

University of Missouri, St. Louis

IRL @ UMSL

Dissertations

UMSL Graduate Works

5-12-2009

Closing the seed dispersal loop for *Guettarda viburnoides* (Rub.): Connecting patterns of avian seed dispersal with population growth in a Neotropical savanna

Andrea Patricia Loayza

University of Missouri-St. Louis, andrea.loayza@umsl.edu

Follow this and additional works at: <https://irl.umsl.edu/dissertation>



Part of the [Biology Commons](#)

Recommended Citation

Loayza, Andrea Patricia, "Closing the seed dispersal loop for *Guettarda viburnoides* (Rub.): Connecting patterns of avian seed dispersal with population growth in a Neotropical savanna" (2009). *Dissertations*. 521.

<https://irl.umsl.edu/dissertation/521>

This Dissertation is brought to you for free and open access by the UMSL Graduate Works at IRL @ UMSL. It has been accepted for inclusion in Dissertations by an authorized administrator of IRL @ UMSL. For more information, please contact marvinh@umsl.edu.

UNIVERSITY OF MISSOURI-ST. LOUIS
Department of Biology
Graduate Program in Ecology, Evolution, and Systematics

Closing the seed dispersal loop for *Guettarda viburnoides* (Rub.): Connecting patterns of avian seed dispersal with population growth in a Neotropical savanna.

A Dissertation Submitted to The Graduate School of the University of Missouri – St. Louis in Partial Fulfillment of the Requirements for the Degree of
Doctor of Philosophy in Biology

by

ANDREA PATRICIA LOAYZA

Dissertation Advisory Committee

Dr. Bette A. Loiselle
(Advisor, Chair)

Dr. John G. Blake

Dr. Eugene W. Schupp

Dr. Tiffany Knight

April 2009

ABSTRACT

Seed dispersal by vertebrates in the tropics is a key ecological process; therefore, understanding its consequences for plant fitness is a central question of plant population ecology. Little is known, however, of how frugivore activity translates into demographic and evolutionary consequences for plants. In this study, I connect data on frugivore activity, post-dispersal seed fate and plant population demography using stage-specific demographic modeling, to examine the role of individual dispersers for plant population dynamics of the fleshy-fruited Neotropical tree *Guettarda viburnoides* (Rubiaceae) in northeastern Bolivian savannas.

In chapter one, I examine avian frugivory and seed dispersal of *G. viburnoides*, focusing on the quantitative and qualitative aspects of disperser effectiveness. The endocarps of this plant are dispersed primarily by two species: *Cyanocorax cyanomelas* and *Pteroglossus castanotis*, which I identify as the quantitatively important dispersers (QID) of *G. viburnoides*. These two species differ in several qualitative aspects of seed dispersal: 1) They select fruits of different sizes; 2) they differ in their fruit handling treatment, which in turn affects the probability of seedling emergence, the temporal pattern of emergence, and the number of emerged seedlings per endocarp and; 3) they differ in their landscape patterns of seed deposition. These results suggest that *C. cyanomelas* and *P. castanotis* differ in the quality of seed dispersal services they provide to *G. viburnoides*.

In chapter two, I analyze how habitat affects the post-dispersal seed fate of *G. viburnoides*. The results show that habitat strongly affects seed dispersal, seed predation,

and seedling emergence. Additionally, uncoupling among different life-stages occurs in all habitats and there is spatial discordance 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. The results also reveal high inter-annual variability in the strength of post-dispersal processes, which leads to a constant shifting of habitat “suitability” from one year to the next; that is, it is context-dependent.

Finally, in chapter three, I determine the individual effect of seed dispersal by *C. cyanomelas* and *P. castanotis* on population growth of *G. viburnoides*, and assess the degree to which these species may be ecologically redundant. The results demonstrate that seed dispersal by *C. cyanomelas* leads to positive population growth of *G. viburnoides*, whereas seed dispersal by *P. castanotis* has a detrimental effect on the population growth of this species. Therefore, *C. cyanomelas* is a key species for the long-term persistence of *G. viburnoides*, and the loss of this dispersal agent would not be compensated by the dispersal services provided by *P. castanotis*. Ultimately, the integration of frugivore activity with plant demography using models such as this one are important for plant ecology because they enable us to close the “seed dispersal loop” and gain a better understanding of the demographic consequences of seed dispersal by different dispersal agents.

ACKNOWLEDGEMENTS

The content of this dissertation represents far more than the culmination of years of graduate school. In more ways than one, this dissertation is an echo of the interactions with many inspiring people I have met throughout my graduate career. The list is long, but I cherish each contribution.

I am extremely grateful to my advisor Bette A. Loiselle for years of unfailing support, for her patience, her commitment and her remarkable guidance throughout my graduate career. I am especially thankful for her friendship and for her generosity... and for so much more Bette: thank you! I want to thank my committee members, John G. Blake, Tiffany Knight, and Eugene W. Schupp, for their insights, help, thoughtful criticism, and continuous support throughout all stages of my Dissertation.

I would like to acknowledge all my professors at UMSL who taught me how to think critically and how to teach others to think. I am grateful also to Dr. Gerardo Camilo, Dr. Matthew Albrecht, Dr. Charlotte Taylor, and Dr. Brett Sandercock, for helpful comments and discussions. I want to thank Kathy Upton for taking care of my plants in the greenhouse. I also want to express my deepest gratitude to Maryann Hempen, Kathy Burney-Miller, and Patricia Hinton: What would we do without you? Thank you for solving just about every issue we come up with!

I owe many thanks to my field assistants, Fransisco Saavedra, Ariel Terán, Alejandro Yarari, and Melanie Houard, not only did they help arduously with the data collection, but they provided entire weeks of fun, laughs, and joy. I am also forever in debt to my field guides, Oliver Burgos, Alejandro Burgos, Alberto Balderrama and

Renato Balderrama. In particular, I want to thank Nataniel Burgos, my friend and right hand in the field; he never finished primary school, yet his knowledge of the area and its natural history far exceeds mine, and the pages of this Dissertation are written in great part thanks to him. I am also extremely thankful to Juana Balderrama and Francisca Averanga. The first, for making the most delicious meals anyone could ever wish for in the field. The second, for helping taking care of my son Gustavo with so much patience and love, both while I was away in the field alone, as well as when he was in the field with me. Thanks to all these wonderful people, when I look back at the three years of fieldwork, I cannot help but smile.

I want to give a very special thanks to my invaluable network of supportive, generous and loving friends, who made life in graduate school an experience I thoroughly enjoyed, and without whom I could not have survived the process. In particular I want to thank Wendy Tori, Jose I. Pareja, Adriana Rodriguez, Adrian Aspiroz, Eloisa Sari, Paulo Camara, Beth Congdon, Jose Hidalgo, Trisha Distler, and Steve Mitten. There are many more people, too many to mention, but I am thankful to all my friends at UMSL.

This work was supported by grants from the National Science Foundation (DEB-0709753), the Rufford Maurice Laing Foundation, the Scott Neotropical Fund of the Cleveland Metropolitan Zoo, the Neotropical Grassland Conservancy, the Webster Groves Nature Study Society, Sigma Xi, and the Whitney R. Harris World Ecology Center at the University of Missouri-St. Louis. Permits were obtained with help from the Herbario Nacional de Bolivia. I want to sincerely thank Kazuya Naoki from the Instituto de Ecología in La Paz, for providing a great space at the University in La Paz where I could work, and for actively including me as an Associate Researcher at the Institute.

Above all I want to thank my family. My parents, Patricia and Javier, for their unconditional love and support. For helping me pursue a life-long dream of becoming a Doctor in Biology. For always standing behind me, no matter what choices I made in life. And to my sister, Veronica, for being a hidden angel in my life, a voice of reason and calm in turbulent times, a true friend, and the second mother of my children. I want to thank all three of you for more things than I can mention here, but most importantly, and quoting from Susan Polis Schutz, I want to thank you because “you were always there to love me and I want to assure you that I am always here to love you”.

And finally, I want to thank from the deepest corner of my heart and with as much love as anyone can possibly give, the five most important “boys” in my life, Rodrigo, Gustavo, Daniel, Alejandro and Matias; my husband and sons. Rodrigo, my soul mate, best friend, drill sergeant, voice of reason, stats coach, manuscript reviewer, field assistant, counselor and life raft. Thank you for always coming to my defense, for letting me fly, and for never giving up on me. Gustavo, my “Tacky the penguin”, thank you for healing my wounds, for showing me the wonders of being a parent, and for helping me clearly distinguish between life and graduate school. Alejandro and Matias, my guardian angels, I have said it before and I’ll say it again, thank you for having showed me what is truly important in life, the lesson will not be forgotten and my love for you will live on forever. Daniel, you will come into this world a few days after all this is finished, but you deserve thanks too. Thank you for inspiring me during the months I was writing these chapters, thank you for your kicks, for making me dream of you, and for giving me something to look forward more than the defense. I love you all.

To all those who have guided me here

TABLE OF CONTENTS

ABSTRACT.....	i
ACKNOWLEDGMENTS.....	iii
CHAPTER 1 — QUANTITY AND QUALITY COMPONENTS OF <i>GUETTARDA</i> <i>VIBURNOIDES</i> (RUBIACEAE) SEED DISPERSAL BY FRUIT-EATING BIRDS IN BOLIVIAN SAVANNAS.....	
	1
Abstract.....	1
Introduction.....	3
Methods.....	5
Study site.....	5
Study species.....	6
Fruit production and fruit traits.....	7
Quantity components of dispersal.....	8
Quality components of dispersal.....	9
Post-feeding movements.....	9
Fruit selection.....	9
Effect of endocarp treatment on seedling emergence.....	10
Results.....	11
Fruit production and fruit traits.....	11
Quantity components of dispersal.....	12
Quality components of dispersal.....	13
Post-feeding movements.....	13
Fruit selection.....	14

Effect of endocarp treatment on seedling emergence.....	15
Discussion.....	15
Quantity components of dispersal.....	16
Quality components of dispersal.....	18
Conclusion.....	21
Acknowledgements.....	22
Literature Cited.....	23
Tables.....	30
Figure legends.....	35
CHAPTER 2 — RECRUITMENT OF A BIRD-DISPERSED TREE (<i>GUETTARDA</i>	
<i>VIBURNOIDES</i>) IN A HETEROGENEOUS LANDSCAPE: SHIFTING PATTERNS OF	
HABITAT SUITABILITY IN TIME.....	42
Summary.....	42
Introduction.....	44
Methods.....	46
Study system.....	46
Seed dispersal.....	48
Post-dispersal seed predation experiments.....	49
Seedling establishment experiments.....	50
Spatial patterns of seed arrival and sapling recruitment.....	50
Statistical analyses.....	51
Results.....	52

Seed dispersal.....	52
Post-dispersal seed predation.....	53
Seedling establishment.....	54
Emergence.....	54
Seedling survival.....	55
Landscape dynamics of recruitment.....	56
Discussion.....	58
Spatial dynamics of recruitment: is there among-habitat variability in early plant recruitment phases?.....	58
Seed rain.....	58
Seed predation.....	59
Seedling emergence.....	61
Seedling survival.....	62
Is the pattern of recruitment among habitats consistent among years?.....	63
Is the pattern of seed dispersal spatially concondant with the pattern of recruitment?.....	64
Acknowledgements.....	66
References.....	67
Tables.....	74
Figure legends.....	77

CHAPTER 3 — SEED DISPERSAL BY PULP CONSUMERS BUT NOT LEGITIMATE SEED DISPERSERS INCREASES POPULATION GROWTH OF <i>GUETTARDA VIBURNOIDES</i> IN A NEOTROPICAL SAVANNA.....	84
Abstract.....	84
Introduction.....	85
Methods.....	88
Study system.....	88
Bird dispersal of <i>Guettarda viburnoides</i>	90
Stage- and Habitat-specific Demography.....	92
Individual-based model.....	93
Results.....	96
Stage- and Habitat-specific Demography.....	96
Individual-based model.....	97
Discussion.....	99
Species-specific consequences of seed dispersal for population growth.....	99
Dissemination limitation and the spatial distribution of <i>G. viburnoides</i>	101
Assumptions of the model.....	103
Conclusions.....	104
Acknowledgements.....	105
Literature Cited.....	106
Tables.....	112
Figure legends.....	114

**CHAPTER 1 — Quantity and quality components of *Guettarda viburnoides*
(Rubiaceae) seed dispersal by fruit-eating birds in Bolivian savannas**

Abstract

For many tropical plant species, birds constitute the most important group of seed dispersers. From a plant's perspective, however, not all birds will be equally effective as dispersal agents. I examined avian frugivory and seed dispersal of *Guettarda viburnoides*, focusing on quantitative and qualitative aspects of disperser effectiveness. Fruits of *G. viburnoides* are consumed by 10 species of birds but two, *Cyanocorax cyanomelas* and *Pteroglossus castanotis*, account for over 80% of the fruits removed. These two species differ in qualitative aspects of seed dispersal. First, they select for fruits of different sizes; *C. cyanomelas* feeds on larger fruits than *P. castanotis*. Second, they differ in the fruit handling treatment; *C. cyanomelas* are pulp consumers, *P. castanotis* swallow the fruit whole. Fruit handling treatment affects the probability of seedling emergence, the temporal pattern of emergence, and the number of emerged seedlings per endocarp. Finally, *C. cyanomelas* and *P. castanotis* differ in their landscape patterns of seed deposition. Even with detailed information on these qualitative differences, however, it is not possible to know which disperser is most effective. To successfully evaluate disperser effectiveness will require connecting the fruit consumption stage, with seed deposition patterns, and habitat-specific post-dispersal seed fate and establishment.

Key words: *Cyanocorax cyanomelas*, disperser effectiveness, frugivory, plant-animal interaction, *Pteroglossus castanotis*.

INTRODUCTION

Seed dispersal by vertebrates in the tropics is a key process for the maintenance of plant populations (Howe & Smallwood 1982). From the standpoint of an individual plant, however, not all dispersers will be equally important (Bas *et al.* 2006, Calviño-Cancela 2002, Figuerola *et al.* 2002, Herrera *et al.* 1994, Wehncke *et al.* 2004, Wenny 1998). The disperser effectiveness, or potential contribution of each frugivore to plant fitness, will depend on the number of seeds dispersed (quantity component), the condition of the dispersed seeds, and the probability that a seed will be dispersed to a habitat where it will survive and produce a new recruit (quality components) (Schupp 1993).

Therefore, the disperser effectiveness of a frugivore will be largely determined by its foraging behavior (Jordano & Schupp 2000, Loiselle & Blake 1999, Wenny 1998). For many tropical plants, which are dispersed by a large assemblage of frugivores (e.g., Loiselle & Blake 1999, Wenny 1998), in order to understand the potential selective role of dispersers on plant traits and recruitment, one must examine the individual (i.e., species-specific) components of dispersal effectiveness.

The number of seeds dispersed away from the parent plant is one of the subcomponents of the dispersal effectiveness of that species (Schupp 1993). To a large extent, this is constrained both by frugivore abundance, and behavior (Jordano and Schupp 2000). Higher frugivore densities can lead to high fruit removal rates, and ultimately higher quantities of seeds dispersed (Carlo & Morales 2008, Loiselle & Blake 1999). Yet frugivore abundance alone is sometimes insufficient to predict the number of seeds dispersed because fruit handling techniques (e.g., swallowing the fruit whole versus consuming only the pulp), and time remaining in a fruiting tree, among others, are also

factors that can affect the number of seeds removed away from the parent plant (Carlo & Morales 2008, Russo *et al.* 2006).

Seed deposition patterns will also depend on the behavior and post-feeding movements of the frugivore. For example, birds that consume the pulp but do not swallow the whole fruit (i.e., pulp consumers) drop the majority of the seeds under the parent plant in the feeding patch (Jordano & Schupp 2000, Levey 1987, Moermond & Denslow 1985). In contrast, frugivorous birds that swallow the fruit whole, and hence retain the seed for longer periods of time, deposit a larger proportion of seeds away from the parent plant and the feeding patch (Holbrook & Loiselle 2007). Through differential survival and growth associated with where seeds are dropped, seed deposition patterns can influence the fate of seeds, and the successful establishment of seedlings, ultimately determining the probability of recruitment of the plant (Levey 1987, Nathan and Müller-Landau 2000, Schupp & Fuentes 1995, Wenny 1998).

In addition to influencing seed rain-patterns, seed handling in the mouth or gut can also have an impact on germination probabilities and thus the qualitative component of effectiveness (Naranjo *et al.* 2003, Traveset & Wilson 1997). Frugivores can influence germination directly in three ways: (1) by scarification of the seed coat; (2) through removal of germination inhibitors by separation of the seeds from the pulp; and (3) through enhancement of germination and seedling growth from fecal material surrounding the seed (Traveset & Verdú 2002; Traveset *et al.* 2007). Although gut passage can inhibit or reduce germination (Ellison *et al.* 1993 [shade-tolerant species], Domínguez-Domínguez *et al.* 2006), most studies have found that it improves

germination rate and/or success (e.g., Ellison *et al.* 1993 [light-demanding species], Bas *et al.* 2006, Webber and Woodrow 2004).

Here, I evaluate avian frugivory and seed dispersal of the fleshy-fruited tree, *Guettarda viburnoides* in northeastern Bolivian savannas, focusing on the quantitative and qualitative aspects of effectiveness. These small trees are patchily distributed across the savanna, and from April to June the fruits of *G. viburnoides* account for the highest proportion of the total fruit biomass available in this habitat (Loayza, unpublished data). Specifically, in this study I address the following questions: 1) Which bird species remove the greatest number of fruits and can be considered quantitatively important dispersers (QID) of *G. viburnoides*? 2) Do QID differ from each other in the fruit selection process? 3) Do QID deposit seeds in similar habitats? and 4) Does seed-handling treatment by QID have an effect on seedling emergence?

METHODS

Study Site. I conducted this study in the savannas of Beni Biological Station-Biosphere Reserve located in Beni, Bolivia (14°30'-14°50' S; 66°40'- 65°50' W; 200 masl) within the region of the Moxos plains. The area receives an annual average of 1900 mm of rain and is characterized by a marked seasonality, with a wet season between November and April, and a dry season during the rest of the year when precipitation is less than 60 mm in any month (Miranda 2000, Sarmiento 2000). The savannas lie between 130-235 m in elevation with local relief ranging from 2 to 6 m (Hanagarth 1993). This relief results in a very heterogeneous landscape, which consists of permanent swamps, areas inundated

from four to ten months, uplands that generally do not flood, forest islands that form on low relief features such as natural levee remnants (Langstroth 1996), and small patches of woody vegetation that commonly form on termite or ant mounds (hereafter, ‘vegetation patches’). Forest islands are isolated units of forest with a canopy height of up to 25 m (Moraes *et al.* 2000); at the study site they range from 0.1-20 ha. They are dominated by *Attalea phalerata* palms (Rios-Aramayo & Loayza-Freire 2000), but also have species typical of forest interior (e.g., *Virola sefibera*) as well as species from savanna habitats (e.g., *Pseudobombax marginatum*). In general, birds and mammals disperse the majority of the plant species in forest islands. Vegetation patches consist of small areas (2-175 m²) occupied by woody vegetation with a canopy height of up to 8 m. Generally, vegetation patches will consist of a few trees (in many cases only 1-4 trees), and small shrubs. As in forest islands, the plant species that occur in vegetation patches typically belong to animal-dispersed genera such as *Guettarda*, *Piper*, *Psidium*, *Clidemia*, *Miconia*, *Nectandra*, and *Cecropia*, among others (*pers. obs.*).

Study Species. *Guettarda viburnoides* Cham. and Schlecht. (Rubiaceae) are small trees (< 6 m) that grow in semi-deciduous forests and grasslands, and are distributed in South America from Brazil to Paraguay (Taylor *et al.* 2004). *G. viburnoides* bears cream-colored tubular flowers (10-25 mm) from October to January. Ripe fruits are available from late March until early July. They are yellow drupes, more or less 1 cm in length but with variable size within the population (*pers. obs.*). Each fruit contains a single, woody endocarp, which contains between 3 and 7 seeds ($\bar{x} = 5$, N= 800). For the plant, the endocarp is the unit of dispersal, and not the individual seeds within it. At the study site,

G. viburnoides grows in the vegetation patches within the savanna, with a very small fraction of the population also occurring in forest islands. The majority of the vegetation patches have only a single adult (i.e., fruit producing) *G. viburnoides* tree; hence, it is very easy to observe frugivore feeding behavior in the trees.

Fruit production and fruit traits. From 2006 through 2008, all adult trees in the population were permanently tagged, measured, and mapped (Figure 1). To estimate fruit production of *G. viburnoides*, I first determined the proportion of adult plants that fruit each season by monitoring reproduction on the tagged trees. Each year, during the first two weeks in March, which correspond to the beginning of the fruiting season before the fruits ripened and were removed, I also counted the total number of fruits on a subset of the reproducing adults ($N_{2006}=16$, $N_{2007}=29$, $N_{2008}=29$). Depending on tree size, I either directly counted the total number of fruits produced or estimated crop size by determining the number of fruits on two to three randomly selected branches of each fruiting individual, and then multiplied this figure by the number of major branches. Additionally, at the beginning, and at the end of the fruiting season in 2007 and 2008, I counted all fruits on two marked branches in each of the selected trees, to calculate the proportion of fruits that were not removed by frugivores by the end of the fruiting season (i.e., non-dispersed fruits hereon). I examined whether the proportion of fruiting adults and fruit production varied among years using a proportions test (Zar 1999), and a one-way ANOVA, respectively.

To determine if fruit size varied among individual *G. viburnoides* plants, in 2008 I selected 15 adult, similar-sized trees from the population. From each tree, I measured

between 25 and 34 randomly selected fruits to the nearest mm with a digital caliper (Mitutoyo, Absolute Digimatic Caliper Series 500, accuracy ± 0.01 mm). I also measured the size of the endocarp of each fruit to determine if endocarp size can be predicted from fruit size. I examined fruit size variation among trees with a one-way ANOVA. For each tree, the relationship between fruit and endocarp size was examined with a linear regression. For both analyses, original data were log-transformed to meet normality requirements.

Quantity components of seed dispersal. Frugivore observations were conducted by two to three independent observers from mid April to early May on a subset of 15, 12, and 5 large, clearly visible trees in vegetation patches during 2006, 2007, and 2008, respectively. The observers were hidden at a distance of 10-20 m, and observed frugivore behavior with binoculars (10 x 50). Each tree was observed for up to three days, and frugivore activity was recorded for three hours in the morning (0645-0945h) and two in the afternoon (1600-1830h), weather conditions permitting. During each visit, we recorded (1) the identity of the frugivore species, (2) the number of fruits consumed per visit, (3) whether the frugivore swallowed the fruits whole or consumed only the pulp, and (4) whether frugivores defecated, dropped or regurgitated seeds before leaving the vegetation patch. I defined quantitatively important dispersers (QID) of *G. viburnoides* based on two criteria: 1) the bird species that accounted for highest percentage of visits and fruits removed, and 2) movement of endocarps away from the feeding site. In this sense, frugivores were considered as seed dispersers if, at least on certain occasions, they dispersed the endocarp out of the vegetation patch where the

fruiting tree was located. Birds that were frequent visitors of *G. viburnoides*, but that always dropped the endocarp within the vegetation patch were not considered as seed dispersers.

Quality components of seed dispersal

Post-feeding movements. To determine the patterns of habitat use by QID following fruit consumption, during each tree visit, observers additionally recorded (1) the post-feeding habitat the frugivore visited, and (2) 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. The physical characteristics of the landscape, open grasslands with distinct, clearly recognizable habitats (i.e., forest islands and vegetation patches), allow easy visualization and following of birds. I used a Chi-square goodness of fit test to determine whether pulp consumers dispersed seeds equally among the different habitats in the landscape.

Fruit selection. To examine if frugivores with different feeding strategies (i.e., swallowing the whole fruit versus consuming the pulp) select for fruits of different size, in 2008 I randomly selected 199 gut-passed endocarps, and 210 endocarps with only the pulp removed, and measured them to the nearest mm with a digital caliper. All endocarps were collected in the study area from multiple locations, and belonged to a larger pool of endocarps collected in 2008. Differences in endocarp size between the two

treatments were examined with a *t*-test using log-transformed data to meet normality requirements.

Effect of endocarp treatment on seedling emergence. To test the effect of endocarp treatment on seedling emergence I established a greenhouse experiment in 2006, and set up 96 replicates each of three treatments: (1) gut-passed endocarps, (2) endocarps with the pulp removed, and (3) endocarps in intact fruits. Gut-passed endocarps came from a pool of endocarps collected in the study area from bird droppings collected in seed traps in forest islands, and occasionally under fruiting *G. viburnoides* trees. Endocarps with the pulp removed were all collected under fruiting *G. viburnoides* trees at the study site. Finally, I collected ripe, intact fruits for the experiment from >25 trees in the population at the end of the fruiting season. Each replicate was placed under identical soil, light and moisture conditions, and I followed seedling emergence for one year.

