	0.5855	2.4544

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-0.61242	0.42562	-1.439	0.150
a\$Ps	-0.01040	0.03649	-0.285	0.776
a\$Qs	-0.04237	0.03100	-1.367	0.172

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 54.286 on 35 degrees of freedom
Residual deviance: 52.396 on 33 degrees of freedom
(12 observations deleted due to missingness)
AIC: 111.50

Number of Fisher Scoring iterations: 4

```
> summary(glm(a$Pm~a$Ps+a$Qs, family=binomial, weights=a$Ps))
```

Call:

```
glm(formula = a$Pm ~ a$Ps + a$Qs, family = binomial, weights = a$Ps)
```

Deviance Residuals:

Min	1Q	Median	3Q	Max
-1.7382	-0.9189	-0.1351	0.3014	3.4247

Coefficients:

	Estimate	Std. Error	z value	Pr(> z)
(Intercept)	-1.61944	0.38894	-4.164	3.13e-05 ***
a\$Ps	0.02595	0.02236	1.161	0.246
a\$Qs	0.02985	0.02924	1.021	0.307

Signif. codes: 0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1

(Dispersion parameter for binomial family taken to be 1)

Null deviance: 52.943 on 47 degrees of freedom
Residual deviance: 51.277 on 45 degrees of freedom
AIC: 135.92

Number of Fisher Scoring iterations: 4

```
> plot(a$Qm,a$Pm)  
> cor.test(a$Qm,a$Pm)
```

Pearson's product-moment correlation

data: a\$Qm and a\$Pm
t = -1.3374, df = 34, p-value = 0.1900
alternative hypothesis: true correlation is not equal to 0
95 percent confidence interval:
-0.5143237 0.1132925
sample estimates:
cor
-0.2235645

Figure 4: R scripts created during the statistical analysis of the data collected throughout the course of this project.

Parashorea
Alternating with *Quercus*
Density depends?

Haiku 1: A summary of our project