Rufford Small Grant

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FINAL REPORT

DETAIL OF EXPENSES FOR THE 2008 FIELD SEASON

Next, I detail the expenses for the 2008 field season; receipts to confirm such expenses are attached at the end.

APRIL
INTERNATIONAL AIRFARE
- *April/13/2008 – August//5/2008*→ American Airlines St. Louis, Missouri – La Paz, Bolivia, St. Louis, Missouri, 1 person @ £86.0/each - £541.0*
- Although original e-ticket shows return date as July/17/2008, which would be incongruent with fieldwork dates. I am attaching a passenger receipt that shows that the actual return date was later changed to August/5/2008.
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JUNE
AIRFARE
- *June/12/2008 – June/29/2008→ AmasZonas La Paz - San Borja – La Paz 2 people @ £86.0/each - £172.0*

FIELD STATION EXPENSES
- *June/12/2008 – June/29/2008→ Food and lodging for 2 people * 17 days, at Beni Biological Station - Biosphere Reserve, @ £ 3.75/person/day – £127.5*

LABOR
- *Hiring of one field guide (including food for guide) * 14 days, @ £5.0/day - – £70*

JULY
AIRFARE
- *July/5/2007 – July/26/2008→ AmasZonas La Paz - San Borja – La Paz 2 people @ £88.0/each - £176.0*

FIELD STATION EXPENSES
- *July/5/2007 – July/26/2008→ Food and lodging for 2 people * 21 days, at Beni Biological Station - Biosphere Reserve, @ £ 3.75/person/day – £157.5*

LABOR
- *Hiring of one field guide (including food for guide) * 16 days, @ £5.0/day – £80.0*
-

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PROJECT RESULTS REPORT

The research supported by the Rufford Small Grants funds resulted into 3 major articles that will be submitted for publication within the next four months. The Journals the articles will be submitted to are: Biotropica, Journal of Ecology, and Ecology. Once the papers are published I will send PDF copies to the Foundation. Next, I present a brief summary of the results obtained from each paper, and then a general conclusion from the whole study. (Note: All the results obtained in the whole study can be submitted in May, once I have defended my Dissertation)

Seed disperser effectiveness: The quantity and quality components of seed dispersal for *Guettarda viburnoides* (RUB.) in a Neotropical savanna. (Will be submitted to Biotropica)

Summary
        In this paper I identify fruit production and fruit traits of *G. viburnoides* at the study site. I also determined the quantitative important dispersers of this species, as well as the seed rain patterns they generate. In addition, I examined the effect of seed treatment in the mouth or gut of the disperser on seedling emergence.
        I quantified fruit production of *G. viburnoides* during three years (2006-2008). For each year, I calculated the proportion of fruiting individuals in the population, and the mean number of fruits produced per tree. In 2007 and 2008, I also examined the proportion of fruits that remain non-dispersed at the end of the fruiting season. Finally, in 2008 I examined whether mean fruit size differed among individual trees.
        To determine which dispersers are quantitatively important, I conducted a total of 402 hrs. of observation to individual *G. viburnoides* trees at the study site from 2006 to 2008. During observation, my field assistants and I recorded (1) the identity of the frugivore species, (2) the number of fruits consumed per visit, (3) whether the frugivore swallowed the fruits or consumed only the pulp, (4) whether frugivores defecated or regurgitated seeds before leaving the vegetation patch where the fruiting tree was located, (5) the post-feeding habitat the frugivore visited, and (6) for pulp consumers only, whether the fruit was consumed in the vegetation patch where the fruiting tree was located or whether it was taken and consumed in another habitat.
        To examine the effects of seed treatment on seedling emergence (seed swallowed and defecated, or pulp consumed without swallowing the seed). In 2006, I conducted a greenhouse experiment and set up 94 replicates of each of three treatments: (1) gut-

passed endocarps, (2) endocarps with the pulp removed, and (3) endocarps in intact fruits. Seedling emergence was followed for a year.