I used several analyses to determine whether endocarp treatment in mouth or gut affects seedling emergence. First, to examine if the temporal pattern of seedling emergence differed among treatments, I conducted a Cox's proportional hazards model. This method allows for comparison of the shape of emergence curves across time, and unlike ANOVA or other statistical models, it does not require normality of the data (Fox 2001). Here, the dependent variable is the hazard function, which describes how the chance of emerging (i.e., hazard) changes with time with respect to endocarp treatment. For this analysis, the hazard functions of gut-passed endocarps, and endocarps with the pulp removed were compared to the hazard function of endocarps in intact *G. viburnoides* fruits (i.e., reference hazard function). Second, to test whether the proportion of emerged

endocarps at the end of the experiment differed among treatments, I conducted a proportions test (Zar 1999). Finally, because each endocarp contains on average 5 seeds, there can be variation in the final number of emerged seedlings per endocarp. Consequently, to examine if the number of seedlings that emerged per endocarp at the end of the experiment differed among treatments, I used a Kruskal-Wallis test (excluding endocarps with zero emergence), and conducted non-parametric multiple comparisons for unequal sample sizes to determine differences between groups (Zar 1999).

RESULTS

Fruit production and fruit traits. During the study period (2006-2008), on average 56% of the trees fruited in any given year (Table 1). The proportion of fruiting adults was similar in 2006 and 2007, but higher in 2008 ($\chi^2=21.308$, $P < 0.05$). 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 (no data available for 2006), on average 23% of the fruits in a tree were not removed by frugivores (Table 1); non-dispersed fruits dried up and remained attached to the branch, eventually falling off.

Mean fruit size differed significantly among trees ($F_{4,370}=69.47$, $P < 0.0009$), ranging from 10 to 21 mm among the sampled individuals (Figure 2). Fruit size

predicted endocarp size in 14 of the 15 selected trees (Figure 3). When performing the analysis for all trees combined, fruit size explained 73% of the variation in endocarp size ($r^2=0.73$, $n=384$, $P<0.001$); therefore, endocarp size can be used as a reliable surrogate of fruit size.

Quantity components of seed dispersal. During the study (402 hours of observation), 10 species of birds were observed handling or consuming the fruits of *G. viburnoides* trees in vegetation patches (Table 2). Based on the total number of visits, the total number of fruits removed, and feeding behavior of these species, I identified two species, *Cyanocorax cyanomelas* (Veilliot) and *Pteroglossus castanotis* (Gould), as quantitatively important dispersers (QID) of *G. viburnoides* at the study site (Table 2). Two other species, *Cyanocorax chrysops* and *Ara severa*, also accounted for a relatively high percentage of visits over the three years, but they were not considered QID of *G. viburnoides* for two reasons. *A. severa* consumed the pulp of *G. viburnoides* fruits without destroying the endocarp, but it dropped 100% of the endocarps under the parent tree; individuals were never observed taking fruits, and hence dispersing the endocarp, out of the vegetation patch. Additionally, although *A. severa* accounts for 16% of the visits in 2006 this is the result of only two visits by two large groups of individuals (each individual was considered one visit). *C. chrysops* is a visitor almost as frequent as *P. castanotis*, but it consumes very few fruits per visit in comparison to *P. castanotis*; therefore, overall it accounts for a small percentage of the total number of fruits removed each year.

I defined *C. cyanomelas* as pulp-consumer-dispersers (PCSD, *sensu* Jordano & Schupp 2000); these birds peel the fruit, and consume the pulp without ingestion of the endocarp. Although they frequently drop the endocarp under the fruiting tree, in some instances they leave the vegetation patch to eat the fruit at another vegetation patch, thus performing infrequent dispersal events (see next section). In contrast, I defined *P. castanotis* as legitimate seed dispersers (SD, *sensu* Jordano & Schupp 2000); members of this species swallow the fruit whole and defecate intact endocarps away from the vegetation patch (see next section). *C. cyanomelas* and *P. castanotis* accounted for approximately 75% and 6.5% of the total bird visits to *G. viburnoides* from 2006 to 2008 (Table 2). *C. cyanomelas* accounted for the vast majority of the visits to *G. viburnoides* trees in vegetation patches, however, *P. castanotis* removed more fruits per visit (almost four times more; $t=15.18$, $P < 0.001$) (Table 3).

Quality components of seed dispersal

Post-feeding movements. Patterns of habitat selection following fruit consumption differed among the two QID of *G. viburnoides*. During the three years, all individuals of *P. castanotis* observed feeding from *G. viburnoides* in vegetation patches ($n=17$), immediately flew and perched in a forest island following fruit consumption. In all instances, *P. castanotis* left the vegetation patch without regurgitating or defecating the endocarps (Table 3). Consequently, it is likely that this species disperses all of the *G. viburnoides* endocarps to forest islands. This result is supported by seed trap data across the study site in 2006 and 2008; endocarps collected in seed traps in forest islands had

been defecated >95% of the time, while those collected in seed traps in vegetation patches had only the pulp removed (Loayza 2009).

On average, 10% of the total visits by *C. cyanomelas* resulted in the dispersal of an endocarp away from the vegetation patch with the fruiting tree. During the three years, this translated into a total of 19 endocarps (2.1% of total fruits consumed) dispersed without ingestion by *C. cyanomelas* to other vegetation patches (Table 3). No visits by *C. cyanomelas* resulted in dispersal to forest islands. There was no difference in the proportion of endocarps dispersed to either vegetation patches with or without *G. viburnoides* ($\chi^2=0.053$, $P > 0.05$).

Fruit selection. Endocarp size was different between gut-passed endocarps and endocarps with the pulp removed ($t=11.3$, d.f.=406, $P < 0.001$). Endocarps processed by *C. cyanomelas* (i.e., with the pulp removed) were on average 1.35 mm larger than gut-passed endocarps processed by *P. castanotis* (Table 3). Given that fruit size can predict endocarp size (see Fruit production and fruit traits section), this suggests that, on average, birds that swallow the fruit whole, feed on smaller fruits than do pulp consumers. Nonetheless, it is also possible that *P. castanotis* regurgitates larger endocarps, although this was never observed in vegetation patches. By considering only the size of defecated endocarps, and the results from the regression of fruit and endocarp size from all trees combined, this suggests that *P. castanotis* feeds mostly on fruits between 11.5-13.5 mm, and can swallow fruits up to approximately 15 mm, whereas *C. cyanomelas* feeds predominantly on fruits ranging from 15.5-17.5 mm, and is able to feed on fruits up to 25 mm (Figure 2).

Effect of endocarp treatment on emergence. The temporal pattern of seedling emergence was significantly affected by endocarp treatment (Likelihood ratio test=48.3, d.f.= 2, $P < 0.001$, Table 4). Seedlings of endocarps with the pulp removed emerged sooner, whereas those from gut-passed endocarps emerged later than endocarps in intact fruits (Figure 4, Table 4). After one year, the proportion of emerged seedlings differed among treatments ($\chi^2=28.35$, $P < 0.001$). The proportion of emerged seedlings was highest for endocarps with the pulp removed, followed by endocarps in intact fruits, and was lowest for gut-passed endocarps (Figure 4). Finally, the number of seedlings emerged per endocarp was also affected by endocarp treatment ($H'=16.19$, d.f. = 2, $P < 0.001$). Specifically, more seedlings emerged per endocarp in endocarps with the pulp removed ($\bar{x} = 1.88$) than in either gut-passed endocarps ($\bar{x} = 1.25$) or endocarps in intact fruits ($\bar{x} = 1.19$) (Figure 5); there was no difference in the final number of seedlings emerged between gut-passed endocarps and endocarps in intact fruits.

DISCUSSION

The results from this study show that only a few species from a frugivore assemblage visiting a plant can account for most of its seed dispersal (Schupp 1993). Moreover, here I show that birds differ in the seed dispersal benefits they provide to *G. viburnoides*. These differences arise from variation of their foraging behavior, specifically in the quantity of fruits they remove, their patterns of fruit selection, their seed handling-treatment, and their post-feeding habitat selection.

Quantity components of seed dispersal. While fruit production varied across years, the overall assemblage of frugivorous birds feeding on *G. viburnoides* was relatively constant in successive years. In terms of the number of fruits removed, the most frequent and reliable visitor to *G. viburnoides* during this study was *C. cyanomelas* (>75% visits). Yet, high frequency of visits alone was not a valid predictor of the relative quantity of fruits removed; the second most frequent visitor, *P. castanotis*, dispersed only 6.5% of the visits, but accounted for almost a third of the fruits removed by *C. cyanomelas*. At a landscape level, these two bird species represent the QID of the *G. viburnoides* population.

At the individual tree level, some trees in the population may be visited either by a moderately different frugivore assemblage, or the relative proportions of frugivores that visit the trees may change for several reasons. First, the number of frugivores that visit individual trees can change with the respect to fruit crop; trees with larger crop sizes frequently attract more dispersal agents (Deckers *et al.* 2008, Ortiz-Pulido and Rico-Gray 2000, Ortiz-Pulido *et al.* 2007, Russo 2003). For this study, all focal trees I selected within a year had similar crop sizes, but fruit production varied considerably among trees in the population (Table 1). Therefore it is reasonable to expect that trees with smaller crops likely attracted fewer frugivores, especially large-bodied species such as toucans. Second, in other areas of its distribution, fruits of *G. viburnoides* are eaten by other frugivores that are present at the study site, but that were not recorded during this study, such as coatis (*Nasua nasua*) (Alves-Costa & Eterovick 2007), *Thraupis sayaca*, *Thlypopsis sordida* and *Dacnis cayana* (Hasui & Hofling 1998). These species are generally forest dwellers, and at the study site they occur in forest islands and continuous

forest. Hence, they may be part of the frugivore assemblage that visits the small fraction of the *G. viburnoides* population that grows in forest islands, but were not detected in the savanna observations. Finally, tree neighborhood density can also affect the number of frugivores visiting a tree, and ultimately fruit removal rates (Carlo & Morales 2008). The distribution of fruiting *G. viburnoides* trees at the study site is very patchy; some trees are highly aggregated, whereas others are relatively isolated (Figure 1). It is possible that aggregated fruit displays (i.e., in areas of high tree density) may be more easily found by frugivores (Denslow 1987), than fruit displays in isolated trees. Ultimately, differences in composition of the frugivore assemblages among trees may have important consequences for individual plant fitness (Jordano & Schupp 2000), and it remains to be explored how much of this variation may occur at the study site.

At the end of the fruiting seasons in 2007 and 2008, between 14 and 32% of the fruits in a tree remained non-dispersed (Table 1). This result suggests that fruit production at the landscape level was sufficient to satiate frugivores (Hampe 2008). Although I did not quantify frugivore abundance during this study, the low number of both species recorded feeding from *G. viburnoides*, as well as the total number of visits per species, suggests a low density of frugivorous birds foraging in the savanna. This may be in part explained by low overall fruit availability in this habitat during the time *G. viburnoides* is fruiting (*pers. obs.*). Although seedlings are able to emerge from endocarps in intact fruits, emergence from intact fruits is lower than from fruits processed by birds (Figure 4). Consequently, the activity of frugivorous birds and the extent of satiation may have important consequences for plant regeneration in this landscape (Hampe 2008).

Quality components of seed dispersal. The two QID of *G. viburnoides* (*C. cyanomelas* and *P. castanotis*) differed significantly in four aspects of the qualitative components of seed dispersal: 1) they chose fruits of different sizes; 2) they had different seed delivery patterns among the habitats in the landscape; 3) they had distinct fruit-handling techniques; and 4) their seed treatment in the mouth or gut had different effects on seedling emergence probabilities. Together, these differences are likely to influence the seed dispersal effectiveness of each species (Schupp 1993).

In this study, I found that *C. cyanomelas* and *P. castanotis* feed on fruits of different sizes, where the former apparently feeds on larger fruits than the latter. Frugivores face foraging decisions on various levels: choice among different plant species, among individual plants from the same species, or among fruits borne on the same plant (Sallabanks 1993, Wheelwright 1985). When feeding from one plant species, fruit selection will presumably be determined by both the behavior of the frugivore and the fruit size (Rey *et al.* 1997). For example, pulp consumers may be able to feed on larger fruits than birds that swallow the fruit whole because gape size constrains the size of fruits that can be swallowed (Wheelwright 1985). The result of size differences between endocarps with the pulp removed and gut-passed endocarps was surprising, however, because gape size would not be a factor limiting *P. castanotis* from consuming larger fruits. Although this species is not the only one that swallows the fruit whole in the study area, and hence some of the gut-passed endocarps measured could have been consumed by other dispersers, the other species recorded swallowing the fruit also have large gape sizes (e.g., *Ramphastos toco* and *Pipile pipile*), or are visitors so infrequent that they would not account for any differences in the analysis. Nonetheless, if the differences I

found in this study between endocarps consumed by legitimate seed dispersers and pulp consumers do represent differences in the fruit selection process, then these results would suggest that *P. castanotis* is either consistently selecting the smallest fruits within a crop, or that this species is feeding more commonly on trees that produce smaller fruits.

Ultimately, by selecting fruits of different sizes, frugivores have the potential to act as agents of selection for fruit size (Jordano 1995, Lord 2004). Additionally, because a single endocarp can contain between three and seven seeds (Loayza 2009), it is possible that larger endocarps contain more seeds than smaller endocarps. In this case, fruit size selection would also have consequences on emergence probabilities, and may even influence the probability that an endocarp is depredated once it is dispersed (Ambrasky 1983).

The endocarp deposition habitats differed between the two QID of *G. viburnoides*; *C. cyanomelas* deposited almost all of the endocarps under or close to the parent tree, and dispersed 2% of the endocarps to other vegetation patches in the savanna, whereas *P. castanotis* presumably dispersed all the endocarps in forest islands, which was consistently the habitat of the first perch used after feeding by this species. Differences in the seed rain pattern generated among frugivores are common for many systems (Alcántara *et al.* 2000, Calviño-Cancela 2002, Wenny 2000). From the plant perspective, these differences can be particularly important depending on the extent to which habitats differ in suitability for recruitment (Schupp 1993). At the study site, vegetation patches are more suitable for recruitment than forest islands (Loayza 2009). Consequently, the spatial pattern of seed deposition by individual dispersers can influence plant fitness. Habitat suitability, however, is context-dependent (Loayza 2009, Schupp 2007) so the

role of individual dispersers for plant recruitment can potentially change in successive years or in different populations.

Frugivore species differed in whether they swallowed fruits whole or only consumed the pulp. *C. cyanomelas* consumed only the pulp and dropped the endocarp; conversely, *P. castanotis* swallowed the fruit and was assumed to only defecate the endocarp, although it is possible it regurgitated endocarps in forest islands. Ultimately, the treatment of the endocarp affected seedling emergence. Gut-passed endocarps had not only the lowest emergence probabilities, and number of emerged seedlings per endocarp, but also the slowest emergence rate in comparison to endocarps that were either in intact fruits or that had only the pulp removed. These results suggest that endocarp ingestion has a negative effect on emergence. Inhibition or reduction of germination after bird ingestion has been reported for some plant species (Domínguez-Domínguez *et al.* 2006, Lieberman & Lieberman 1986). Differences in germination among seed treatments, however, may also be a consequence of indirect effects of the fecal material in which seeds are embedded at the time of deposition. In this sense, Meyer and Witmer (1998) found that the fecal material of cedar waxwings (*Bombycilla cedrorum*) surrounding *Lindera* and *Prunus* seeds reduced germination success by promoting fungal and/or bacterial growth, rather than by direct effects of ingestion on the seed coat. This hypothesis remains to be tested for *G. viburnoides* endocarps in *P. castanotis* faeces. Finally, because gut-passed endocarps were on average smaller than endocarps with the pulp removed, lower emergence probabilities, and final number of emerged seedlings per endocarp, may also reflect a smaller number of seeds in the

endocarps that had been ingested and defecated in comparison to those with the pulp removed.

Conclusion. Understanding the roles of individual dispersers for plant recruitment requires dissecting the components of dispersal effectiveness (Schupp 1993). In this study, I found an assemblage of 10 species of birds feeding on *G. viburnoides* trees in vegetation patches within the savanna. Only two of these species, however, were frequent enough visitors to the trees to be considered quantitatively important dispersers of *G. viburnoides*. These two species, *C. cyanomelas* and *P. castanotis*, differed in several aspects of the quality components of seed dispersal. Nonetheless, even detailed information of these qualitative differences is insufficient to adequately assess disperser effectiveness. Seeds processed by *C. cyanomelas* have the highest emergence probability, but this species drops 98% of the endocarps under the parent tree. Seeds processed by *P. castanotis* have the lowest emergence probability, but this species disperses 100% of the endocarps away from the parent tree. Thus, it is not clear which species is the most effective disperser. The ecology of seed dispersal is complex; ultimately our ability to understand the relative importance of different frugivores for plant fitness will require connecting for each disperser the fruit consumption and seed removal stages, with landscape patterns of seed deposition, and habitat-specific post-dispersal seed fate and establishment. Only then, will we be able to effectively determine how different dispersal agents affect the population dynamics of the plant they consume.

ACKNOWLEDGEMENTS

I am very grateful to the people who assisted me with the field data collection, particularly F. Saavedra, N. Burgos, R. Balderrama, A. Terán, O. Burgos, A. Yarari, and M. Houard. Fieldwork was facilitated by logistic support of the Instituto de Ecología in La Paz, Bolivia and the Estación Biológica Beni. I also thank Bette Loiselle, Rodrigo Rios, Tiffany Knight, John Blake, and Eugene Schupp for critical comments that helped improve an earlier version of this paper. This study was supported by grants from the National Science Foundation (DEB-0709753), the Rufford Maurice Laing Foundation, the Scott Neotropical Fund from the Cleveland Metropolitan Zoo, the Neotropical Grassland Conservancy, the Webster Groves Nature Study Society, Sigma Xi, and the Whitney R. Harris World Ecology Center at the University of Missouri-St. Louis.

LITERATURE CITED

- ALCÁNTARA, J. M., REY P. J., VALERA, F. & SANCHEZ-LAFUENTE, A. M. 2000. Factors shaping seedfall pattern of a bird-dispersed plant. *Ecology* 81:1937–1950.
- ALVES-COSTA, C. P. & ETEROVICK, P. C. 2007 Seed dispersal services by coatis (*Nasua nasua*, Procyonidae) and their redundancy with other frugivores in southeastern Brazil. *Acta Oecologica* 32: 77–92.
- AMBRASKY, Z. 1983. Experiments on seed predation by rodents and ants in the Israeli desert. *Oecologia* 57: 328–332.
- BAS, J. M., PONS, P. & GÓMEZ, C. 2006 Exclusive frugivory and seed dispersal of *Rhamnus alaternus* in the bird breeding season. *Plant Ecology* 183: 77–89.
- CALVIÑO-CANCELA, M. 2002 Spatial patterns of seed dispersal and seedling recruitment in *Corena album* (Empetraceae): the importance of unspecialized dispersers for regeneration. *Journal of Ecology* 90: 775–784.
- CARLO, T. A. & MORALES, J. M. 2008. Inequalities in fruit removal and seed dispersal: consequences of bird behaviour, neighborhood density and landscape aggregation. *Journal of Ecology* 96: 609–618.
- DECKERS, B., VERHEYEN, K., VANHELLEMONT, M., MADDENS, E., MUYS, B. & HERMY, M. 2008. Impact of avian frugivores on dispersal and recruitment of the invasive *Prunus serotina* in an agricultural landscape. *Biological Invasions* 10:717–727.
- DENSLOW, J. S. 1987. Fruit removal rates from aggregated and isolated bushes of the red elderberry, *Sambucus pubens*. *Canadian Journal of Botany* 65: 1229–1235.
- DOMÍNGUEZ-DOMÍNGUEZ, L. E., MORALES-MÁVIL, J. E. & ALBA-LANDA, J. 2006. Germinación de semillas de *Ficus insipida* (Moraceae) defecadas por tucanes

- (*Ramphastos sulfuratus*) y monos araña (*Ateles geoffroyi*). *Revista de Biología Tropical* 54: 387–394.
- ELLISON, A. M., DENSLOW, J. S., LOISELLE, B. A. & BRENES, M. D. 1993. Seed and seedling ecology of Neotropical Melastomataceae. *Ecology* 74:1733–1749.1
- FIGUEROLA, J. A., GREEN, J. & SANTAMARIA, L. S. 2002. Comparative dispersal effectiveness of wigeongrass seeds by waterfowl wintering in south-west Spain: quantitative and qualitative aspects. *Journal of Ecology* 90: 989–1001.
- FOX, G. A. 2001. Failure-time analysis. Pp. 235–266 in Scheiner, S. M., & Gurevitch, J. (eds). *Data analysis of ecological experiments*. Oxford University Press, New York.
- HANAGARTH, W. 1993. *Acerca de la geoecología de las sabanas del Beni en el Noreste de Bolivia*. Instituto de Ecología, La Paz, Bolivia. 186 pp.
- HAMPE, A. 2008. Fruit tracking, frugivore satiation, and their consequences for seed dispersal. *Oecologia* 156: 137–145.
- HASUI, E. & HÖFLING, E. 1998. Preferência alimentar das aves frugívoras de um fragmento de floresta estacional semidecídua secundária, São Paulo, Brasil. *Iheringia, Série Zoologia, Porto Alegre* 84: 43–64.
- HERRERA, C. M., JORDANO, P., LÓPEZ-SORIA & L., AMAT, J. A. 1994. Recruitment of a mast fruiting, bird-dispersed tree: Bridging frugivore activity and seedling establishment. *Ecological Monographs* 64: 315–344.
- HOLBROOK, K. M. & LOISELLE B. A. 2007. Using toucan-generated dispersal models to estimate seed dispersal in Amazonian Ecuador. Pp 391–406 in Dennis, A. J.,

- Schupp, E. W., Green R. J., & Westcott, D. A. (eds) *Seed dispersal: Theory and its application in a changing world*. CABI. Oxfordshire, UK.
- HOWE, H. F. & SMALLWOOD, J. 1982 Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.
- JORDANO, P. 1995. Frugivore-mediated selection on fruit and seed size: Birds and St. Lucie's cherries, *Prunus mahaleb*. *Ecology* 76: 2627–2639.
- JORDANO, P. & SCHUPP, E. W. 2000. Seed disperser effectiveness: the quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70: 591–615.
- LANGSTROTH, R. P. 1996. *Forest islands in an Amazonian savanna of northeastern Bolivia*. Ph. D. Dissertation. University of Wisconsin-Madison.
- LEVEY, D. 1987. Seed Size and Fruit-Handling Techniques of Avian Frugivores. *The American Naturalist* 129: 471–485.
- LIEBERMAN, M. & LIEBERMAN, D. 1986. An experimental study of seed ingestion and germination in a plant-animal assemblage in Ghana. *Journal of Ecology* 2: 113–126.
- LOAYZA, A. P. 2009. *Closing the seed dispersal loop for Guettarda viburnoides (Rub.): Connecting patterns of avian seed dispersal with population growth in a Neotropical savanna*. Ph.D. Dissertation, University of Missouri-St. Louis.
- LOISELLE, B. A. & BLAKE, J. G. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology* 80: 330–336.
- LORD, J. M. 2004 Frugivore gape size and the evolution of fruit size and shape in southern hemisphere floras. *Austral Ecology* 29: 430–436.

- MCDONNELL, M. J. & STILES, E. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. *Oecologia* 56:109–116.
- MEYER, A. M. & WITMER, M. C. 1998. Influence of seed processing by frugivorous birds on germination success of three North American shrubs. *American Midland Naturalist* 140: 129–139.
- MIRANDA, C. L. 2000. La Reserva de la Biósfera Estación Biológica del Beni, Bolivia. Pp 21–25 in Herrera-MacBryde, O., Dallmeier, F., MacBryde, B., Comiskey, J. A. & Miranda, C. (eds). *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia*. Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB).
- MOERMOND, T. C. & DENSLOW, J. S. 1985. Neotropical avian frugivores: patterns of behavior, morphology and nutrition, with consequences for fruit selection. Neotropical Ornithology: 865–897 in Buckley, P. A., Foster, M. S., Morton, E. S., Ridgely, & R. S., Buckley, F. G. (eds). *Ornithological Monograph No. 36*. American Ornithologists Union, Washington D.C.
- MORAES, M. R., RIBERA, M. O. & VILLANUEVA, E. 2000. La vegetación de la Reserva de la Biosfera Estación Biológica del Beni y su importancia para la conservación. Pp 59–73 in Herrera-MacBryde, O., Dallmeier, F., MacBryde, B., Comiskey, J. A. & Miranda, C. (eds). *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia*. Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB).

- NARANJO, M. E., RENJIFO, C. & SORIANO, P. J. 2003 Effect of ingestion by bats and birds on seed germination of *Stenocereus griseus* and *Subpilocereus repandus* (Cactaceae). *Journal of tropical Ecology* 19: 19–25.
- NATHAN, R. & MÜLLER-LANDAU, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285.
- ORTIZ-PULIDO, R. & RICO-GRAY, V. 2000. The effect of spatiotemporal variation in understanding the fruit crop size hypothesis. *Oikos* 91:523–527.
- ORTIZ-PULIDO, R., ALBORES-BARAJAS, Y. V. & DÍAZ, S. A. 2007. Fruit removal efficiency and success: influence of crop size in a neotropical treelet. *Plant Ecology* 189: 147–154.
- REY, P. J., GUTIERREZ, J. E., ALCANTARA, J. & VALERA, F. 1997. Fruit Size in Wild Olives: Implications for Avian Seed Dispersal. *Functional Ecology* 11: 611–618.
- RIOS-ARAMAYO, R. & LOAYZA-FREIRE, A. 2000. Depredación de semillas de *Attalea phalerata* por brúquidos en islas de bosque de la Estación Biológica Beni. *Ecología en Bolivia* 33: 78–89.
- RUSSO, S. E. 2003. Responses of dispersal agents to tree and fruit traits in *Virola calophylla* (Myristicaceae): implications for selection. *Oecologia* 136:80–87.
- RUSSO, S. E., S. PORTNOY, & C. K. AUGSPURGER. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* 87: 3160–3174.
- SALLABANKS, R. 1993. Hierarchical mechanisms of fruit selection by an avian frugivore. *Ecology* 74: 1326–1336.

- SARMIENTO, J. 2000. Observaciones preliminares sobre la composición y distribución de la ictiofauna de la Estación Biológica del Beni, Bolivia. Pp 129–150 in Herrera-MacBryde, O., Dallmeier, F., MacBryde, B., Comiskey, J. A. & Miranda, C. (eds). *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia*. Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB).
- SCHUPP, E. W. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15–29.
- SCHUPP, E. W. 2007 The suitability of a site for seed dispersal is context-dependent. Pp. 445–462 in Dennis, A. J., Schupp E. W., Green R. J., & Westcott, D. A. (eds). *Seed dispersal: theory and its application in a changing world*. CABI International, Wallingford, Oxfordshire.
- SCHUPP, E. W. & FUENTES, M. 1995. Spatial patterns of seed dispersal and the unification of plant ecology. *EcoScience* 2: 267–275.
- TAYLOR, C., DELPRETE, P. G., VINCENTINI, A., CORTÉS, R., ZAPPI, D., PERSSON, C., BESTETTI COSTA, C. & ARAUJO DE ANUNCIAÇÃO, E. 2004. Pp 497–847 in Steyermark, J. A., Berry, P. E., Yatskievych, K., Holst, B. K. (eds). *Rubiaceae. Flora of the Venezuelan Guayana: Volume 8 – Poaceae-Rubiaceae*. Missouri Botanical Garden Press, St. Louis.
- TRAVASET, A. & WILSON, M. F. 1997. Effect of birds and bears on seed germination of fleshy-fruited plants in temperate rainforests of southeast Alaska. *Oikos* 80: 89–95.

- TRAVERSE, A. & VERDÚ, M. 2002. A meta-analysis of the effect of gut treatment on seed germination. Pp 339–350 in Levey, D. J., Silva W. R., & Galetti, M. (eds). *Seed dispersal and frugivory: Ecology, evolution, and conservation*. CABI Publishing, Wallingford, Oxfordshire, UK.
- TRAVASET, A., ROBERTSON, A. W. & RODRIGUEZ-PÉREZ, J. 2007. A review of the role of endozoochory in seed germination. Pp 78–1103 in Dennis, A. J., Schupp, E. W., Green, R. J., & Westcott, D. A. (eds). *Seed dispersal: Theory and its application in a changing world*. CABI. Oxfordshire, UK.
- WEBBER, B. L. & WOODROW, I. E. 2004. Cassowary frugivory, seed defleshing and fruit fly infestation influence the transition from seed to seedling in the rare Australian rainforest tree, *Ryparosa* sp. nov. 1 (Achariaceae). *Functional Plant Biology* 31: 505–516.
- WENNY, D. G. 1998. Directed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the Natural Academy of Sciences, USA* 95: 6204–6207.
- WENNY, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs* 70: 331–351.
- WEHNCKE, E. V., Valdez, C. N. & Dominguez, C. A. 2004. Seed dispersal and defecation patterns of *Cebus capucinus* and *Alouatta palliata*: consequences for seed dispersal effectiveness. *Journal of Tropical Ecology* 20: 535–543.
- WHEELWRIGHT, N. 1985. Fruit size, gape width and the diet of fruit-eating birds. *Ecology* 66: 808–818.
- ZAR, J. H. 1999. *Biostatistical Analysis*. 4th Edition. Prentice-Hall, Inc., Upper Saddle River, NJ. 931 pp.

Table 1. Yearly variation in mean individual plant fecundity of the *G. viburnoides* population from 2006-2008 at Beni Biological Station-Biosphere Reserve

Year	Proportion of fruiting adults	Mean # fruits/adult (range)	Proportion of non-dispersed fruits (Mean \pm SD)
2006	0.486	2273 (10-6000)	-
2007	0.489	1089 (10-7000)	0.14 \pm 0.10
2008	0.712	2722 (10-6350)	0.32 \pm 0.15

Table 2. Percent of visits by fruit-eating birds to *G. viburnoides* trees in vegetation patches at Beni Biological Station-Biosphere Reserve from 2006 to 2008

Species	Frugivory type [†]	Percent of visits			
		2006	2007	2008	Mean
		(170 hrs)	(173 hrs)	(59 hrs)	
<i>Ara severa</i>	PC	16.00	3.30	-	6.43
<i>Columba cayannensis</i>	SP*	0.67	-	-	0.22
<i>Cyanocorax cyanomelas</i>	PCSD	64.67	83.52	77.78	75.32
<i>Cyanocorax chrysops</i>	PCSD	5.33	2.20	7.41	4.98
<i>Ortalis motmot</i>	SD	-	2.20	-	0.73
<i>Pipile pipile</i>	SD	1.33	-	-	0.44
<i>Psarocolius decumanus</i>	PC	2.67	-	3.70	2.12
<i>Pteroglossus castanotis</i>	SD	6.67	5.49	7.41	6.52
<i>Ramphastos toco</i>	SD	2.67	3.30	-	1.99
<i>Tyrannus melancholicus</i>	SD	-	-	3.70	1.23

† SD, seed disperser; SP, seed predator; PC, pulp consumer; PCSD, pulp-consumer disperser (*sensu* Jordano and Schupp 2000)

* This species swallows the fruit whole, but likely destroys the endocarp in the gizzard.

Table 3. Foraging behavior of the two quantitatively important dispersers of *G. viburnoides* feeding in vegetation patches at Beni Biological Station-Biosphere Reserve (data from 2006 through 2008 combined)

	<i>Cyanocorax cyanomelas</i>	<i>Pteroglossus castanotis</i>
Total visits	194	17
Visits with handled fruits	190	17
Total visits which result in the dispersal of an endocarp out of the vegetation patch (%)	19 (9.7%)	17 (100%)
Handled fruits/visit (mean \pm SE)	4.62 \pm 0.24	18.06 \pm 2.19
Total number of fruits consumed	897	307
Endocarp diameter [†] (mean \pm SE)	10.37 \pm 0.10	9.02 \pm 0.07
[range]	[7.10-14.82]	[6.89-11.58]
Fruit treatment (%)	Swallowed	0
	Pulp removed	100
% Endocarps dropped or defecated ^a (total)	Feeding site	97.9 (876)
	GV	1.0 (9)
	No GV	1.1. (10)
	ISL	0
		100*

[†] Indicates mean size (mm) of gut-passed endocarps (i.e., processed by *P. castanotis*) and endocarps with the pulp removed (i.e., processed by *C. cyanomelas*)

^a Dispersed to other vegetation patches with (GV) or without (No GV) *G. viburnoides*, and to forest islands (ISL).

* *P. castanotis* was always observed to fly to forest islands after consuming fruits in vegetation patches with *G. viburnoides*. This observation together with the absence of any evidence that *G. viburnoides* endocarps were defecated or regurgitated in vegetation patches and seed trap data in forest islands that revealed endocarps arriving in this habitat were almost always defecated, suggest that *P. castanotis* was primarily responsible for dissemination into forest islands.

Table 4. Cox proportional hazards regressions of seedling emergence for endocarp treatment. Note that because the dependent variable in the model is a hazard rate, a positive coefficient (β) means that the endocarp treatment increases the hazard, thereby decreasing failure time (i.e., time to emergence) in comparison to the control group (i.e., endocarps in intact fruits).

Endocarp treatment	β	β_{exp}	$SE_{(\beta)}$	d.f.	P
Gut-passed endocarps	-0.78	0.46	0.29	2	0.007
Endocarps with pulp removed	0.87	2.40	0.21	2	< 0.001

FIGURE LEGENDS

Figure 1. Map of the study area at Beni Biological Station-Biosphere Reserve. White circles and black triangles denote the location of vegetation patches with and without *G. viburnoides*, respectively. Dark grey areas are forest islands. The light grey background represents the savanna matrix, and the white rectangle is a lake.

Figure 2. Distribution of mean fruit sizes among sampled trees. Error bars indicate $1 \pm$ SE. Box with diagonal lines indicates predicted range of fruit sizes that *P. castanotis* mostly selects (based on sizes of gut-passed endocarps). Box with crosshatch shows the predicted range of fruit sizes on which *C. cyanomelas* most commonly feeds (based on sizes of endocarps with the pulp removed). Dashed and dotted vertical lines indicate the maximum predicted fruit size *P. castanotis* and *C. cyanomelas*, respectively, feed on (based on the maximum size of gut-passed endocarps and endocarps with the pulp removed).

Figure 3. Relationship between fruit and endocarp size in each of the 15 selected trees. Endocarp size can be predicted from fruit size in all but one of the trees (T15).

Figure 4. Survival curves for *G. viburnoides* seedling emergence. Circles represent gut-passed endocarps; triangles symbolize endocarps from intact fruits; and squares denote endocarps with the pulp removed. Bars represent 95% confidence intervals. All curves end when the last seedling emerged. The experiment ended at 366 days.

Figure 5. Distribution of number of emerged seedlings per endocarp in each of the treatments.

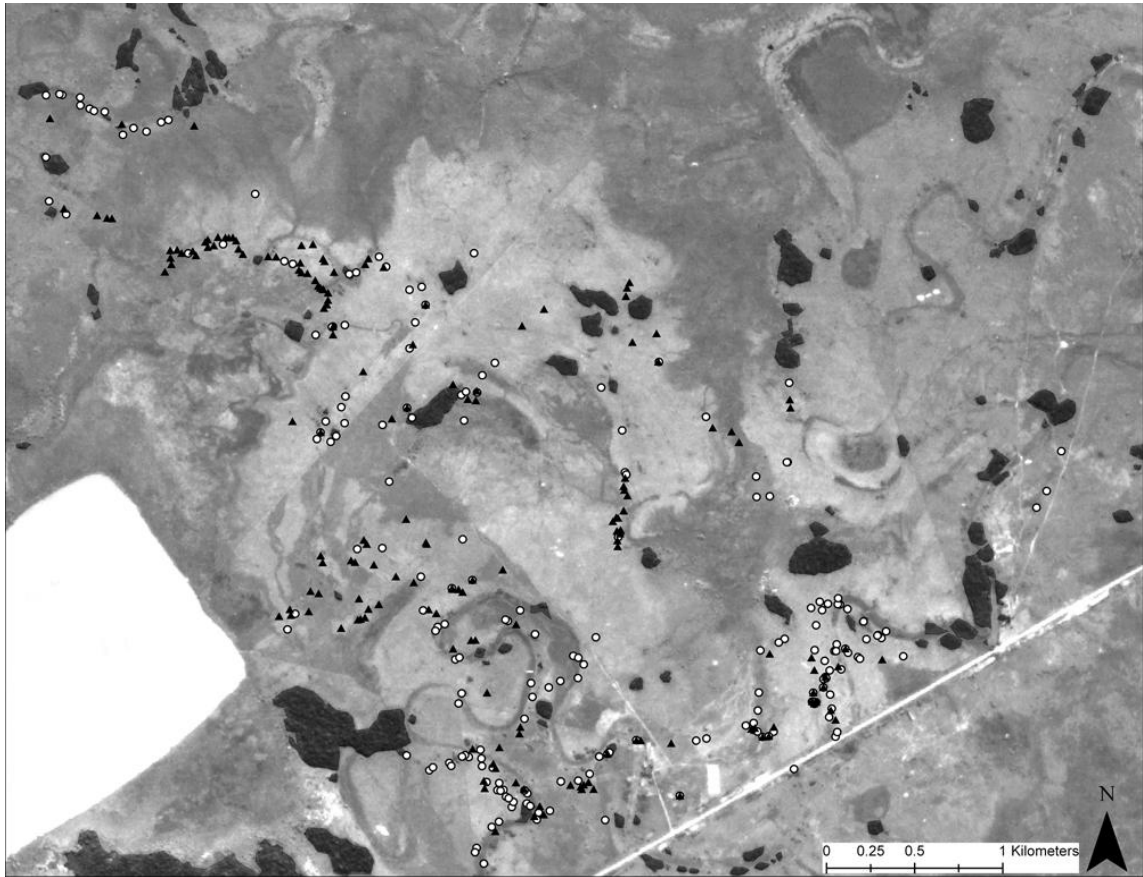


Figure 1

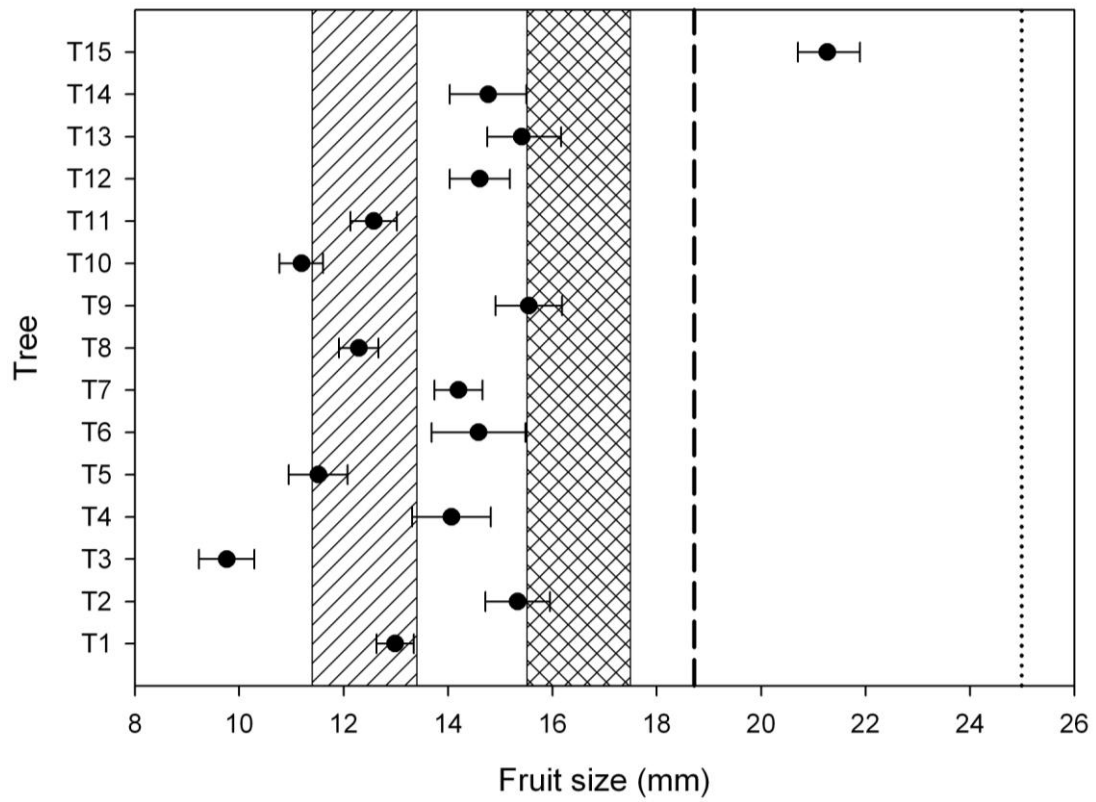


Figure 2

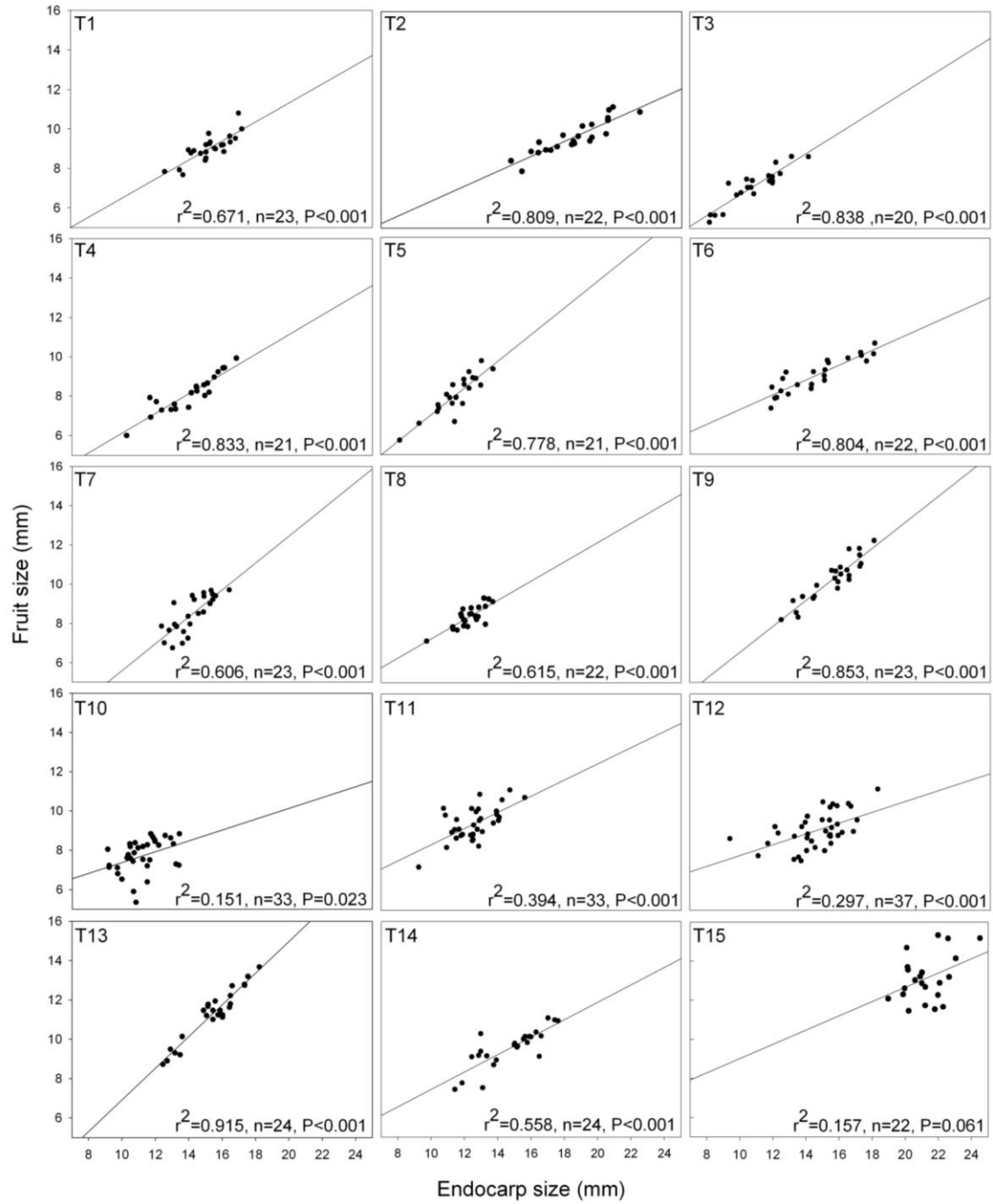


Figure 3

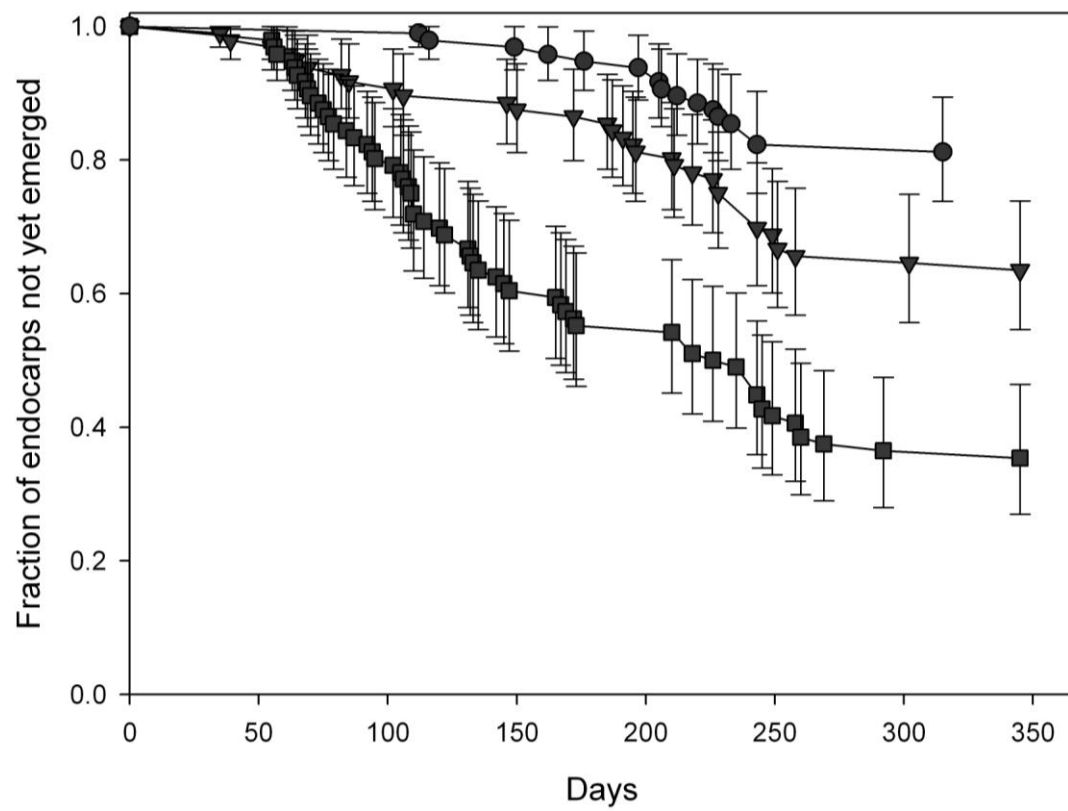


Figure 4

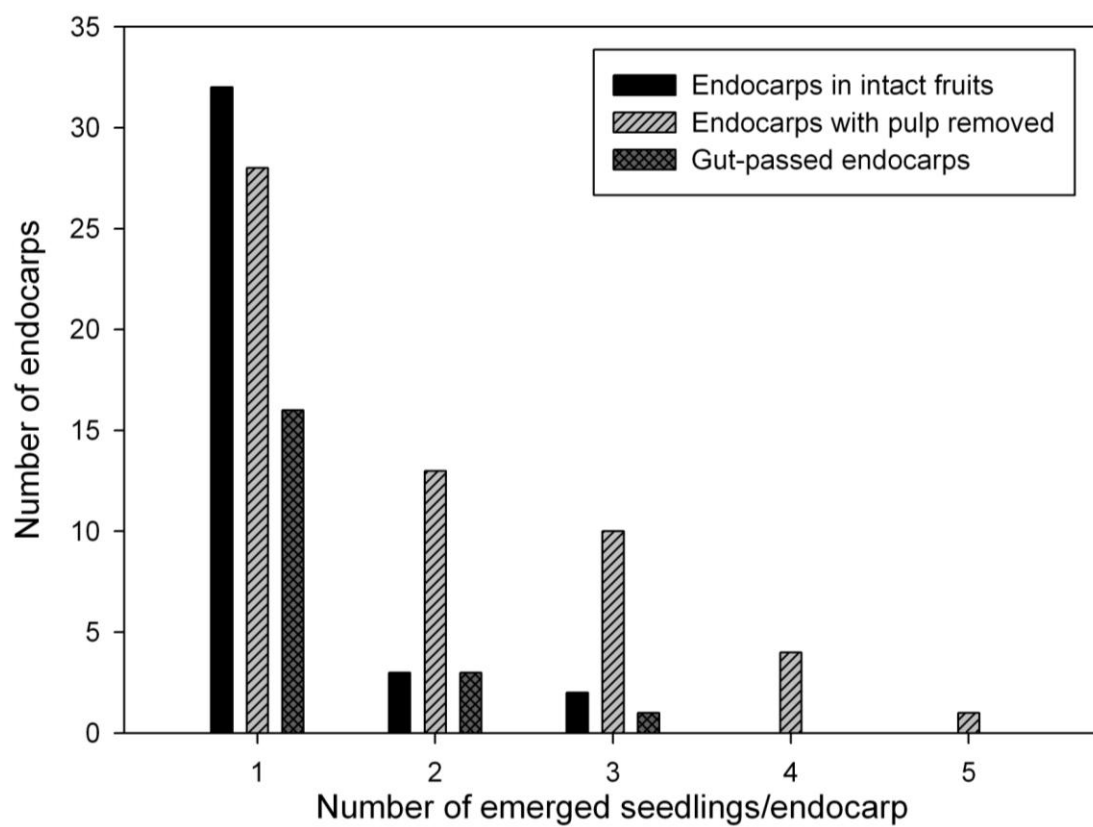


Figure 5

CHAPTER 2 — Recruitment of a bird-dispersed tree (*Guettarda viburnoides*) in a heterogeneous landscape: Shifting patterns of habitat suitability in time.