Results

During the study period, on average 56% of the adult *G. viburnoides* trees in the population produced fruit each year. Fruit crops of individual trees were very variable, ranging between 10 and 7000 fruits ($\bar{x}_{2006-2008} = 1981$). Fruit production differed among years ($F_{2,70}=6.42$, P=0.003); specifically, the number of fruits produced by individual trees was lower in 2007 compared to 2006 and 2008 (P<0.001). At the end of the fruiting seasons in 2007 and 2008, approximately 23% of the fruits in a tree were not removed by frugivores; non-dispersed fruits dried up and remained attached to the branch, eventually falling off. Fruit size differed significantly among trees ($F_{4,370} = 69.47$, P < 0.0009), ranging from 10 to 21 mm among the sampled individuals.

A total of 17 species of birds were recorded visiting *G. viburnoides* trees. Of these, 10 were observed handling or consuming the fruits. Based on the total number of visits observed over the three years, and the number of fruits consumed per visit, I identified *Cyanocorax cyanomelas* (Veilliot) and *Pteroglossus castanotis* (Gould) as quantitative important dispersers (QID) of *G. viburnoides* in the study site. There were no between-year differences in the proportion of visits by these species.

C. cyanomelas (Photo: Andrea Loayza)

P. castanotis (Photo: Andrea Loayza)

C. cyanomelas are pulp-consumers that deposited the seeds 95% of the time in the same vegetation patch where the fruiting tree was located, and dispersed to remaining 5% of seeds at other vegetation patches within the savanna. In contrast, *P. castanotis* are legitimate dispersers (i.e., the swallow and defecate the seed, *sensu* Jordano and Schupp 2000) that dispersed 100% of the seeds in large forest islands in the landscape.

Contrary to what was expected, greenhouse experiments revealed that highest seedling emergence was observed in endocarps with the pulp removed (25% emergence), then in endocarps in intact fruits (9% emergence), and least in swallowed and passed endocarps (5% emergence).

Synthesis

At the study site, *G. viburnoides* seeds are dispersed primarily by two species: *C. cyanomelas* and *P. castanotis*. These species differ not only in the treatment of the seed in mouth or gut (pulp consumers versus fruit swallowing), but also where they deposit/disperse the seeds. *C. cyanomelas* disperses them in vegetation patches within the

savanna, whereas *P. castanotis* disperses the seeds in forest islands. Finally, seed treatment significantly affects germination of this species. Seeds are more likely to germinate and emerge if they are processed by *C. cyanomelas* than by *P. castatnotis*.

Recruitment of a bird-dispersed tree (*Guettarda viburnoides*) in a heterogeneous landscape: Shifting patterns of habitat suitability in time. (Will be submitted to Journal of Ecology)

Summary

Seed dispersal results in a non-random distribution of seeds among different habitats. Depending on the habitat, patterns of seed dispersal may cascade through the entire recruitment phase so that they are concordant with patterns of recruitment or, uncoupling between developmental stages may occur, so that patterns of seed dispersal will be discordant with patterns of recruitment. In this study, I analyzed how habitat affects the recruitment dynamics of *Guettarda viburnoides*. The objective was to link landscape patterns of seed dispersal to patterns of seedling establishment of *G. viburnoides* over two years. I determined the habitats into which seeds were naturally dispersed, and then followed the post-dispersal fate of seeds experimentally dispersed into these habitats. Specifically, I quantified seed rain patterns, post-dispersal seed predation, seedling emergence and seedling survival in four different: (1) open savanna sites, (2) vegetation patches with an adult *G. viburnoides* tree, (3) vegetation patches without an adult *G. viburnoides tree*, and (4) forest islands.

To examine seed rain patterns in the landscape, in 2006 and 2008 I installed a system of 430 seed traps across the study site as follows: two seed traps in each of 25 vegetation patches without *G. viburnoides*; two seed traps in each of 25 vegetation patches with *G. viburnoides*; a group of six seed traps at each of 35 savanna sites with no woody vegetation and at least 70 m from a vegetation patch or a forest island; and two groups of four seeds traps in each of 15 forest islands.

Example of seed traps placed in the savanna (Photo: Andrea Loayza).