Summary

1. 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.

2. In this study, we analyzed how habitat affects the recruitment dynamics of a bird-dispersed tree *Guettarda viburnoides* (RUB.). Seed dispersal, post-dispersal seed predation, seedling emergence and seedling survival were quantified in four different habitats in a Neotropical forest-savanna mosaic during three years.

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

4. 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.

5. Synthesis: This study shows that habitat can affect seed dispersal, post-dispersal processes and, ultimately, the recruitment dynamics of a Neotropical tree in a heterogeneous landscape. Most importantly, our results also show high inter-annual

variability in the strength of post-dispersal processes, which leads to a constant shifting of habitat “suitability” from one year to the next. Therefore, in order to better understand the role of site suitability for recruitment, we need to explicitly consider not only variation in habitat-specificity in dispersal and post dispersal processes, but also how this variation can shift under different environmental conditions; that is, the context dependence of suitability.

Key words: *Guettarda viburnoides*, context-dependence, habitat suitability, plant recruitment, savanna, seed dispersal, seed predation, seedling emergence, seedling survival, spatial discordance.

Introduction

Seed dispersal is a multi-staged process that links consecutive generations of plants (Nathan & Müller-Landau 2000; Wang & Smith 2002). The most immediate outcome of dispersal is a non-random distribution of seeds among the different habitats in a landscape. Seed arrival to a particular habitat, however, is no guarantee of recruitment (Nathan & Müller-Landau 2000). Habitats vary in their biotic and abiotic environments, which in turn affect the probability of recruitment (Schupp 1995; Schupp & Fuentes 1995; Kollmann 2000). Thus, depending on the habitat into which a seed is dispersed, a seed may encounter different abiotic conditions, such as soil characteristics (Herrera 2002; Russo *et al.* 2008) or light levels (Páez & Marco 2000), as well as differences in the biotic environment, such as predation (Kennedy 2005) and seedling herbivory (Nickel *et al.* 2003). This variation may ultimately lead to habitat-dependent differences in recruitment probabilities, and may be particularly important for early plant recruitment phases, such as seed survival, germination and seedling establishment, which have long been recognized as the most critical periods for population dynamics in plants (Harper 1977).

Differences in the extent of post-dispersal processes among habitats can alter, if not erase, the initial landscape pattern of seed rain. For example, due to life stage conflicts (Schupp 1995, 2007) seeds may be deposited in habitats adequate for seedling emergence but unfavorable for seedling survival and, as a result, the probability of recruitment into such habitats is low (Fuchs *et al.* 2000; Gómez *et al.* 2008). Such a situation, where the processes that affect one demographic stage obscure the effects of

processes in previous stages, is an example of uncoupling (Jordano & Herrera 1995). Eventually, uncoupling can lead to recruitment patterns that are discordant with those of seed rain and may result in patterns of adult establishment that bear little resemblance to those of seed rain (Schupp 1995; Schupp & Fuentes 1995; García 2001).

Suitability of a habitat for different developmental stages can also vary over time. That is, habitat suitability can be context-dependent, whereby a habitat may favor or promote recruitment in some years but not others (Schupp 2007). Although a number of recent studies have analyzed patterns of seed dispersal and seedling recruitment across years (*e.g.* Hampe 2004; Gómez-Aparicio *et al.* 2005; Hampe *et al.* 2008), we still lack a clear understanding of why differences in seed dispersal, seed survival, germination and seedling establishment among habitats can be strong in some years but not in others. Ultimately, the consequences of seed dispersal for plant population ecology can only be fully understood by assessing the extent to which habitat affects the number of potential new recruits at different developmental stages, and how this relationship varies across years.

The objective of this study was to link landscape patterns of seed dispersal to patterns of seedling establishment of *Guettarda viburnoides* (Rubiaceae) over two years in a neotropical savanna. We determined the habitats into which seeds were naturally dispersed, and then followed the post-dispersal fate of seeds experimentally dispersed into these habitats. We hypothesized that the spatial pattern of recruitment would be initially established by the seed rain pattern, but that this pattern may be altered by variation in post-dispersal processes among habitats (spatial discordance). Further, due to climatic variability across years in the region, we hypothesized that differences in the

impact of post-dispersal processes among habitats would vary between years. To test these hypotheses, we addressed the following specific questions: (i) Is there among-habitat variability in seed dispersal, seed predation, seedling emergence, and seedling survival? (ii) Are the stage-dependent suitabilities of habitats consistent among years? (iii) Is there evidence of uncoupled recruitment within habitats? If so, does it lead to patterns of spatial discordance?

Methods

STUDY SYSTEM

This research was conducted in Beni Biological Station-Biosphere Reserve (BBSBR) located in Beni, Bolivia (14°30' -14°50' S; 66°40' - 65°50' W; 200m), within the region of the Moxos plains. Shallow floodwaters cover large portions of the land in the plains during the rainy season (November to February), but the rest of the year dry conditions prevail and water is limited (Hanagarth 1993; Langstroth 1996). The plains form a complex mosaic of habitats that include terra firme forest, naturally occurring forest islands, gallery forest, open and wooded grasslands (Beck & Moraes 1997).

For this study we selected four habitats in the savanna complex. 'Forest islands' consist of isolated units of forest (0.1-20 ha in the study site) with a canopy height from 15 to 25 m. The dominant species in these forest islands is *Attalea phalerata* palms (Rios-Aramayo & Loayza-Freire 2000), but species in the genera *Ceiba*, *Ficus*, *Guarea*, *Rheedia*, *Celtis*, *Salacia*, *Trichilia*, as well as *Virola sebifera*, *Sterculia apetala*, *Vitex cymosa*, *Copernicia alba* and *Guazuma ulmifolia* are also common (Comiskey *et al.*

2000). ‘Vegetation patches’ are habitats where woody species have established. These constitute small (2-175 m²) stands of trees and shrubs with a canopy height of up to 8 m. A vegetation patch can have from three to approximately 40 species, and they are composed primarily of animal-dispersed genera such as *Guettarda*, *Virola*, *Piper*, *Psidium*, *Clidemia*, *Miconia*, *Nectandra*, *Solanum*, *Ficus*, *Cecropia*, *Pourouma* and several species of palms (*pers. obs.*). We distinguished between two types of vegetation patches, ‘vegetation patches with an adult *G. viburnoides*’ and ‘vegetation patches without adult an *G. viburnoides*’ (vegetation patches with and without *G. viburnoides* hereon). Finally, the ‘savanna’ habitat is a herbaceous formation, which is the most widespread landscape element of the Moxos plains. Sedges, grasses and other herbaceous plants dominate this habitat (Hanagarth 1993).

Guettarda viburnoides Cham. & Schlecht. (Rubiaceae) are small trees distributed from Brazil to Paraguay. They typically occur in semi-deciduous forests and grasslands (Taylor *et al.* 2004). At the study site, *G. viburnoides* trees grow in vegetation patches, and rarely in forest islands or as isolated trees in the savanna (*pers. obs.*). Moreover, vegetation patches have generally only one adult tree; very rarely does a vegetation patch have two or more adults. Trees bear fragrant, tubular, cream-yellow colored flowers (10-25 mm) from October to January. Fruits are subglobose drupes (8–25 mm), which ripen from late March until early July (*pers. obs.*). Each fruit contains a single, woody endocarp (0.7–15 mm), which contains between 3 and 7 “true” seeds ($n = 800$). Birds consume the fruit and either drop or swallow and pass the whole endocarp; thus, for the purposes of the plant, the endocarp constitutes the unit of dispersal, and will be referred to as the “seed” from hereon. At the study site fruits are consumed by 10 species of

birds, but > 80% of seed dispersal is by two species: *Cyanocorax cyanomelas* Vieillot, and *Pteroglossus castanotis* Gould (Loayza 2009).

SEED DISPERSAL

Seed dispersal into different habitats was monitored in 2006 and 2008. In both years, we established a system of 430 seed traps spread among the four habitats selected. Specifically, we placed 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. The unequal sample sizes both of seeds traps and habitat replicates were an effort to maximize the number of seeds arriving at these traps and to account for the relative area that each habitat represents.

In 2006, seed traps consisted of funnels made out of plastic mosquito mesh, whereas in 2008 they were built from cotton cloth, which let the water through. The funnels were 80 cm deep, had a 0.20 m² surface area, and were placed one meter above the ground. This design minimized possible seed removal (e.g., by ants or rodents) from the sampled area between censuses; thus, we considered this a reliable method of estimating seed rain density for the purposes of this study. Seed traps were checked bimonthly during both fruiting seasons.

POST-DISPERSAL SEED PREDATION EXPERIMENTS

We estimated post-dispersal seed predation in the four habitats during three consecutive years (2006, 2007, and 2008). In 2006, we conducted a preliminary experiment to identify the most important seed predators of *G. viburnoides*. We determined that in our study area, the main seed predators of this species were ants of the genus *Pheidole* and, to a lesser extent, *Atta* (Saavedra 2008); thus, for all subsequent experiments we quantified seed predation by using seeds protected by wire exclosures. The exclosures were made of wire with a 25mm² mesh size, which allowed ants to depredate 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 first week, and then on days 10, 17 and 40. Note that for this study we considered the whole endocarp as “dead” if at least one of the “true” seeds in the endocarp was depredated. Although this method gives a conservative estimate of survival, because other living/intact “true” seeds can remain in the endocarp, it allows a standardized comparison of seed predation among habitats. Ants remove the true seeds by chewing holes through the germination pores, allowing the actual number of “true” seeds depredated per endocarp to be estimated. However, because the number of intact “true” seeds that remain in the endocarp cannot be measured without destructive sampling, one cannot establish in the field if any seeds remain undamaged in an endocarp.

SEEDLING ESTABLISHMENT EXPERIMENTS

Seedling emergence was quantified for the 2006 and 2007 fruiting seasons. In each habitat replicate (15 in 2006 and 25 in 2007), we established an emergence experiment by sowing a group of 40 seeds in 2006, and 10 seeds in 2007, three centimeters below ground. In both years, seeds were planted 3 cm apart so as to recognize seedlings that emerged from the same endocarp. For both years, emergence was examined once a month for a year (June 2006 – June 2007, and June 2007 – June 2008). In every survey, the presence of emerged seedlings was recorded (seedlings of *G. viburnoides* are easily identified from the time they emerge). 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.

Each year, seeds for both seed predation and seedling establishment experiments came from a unique seed pool, which was established by collecting seeds from several trees (>30) from areas adjacent to the study area. This minimized any potential difference of the number of “true seeds” per endocarp, among replicates or habitats.

SPATIAL PATTERNS OF SEED ARRIVAL AND SAPLING RECRUITMENT

To explore the spatial dynamics of *G. viburnoides*’ recruitment, we estimated habitat-specific transition probabilities (TPs). TPs were calculated for each of the four habitats as the mean number of individuals completing a stage divided by the number of individuals entering that stage (Rey & Alcántara 2000; Travaset *et al.* 2003). For a given

habitat, the probability of seed arrival was defined as the ratio of mean seed density per m² in the habitat to the sum of mean seed densities in all four habitats. The cumulative probability of recruitment (CP) for each habitat was defined as the product of the individual TPs. Finally, the overall probability of recruitment (OPR) for the population was estimated as:

$$OPR = \sum_{i=1}^4 (CP_i * A_i)$$

where CP_i is the cumulative probability in habitat _i, and A_i is the proportional area represented by habitat *i* in the landscape.

STATISTICAL ANALYSES

We evaluated variation in seed rain, seed predation, and seedling emergence among habitats by means of Generalized Linear models (GLM Crawley 1993) considering habitat as the main factor, and the density of dispersed seeds, the percentage of seed predation at the end of the study, and the number of seedlings emerged as the response variables. Poisson error distributions were considered for seed rain and emergence response variables, whereas for seed predation we used binomial error distributions. To examine if seedling survival differed among habitats, we used a proportions test (Zar 1996). Additionally, to determine if levels of seed predation, seedling emergence and seedling survival varied with time across habitats, we conducted Cox's proportional hazards models (clustered by habitat replicate for the first two variables). This analysis allows for certain aspects of survival analysis data, such as censoring and non-normality that cause difficulty when analyzing with other statistical models such as GLM (Lagakos 1992; Fox 2001). Here, the dependent variable is the hazard function, which describes

how the hazard (*e.g.* risk of a seed being depredated) changes over time, and the effect parameter describes how hazard relates to habitat. For these analyses all comparisons were made against vegetation patches with *G. viburnoides*. We choose vegetation patches with *G. viburnoides* as the standard for the comparisons because seeds are more likely to remain in this habitat (*i.e.* the home site). We examined the concordance across habitats in the stage-specific transition probabilities using a Kendall's concordance test. Finally, we determined whether patterns of seed rain were concordant with those of one year-old plant survival using a Spearman rank correlation.

Results

SEED DISPERSAL

No seed dispersal was observed into savanna seed traps in either year; therefore, we 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 [χ^2] statistic = 898.44, d.f. = 2, $P < 0.001$) and 2008 (GLM: habitat effects Wald [χ^2] statistic = 2073.05, d.f. = 2, $P < 0.001$). In both years, seeds were more likely to be dispersed in vegetation patches with *G. viburnoides* than in any other habitat (Fig. 1). Although sometimes these seeds were from other nearby fruiting *G. viburnoides* trees (Saavedra 2008), most seeds came from the adult tree in the vegetation patch. Additionally, seed dispersal was between 2- and 10-fold higher in vegetation patches without *G. viburnoides* than in forest islands (Fig. 1). The 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 proportion of seeds preyed upon at the end of the experiment (40 days) differed among habitats in 2006 (GLM: habitat effects Wald [χ^2] statistic = 103.36, $P < 0.001$) and 2008 (GLM: habitat effects Wald [χ^2] statistic = 8.28, $P = 0.04$), but not in 2007 (GLM: habitat effects Wald [χ^2] statistic = 3.01, $P = 0.39$). In 2006, predation was higher in vegetation patches with *G. viburnoides* and forest islands than in vegetation patches without *G. viburnoides* or savanna, whereas a different pattern is observed in 2008 where savanna sites and forest islands had higher predation levels than the other two habitats (Fig. 2).

In 2006, the distribution of seed mortality rates through time (i.e. seed survivorship-curves) differed significantly between vegetation patches with *G. viburnoides* and two of the other habitats (Wald test₂₀₀₆ = 31.4, d.f. = 3, $P < 0.0009$; Fig. 3). Overall, the risk of seed predation (i.e. the hazard) was *ca.* 64% lower ($1-\beta_{exp}$) in the savanna, and 55% lower than seeds in vegetation patches without *G. viburnoides*, than in vegetation patches with *G. viburnoides* (Table 1). The predation risk for seeds in forest islands was not significantly different from that in vegetation patches with *G. viburnoides* (Table 1). In contrast, in 2007 there was no significant difference between the seed survivorship curves between vegetation patches with *G. viburnoides* and the other three habitats (Wald test₂₀₀₇ = 1.79, d.f. = 3, $P = 0.618$; Table 1). The temporal pattern of seed predation also did not differ among habitats in 2008 (Wald test₂₀₀₈ = 2.6, d.f. = 3, $P = 0.458$; Table 1). Therefore, in 2008 there was a significant difference in final seed

survival probabilities, despite there being no difference in the temporal patterns of mortality among habitats.

SEEDLING ESTABLISHMENT

Emergence. Seedling emergence was extremely low in 2007, with a total of 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 [χ^2] statistic = 46.77, $P < 0.0001$). More seedlings emerged in vegetation patches with *G. viburnoides*, and significantly less overall emergence was recorded in savanna than any other habitat (Fig. 4). The temporal pattern (i.e. emergence curves) of seedling emergence was also affected by habitat (Wald test₂₀₀₇ = 25.8, d.f. = 3, $P < 0.0009$). In comparison to vegetation patches with *G. viburnoides*, cumulative seedling emergence was lower in forest islands and savanna habitats by 80% and 93% respectively, but did not differ with respect to the cumulative emergence in vegetation patches without *G. viburnoides* (Table 2).

In 2008, seedling emergence was over five-fold higher than 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 [χ^2] statistic = 41.86, $P < 0.0001$). In contrast to 2007, seedlings emerged more in savanna sites than in vegetation patches with or without *G. viburnoides*, where emergence was lowest (Fig. 4).

Additionally, the temporal pattern of seedling emergence also differed significantly between vegetation patches with *G. viburnoides* and the other habitats (Wald test₂₀₀₈ = 14.9, d.f. = 2, P = 0.0006). Seedling emergence curves were different between vegetation patches with and without *G. viburnoides*, but did not differ between savanna sites and vegetation patches with *G. viburnoides* (Table 2). Thus, in 2008 final savanna emergence probabilities differ from those in vegetation patches with *G. viburnoides*, even though there are no differences in the temporal patterns of seedling emergence between those two habitats.

Seedling survival. Between September 15 and 17, 2008, an uncontrolled fire burned through the entire study site killing many of the adult trees, and almost all of the seedlings and saplings that emerged in 2007 and 2008; hence, we present results on 18-month survival for the 2007 cohort, and 6-month survival for the 2008 cohort.

Of the 2007 cohort, approximately 50% of seedlings died within the first 6 months after emergence, 10% survived the first year, and only 6 % survived to 18 months. Because of the low number of emerged seedlings in the savanna ($n = 4$), and because they all emerged in a single savanna site, we excluded this habitat from the statistical analysis. Additionally, all seedlings (for both cohorts) were considered independent observations (i.e. analysis of survival data using Cox's proportional hazards models was not clustered by habitat replicate). For the 2007 cohort, neither the proportion of plants that survived to 18 months ($\chi^2=5.66$, d.f.=2, $P>0.05$), nor the temporal pattern of seedling mortality was affected by habitat (Wald test₂₀₀₇= 4, d.f. = 2, $P = 0.136$; Table 3). In 2008, comparatively more seedlings survived to six months than in 2007 (ca. 61%). For this cohort, seedling survival during the first six months differed

among habitats ($\chi^2=6.36$, d.f.=2, $P<0.05$); specifically, the proportion of surviving seedlings was lower in vegetation patches with *G. viburnoides* (0.47) than in vegetation patches without *G. viburnoides* (0.74), but did not differ between the latter and savanna sites (0.64), or between savanna and vegetation patches with *G. viburnoides*. The temporal pattern of seedling mortality did not differ between vegetation patches with *G. viburnoides* and the other two habitats (Wald test₂₀₀₈ = 4.56, d.f. = 2, $P = 0.102$; Table 3).

LANDSCAPE DYNAMICS OF RECRUITMENT

Habitat-specific first-year recruitment for the 2006-2007 season is summarized in Figure 5A. In general there was uncoupling between seed and seedling stages across all habitats, indicating that habitats that are suitable for one stage of recruitment are unsuitable for others; that is, life stage conflicts exist. For example, vegetation patches with *G. viburnoides* were the worst habitats for seed survival, but the best for seedling emergence (Fig. 5A). Moreover, there was a lack of concordance among habitats in the stage-specific transition probabilities (Kendall's $W = 0.12$, $P > 0.05$, $n = 5$, d.f. = 2; savanna sites excluded); therefore, there is no overall trend across habitats with respect to suitability for one or more stages. Finally, there was no correlation between seed rain and 18-month plant establishment ($r_s = 0.63$, $P = 0.37$, $n = 4$), revealing spatial discordance between the initial seed rain patterns and early establishment.

Recruitment for the 2007-2008 season was examined only for the first six months after emergence (see above). Like the previous year, early plant recruitment across all habitats reveals uncoupling events (Fig. 5B). Again, the worst habitat for seed survival becomes the best habitat for seedling emergence, although the actual habitat where this

switch occurred differed from the previous year (i.e. patches with *G. viburnoides* in 2007 and savanna sites in 2008) (Fig. 5B). This clearly demonstrates context dependence of the processes determining site suitability.

The cumulative probability of recruitment for the 2006-2007 season revealed that seeds dispersed into patches with *G. viburnoides* had the highest probability of establishing as 18-month plants, whereas those dispersed into savanna sites and vegetation patches without *G. viburnoides* had the lowest probability (Fig. 5A). Across habitats, the most critical process during recruitment was seedling emergence; the mean transition probability for all habitats indicates that more than 95% of the potential seeds in the cohort did not emerge. The overall probability of recruitment (18 months) for *G. viburnoides* in this landscape during this season was very low (OPR=0.000027). This result is mainly driven by the large fraction of area represented by savanna habitat (96%), all of which is unsuitable for the establishment of *G. viburnoides*, and the low emergence rates of seedlings.

For the 2007-2008 season, the cumulative probability of recruitment again shows that seeds dispersed into vegetation patches with *G. viburnoides* had the highest probability of surviving to six-month seedlings. There was no recruitment for this season in vegetation patches without *G. viburnoides* or in forest islands. Finally, the overall probability of recruitment (6 months) was 0.000019.

Discussion

SPATIAL DYNAMICS OF RECRUITMENT: IS THERE AMONG-HABITAT VARIABILITY IN EARLY PLANT RECRUITMENT PHASES?

In general, we found that seed dispersal, seed predation, seedling emergence and survival varied strongly among habitats across years.

Seed rain. Seeds of *G. viburnoides* were dispersed into all but the savanna habitat. This finding supports a general trend in open ecosystems, where seed rain depicts a non-random pattern, with increased abundance and diversity of seeds in woody habitats or under isolated trees and few, if any, seeds in open interspaces (Alcántara *et al.* 2000a; Jordano & Schupp 2000; García *et al.* 2005). Woody habitats attract seed dispersers by providing perches, shade and/or fruits and, as a result, seed arrival at these sites is higher than in open areas (Nepstad *et al.* 1996; Slocum 2000; Slocum & Horvitz 2000).

Ultimately, this translates into dissemination limitation (Schupp *et al.* 2002) in the savanna, as very few seeds are dispersed into this habitat (but see Arteaga *et al.* 2006).

Seed rain was highest in vegetation patches with *G. viburnoides*. This result is consistent with other studies that also report high densities of seeds under or close to conspecifics (Alcántara *et al.* 2000a; Wenny 2000; Travaset *et al.* 2003; Gómez-Aparicio 2008). The spatial variation in the seed rain pattern of *G. viburnoides* in this landscape was mainly determined by the post-feeding behavior of its main disperser, *C.*

cyanomelas. These tufted jays are pulp consumers that deposit the majority (98%) of the seeds from the fruits they consume under the fruiting tree (Loayza 2009). In some cases, however, *C. cyanomelas* will remove a fruit and usually fly < 100 m to a nearby

vegetation patch where it consumes the pulp and drops the seed (Loayza 2009). Seeds arriving in forest islands were most likely dispersed by toucans: mostly *Pteroglossus castanotis* and, to a lesser extent, *Ramphastos toco* (Loayza 2009). Seeds processed by toucans, as compared to tufted jays, are easily recognizable, because the first are deposited in clumps surrounded by fecal material, whereas the latter are completely clean, and deposited individually. In all but one case, seeds collected in forest island seed traps clearly had been defecated.

Although no seeds were collected in savanna seed traps, extensive seed searches in the savanna, as well as frugivore observations, revealed at least two independent events of dispersal into this habitat. Moreover, rare dispersal events in the savanna may occur at the study site, given that three of the 175 individuals recorded in the population occur completely isolated in this habitat (i.e. not in a vegetation patch). Although not conclusive, this suggests that on rare occasions seeds arrive and establish in open savanna.

Seed predation. After dispersal, seed predation is generally a pervasive, and often extensive, process for both tropical and temperate plants (Balcomb & Chapman 2003; Travaset *et al.* 2003; Russo & Augspurger 2004; Orrock *et al.* 2006). In this study, the risk of predation varied among habitats and between years. Among habitat differences in predation have been found in a number of studies (Alcántara *et al.* 2000b; Calviño-Cancela 2002; Walters *et al.* 2005). Habitats can differ in their intensity of seed predation because of differences in habitat-specific predator activity and/or abundance. In 2006, seed predation was highest in vegetation patches with *G. viburnoides* and lowest in savanna sites. This pattern was expected because 1) ants are more likely to be found in

woody habitats or under isolated trees than in open spaces (Dunn 2000) and 2) predation is predicted to be more intense under conspecifics where abundant resources attract more predators (Janzen 1970; Connell 1971).