I estimated post-dispersal seed predation in the four habitats during three consecutive years (2006, 2007, and 2008). I quantified seed predation by using seeds protected by wire exclosures, which allowed ants to deprecate the seed (i.e. the endocarp) but impeded them from taking it elsewhere. In 2006, 20 seeds were put inside each cage, which was then placed on the soil surface in each of 15 replicates per each of the four habitats. In 2007 and 2008, we increased replication to 25 per habitat, but due to the low fruit availability in 2007, that year each exclosure contained only 10 seeds. For all three years, experiments were installed simultaneously during the peak of the fruiting season (May) and seed predation was monitored every other day the

Example of wire exclosure placed on a forest islands (Photo: Andrea Loayza

first week, and then on days 10, 17 and 40.

I quantified seedling emergence for the 2006 and 2007 fruiting seasons. In each habitat replicate, I established an emergence experiment by sowing a group of 40 seeds in 2006, and 10 seeds in 2007, three centimeters below ground. For both years, emergence was examined once a month for a year. In every survey, I recorded the presence of emerged seedlings. Each seedling was individually tagged with an aluminum tag and the fate of each marked seedling was followed in successive surveys. Seedling fate was followed for two years for the 2007 cohort and for one year for the 2008 cohort.

Results
SEED DISPERSAL

No seed dispersal was observed into savanna seed traps in either year; therefore, I excluded this habitat from the statistical analysis. The density of dispersed seeds differed significantly among the other three habitats for both 2006 (GLM: habitat effects Wald $[\chi^2]$ statistic = 898.44, d.f. = 2, P < 0.001) and 2008 (GLM: habitat effects Wald $[\chi^2]$ statistic = 2073.05, d.f. = 2, P < 0.001). In both years, seeds were more likely to be dispersed in patches with *G. viburnoides* than in any other habitat (Fig. 1). These results reveal that seed dispersal in this landscape is very asymmetrical; some habitats receive many seeds, whereas others receive none or few.

POST-DISPERSAL SEED PREDATION

The average proportion of seeds preyed upon at the end of the experiment differed among habitats in 2006 (GLM: habitat effects Wald $[\chi^2]$ statistic = 103.36, P < 0.001) and 2008 (GLM: habitat effects Wald $[\chi^2]$ statistic = 8.28, P = 0.04), but not in 2007 (GLM: habitat effects Wald $[\chi^2]$ statistic = 3.01, P = 0.39). In 2006, predation was higher in patches with *G. viburnoides* and forest islands than in patches without *G. viburnoides* or savanna, whereas in 2008, savanna sites and forest islands had higher predation levels than the other two habitats (Fig. 2).

SEEDLING ESTABLISHMENT

Seedling emergence was extremely low in 2007, with only 86 seedlings emerging out of 2400 endocarps sown in 2006. Thus, given an average of 5 "true" seeds per endocarp ($\bar{x}$ = 4.9, s.d.= 0.94, *n* = 800), less than 1% of the seeds produced an emerged seedling (0.72%). In 2007, seedling emergence was significantly affected by habitat (GLM: habitat effects, Wald $[\chi^2]$ statistic = 46.77, P < 0.0001). More seedlings emerged in patches with *G. viburnoides* than in any other habitat (Fig. 3).

In 2008, seedling emergence was over five-fold higher that in 2007; 178 seedlings emerged out of 1000 endocarps sown. Considering five true seeds per endocarp, *ca*. 4% of the seeds produced emerged seedlings. No seedlings emerged in forest islands; hence this habitat was excluded from the 2008 analysis. Seedling emergence was significantly different among the other three habitats (GLM: habitat effects, Wald $[\chi^2]$ statistic = 41.86, P < 0.0001). In contrast to 2007, seedlings emerged more in savanna sites than in patches with and without *G. viburnoides* (Fig. 3).

Synthesis

Habitat strongly affected seed dispersal, seed predation, seedling emergence and survival. The strength of post-dispersal processes, however, also varied significantly among years, and no consistent within-habitat pattern emerged.