In contrast, in 2007, seed predation did not differ among habitats. Although possible, we do not attribute this result to the lower number of endocarps used for this experiment in 2007 compared to 2006 ($n_{2007}=10$ vs. $n_{2006}=20$ per replicate). This is because in 2006, no differences were observed in the amount of seed predation between our study using 20 endocarps per replicate, and a simultaneous study of seed predation at the study site using 10 endocarps per replicate (Saavedra 2008). This suggests that the difference in the amount of resource offered did not lead to changes in predation levels. Compared to 2006, there was a decrease in predation in vegetation patches with *G. viburnoides* and forest islands, and an increase in seed predation levels in the savanna. While the mechanisms that caused this shift are uncertain, the consequences of two independent events in this season may provide a preliminary explanation for this pattern. First, in November 2006, there was a large fire across the study area that extended over 5 days, burning through vegetation patches as well as entire forest islands. Second, 2007 was an El Niño year, and some forest islands, as well as areas of the savanna (including the vegetation patches) that are not usually under water were completely submerged for several months (from December 2006 to March 2007). The combined effects of these events likely resulted in the lower fruit production we observed that year; burnt trees had to produce new foliage, and many of them did not flower or fruit (although, we do not have data for other plants, significantly lower fruit production was also recorded for *A. phalerata* in 2007; R. Rios *pers. comm.*). In turn, lower fruit production in forest islands

and vegetation patches ultimately results in lower seed availability in these habitats, which may have caused a shift in the foraging behavior of ants. Harvester ants, such as *Pheidole*, usually select seeds that are abundant and available throughout the foraging season (Whitford 1978). If seeds are not abundant in one habitat, ants will shift their foraging activity to different habitats (Wilby & Shachak 2000). Consequently, it is possible that because of a shortage of resources in forest islands and vegetation patches, ants may have shifted their foraging activity to savanna sites, where seeds of grasses and forbs were readily available.

In 2008, seed predation intensity again varied among habitats, and the mean proportion of depredated seeds was higher across all habitats than in 2007. This was an expected result, as more intense foraging activity (i.e. resulting in higher seed predation) following periods of low seed production has been observed for other harvester ants (Whitford 1978). Contrary to 2006, however seed predation was lowest in vegetation patches with *G. viburnoides* and highest in forest islands and savanna sites. Fruit production levels were similar to 2006, so it is unlikely that resource availability alone determined the foraging habitat of ants. Other factors, such as differences in soil surface temperature, saturation deficit and light intensity (Whitford 1978) may have regulated the foraging activity of ants.

Seedling emergence. The probability of seedling emergence also differed significantly among habitats, and as for seed predation, there was no consistent pattern among years. Habitat-dependent differences in seedling emergence have been shown in various studies (Fuchs *et al.* 2000; García 2001; Gómez-Aparicio *et al.* 2005; García *et al.* 2005; Gómez-Aparicio 2008). In certain habitats, seedlings from woody species are more likely to

emerge in habitats where pre-existing vegetation exists, and are less likely to do so in bare or open areas. For example, vegetation cover usually facilitates seedling emergence in arid or semi-arid environments (Flores & Jurado 2003; Padilla & Pugnaire 2006). In the study area, woody vegetation can facilitate emergence by reducing trampling by cattle, and also because both forest islands and vegetation patches are usually above the flood line during the rainy season. Higher emergence in savanna sites in 2008 was unexpected for this species but may have resulted from variation in soil moisture conditions across years. As mentioned above, 2007 was an El Niño year and 2008 was a La Niña year. Both El Niño and La Niña periods are characterized in the region by heavy rainfall, which results in the study area being flooded for several months. High water content in the poorly drained savanna soils may have triggered higher germination of *G. viburnoides* seeds. The relationship between seed germination and soil moisture conditions in this species, however, remains to be experimentally tested.

Seedling survival. For the 2007 cohort, habitat did not have an effect on the probability of seedling survival to 18 months (savanna sites excluded). Habitat would be expected to influence seedling survival in at least two scenarios. First, if density-dependent factors are operating (Janzen 1970; Connell 1971). In this case, seedling mortality would be expected to be higher in vegetation patches with *G. viburnoides* than in the other habitats because predators are more likely to concentrate around dense seedling aggregations. In our study system, the density of *Pheidole* and *Atta* ants was higher in vegetation patches both with and without *G. viburnoides* than in savanna sites (Saavedra 2008), but it is not known whether herbivory of *G. viburnoides* seedlings is the result of activity by these ant genera. Second, if environmental conditions important for seedling survival, such as

availability of habitat that does not flood or presence of cattle, differ among habitats. Both vegetation patches with and without *G. viburnoides*, as well as forest islands are formed upon low-relief features in the landscape hence, in contrast to many sites in the savanna, none of these three habitats flood during the rainy season. Additionally, the landscape at the study site is subject to low-intensity cattle grazing, therefore all habitats where the experiments were conducted are exposed to more or less similar intensities of grazing and trampling by cattle.

For the 2008 cohort, seedling survival was higher in vegetation patches without- than in vegetation patches with *G. viburnoides*. This, however, represents six-month seedling survival before the onset of the rainy season, and before the generally moderate fires that are part of the ecosystem dynamics, and that influence seedling survival. Additionally, we do not have data on ant abundance in these habitats for 2008. Consequently, further information is warranted to draw any biological inferences to this result.

IS THE PATTERN OF RECRUITMENT AMONG HABITATS CONSISTENT AMONG YEARS?

Many studies of plant regeneration dynamics have assessed inter-annual variation in early plant recruitment stages, and shown that recruitment rates are highly variable across years (e.g. Schupp 1990; Beckage *et al.* 2005; Wright *et al.* 2005; Hampe *et al.* 2008), and are therefore strongly context-dependent (Schupp 2007). Although not tested directly, here we show that the strength of post-dispersal processes varies not only with habitat but also among years. Our results provide further empirical evidence to the

growing body of literature that emphasizes caution when categorizing specific habitats as “safe sites” for recruitment (*e.g.* Fowler 1988; Schupp 2007).

In our study, we document that habitat suitability shifted from year to year, and that temporal variability in habitat suitability appears not to affect all habitats in the same way. For example, mean proportion of depredated seeds tended to decrease in vegetation patches with *G. viburnoides* from 2006 to 2007 (hence habitat suitability for this stage increased in 2007; $U' = 121$, $P = 0.057$), whereas the opposite occurred in savanna sites, where predation significantly increased from 2006 to 2007 (thus savanna suitability decreased in 2007; $U' = 115$, $P = 0.038$). Therefore, we show that in this landscape too, the outcome of the post-dispersal processes is also context-dependent. Ultimately, this result stresses the difficulty of making any generalizations about habitat suitability for recruitment (Schupp 2007).

IS THE PATTERN OF SEED DISPERSAL SPATIALLY CONCORDANT WITH THE PATTERN OF RECRUITMENT?

In this study, we asked whether landscape patterns of seed rain are concordant with those of sapling establishment. By connecting different stages in the seed dispersal loop (Wang & Smith 2002), we explore the early consequences of seed dispersal for a Neotropical tree.

For the 2006-2007 cohort, the seed dispersal pattern of *G. viburnoides* is discordant with the pattern of one-year old and 18-month plant establishment. The absence of spatial concordance between the initial template of seed rain and the habitat of recruitment may indicate microsite limitation (Gómez-Aparicio 2008). In other words, in

a highly heterogeneous landscape such as this forest-savanna mosaic, habitat available for early recruitment of *G. viburnoides* may be strongly limited. It is important to highlight, however, that these results are for one cohort only, and given the high inter-annual variability we observed in post-dispersal processes, the degree of concordance may change across years.

Spatial discordance is predicted to occur when seed rain is less heterogeneous than post-dispersal losses, and/or when life stage conflicts exist (García *et al.* 2005). Here, we observed uncoupled recruitment and life-stage conflicts throughout the recruitment phase and across habitats. For example, on both years, the worst habitat for seed survival became one of the best for seedling survival. This pattern indicates seed-seedling conflicts in these habitats (Schupp 1995, Schupp 2007). Uncoupled recruitment has been documented in many studies (Fuchs *et al.* 2000; Rey & Alcántara 2000; Travaset *et al.* 2003; García 2001; Jordano & Herrera 1995), and it has been suggested to be the generalized pattern for bird-dispersed woody plants in Mediterranean areas (García *et al.* 2005). To our knowledge, this is the first study to connect patterns of dispersal and seedling recruitment in Neotropical forest-savanna mosaic, and more research needs to be carried out in these ecosystems to determine general patterns.

In summary, our results suggest that the consequences of seed dispersal for plant demography are strongly context-dependent. Seed dispersal and early post-dispersal seed fate can vary across habitats, across years, and that there can also be an interaction where the effect of habitat can differ across years. Although general patterns can be established from short-term studies, a full understanding of the effect of habitat heterogeneity on plant recruitment dynamics will require an integrative approach that connects all the

stages in plant recruitment across several years. Inter-annual variability in plant recruitment rates seems to be the norm rather than the exception in both temperate and tropical systems, and should therefore explicitly considered in studies of plant regeneration dynamics.

Acknowledgements

This chapter was prepared in collaboration with B. A. Loiselle. We would like to thank the people who assisted with the field data collection, particularly F. Saavedra, N. Burgos, R. Balderrama, A. Terán, O. Burgos, A. Yarari, and M. Houard. Fieldwork was possible through logistic support of the Instituto de Ecología in La Paz, Bolivia and the Estación Biológica Beni. Comments from Rodrigo Rios, Tiffany Knight, John Blake, and Eugene Schupp helped improve an earlier version of this paper. This research was supported by grants from the National Science Foundation (DEB-0709753), the Rufford Maurice Laing Foundation, the Scott Neotropical Fund from the Cleveland Metropolitan Zoo, the Neotropical Grassland Conservancy, the Webster Groves Nature Study Society, Sigma Xi, and the Whitney R. Harris World Ecology Center at the University of Missouri-St. Louis.

References

- Alcántara, J.M., Rey, P.J., Valera, F. & Sánchez-LaFuente, A.M. (2000a) Factors shaping the seedfall patterns of a bird-dispersed plant. *Ecology*, **81**, 1937–1950.
- Alcántara, J.M., Rey, P.J., Sánchez-LaFuente, A.M. & Valera, F. (2000b) Early effects of rodent post-dispersal seed predation on the outcome of the plant-seed disperser interaction. *Oikos*, **88**, 362–370.
- Arteaga, L.L., Aguirre, L.F. & Moya, M.I. (2006) Seed rain produced by bats and birds in forest islands in a Neotropical savanna. *Biotropica*, **38**, 718–724.
- Balcomb, S.R. & Chapman, C.H. (2003) Bridging the gap: Influence of seed deposition in seedling recruitment in a primate-tree interaction. *Ecological Monographs*, **73**, 625–642.
- Beck, S.G. & Moraes, M. (1997) Llanos de Mojos Region, Bolivia. *Centers of Plant Diversity: A Guide and Strategy for their Conservation, Volume 3, The Americas* (eds S.D. Davis, V.H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos & A.C. Hamilton), WWF, IUCN, Oxford, U.K.
- Beckage, B., Lavine, M. & Clark, J.S. (2005) Survival of tree seedlings across space and time: estimates from long-term count data. *Journal of Ecology*, **93**, 1177–1184.
- Calviño-Cancela, M. (2002) Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): the importance of unspecialized dispersers for regeneration. *Journal of Ecology*, **90**, 775–784.
- Connell, J.H. (1971) On the role of natural enemies in preventing competitive exclusion in some marine animals and in rainforest trees. *Dynamics of populations* (eds P.J. den Boer & G.B. Gradwell), pp 298–231 PUDOC, Wageningen, The Netherlands.

- Crawley, M.J. (1993) *GLIM for Ecologists*. Balckwell Oxford.
- Dunn, R.R. (2000) Isolated trees as foci of diversity in active and fallow fields. *Biological Conservation*, **95**, 317–321.
- Fox, G.A. (2001) Failure-time analysis. *Data analysis of ecological experiments* (eds S.M. Scheiner & J. Gurevitch), pp. 235–266, Oxford University Press, New York.
- Flores, J. & Jurado, E. (2003) Are nurse-protégé interactions more common among plants from arid environments? *Journal of Vegetation Science*, **14**, 911–916.
- Fowler, N.L. (1988) What is a safe site?: Neighbor, litter, germination date, and patch effects. *Ecology*, **69**, 947–961.
- Fuchs, M.A., Krannitz, P.G. & Harestad, A.S. (2000) Factors affecting emergence and first-year survival of seedlings of Garry oaks (*Quercus garryana*) in British Columbia, Canada. *Forest Ecology and Management*, **137**, 209–219.
- García, D. (2001) Effects of seed dispersal on *Juniperus communis* recruitment on a Mediterranean mountain. *Journal of Vegetation Science*, **12**, 839–2848.
- García, D., Obeso, J.R. & Matínez, I. (2005) Spatial concordance between seed rain and seedling establishment in bird-dispersed trees: does scale matter? *Journal of Ecology*, **93**, 693–704.
- Gómez, J.M., Puerta-Piñero, C. & Schupp, E.W. (2008) Effectiveness of rodents as local seed dispersers of Holm oaks. *Oecologia*, **155**, 529–537.
- Gómez-Aparicio, L. (2008) Spatial patterns of recruitment in Mediterranean plant species: linking the fate of seeds, seedlings and saplings in heterogeneous landscapes at different scales. *Journal of Ecology*, **96**, 1128–1140.

- Gómez-Aparicio, L., Gómez, J.M. & Zamora, R. (2005) Microhabitats rank in suitability for seedling establishment depending on habitat type and climate. *Journal of Ecology*, **93**, 1194–1202.
- Hampe, A. (2004) Extensive hydrochory uncouples spatiotemporal patterns of seedfall and seedling recruitment in a ‘bird-dispersed’ riparian tree. *Journal of Ecology*, **92**, 797–807.
- Hampe, A., García-Castaño, J.L., Schupp, E.W. & Jordano, P. (2008) Spatio-temporal dynamics and local hotspots of initial recruitment in vertebrate-dispersed trees. *Journal of Ecology*, **96**, 668–678.
- Hanagarth, W. 1993. Acerca de la geoecología de las sabanas del Beni en el Noreste de Bolivia. Instituto de Ecología, La Paz, Bolivia. 186 p.
- Harper, J.L. (1977) Population biology of plants. Academic Press, London, England.
- Herrera, C.M. (2002) Topsoil properties and seedling recruitment: stage-dependence and spatial decoupling of influential parameters. *Oikos*, **97**, 260–270.
- Janzen, D.H. (1970) Herbivores and the Number of Tree Species in Tropical Forests. *The American Naturalist*, **104/940**, 501–527.
- Jordano, R. & Herrera, C.M. (1995) Shuffling the offspring; Uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. *EcoScience*, **2**, 1–8.
- Jordano, P., & Schupp, E.W. (2000) Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs*, **70**: 591–615.

- Kennedy, P.G. (2005) Post-dispersal seed predation varies by habitat not acorn size for *Quercus chrysolepis* (Fagaceae) and *Lithocarpus densiflora* (Fagaceae) in central coastal California. *Madroño*, **52**, 30–34.
- Kollman, J. (2000) Dispersal of fleshy-fruited species: a matter of spatial scale? *Perspectives in Plant Ecology, Evolution and Systematics*, **3**, 29–5.
- Lagakos S.W. (1992) Statistical analysis of survival data. *Medical uses of statistics* (eds C. Bailar III & F. Mosteller), pp. 282–291, NEJM Books, Boston, Massachusetts.
- Loayza, A.P. (2009) Closing the seed dispersal loop for *Guettarda viburnoides* (Rub.): Connecting patterns of avian seed dispersal with population growth in a Neotropical savanna. Ph.D. Thesis, University of Missouri-St. Louis.
- Nathan, R. & Müller-Landau, H.C. (2000) Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution*, **15**, 278–285.
- Nepstad, D.C., Uhl, C., Pereira, C.A. & Cardoso da Silva, J.M. (1996) A comparative study of tree establishment in abandoned pasture and mature forest of eastern Amazonia. *Oikos*, **76**, 25–39.
- Nickel, A.M., Danielson, B.J. & Moloney, K.A. (2003) Wooded habitat edges as refugia from microtine herbivory in tallgrass prairies. *Oikos*, **100**, 525–533.
- Orrock, J.L., Levey, D.J., Danielson, B.J. & Damschen, E.I. (2006) Seed predation, not seed dispersal, explains the landscape level abundance of an early-successional plant. *Journal of Ecology*, **94**, 838–845.
- Padilla, F.M. & Pugnaire, F.I. (2006) The role of nurse plants in the restoration of degraded environments. *Frontiers in Ecology and the Environment*, **4**, 196–202.

- Páez, S.A. & Marco, D.E. (2000) Seedling habitat structure in dry Chaco forest (Argentina). *Journal of Arid Environments*, **46**, 57–68.
- Rey, P.J. & Alcántara, J. (2000) Recruitment dynamics of a fleshy-fruited plant (*Olea europaea*): connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*, **88**, 622–633.
- Rios-Aramayo, R., & Loayza-Freire, A. 2000. Depredación de semillas de *Attalea phalerata* por brúquidos en islas de bosque de la Estación Biológica Beni. *Ecología en Bolivia*, **33**, 78–89.
- Russo, S.E. & Augspurger, C.K. (2004) Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Viola calophylla*. *Ecology Letters*, **7**, 1058–1067.
- Russo, S.E., Brown, P., Tan, S. & Davies, S.J. (2008) Interspecific demographic trade-offs and soil-related habitat associations of tree species along resource gradients. *Journal of Ecology*, **96**, 192–203.
- Saavedra, F. (2008) Patrones de reclutamiento – Dispersión, sobrevivencia y establecimiento – de *Guettarda viburnoides* (Rubiaceae) en las sabanas de la Reserva de la Biósfera Estacion Biológica del Beni (RE-EBB). Licenciatura Thesis, Universidad Mayor de San Andres, La Paz, Bolivia.
- Schupp, E.W. (1995) Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *American Journal of Botany*, **82**, 399–409.
- Schupp E.W. (2007) The suitability of a site for seed dispersal is context-dependent. *Seed dispersal: theory and its application in a changing world* (eds A.J. Dennis, E.W.

- Schupp, R.J. Green & D.A. Westcott), pp. 445–462, CABI International, Wallingford, Oxfordshire.
- Schupp E.W. & Fuentes, M. (1995) Spatial patterns of seed dispersal and the unification of plant ecology. *EcoScience*, **2**, 267–275.
- Schupp, E.W., Milleron, T. & S.E. Russo. (2002) Dissemination limitation and the origin and maintenance of species-rich tropical forests. *Seed dispersal and frugivory: Ecology, evolution, and conservation* (eds D.J. Levey, W.R. Silva & M. Galetti), pp. 394–406. CABI Publishing, Wallingford, Oxfordshire.
- Slocum, M.G. (2000). Logs and fern patches as recruitment sites in a tropical pasture. *Restoration Ecology* **8**, 408–413.
- Slocum, M.G. & Horvitz, C.C. (2000). Seed arrival under different genera of trees in a Neotropical pasture. *Plant Ecology*, **149**, 51–62.
- Taylor, C., Delprete, P.G., Vincentini, A., Cortés, R., Zappi, D., Persson, C., Bestetti Costa, C. & Araujo de Anunciação, E. (2004) Rubiaceae. *Flora of the Venezuelan Guayana: Volume 8 – Poaceae-Rubiaceae* (eds A. Steyermark, P.E. Berry, K. Yatskievych & B.K. Holst), pp. 497–847, Missouri Botanical Garden Press, St. Louis.
- Travaset, A., J. Gulias, N. Riera and, M. Mus. (2003) Transition probabilities from pollination to establishment in a rare dioecious species (*Rhamnus ludovicisalvatoris*) in two habitats. *Journal of Ecology*, **91**, 427–437.
- Walters, M., Milton, S.J., Somers, M.J. & Midgley, J.J. (2005) Post-dispersal seed fate in a African savanna. *South African Journal of Wildlife Research*, **35**, 191–199.

- Wang, B.C. & Smith, V. (2002) Closing the seed dispersal loop. *Trends in Ecology and Evolution*, **17**, 379–385.
- Wenny, D. G. (2000) Seed dispersal, seed predation, and seedling recruitment of a neotropical montane tree. *Ecological Monographs*, **70**, 331–351.
- Whitford, W.G. (1978) Foraging by seed harvesting ants. *Production ecology of ants and termites* (ed M.V. Brain), pp. 107–110, Cambridge University Press, Cambridge, New York.
- Wilby, A. & Shachak, M. (2000) Harvester ant response to spatial and temporal heterogeneity in seed availability: pattern in the process of granivory. *Oecologia*, **125**, 495–503.
- Wright, S.J., Muller-Landau, H.C., Calderón, O. & Hernández, A. (2005) Annual and spatial variation in seedfall and seedling recruitment in a neotropical forest. *Ecology*, **86**, 848–860.
- Zar, J.H. (1999) *Biostatistical Analysis*. 4th Edition. Prentice-Hall, Inc., Upper Saddle River, NJ. 931 pp.

Table 1. Cox proportional hazards regressions of seed survival clustered by habitat replicate. Note that because the dependent variable in the model is a hazard rate, negative coefficients (β) indicate that a factor has a positive effect upon survival and vice-versa when compared against the risk of a seed being predated in a vegetation patch with *G. viburnoides*.

Habitat	β	β_{exp}	$SE_{(\beta)}$	d.f.	P
2006					
Forest Islands	-0.298	0.742	0.177	3	0.56
Savanna	-1.016	0.362	0.217	3	0.0012
Vegetation patches without <i>G. viburnoides</i>	-0.809	0.445	0.204	3	0.0015
2007					
Forest Islands	-0.253	0.777	0.262	3	0.31
Savanna	0.009	1.101	0.241	3	0.70
Vegetation patches without <i>G. viburnoides</i>	-0.109	0.897	0.252	3	0.55
2008					
Forest Islands	0.279	1.32	0.130	3	0.18
Savanna	0.258	1.29	0.130	3	0.17
Vegetation patches without <i>G. viburnoides</i>	0.255	1.29	0.132	3	0.24

Table 2. Cox proportional hazards regressions of seedling emergence (2007 and 2008 cohorts) clustered by habitat replicate. Note that because the dependent variable in the model is a hazard rate, negative coefficients (β) indicate that a factor has a positive effect upon survival and vice-versa when compared against the risk of a seed being predated in a vegetation patch with *G. viburnoides*.

Habitat	β	β_{exp}	$\text{SE}_{(\beta)}$	d.f.	P
2007					
Forest Islands	-1.61	0.198	0.332	3	0.014
Savanna	-2.63	0.072	0.519	3	0.017
Vegetation patches without <i>G. viburnoides</i>	-1.10	0.333	0.273	3	0.200
2008					
Savanna	0.690	1.994	0.171	2	0.110
Vegetation patches without <i>G. viburnoides</i>	-0.748	0.473	0.236	2	0.005

Table 3. Cox proportional hazards regressions of seedling survival for the 2007 and 2008 cohorts. Note that because the dependent variable in the model is a hazard rate, negative coefficients (β) indicate that a factor has a positive effect upon survival and vice-versa when compared against the risk of a seed being predated in a vegetation patch with *G. viburnoides*.

Habitat	β	β_{exp}	$\text{SE}_{(\beta)}$	d.f.	P
2007 cohort (18 month survival)					
Forest Islands	-0.767	0.464	0.390	2	0.066
Vegetation patches without <i>G. viburnoides</i>	-0.052	1.054	0.281	2	0.810
2008 cohort (6 month seedling survival)					
Savanna	0.655	1.53	0.394	2	0.100
Vegetation patches without <i>G. viburnoides</i>	0.488	2.05	0.231	2	0.060

FIGURE LEGENDS

Figure 1. Number of seeds deposited per m² 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 surviving seeds in four different habitats over 40 days: Vegetation patches with *G. viburnoides* [solid circles], vegetation patches without *G. viburnoides* [solid triangles], forest islands [open circles], and savanna [open triangles]) for each of 6 censuses in 2006 (Means + SE, 15 sampling stations per habitat).

Figure 4. 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).

Figure 5. Seed fate diagram of *G. viburnoides*' recruitment in different habitats: (1) Vegetation patches with *G. viburnoides* (GV), (2) vegetation patches without *G. viburnoides* (No GV), (3) forest islands (ISL), and (4) savanna (SAV). Each column reflects the recruitment in one of the four selected habitats. The values represent transition probabilities estimated from the: A. 2006 experiments, and B. 2007 experiments. The width of the border of the box represents the relative suitability of each habitat for overall recruitment within a stage. The boxes and values beneath the line represent the cumulative probability of recruitment in each habitat. D, dispersal; PostD, probability of escaping post-dispersal predation; E, seedling emergence; SdlS, seedling survival; SapS, sapling survival. Diagram based on Fig. 2. In Rey and Alcántara 2000.