Uncoupling among different life-stages was observed across all habitats and spatial discordance was found between the seed rain and sapling recruitment patterns. This discordance suggests that, in certain years at least, habitat available for recruitment of *G. viburnoides* in this landscape is limited.
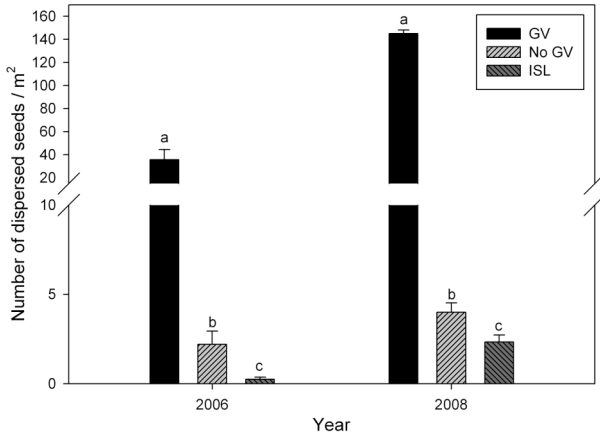
Figure 1. Number of seeds deposited per m^2 in three different habitats: (1) Vegetation patches with *G. viburnoides* (GV), (2) vegetation patches without *G. viburnoides* (No GV), and (3) forest islands (ISL); no seeds were dispersed into the savanna. Lowercase letters indicate among habitat differences within a year. (Means + SE).
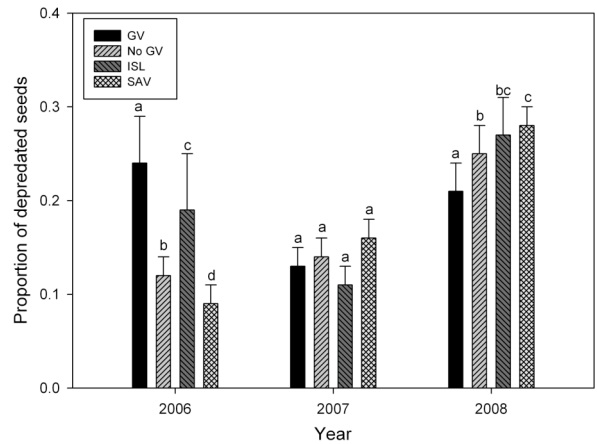

Figure 2. Mean proportion of depredated seeds after 40 days in: (1) Vegetation patches with *G. viburnoides* (GV), (2) vegetation patches without *G. viburnoides* (No GV), (3) forest islands (ISL), and savanna (SAV) in 2006, 2007 and 2008. Lowercase letters indicate among habitat differences within a year. (Means + SE, $n_{2006} = 15$, $n_{2007} = 25$, $n_{2008} = 25$ sampling stations per habitat).
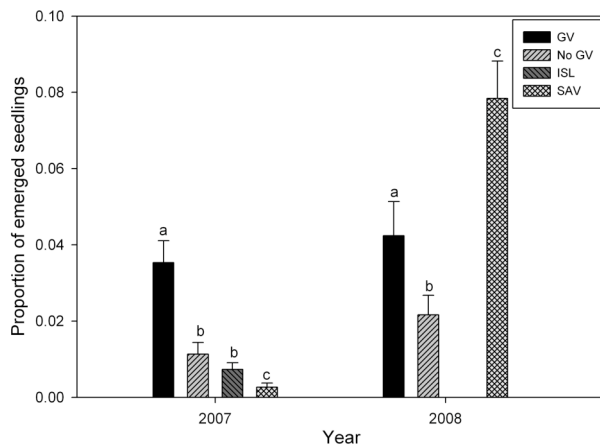

Figure 3. Proportion of emerged seedlings in four different habitats: (1) vegetation patches with *G. viburnoides* (GV), (2) vegetation patches without *G. viburnoides* (No GV), (3) forest islands (ISL), and savanna (SAV). Lowercase letters indicate among habitat differences within a year. (Means + SE, $n_{2007} = 15$, $n_{2008} = 25$, sampling stations per habitat).

Species-specific consequences of seed dispersal for population growth rate of *G. viburnoides*: When a good disperser turns bad (Will be submitted to Ecology)

Summary

In this study, I examined the demographic consequences of seed dispersal by the two quantitative important dispersers of *Guettarda viburnoides* at the study site. My primary goal was to determine the impact of each dispersal agent on the population dynamics of *G. viburnoides*, and assess the degree to which these species may be ecologically redundant. To do so, I conducted demographic simulations by incorporating dispersal effectiveness of each species into a population projection matrix model for *G. viburnoides*.