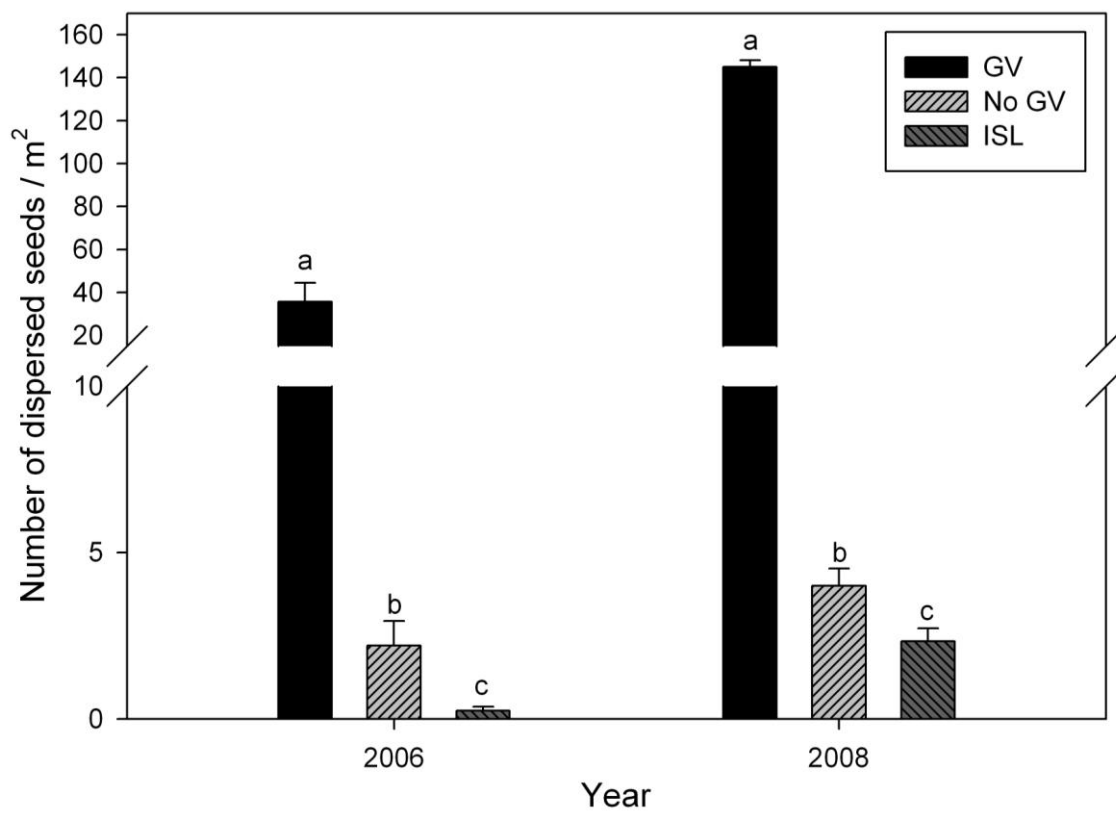


Figure 1

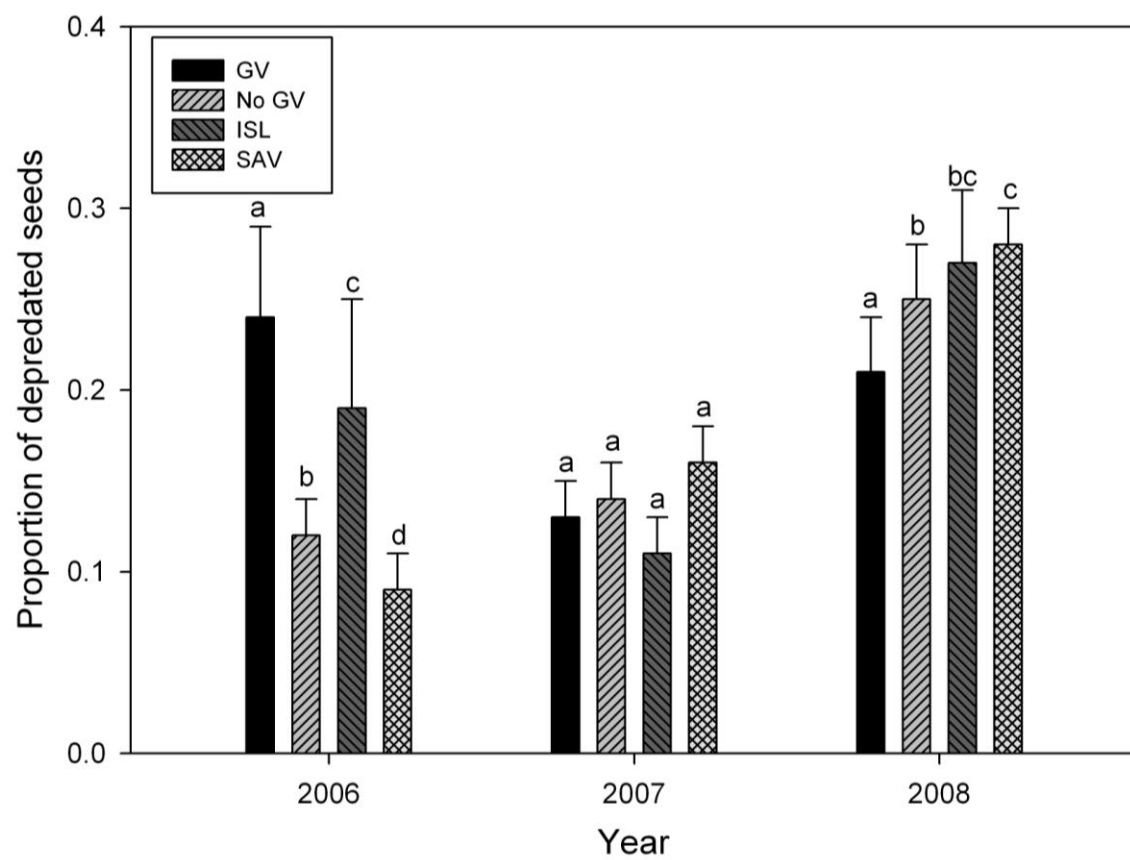


Figure 2

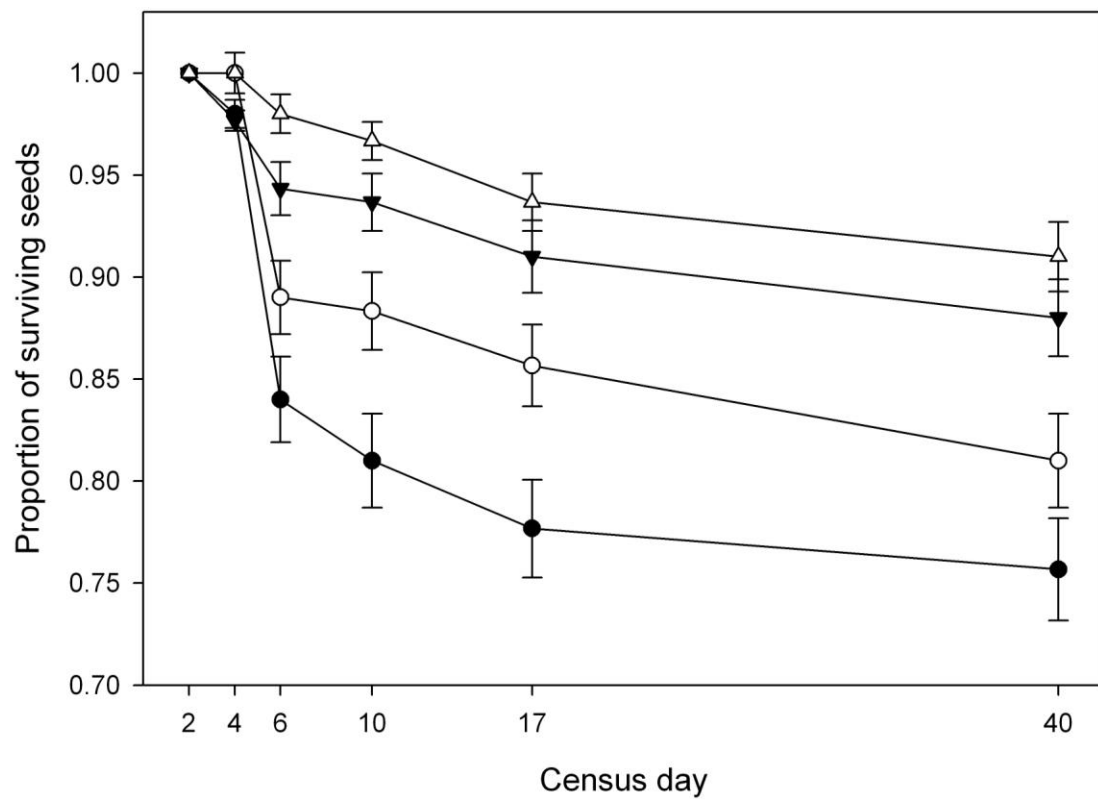


Figure 3

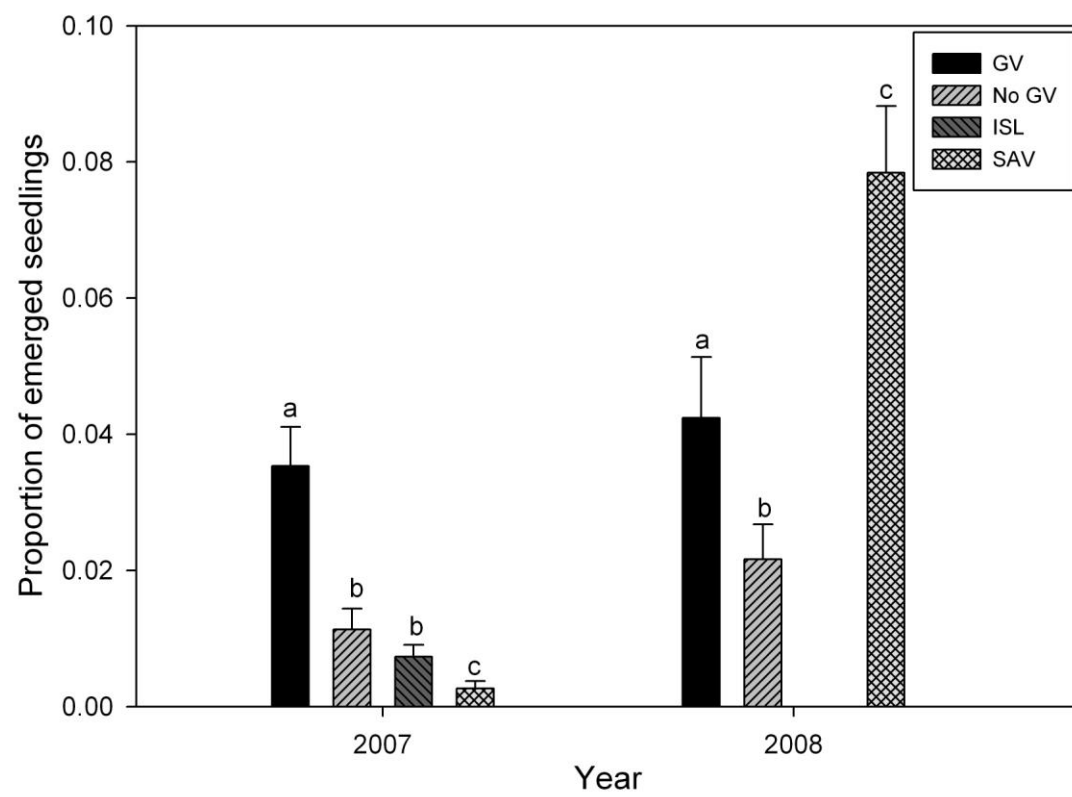


Figure 4

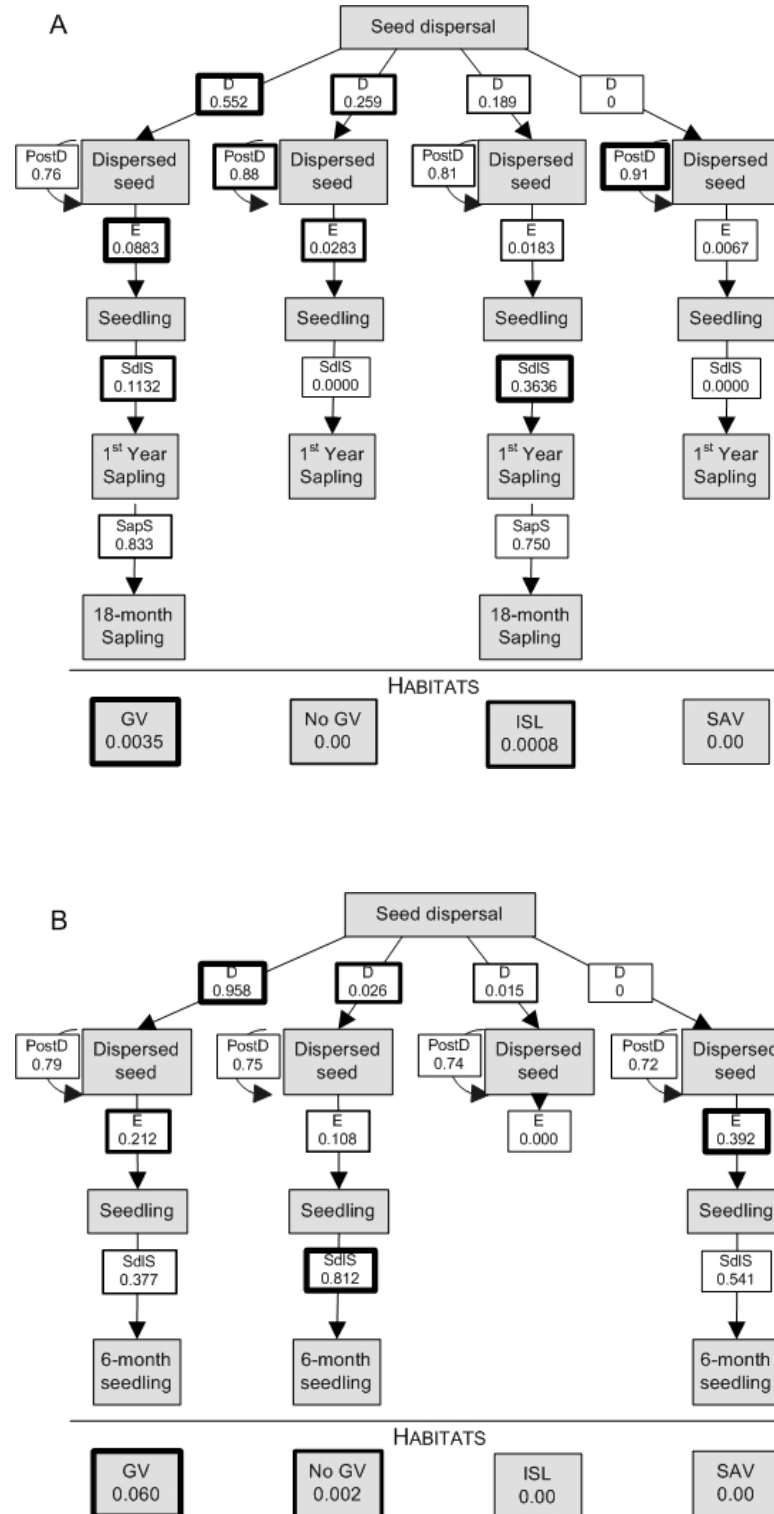


Figure 5

CHAPTER 3 — Seed dispersal by pulp consumers but not legitimate seed dispersers increases population growth of *Guettarda viburnoides* in a neotropical savanna.

Abstract. We examined the effect of seed dispersal by tufted jays (*Cyanocorax cyanomelas*; pulp consumers) and the Chestnut-eared Araçari (*Pteroglossus castanotis*; legitimate seed dispersers) on population growth of *Guettarda viburnoides* (Rub.) in northeastern Bolivian savannas. Because each bird species differs with respect to feeding and post-feeding behavior, we hypothesized that seed dispersal by each species will contribute differently to the rate of increase of *G. viburnoides*, but that seed dispersal by either species will increase population growth when compared to a scenario with no seed dispersal. To examine the effects of individual dispersers on the future population size of *G. viburnoides*, we projected population growth rate using demographic models for *G. viburnoides* that explicitly incorporate data on quantitative and qualitative aspects of seed dispersal by each frugivore species. We found that seed dispersal by *C. cyanomelas* leads to positive population growth of *G. viburnoides*, whereas seed dispersal by *P. castanotis* has a detrimental effect on the population growth of this species. To our knowledge, this is the first study to report negative effects of a legitimate seed disperser on the population dynamics of the plant it consumes. Our results stress the importance of incorporating frugivore effects into population projection matrices, to allow a comprehensive analysis of the effectiveness of different dispersers for plant population dynamics.

Key words: Bolivia, birds, *C. cyanomelas*, disperser effectiveness, frugivory, matrix models, *P. castanotis*.

INTRODUCTION

Seed dispersal has long been recognized to have a critical role in the demography of plant populations (Harper 1977). However, in spite of the large amounts of information on seed dispersal in the literature, there are still significant gaps in our understanding of how frugivore activity translates into demographic and evolutionary consequences for plants (Schupp and Fuentes 1995, Levey et al. 2002). The extent to which seed dispersal influences plant population dynamics has been difficult to quantify because, until recently, research failed to establish robust links between the seed dispersal stage and patterns of recruitment (Godínez-Alvarez et al. 2002, Howe and Miriti 2004).

Frugivores can influence the demography of plants by determining the habitats and conditions in which seeds are deposited (Wenny 2000, Godínez-Alvarez and Jordano 2007). Thus, not all dispersers are expected to provide equal benefits to plants, and differences in behavior can lead to differences in disperser effectiveness (e.g., Loiselle and Blake 1999, Wenny 1998, 2000, Calviño-Cancela 2002), which is a measure of the contribution of a particular disperser to the recruitment of a plant. The effectiveness of a dispersal agent will be determined by two components: 1) the quantity of seeds removed, and 2) the quality (i.e., probability that a seed will survive and produce a new recruit) of dispersal provided to each seed (Schupp 1993). When both components are thoroughly examined, it becomes possible to analyze the individual effect of frugivores on plant recruitment.

Because seed dispersal by animals is the result of a mutualistic relationship between the frugivores and the fruiting plants they consume, it is expected that seed dispersal will have a positive effect on the populations of each participating species

(Godínez-Alvarez and Jordano 2007). Plants can benefit from having several species of seed dispersers, regardless of differences in disperser effectiveness, for several reasons. Multiple seed dispersers can diversify the habitats where seeds arrive (Jordano and Schupp 2000, Wenny 2000), reduce seed aggregations under parental crowns, and increase the total number of seeds removed, as well as the distances seeds are dispersed (Bleher and Böhning-Gaese 2001, Cordeiro and Howe 2003, Loiselle et al. 2007, Holbrook and Loiselle in press). From a plant perspective, when multiple frugivores are present, some ecological redundancy may occur, where all or some of the frugivores that consume the fruits provide more or less similar seed dispersal services to the species (Loiselle et al. 2007) and, thus, presumably have equivalent effects on its population dynamics. Such redundancy may buffer plants from years of low abundance of any one seed disperser or loss of a seed disperser from the system (Loiselle & Blake 2001). Therefore, the number and diversity of frugivores can be a major determinant of dispersal success and, ultimately, of the fitness of animal-dispersed species.

Recent studies have examined the link between seed dispersal and patterns of recruitment (Nathan and Müller-Landau 2000, Wang and Smith 2002, Tews et al. 2004), which is the first step towards understanding how frugivore activity translates into demographic consequences for plants. To date, however, only one study has quantified the effects of seed dispersal on plant population dynamics. One way to close the “seed dispersal loop” (Wang and Smith 2002) and examine the consequences of seed dispersal is to connect landscape patterns of seed deposition and post-dispersal seed fate, with population demography through stage-specific demographic modeling that incorporates individual disperser effects (Godínez-Alvarez et al. 2002, Wang and Smith 2002, Howe

and Miriti 2004, Godínez-Alvarez and Jordano 2007). Frugivore effects can be incorporated into population projection matrices by considering data on quantitative and qualitative aspects of seed dispersal by each species. Thus, it is necessary to know 1) the probability of seed removal by each disperser, 2) the probability of germination with respect to seed treatment, 3) the probability that seeds move to each habitat type with respect to each disperser, and 4) the probability of making the transition from seed to seedling with respect to their dispersal agent and their habitat. With these data at hand we can begin to evaluate the effects of frugivores on plant recruitment.

In plants whose dispersers generate largely different seed deposition patterns in the landscape, the question is open as to how the demography of the plant is influenced by different disperser species or functional groups. By projecting population growth under different scenarios (e.g., with and without a particular frugivore) we can thus determine the relative importance of given dispersers to the maintenance of plant populations (Godínez-Alvarez et al. 2002, Loiselle and Blake 2002). Further, we can examine whether the loss of one disperser species would be compensated by the presence of another, as would be expected if dispersers are ecologically redundant.

In this study, we examine the demographic consequences of seed dispersal by the two quantitatively important dispersers of *Guettarda viburnoides* (Rubiaceae) in northeastern Bolivian savannas. Our primary goal is to determine the effect 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, we project population growth rate using demographic models for *G. viburnoides* that explicitly incorporate dispersal effectiveness of each frugivore species. We predicted that (1) differences in

dispersal effectiveness by each frugivore will lead to differences in the rate of increase of *G. viburnoides* and the distribution of individuals in different habitats, and (2) regardless of these differences, seed dispersal by each species will increase population growth, as compared to a scenario where no seed dispersal occurs.

METHODS

Study system

The demographic and seed dispersal data for *G. viburnoides* was collected between 2005 and 2008 at Beni Biological Station-Biosphere Reserve (BBSBR) in Beni, Bolivia (14°30'-14°50' S; 66°40'- 65°50' W; 190-220m). The reserve is located within the Moxos plains, a region of seasonally inundated savannas, located in the southwestern corner of the Amazon Basin. The area has a mean annual temperature of 26°C and receives approximately 1900 mm of rain, with a pronounced wet and dry season (Miranda 2000). Almost 60% of the Reserve (80,000 ha) is represented by a large tract of continuous forest, while the rest consists of savanna (Ribera et al. 1990), which is partially covered by floodwaters from four to up to 10 months per year. Within the savanna, the landscape is very heterogeneous with naturally occurring forest islands, small vegetation patches, as well as open and wooded grasslands (Hanagarth 1993, Beck and Moraes 1997, see Plate 1). 'Forest islands' are isolated units of forest (0.1-20 ha in the study site) upon low-relief features (e.g., natural levee remnants; Langstroth 1996). These islands have a canopy height of up to 25m (see Plate 1); common plant species present in the islands include *Attalea phalerata*, *Virola sebifera*, *Sterculia apetala*, *Vitex cymosa*, *Copernicia alba* and *Guazuma ulmifolia*, as well as species from the genera

Ceiba, *Ficus*, *Guarea*, *Rheedia*, *Celtis*, *Salacia*, and *Trichilia* (Comiskey et al. 2000).

‘Vegetation patches’ are sites where woody species have established (see Plate 1). These are small (2-175 m²) stands of shrubs and trees with a canopy height of up to 8 m; like forest islands, vegetation patches generally form on slightly (i.e., 1-2m) elevated terrain, such as termite and ant mounds. The plant species found in vegetation patches are commonly from animal-dispersed genera such as *Guettarda*, *Virola*, *Piper*, *Psidium*, *Clidemia*, *Miconia*, *Solanum*, *Cecropia*, *Pourouma*, and a couple of species of palms (*pers. obs.*). Both forest islands and vegetation patches are generally above the flood line, remaining dry throughout the year except during extreme weather events such as during El Niño or La Niña years.

Guettarda viburnoides Cham. & Schlecht. (Rubiaceae) are small trees, distributed from Brazil to Paraguay, generally occurring in semi-deciduous forests and grasslands (Taylor et al. 2004). At BBSBR, *G. viburnoides* grows in the vegetation patches within the savanna, and typically a single adult tree is found per vegetation patch. A small proportion of the *G. viburnoides* population at the study site also occurs in forest islands (*pers. obs.*). Trees bear tubular, cream colored flowers (10-25 mm) from October to January. Fruits are subglobose drupes (8-25 mm) that turn yellow when ripe from late March until early July (*pers. obs.*). Each fruit contains a single woody endocarp (0.7-15 mm), which contains on average 5 seeds (range 3-7). For the purposes of this study, we explicitly consider three habitats that correspond to differences in demographic vital rates for *G. viburnoides* (see below): forest islands, vegetation patches with an adult *G. viburnoides* tree, and vegetation patches without an adult *G. viburnoides* tree (vegetation patches with- and without *G. viburnoides* hereon).

Bird dispersal of Guettarda viburnoides

At our study site, fruits are consumed by ten species of birds, but >80% of the seed dispersal is due only to two species that we consider the quantitatively important dispersers (QID) of *G. viburnoides* (Loayza 2009): *Cyanocorax cyanomelas* (Veilliot) (tufted jay) and *Pteroglossus castanotis* (Gould) (chestnut-eared araçari). Hence, for the purposes of our study and model, we consider that fruits of *G. viburnoides* in our study area are consumed and dispersed solely by these two species. *C. cyanomelas* are pulp consumers; once they remove the fruits' skin and consume the pulp, they drop the intact endocarp. Conversely, *P. castanotis* swallow and pass the whole endocarp. Consequently, the endocarp constitutes the unit of dispersal.

C. cyanomelas consumes 56% of fruits produced by a *G. viburnoides* tree (based on 402 hours of observation from 2006-2008; Loayza 2009). *C. cyanomelas* feeding within vegetation patches with *G. viburnoides* will drop 97.9% of the endocarps below or near the parent tree (i.e., no dispersal), and will disperse 1.00% and 1.11% of the endocarps to other vegetation patches, either with or without *G. viburnoides*, respectively (the minimum distance between two vegetation patches where the observations were conducted ranged from 50-100m). Therefore, in total 98.9% of the endocarps processed by *C. cyanomelas* remain in vegetation patches with *G. viburnoides*. No observations of *C. cyanomelas* feeding within forest islands were carried out; we assume, however, that *C. cyanomelas* feeding in this habitat drop 100% of the endocarps without leaving the forest island (i.e., no dispersal). Based on the behavior of this species, we consider an individual is more likely to perch and consume the fruit in a large, adjacent or nearby tree

within the forest island, than to remove the fruit from a *G. viburnoides* tree in a forest island, and fly between 100 to 200 m over open savanna to feed in a vegetation patch.

P. castanotis consumes 21% of the fruits produced by a *G. viburnoides* tree. *P. castanotis* feeding in vegetation patches with *G. viburnoides* disperse 100% of the endocarps to forest islands (based on 402 hours of observation of the feeding behavior of *P. castanotis* in vegetation patches; *P. castanotis* neither regurgitated nor defecated endocarps in this feeding habitat, Loayza 2009). Again, we have no observations of *P. castanotis* feeding within forest islands, but we assume that this species defecates 100% of the endocarps in this habitat (i.e., no dispersal or dispersal to another forest island). Data from seed traps placed in different habitats at the study site in 2006 and 2008 reveal that in forest islands, the majority of the endocarps collected had been defecated. In contrast, the endocarps collected in seed traps in vegetation patches had only the pulp removed.

Our greenhouse experiments indicate that endocarps processed by *C. cyanomelas* have higher emergence than those processed by *P. castanotis* and those not processed by any birds (i.e., endocarps in intact fruits). In contrast, endocarps processed by *P. castanotis* have lower emergence than those not processed by any birds (Loayza 2009).

At the end of the fruiting season approximately 24% of the fruits in each tree are not removed by either disperser (non-dispersed fruits hereon); these, dry up and remain attached to the branch and eventually fall off (Loayza 2009).

Stage- and Habitat-specific Demography

To study population dynamics, fecundity, growth and survival were estimated from marking and following the fate of selected plants in each of the three habitats described above. Specifically, in 2005 we selected and permanently tagged 278 individuals in the study area; in 2006, we added an additional 94 new plants, and in 2007 added another 108 individuals. Therefore, a total of 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. Seedlings are small (less than 15 cm in height), have narrow, pilose leaves, and lack a woody stem. Saplings are generally larger (10-100 cm in height), have broader, thicker leaves and a woody stem. Small trees are non-reproductive individuals that can be up to 2m in height. When small, they are distinguished from saplings because the base of the trunk is engorged and presents distinct rings; additionally, unlike saplings, small trees present ramification. Adult plants are generally over 2m in height and have a probability of producing fruit in a given year. All stage classes can enter the sprout stage class if these individuals lose all of their foliage and re-sprout the following year. Plants were censused in July 2006, 2007, and 2008, and surviving individuals were reclassified into each stage class. For each habitat, the average stage transition probabilities from all three years were used for our individual based model (see below, results presented in Fig. 1).

To estimate fruit production of the adult plants in the population, we determined the proportion of adult trees that reproduce in each season by monitoring reproduction on our tagged adult trees, and then counted the number of fruits on a subset of reproducing adults. We selected 16 reproductive trees in 2006, and 29 in both 2007 and 2008, and

calculated the total number of endocarps produced per tree at the beginning of the fruiting season before the fruits ripened and were removed (results presented in Table 1).

From 2006 to 2008, we quantified the proportion of endocarps that escape predation by ants, and the proportion of endocarps that germinate (i.e., emergence of an above-ground seedling) and produce an established seedling in all three habitats (results presented in Table 1). We monitored 3150 endocarps across all three years and habitats to create an average level of ant predation for each habitat. Ant predation typically resulted in a loss of most seeds within the endocarp. In 2006 we planted 40 endocarps per habitat * 3 habitats * 15 replicates of each habitat and scored these seeds for emergence (assuming a mean of 5 seeds/endocarp), and seedling survival until the next census period (July 2007). We repeated this in 2007 with higher replication (10 endocarps * 25 replicates for each habitat). All of these monitored endocarps were processed by *C. cyanomelas* (Loayza 2009).

Individual-based model

To project the population trajectory and the role of each disperser in future population size of *G. viburnoides*, we 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.

We 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 *G. viburnoides*, and vegetation patches without *G. viburnoides*; and rows represent the five stage classes, seedlings, saplings, sprouts, small trees and adult trees.

In each time step (year), individuals in each stage class would die or live and be placed into stage classes for the next year based on probabilities generated from demographic data collected at our study site (see Fig. 1). Adult plants reproduce with probability p . All reproductive adult plants produce 1981 endocarps (see Table 1). Endocarps are processed by *P. castanotis* with probability p_t , by *C. cyanomelas* with probability p_j or not processed by birds with probability $1-p_t-p_j$. Movement of endocarps by seed dispersers depends on the species of seed disperser and the habitat, and these parameters are described in Table 1 (parameters t_{ii} , t_{gi} , j_{ii} , j_{gg} , j_{gn}). Endocarps on the ground have a probability of escaping predation by ants that is habitat-specific (parameters e_i , e_g , e_n). Each endocarp contains 5 seeds. Germination of seeds depends on how the endocarp was processed (by *P. castanotis*, by *C. cyanomelas*, or not processed by birds) and the habitat where it is dispersed. Parameter estimates for germination use both greenhouse data that distinguish between endocarps processed in different ways and field data that are habitat specific. For example, in our model the germination of seeds in endocarps processed by *P. castanotis* in forest islands is equal to: (the emergence

probabilities of seeds in endocarps processed by *P. castanotis* / the emergence
probabilities of seeds in endocarps processed by *C. cyanomelas*) * the emergence
probabilities of seeds in forest islands. Germination parameters are presented in Table 1
(parameters g_{ti} , g_{ji} , g_{ni} , g_{jg} , g_{ng} , g_{jn}). Seedling establishment rates (survival of seedlings
until the start of the next time step; approximately six months) were habitat-specific
(parameters y_i , y_g , y_n).

We used our individual-based model to project population size of *G. viburnoides*
10 years into the future. We chose this short time frame for two reasons. First, over
longer time periods, vegetation patches without *G. viburnoides* are likely to transition
into vegetation patches with *G. viburnoides*, and vice versa. It is reasonable to ignore
such changes in habitat over shorter time periods because we find that over short periods
of time the proportion of vegetation patches that switch from one type to the other (i.e.,
patches with *G. viburnoides* to patches without *G. viburnoides*, and vice versa, is
approximately equal). Second, in cases for which the population is projected to grow,
our model ignores environmental constraints to this growth that we know are important in
this system, such as the availability of habitat that will not flood. Thus, our model
provides a reasonable projection over short-time periods and for moderate increases in
population size.

To project the population size of *G. viburnoides* into the future in the presence of
normal seed disperser dynamics (i.e., both QID present), we 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). We performed 1000 runs of our individual-based model, and for
each year, we present the mean population size 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* (setting parameter $p_i=0$), absence of only *C. cyanomelas* (setting parameter $p_j=0$), and absence of both QID ($p_i=p_j=0$). In our model we assumed that when one of the dispersers was absent, the proportion of fruits this species removed was not removed by the remaining species; instead those fruits remained as non-dispersed. This assumption was based on the fact that 23% of the fruits remained non-dispersed at the end of the fruiting season with all dispersers present, suggesting there are enough fruits to satiate the frugivore community (Loayza 2009). As with the original model, we projected 10 years into the future and performed 1000 runs of the individual-based model to generate 95% confidence intervals. Lack of overlap between 95% confidence intervals indicates statistically significant differences in the projected population size for different seed disperser scenarios.

RESULTS

Stage- and Habitat-specific Demography

Because of low sample size (i.e., rare occurrence) of adult trees in forest islands ($N=6$), survivorship and sprouting of adult plants were calculated at the landscape rather than the habitat level, and these values were used for all habitats. Additionally, because we never observed a small tree to adult transition in forest islands during the study (2 small trees present in forest islands from 2005-2008), the value we used for our model is approximately a third of the probability of the same transition in patches with adult *G.*

viburnoides (0.01). In general, there were distinct among-habitat differences across all the transitions in the *G. viburnoides* life cycle, with forest islands having the lowest growth and survivorship values for the seedling and sapling stages in the landscape. For example, over the three years seedlings were between five and six times more likely to transition to saplings in vegetation patches with and without *G. viburnoides*, respectively, than in forest islands (Fig. 1). Seedlings were also more likely to lose all their foliage, and re-sprout the next year in forest islands than in the other two habitats, which points to a higher probability of above ground mortality in forest islands. Moreover, on average both sapling survival and the probability of a sapling becoming a small tree were also about 1.7 and two times lower in forest islands than in vegetation patches. These results strongly indicate that, compared to vegetation patches, forest islands are unfavorable for the recruitment and establishment of the earliest plant stages of *G. viburnoides*.

Growth and survival values for different plant stages were similar in vegetation patches with and without *G. viburnoides*, with two exceptions. First, the probability that small trees would die aboveground and re-sprout the next year was three times higher in vegetation patches with than without *G. viburnoides*. Second, sprouts were twice as likely to die and re-sprout the following year in vegetation patches without than with *G. viburnoides*. Besides those differences, vegetation patches with and without *G. viburnoides* had comparable demographic vital rates.

Individual-based model

The values for the parameters we used for the model (Table 1) are discussed in detail elsewhere (Loayza 2009). At the landscape level (individuals summed across all

three habitats), the population is projected to double in size in the presence of both QIDs in the next 10 years (Fig. 2). Interestingly, the population can grow even in the scenario for which neither of the QID are present (i.e., no seed dispersal). Highest population growth (almost a four-fold increase) is predicted to occur in the scenario in which only *C. cyanomelas* consumes the fruits and disperses the seeds, whereas negative growth will occur if the fruits of *G. viburnoides* are solely consumed by *P. castanotis* (Fig. 2).

When we examined the effects of seed dispersal for each habitat separately, the population trajectories varied among habitats for each scenario (Fig. 3). Predicted population trajectories in vegetation patches with *G. viburnoides*, paralleled those at the landscape level; the population was projected to grow under all scenarios, except if seeds are dispersed only by *P. castanotis*. After 10 years, population size was largest (462% increase) when fruits were exclusively consumed by *C. cyanomelas*, but remained at equilibrium when they were consumed only by *P. castanotis* (Fig. 3A). In vegetation patches without *G. viburnoides*, seed dispersal is not sufficient to sustain population size. Therefore, over time the total number of individuals was predicted to decline in all scenarios (Fig. 3B); this result indicates severe dissemination limitation into vegetation patches without *G. viburnoides*. The population declines towards zero if no QID are present or if fruits are solely consumed by *P. castanotis*, because in this habitat all *G. viburnoides* are small, non-reproductive plants, and the only influx of seeds is provided by *C. cyanomelas*. Seed dispersal by *C. cyanomelas* into vegetation patches without *G. viburnoides*, however, is so low that it does not allow for population growth. Nonetheless, if seeds are dispersed only by *C. cyanomelas*, following an initial decrease in the number of individuals occurring in this habitat, population size appears to stabilize

(Fig. 3B). Similarly, in forest islands the population is predicted to decline in all scenarios, but the decline is steeper if only *P. castanotis* consumes the fruits or if there is no seed dispersal by QID (Fig. 3C).

DISCUSSION

We found that the two quantitatively important dispersers of *G. viburnoides* in the Beni savannas were not ecologically redundant in their seed dispersal services. Instead, seed dispersal by *P. castanotis* has a detrimental effect on the population growth of this species. To our 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 whose fruits it consumes. In many plant communities in the tropics, frugivores disperse the seeds of up to 90% of the woody species (Howe and Smallwood 1982), and seed dispersal is generally considered a diffuse mutualism (but see Wenny 2001), where the seeds of a plant are dispersed by an array of frugivores (e.g., Wheelwright and Orians 1982, Whitney et al. 1998, Loiselle et al. 2007). Our results stress the importance of linking species-specific seed dispersal patterns with their demographic consequences in different habitats to fully determine the net effect of seed dispersal by multiple agents.

Species-specific consequences of seed dispersal for population growth. The consequences of seed dispersal for the population dynamics of *G. viburnoides* differed between *C. cyanomelas* and *P. castanotis*. Tufted jays (i.e., *C. cyanomelas*) are pulp consumers that deposit 99% of the endocarps in vegetation patches with a fruiting adult (Loayza 2009). Therefore, considering that one of the advantages of seed dispersal is escape from enemies that live near the parent plant or that search for high concentrations

of seeds or seedlings (Janzen 1970, Connell 1971), this species would undoubtedly be regarded as a non-effective disperser. Toucans (i.e., *P. castanotis*), in contrast, are typically regarded as effective dispersers because they swallow and defecate the seeds, transporting them large distances away from the parent plant and hence potentially allowing them to colonize new areas, and escape from predators (Howe 1993, Howe et al. 1995, Holbrook and Loiselle 2009). By linking frugivore behavior and post-dispersal seed fate in different habitats with a demographic model, here we show a pattern opposite to what is expected under the previous considerations; the success of seeds taken by *C. cyanomelas* is ultimately higher than those of *P. castanotis*. Two factors explain this pattern. First, seedling emergence was almost five times higher for endocarps processed by *C. cyanomelas* than by *P. castanotis* (Loayza 2009). Although, generally germination is typically enhanced after a seed has passed through a vertebrate's gut (Travaset 1998, Bas et al. 2006, Travaset *et al.* 2007), this was not the case in our system. Our results concur with the results of Domínguez-Domínguez and colleagues (2006); they show that seed ingestion by another species of toucan also lowers germination in the neotropical tree *Ficus insipida*. Conversely, pulp removal by tufted jays leads to higher emergence rates than endocarps processed by *P. castanotis* or not processed by frugivores. Second, in our system, toucans disperse all of the endocarps to forest islands; this habitat is characterized by lower emergence probabilities and lower rates of seedling and sapling survivorship compared to vegetation patches. Additionally, even though *C. cyanomelas* deposit the vast majority of the endocarps under the parent or a conspecific tree, the remaining 1% are dispersed to vegetation patches without *G. viburnoides*, a habitat where plants of all stage classes have some of the highest rates of survival and growth. This last

result clearly demonstrates that rare dispersal events, which are often accidentally neglected in empirical studies, can have critical consequences for plant population dynamics.

Dissemination limitation and the spatial distribution of G. viburnoides. Our individual-based model shows that, at the landscape level, the population of *G. viburnoides* is predicted to grow even in a scenario with no seed dispersal; this suggests that seed dispersal may be dispensable for the short-term maintenance of this population. A lack of dispersal agents, however, would have dramatic consequences on the spatial distribution of this species. First, even with the dispersal services provided by both QID, the population of *G. viburnoides* is strongly dispersal limited (Jordano and Godoy 2002); 98% endocarps fall directly under the parent tree and thus, can only establish in the home patch, unable to reach all available habitats for recruitment. In a scenario with a complete lack of dispersal agents, *G. viburnoides* would not establish in patches without existing adult *G. viburnoides*. Further, all *G. viburnoides* plants in a vegetation patch with an adult tree present would eventually be the offspring of the resident maternal tree, which would result in spatial isolation of close relatives, and eventually lead to within-patch reduction of genetic diversity (Jordano and Godoy 2002, Holbrook 2006). *G. viburnoides* is an outcrossing species presumably pollinated by night-active moths (Charlotte Taylor, Missouri Botanical Gardens, *pers. comm.*), therefore cross-pollination from other *G. viburnoides* trees in the landscape may slow the loss of within-patch genetic diversity. It is uncertain, however, how far pollen can move in this landscape. Second, although the population is predicted to grow within the first 10 years in the no disperser scenario, this result needs to be interpreted with caution because certain

environmental constraints will impede growth. Specifically, the vegetation patches where *G. viburnoides* occurs are sites where woody species have established because they are above the floodwaters during the wet season. These habitats are limited in area, and generally cannot expand because the surrounding savanna prevents recruitment of woody species (i.e., it is submerged from 4-8 months a year). We find that at our study site, the majority of vegetation patches have only one adult *G. viburnoides* tree; consequently, population growth and expansion of this species in the landscape is most likely explained by the rare colonization events of “empty” available habitats (e.g., vegetation patches without *G. viburnoides*) rather than by the establishment of new adults in already “occupied” vegetation patches. Third, *G. viburnoides* plants of all stage classes frequently die in vegetation patches due to the yearly fire regime in the study area; therefore, without seed dispersal, and specifically without seed dispersal by *C. cyanomelas* to vegetation patches without *G. viburnoides* as they become available, in time the population size of this species may be significantly reduced.

The effects of dissemination limitation in the landscape can also be clearly determined by examining the projected population trajectory in vegetation patches without *G. viburnoides*. This habitat allows plants to have high rates of establishment, survival and growth. Yet, the declining fraction of the population that occurs in this habitat with time reveals that new recruitment is limited by seed dispersal. Further exploration of these results (results not shown) indicate that small increases in seed dispersal to patches without adult *G. viburnoides* (from 1.1% to 4%) by *C. cyanomelas*, would be sufficient for the population to remain at numerical equilibrium in this habitat. Although in our direct observations of the feeding behavior by *C. cyanomelas*, we

recorded movement of only 1.1% of the endocarps to vegetation patches without *G. viburnoides*, data from seed traps placed across the study area in 2006 and 2008 reveal that seed dispersal into this habitat is slightly higher; between 3 and 4% of the dispersed seeds arrive to vegetation patches without *G. viburnoides*, probably as a result of the actions of the other frugivores that feed on this plant species (Loayza 2009). Therefore, although it is rare, dispersal to vegetation patches without *G. viburnoides* may be very important for population growth in the landscape.

Assumptions of the model. We emphasize caution when interpreting results from our model, as this approach has some assumptions, which can limit our interpretations (Godínez-Alvarez and Jordano 2007). First, the survival, growth and fecundity values of individuals are assumed to be constant through time. In our model, we used averaged values from three years of data for each habitat; however, there was high environmental variability during the study period; we consider 2006 an average year, while 2007 and 2008 were El Niño and La Niña years, respectively. This variability may give rise to among-year differences in some vital rates and processes (e.g., emergence), which can in turn lead to shifts in habitat suitability across years (i.e., context dependence, Schupp 2007). Therefore, although forest islands are generally habitats that are unfavorable for seedlings and saplings of *G. viburnoides*, depending on the environmental conditions, some years may not be as negative as the ones we observed here, and this may explain the proportion of adults in the population that presently occur in this habitat. Second, these models assume the population grows at a constant rate, and do not consider other factors, such as density-dependent effects or environmental constraints that may inhibit or slow down growth. As mentioned before, these savannas are very heterogeneous

landscapes, where the available habitat that does not flood during the rainy season is a limiting factor for the establishment of woody species, and can thus ultimately constrain population growth of *G. viburnoides*. Each vegetation patch likely hold a certain carrying capacity of trees and shrubs, and additional recruits will probably be unable to establish unless other plants in the vegetation patch die.

Conclusions. The seed dispersal cycle of *G. viburnoides* in heterogeneous landscapes, such as Neotropical savannas, is complex. Landscape heterogeneity induces spatial variation in demographic rates; habitats vary in their suitability for different plant stages, and ultimately in their overall probability for plant recruitment. The fruits are consumed in varying quantities by bird species that process the seeds in different ways, and deliver them unevenly among different habitats. As a result population recruitment can be attributed to the activity of only a restricted set of species within the disperser assemblage.

Our model enabled us to address a key question on the ecological consequences of seed dispersal: What are the relative contributions of different dispersers to the future population growth of the plant they consume? Through this integrative approach we examined the degree to which ecological function can be substituted by different members of an ecological guild and determined that dispersers can have not only different, but opposite effects for plant fitness. Considering its dispersal effectiveness and its impacts on the population dynamics of *G. viburnoides* in our study area, we conclude that *C. cyanomelas* is a key species for the persistence of this tree; the loss of this dispersal agent would not be compensated by the dispersal services provided by *P. castanotis*.

Ultimately, the integration of frugivore activity with plant demography using spatially explicit models such as this one and others (e.g., Godínez-Alvarez et al. 2002) can be extremely valuable for plant ecology. Such models enable us to close the “seed dispersal loop” (Wang and Smith 2004) and gain a better understanding of the demographic consequences of seed dispersal by different dispersal agents. This information becomes particularly relevant when the set of potential dispersers of a plant species, such as *G. viburnoides*, is small, and the loss of a single disperser may affect the long-term persistence of the species.

ACKNOWLEDGEMENTS

This chapter was prepared in collaboration with Tiffany Knight. This research was supported by grants from the National Science Foundation (DEB-0709753), the Rufford Maurice Laing Foundation, the Scott Neotropical Fund from the Cleveland Metropolitan Zoo, the Neotropical Grassland Conservancy, the Webster Groves Nature Study Society, Sigma Xi, and the Whitney R. Harris World Ecology Center at the University of Missouri-St. Louis. We are grateful to the people who assisted with the field data collection in Bolivia, in particular F. Saavedra, N. Burgos, R. Balderrama, A. Terán, O. Burgos, A. Yarari, and M. Houard. Fieldwork was facilitated through logistic support of the Instituto de Ecología in La Paz, Bolivia and the Estación Biológica Beni. Suggestions from Bette Loiselle, Rodrigo Rios, John Blake, and Eugene Schupp helped improve and earlier version of this manuscript.

LITERATURE CITED

- Bas, J. M., P. Pons, and C. Gómez. 2006. Exclusive frugivore and seed dispersal of *Rhamnus alaternus* in the bird breeding season. *Plant Ecology* 183:77–89.
- Beck, S. G. & Moraes, M. 1997. Llanos de Mojos Region, Bolivia. *in* S. D. Davis, V. H. Heywood, O. Herrera-MacBryde, J. Villa-Lobos and A. C. Hamilton, editors. *Centers of Plant Diversity: A Guide and Strategy for their Conservation*, Volume 3, The Americas. WWF, IUCN, Oxford, U.K.
- Bleher, B., and K. Böhning-Gaese. 2001. Consequences of frugivore diversity for seed dispersal, seedling establishment and the spatial pattern of seedlings and trees. *Oecologia* 129: 385–394.
- Calviño-Cancela, M. 2002. Spatial patterns of seed dispersal and seedling recruitment in *Corema album* (Empetraceae): the importance of unspecialized dispersers for regeneration. *Journal of Ecology* 90: 775–784.
- Comiskey, J. A., F. Dallmeier, and G. Aymard. 2000. Floristic composition and diversity of forested habitats in the Estación Biológica del Beni, Amazonian Bolivia. Pages 89–312 *in* O. Herrera-MacBryde, F. Dallmeier, B. MacBryde, J. A. Comiskey and C. Miranda, editors. *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia*. Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB).
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine mammals and in rain forest trees. Pages 298–312 *in* P. J. Den Boer and G. Gradwell G, editors. *Dynamics of Populations*. Wageningen (The Netherlands): Pudoc.