To conduct this analysis I used all the ecological data gathered from the previous two sections and incorporated it in a matrix model. To study population dynamics, fecundity, growth and survival were estimated from marking and following the fate of selected plants in each of the habitats described above. Specifically, I selected and permanently tagged 278, 94 and 108 plants from the population in 2005, 2006, and 2007 respectively; thus, a total 480 individuals were followed during a three-year period across all habitat types. Plants were classified into 5 relatively discrete stage classes: seedling, sapling, small tree, sprout, and adult. Plants were censused in July 2006, July 2007, and July 2008, and surviving individuals were reclassified into each stage class. For each habitat type, the average stage transition probabilities from all three years were used for the individual based model.

Individual-based model. To project the population trajectory and the role of each disperser in future population size of *G. viburnoides*, I created an individual-based model that incorporated stage- and habitat-specific demography, endocarp movement between habitats by dispersers, and differential emergence of seeds based on whether endocarps were processed by birds and by which species.

I began with 1000 individuals in the population, distributed unequally between habitats and stage classes based on the distribution of individuals found naturally at our study site. Specifically, the initial population size can be described by the matrix:
[27 360 28
 26 249 50
 9 98 30
 3 86 12
 5 17 0]
where columns represent the three habitat types, forest islands, vegetation patches with an adult *G. viburnoides*, and vegetation patches without an adult *G. viburnoides*; and rows represent the five stage classes, seedlings, saplings, sprouts, small trees and adult trees. In each time step individuals in each stage class would die or live and be placed into stage classes for the next year based on probabilities found in the demographic data collected for our study site (Fig. 4). I used the individual-based model to project population size of *G. viburnoides* 10 years into the future. To project the population size of *G. viburnoides* into the future in the presence of normal seed disperser dynamics (i.e., both QID present), I kept track of the total number of individuals in each habitat in each time step of the model for a total of 10 times steps (10 years). I performed 1000 runs of the individual-based model, and for each year, I present the mean and 95% confidence

intervals of these 1000 runs.

To examine the effects of individual dispersers on the future population size of *G. viburnoides*, we considered three scenarios: absence of only *P. castanotis*, absence of only *C. cyanomelas*, and absence of both seed dispersers. Lack of overlap between 95% confidence intervals indicates statistically significant differences in the projected population size for different seed disperser scenarios.

Results

In general, there were distinct among-habitat differences across all the transitions in the *G. viburnoides* life cycle (Fig. 4). These differences resulted in different population growth rates in each of the habitats.

Individual based model. At the landscape level, the population is predicted to grow even when neither of the QID are present (i.e., a no seed dispersal scenario). This result however needs to be interpreted with extreme caution as the model does not consider certain environmental conditions witch can constrain population growth, and hence making growth in a scenario with no dispersers unrealistic.

Highest population growth (i.e., a three-fold increase) will occur if only *C. cyanomelas* consumes the fruits, whereas the lowest growth is predicted to occur if the fruits of *G. viburnoides* are solely consumed by *P. castanotis* (Fig. 5). When I examined the effects of seed dispersal in each habitat individually, the population trajectories varied among habitats.

Summary

The major finding this part of the study was that the two quantitative important dispersers of *G. viburnoides* in the Beni savannas are not only non-ecologically redundant in terms of the seed dispersal services they provide to the plant, but also that seed dispersal by *P. castanotis* has a detrimental impact on the population growth of this species. To my knowledge, this is the first study to report negative effects of a legitimate seed disperser (*sensu* Jordano and Schupp 2000) on the population dynamics of the plant it consumes, being the rate of population increase when seeds are dispersed by *P. castanotis* lower than in a scenario with no seed dispersal at all (Fig. 5).
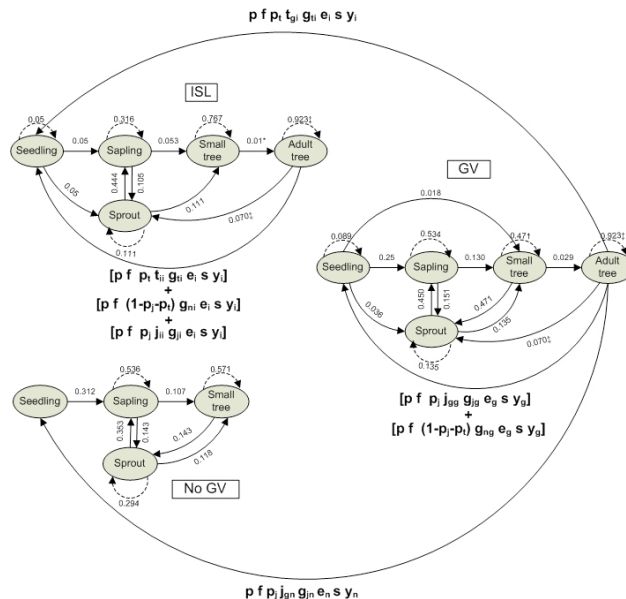