- Cordeiro, N. J., and H. F. Howe. 2003. Forest fragmentation severs mutualism between seed dispersers and an endemic African tree. *Proceedings of the National Academy of Sciences* 100: 14052–14056.
- Domínguez-Domínguez, L. E., J. E. Morales-Mávil, and J. Alba-Landa. 2006. Germinación de semillas de *Ficus insipida* (Moraceae) defecadas por tucanes (*Ramphastos sulfuratus*) y monos araña (*Ateles geoffroyi*). *Revista de Biología Tropical* 54: 387–394.
- Godínez-Alvarez, H., and P. Jordano. 2007. An empirical approach to analysing the demographic consequences of seed dispersal by frugivores. Pages 391–406 in A. J. Dennis, E. W. Schupp, R. J. Green and D. A. Westcott, editors. *Seed dispersal: Theory and its application in a changing world*. CABI. Oxfordshire, UK.
- 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.
- Hanagarth, W. 1993. *Acerca de la geoecología de las sabanas del Beni en el Noreste de Bolivia*. Instituto de Ecología, La Paz, Bolivia. 186 p.
- Harper, J. L. 1977. *Population biology of plants*. Academic Press, London, UK. 892 p.
- Holbrook, K. M. 2006. Seed dispersal limitation in a Neotropical nutmeg, *Virola flexuosa* (Myristicaceae): and ecological and genetic approach. Ph. D. Dissertation, University of Missouri-St. Louis. (USA).
- Holbrook, K. M., and B. A. Loiselle. 2009. Seed dispersal in a neotropical tree, *Virola flexuosa* (Myristicaceae): does hunting of large vertebrates limit seed removal? *Ecology*, *In Press*.

- Howe, H. F. 1993. Aspects of variation in a neotropical seed dispersal system. *Vegetatio* 107/108: 149–162.
- Howe, H. F., and M. N. Miriti. 2004. When seed dispersal matters. *Bioscience* 54: 651–660.
- Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. *Annual Review of Ecology and Systematics* 13: 201–228.
- Howe, H. F., E. W. Schupp, and L. C. Westley. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66: 781–791.
- Janzen D. H. 1970. Herbivores and the number of tree species in tropical forests. *The American Naturalist* 104: 501–528.
- Jordano, P., and E. W. Schupp. 2000. Seed disperser effectiveness: The quantity component and patterns of seed rain for *Prunus mahaleb*. *Ecological Monographs* 70: 591–615.
- Jordano, P., and J. A. Godoy. 2002. Frugivore-generated seed shadows: A landscape view of demographic and genetic effects. Pages 305–321 in D. J. Levey, W. R. Silva and M. Galetti, editors. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK.
- Langstroth, R. P. 1996. Forest islands in an Amazonian savanna of northeastern Bolivia. Ph. D. Dissertation. University of Wisconsin-Madison. (USA).
- Levey, D. J., W. R. Silva, and M. Galetti (eds.) 2002. *Seed dispersal and frugivory: Ecology, evolution, and conservation*. CABI Publishing, New York. 511 p.
- Loayza, A. P. 2009. Closing the seed dispersal loop for *Guettarda viburnoides* (Rub.): Connecting patterns of avian seed dispersal with population growth in a

- Neotropical savanna. Ph.D. Dissertation, University of Missouri-St. Louis.
(USA).
- Loiselle, B. A., and J. G. Blake. 1999. Dispersal of melastome seeds by fruit-eating birds of tropical forest understory. *Ecology* 80: 330–336.
- Loiselle, B. and J. Blake. 2001. Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. Pages 397–406 *in* D. J. Levey, W. R. Silva and M. Galetti, editors. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK.
- Loiselle, B. A., and J. G. Blake. 2002. Potential consequences of extinction of frugivorous birds for shrubs of a tropical wet forest. Pages 397–405 *in* D. J. Levey, W. R. Silva and M. Galetti, editors. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation*. CAB International, Wallingford, UK.
- Loiselle, B. A., P. G. Blendinger, J. G. Blake, and T. B. Ryder. 2007. Ecological redundancy in seed dispersal systems: A comparison between manakins (Aves: Pipridae) in two tropical forests. Pages 178–195 *in* A. J. Dennis, E. W. Schupp, R. J. Green and D. A. Westcott, editors. *Seed dispersal: Theory and its application in a changing world*. CABI. Oxfordshire, UK.
- Miranda, C. L. 2000. La Reserva de la Biósfera Estación Biológica del Beni, Bolivia. Pages 21–25 *in* O. Herrera-MacBryde, F. Dallmeier, B. MacBryde, J. A. Comiskey and C. Miranda, editors. *Biodiversity, conservation and management in the region of the Beni Biological Station Biosphere Reserve, Bolivia*. Smithsonian Institution/Monitoring and Assessment of Biodiversity Program (SI/MAB).

- Nathan, R., and H. C. Müller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15: 278–285.
- Schupp, E. W. 1993. Quantity, quality, and the effectiveness of seed dispersal by animals. *Vegetatio* 107/108: 15–29.
- Schupp E. W. 2007. The suitability of a site for seed dispersal is context-dependent. Pges 445–462 in A. J. Dennis, E. W. Schupp, R. J. Green and D. A. Westcott, editors. *Seed dispersal: theory and its application in a changing world*. CABI International, Wallingford, Oxfordshire.
- Schupp E. W., and M. Fuentes. 1995. Spatial patterns of seed dispersal and the unification of plant ecology. *EcoScience* 2: 267–275.
- Taylor, C., P. G. Delprete, A. Vincentini, R. Cortés, D. Zappi, C. Persson, C. Bestetti Costa, and E. Araujo de Anunciação. 2004. Rubiaceae. Pages 497–847 in J. A. Steyermark, P. E. Berry, K. Yatskievych and B. K. Holst, editors. *Flora of the Venezuelan Guayana: Volume 8 – Poaceae-Rubiaceae*. Missouri Botanical Garden Press, St. Louis.
- Tews, J., K. Moloney, and F. Jeltsch. 2004. Modeling seed dispersal in a variable environment: a case study of the fleshy-fruited savanna shrub *Grewia flava*. *Ecological Modeling* 175: 65–76.
- Traveset, A. 1998. Effect of seed passage through vertebrate frugivores' guts on germination: a review. *Perspectives in Plant Ecology, Evolution, and Systematics* 1/2: 151–190.

- Travaset, A., A. W. Robertson, and J. Rodriguez-Pérez. 2007. A review of the role of endozoochory in seed germination. Pages 78–1103 in A. J. Dennis, E. W. Schupp, R. J. Green and D. A. Westcott, editors. *Seed dispersal: Theory and its application in a changing world*. CABI. Oxfordshire, UK.
- Wang, B. C., and T. B. Smith. 2002. Closing the seed dispersal loop. *Trends in Ecology and Evolution* 17: 379–385.
- Wenny, D. G. 1998. Directed dispersal by bellbirds in a tropical cloud forest. *Proceedings of the Natural Academy of Sciences USA* 95: 6204–6207.
- Wenny, D. G. 2000. Seed dispersal, seed predation, and seedling recruitment of a Neotropical montane tree. *Ecological Monographs* 70: 331–351.
- Wenny, D. G. 2001. Advantages of seed dispersal: A re-evaluation of directed dispersal. *Evolutionary Ecology Research* 3: 51–74.
- Wheelwright, N. T., and G. H. Orians. 1982. Seed dispersal by animals: Contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *American Naturalist* 119: 402–413.
- Whitney, K. D., M. K. Fogiel, A. M. Lamperti, K. M. Holbrook, D. J. Stauffer, B. D. Hardesty, V. T., and T. B. Smith. 1998. Seed dispersal by *Ceratogymna* hornbills in the Dja Reserve, Cameroon. *Journal of Tropical Ecology* 14:351–371.

TABLE 1. Parameters used to develop the individual-based model of the consequences of seed dispersal of *G. viburnoides* by *C. cyanomelas* and *P. castanotis*. The table shows the value we used for each parameter and a description of how it was parameterized. GV, vegetation patches with *G. viburnoides*; No GV vegetation patches without *G. viburnoides*; ISL, forest islands.

Parameter	Description	Value	How was it parameterized
p	Mean proportion of adult plants that fruit from 2006-2008	0.56	$p = \left[\sum_3 (\# \text{ fruiting adults} / \text{total} \# \text{ adults}) \right] / 3 (\text{years})$
f	Fertility- mean number of endocarps per adult plant	1981	Mean number of endocarps per adult tree ($N_{2006}=16$, $N_{2007,2008}=29$)
p _t	Mean proportion of endocarps consumed by <i>P. castanotis</i> from 2006-2008	0.21	$p_t = \left[\sum_3 (n_t / n_t + n_j) \right] / 3$ where n_t is the total of fruits consumed by <i>P. castanotis</i> , and n_j is the total number of fruits consumed by <i>C. cyanomelas</i> .
p _j	Mean proportion of endocarps consumed by <i>C. cyanomelas</i> from 2006-2008	0.56	$p_j = \left[\sum_3 (n_j / n_t + n_j) \right] / 3 (\text{years})$
t _{ii}	Proportion of endocarps from ISL that remain in ISL after being processed by <i>P. castanotis</i>	1	Estimation*
t _{gi}	Proportion of endocarps from GV that move to ISL after being processed by <i>P. castanotis</i>	1	Based 402 hours of observation of fruiting <i>G. viburnoides</i> from 2006-2008, and seed trap data.
j _{ii}	Proportion of endocarps from ISL that remain in ISL after being processed by <i>C. cyanomelas</i>	1	Estimation*
j _{gg}	Proportion of endocarps from GV that remain in GV after being processed by <i>C. cyanomelas</i>	0.989	Based on observations of 888 out of 897 endocarps either dropped or dispersed to a GV patch by <i>C. cyanomelas</i> [‡] (2006-2008)
j _{gn}	Proportion of endocarps from GV that are moved to No GV after being processed by <i>C. cyanomelas</i>	0.011	Based on observed movement of 11 out of 897 endocarps from GV to No GV patches by <i>C. cyanomelas</i> (2006-2008)
e _i	Mean probability an endocarp escapes predation in ISL	0.81	Based on seed predation experiments from 2006-2008. The fate of a group of 20 (2006, 2008) and 10 endocarps (2007) was followed for 40 days in each habitat replicate ($N_{2006}=15$, $N_{2007,2008}=25$)

e_g	Probability endocarp escapes predation in GV	0.81	<i>Same as above</i>
e_n	Probability endocarp escapes predation in No GV	0.83	<i>Same as above</i>
s	Seeds per endocarp	5	Based on 800 endocarps
g_{ti}	Emergence probability of seeds processed by <i>P. castanotis</i> in ISL	0.000758	$g_{ti} = (\text{emergence prob. of seeds processed by } P. \text{ castanotis}^\circ / \text{emergence prob. of seeds processed by } C. \text{ cyanomelas}) \times \text{emergence probability of seeds in forest islands}^\dagger$
g_{ji}	Emergence probability of seeds processed by <i>C. cyanomelas</i> in ISL	0.0036	$g_{ji} = \text{emergence probability of seeds in ISL}^\dagger$
g_{ni}	Emergence probability of seeds not processed by birds (i.e. whole fruits) in ISL	0.001334	$G_{ni} = (\text{emergence prob. of seeds not processed by birds}^\circ / \text{emergence prob. of seeds processed by } C. \text{ cyanomelas}) \times \text{emergence probability of seeds in ISL}^\dagger$
g_{ig}	Emergence probability of seeds processed by <i>C. cyanomelas</i> in GV	0.038	$g_{ig} = \text{emergence probability of seeds in GV}^\dagger$
g_{ng}	Emergence probability of seeds not processed by birds in GV	0.014086	$G_{ng} = (\text{emergence prob. of seeds not processed by birds}^\circ / \text{emergence prob. of seeds processed by } C. \text{ cyanomelas}) \times \text{emergence probability of seeds in GV}^\dagger$
g_{jn}	Emergence probability for seeds processed by <i>C. cyanomelas</i> in No GV	0.0164	$G_{jn} = \text{emergence probability of seeds in No GV}^\dagger$
y_i	Mean probability that emerged seedlings survive and establish in ISL	0.54	$y_i = \left(\sum_2 \# \text{surviving seedlings (6 months)} / \text{total} \# \text{emerged seedlings} \right) / 2$ Based on emergence data from 2007 and 2008.
y_g	Mean probability that emerged seedlings survive and establish GV	0.30	<i>Same as above</i>
y_n	Mean probability that emerged seedlings survive and establish in No GV	0.61	<i>Same as above</i>

* See text

† Fruit processing by *C. cyanomelas* was considered a dispersal event even if the endocarp remained in the feeding site.

° From greenhouse experiments established in 2006 (n=96 endocarps/treatment; i.e. processed by *P. castanotis*, by *C. cyanomelas*, or whole fruits)

† From field experiments established in 2006 and 2007

FIGURE LEGENDS

PLATE. 1. A. Map of the study area at Beni Biological Station-Biosphere Reserve. White circles and black triangles show the location of vegetation patches with and without *G. viburnoides*, respectively. Dark grey areas are forest islands. The light grey background is the savanna matrix. B. Forest island. C. Vegetation patch. Photographs by Andrea P. Loayza.

FIG. 1. 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. Ovals 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 (see Table 1). [‡]Transition estimated at the landscape, rather than habitat level. ^{*} Estimated transition (see text).

FIG. 2. Projected population growth of *G. viburnoides* at the landscape level in four seed disperser scenarios.

FIG. 3. Projected population trajectories of *G. viburnoides* under four seed dispersal scenarios in three habitats: A. Vegetation patches with an adult *G. viburnoides*; B. Vegetation patches without an adult *G. viburnoides*; and C. Forest islands.

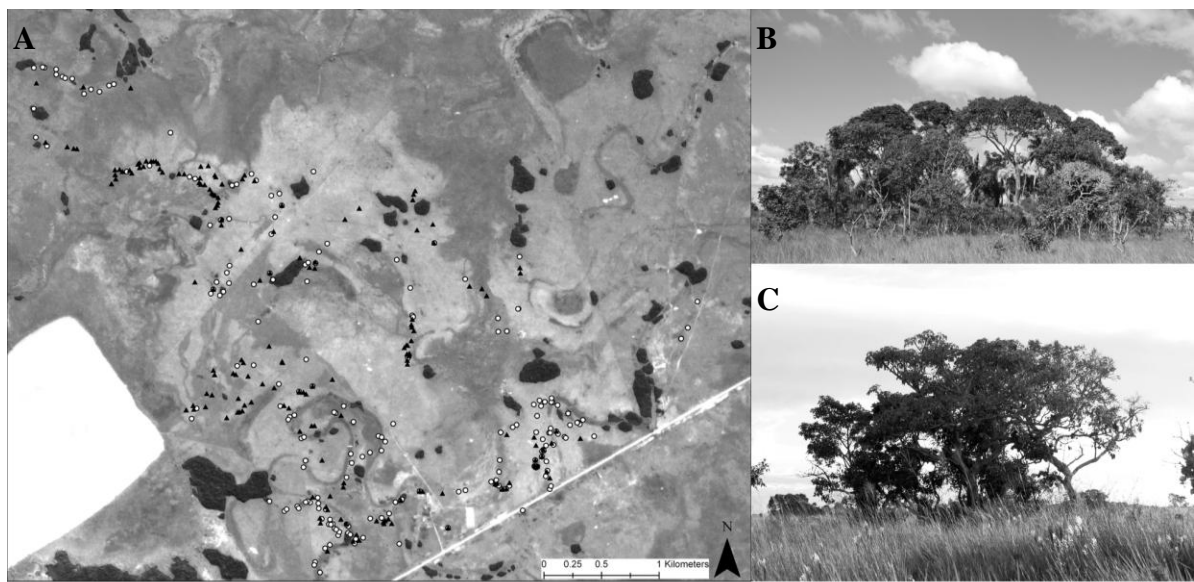


Plate 1

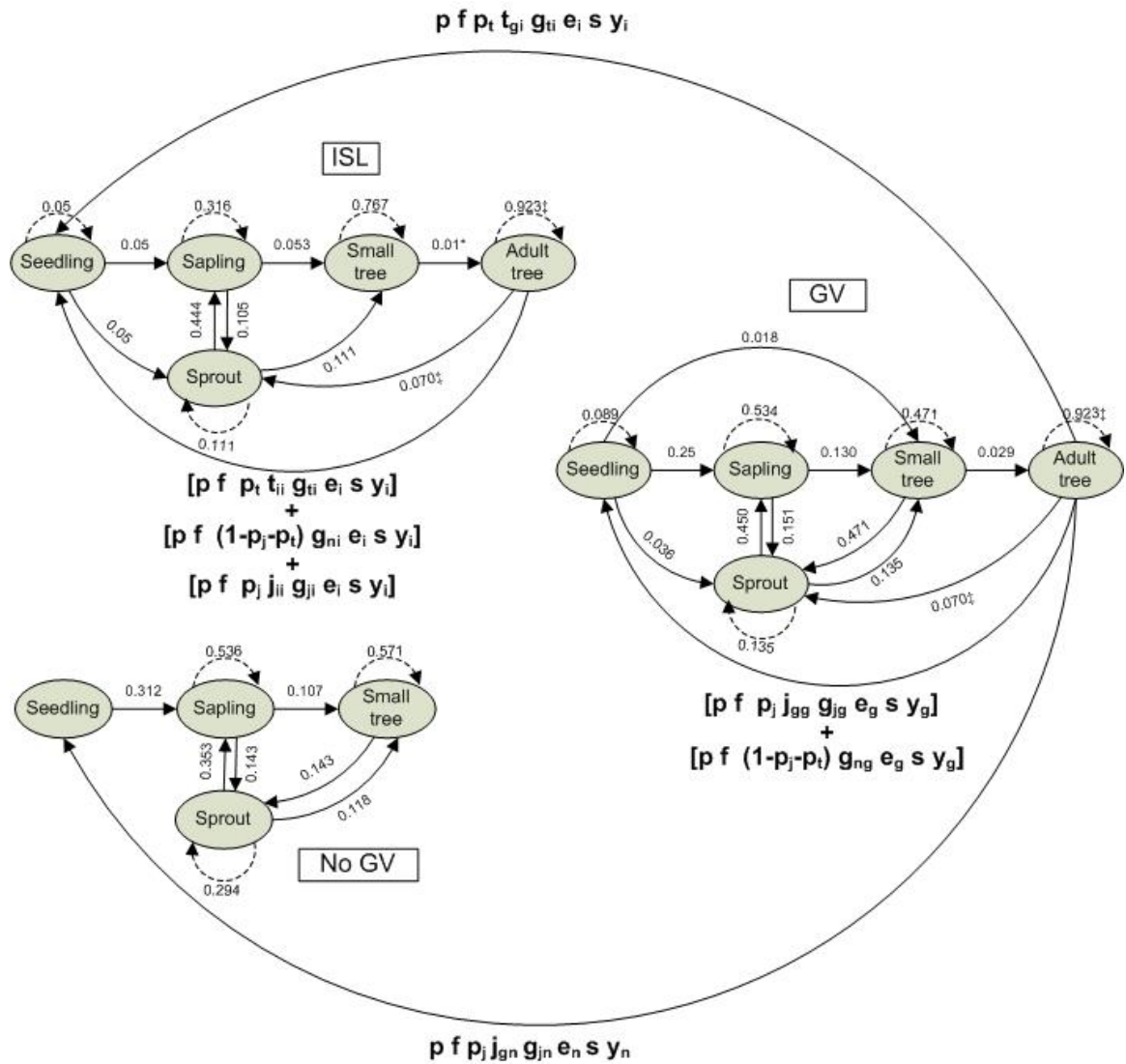


Figure 1

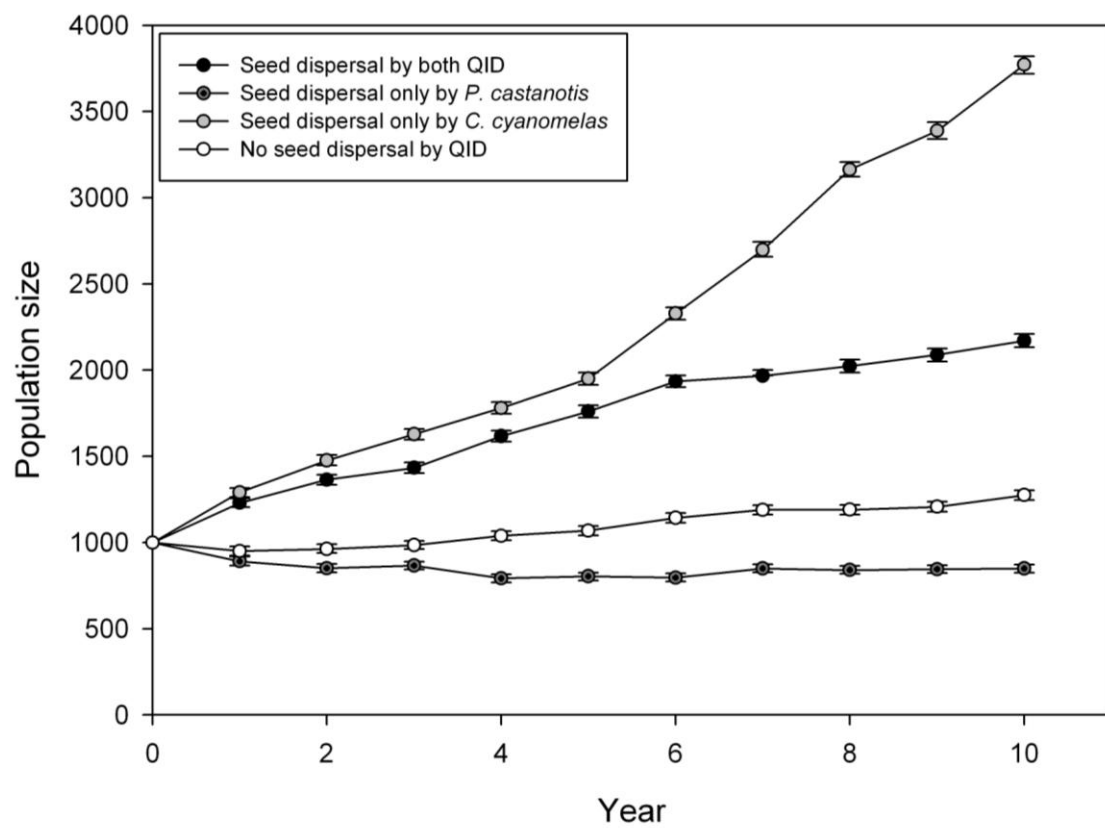


Figure 2

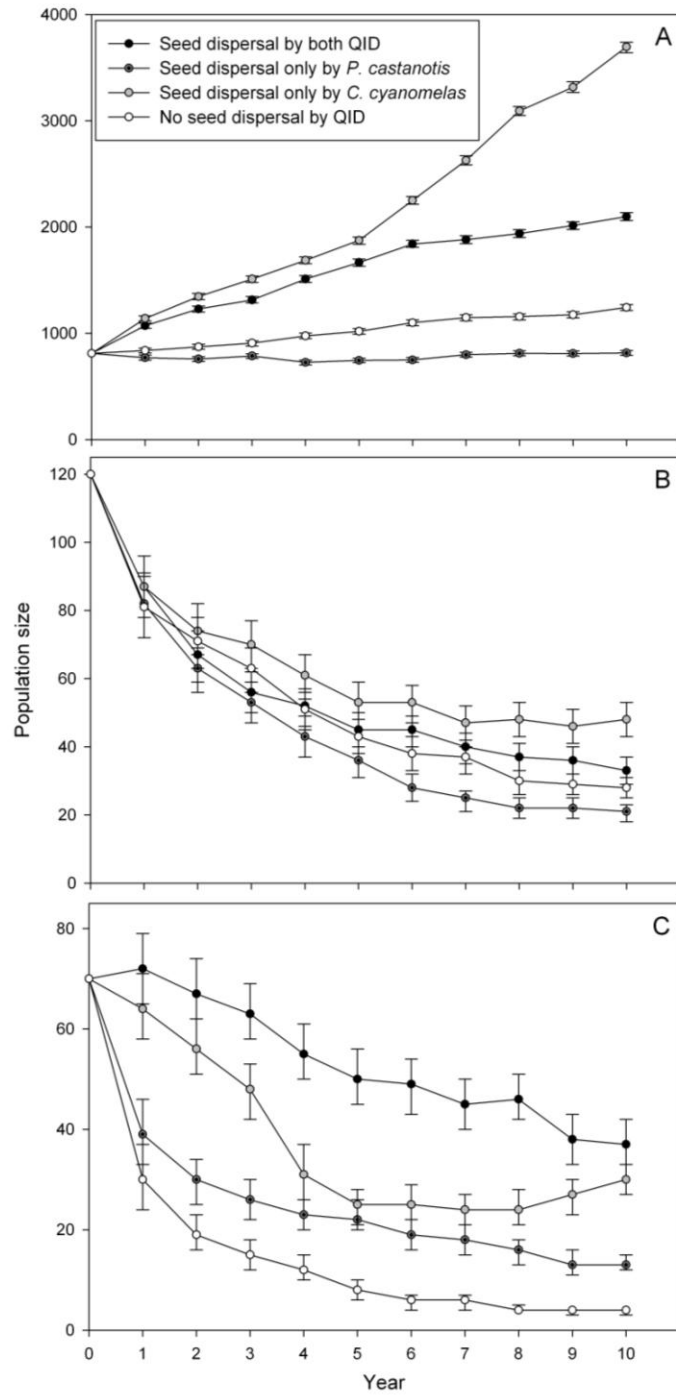


Figure 3