Figure 4. Life cycle transitions of *G. viburnoides* in three habitats (parameters defined in Table 1): 1) vegetation patches with an adult *G. viburnoides* (GV); 2) vegetation patches without an adult *G. viburnoides* (No GV); and 3) forest islands. Circles represent five demographic stages. Numbers on the arrows represent the mean probability that plants transition to different stages from one year to the next. Seed dispersal in the landscape is represented by modifying the fecundity values. Bold face letters indicate the parameters used to calculate fecundity.
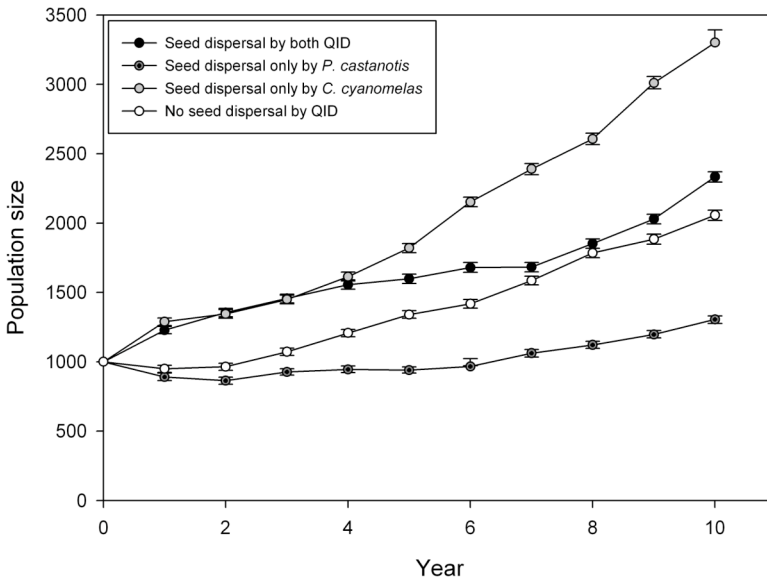
Figure 5. Projected population growth of *G. viburnoides* at the landscape level under four seed dispersal scenarios.

GENERAL CONCLUSION

This study is one of the first (if not the first) to analyze all the sequential stages of the seed dispersal cycle and determine their consequences for population dynamics by means of an explicitly demographic approach. Here, I determined which species consume the fruits of *G. viburnoides*, and through an observational, experimental, and modeling approach was able to link how frugivore activity translates into demographic and potentially evolutionary consequences for plants.

In terms of conservation, this study has several implications. Foremost, it shows that even though a plant may have several dispersers, not all fulfill the same function. Moreover, the loss of just one of those dispersers (in this case *C. cyanomelas*) can cause a dramatic decline in the population, even if other dispersers remain in the system. From a theoretical point of view, this study shows that ecological redundancy may not be as prevalent as previously thought for a seed-dispersal system.

Ultimately, the integration of frugivore activity with plant demography using models such as this one and others (e.g., Godínez-Alvarez et al. 2002) can be extremely valuable for plant ecology, as they enable us to close the "seed dispersal loop" (Wang and Smith 2004) for an understanding of demographic consequences of seed dispersal.

References Cited

Godínez-Alvarez, H., A. Valiente-Banuet, and A. Rojas-Martínez. 2002. The role of seed dispersers in the population dynamics of the columnar cactus *Neobuxbauma tetetzo*. Ecology 83: 2617–2629.

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