

2010

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Seed dispersal by pulp consumers, not “legitimate” seed dispersers, increases *Guettarda viburnoides* population growth

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Abstract. We examined the effect of seed dispersal by Purplish Jays (*Cyanocorax cyanomelas*; pulp consumers) and the Chestnut-eared Araçari (*Pteroglossus castanotis*; “legitimate” seed dispersers) on population growth of the small tree *Guettarda viburnoides* (Rubiaceae) 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. Our model suggests 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: avian seed dispersal; Bolivian savanna; *Cyanocorax cyanomelas*; disperser effectiveness; frugivory; *Guettarda viburnoides*; matrix models; Neotropical birds; *Pteroglossus castanotis*; Rubiaceae.

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 will provide equal benefits to plants, and differences in behavior can lead to differences in disperser effectiveness (e.g., Wenny

1998, 2000, Loiselle and Blake 1999, 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.

For seed dispersal by animals to be the result of a mutualistic relationship between the frugivores and the fruiting plants that they consume, it needs to 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 because multiple 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 and the distances seeds are dispersed (Bleher and Böhning-Gaese 2001, Cordeiro and Howe 2003, Loiselle et al. 2007, Holbrook and Loiselle 2009). However, when multiple frugivores are present, some ecological redundancy may also occur, in which frugivores provide more or less similar seed dispersal services to the plant (Loiselle et al. 2007) and, thus, presumably have equivalent effects on its population dynamics. Such

Manuscript received 19 March 2009; revised 1 December 2009; accepted 4 December 2009. Corresponding Editor: T. P. Young.

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redundancy may buffer plants from years of low abundance of any one seed disperser or loss of a seed disperser from the system (Loiselle and 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 toward understanding how frugivore activity translates into demographic consequences for plants. To date, however, only one study has quantified the net effects of seed dispersal on plant population dynamics (Godínez-Alvarez et al. 2002). 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 by the disperser, (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 habitat. With these data in 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 estimate the relative importance of given dispersers to the maintenance of plant populations (Godínez-Alvarez et al. 2002, Loiselle and Blake 2002) and determine whether different disperser species provide similar dispersal services to the plant, 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 model 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 predict that (1) differences in dispersal effectiveness by each frugivore will lead to

modeled 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 probably increase modeled population growth, as compared to a scenario where no seed dispersal occurs.

METHODS

Study system

The demographic and seed dispersal data for *G. viburnoides* were collected between 2005 and 2008 at Beni Biological Station-Biosphere Reserve in Beni, Bolivia (14°30′–14°50′ S; 66°40′–65°50′ W; 190–220 m elevation). 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 ~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 for 4–10 months per year. Within the savanna, the landscape is heterogeneous, with naturally occurring forest islands, small woody patches, as well as open and wooded grasslands (Hanagarth 1993, Beck and Moraes 1997). “Forest islands” are isolated units of forest (0.1–20 ha in the study site) with a canopy height of up to 25 m (see Fig. 1), located on low-relief features (e.g., natural levee remnants; Langstroth 1996). “Woody patches” are sites where woody species have established (see Fig. 1). These are small (2–175 m²) stands of shrubs and trees with a canopy height of up to 8 m; like forest islands, woody patches generally form on slightly elevated (i.e., 1–2 m) terrain, such as termite and ant mounds. Both forest islands and woody patches are generally above the flood line, except during extreme weather events such as during El Niño or La Niña years.

Guettarda viburnoides Cham. & Schlecht. (Rubiaceae) is a small tree, distributed from Brazil to Paraguay, generally occurring in semideciduous forests and grasslands (Taylor et al. 2004). At the study site, *G. viburnoides* grows in the woody patches, and typically only a single adult tree is found per woody patch. A small proportion of the *G. viburnoides* population at the study site also occurs in forest islands. Trees bear ripe yellow fruits (13.95 ± 2.84 mm, mean \pm SD) from late March until early July. Each fruit contains a single woody endocarp (9.20 ± 1.67 mm), which contains, on average, 5 seeds (range 3–7). Sown in greenhouse conditions, seeds germinated between within 1–11 months after sowing; whereas those sown at the study site germinated within 2–15 months after sowing (Loayza 2009). No germination was observed after 15 months, suggesting that *G. viburnoides* does not form a persistent seed bank. Based on our demographic data, it takes an average of 7.5 years for seedlings to mature into adult (reproductive) plants in woody patches and 8.6

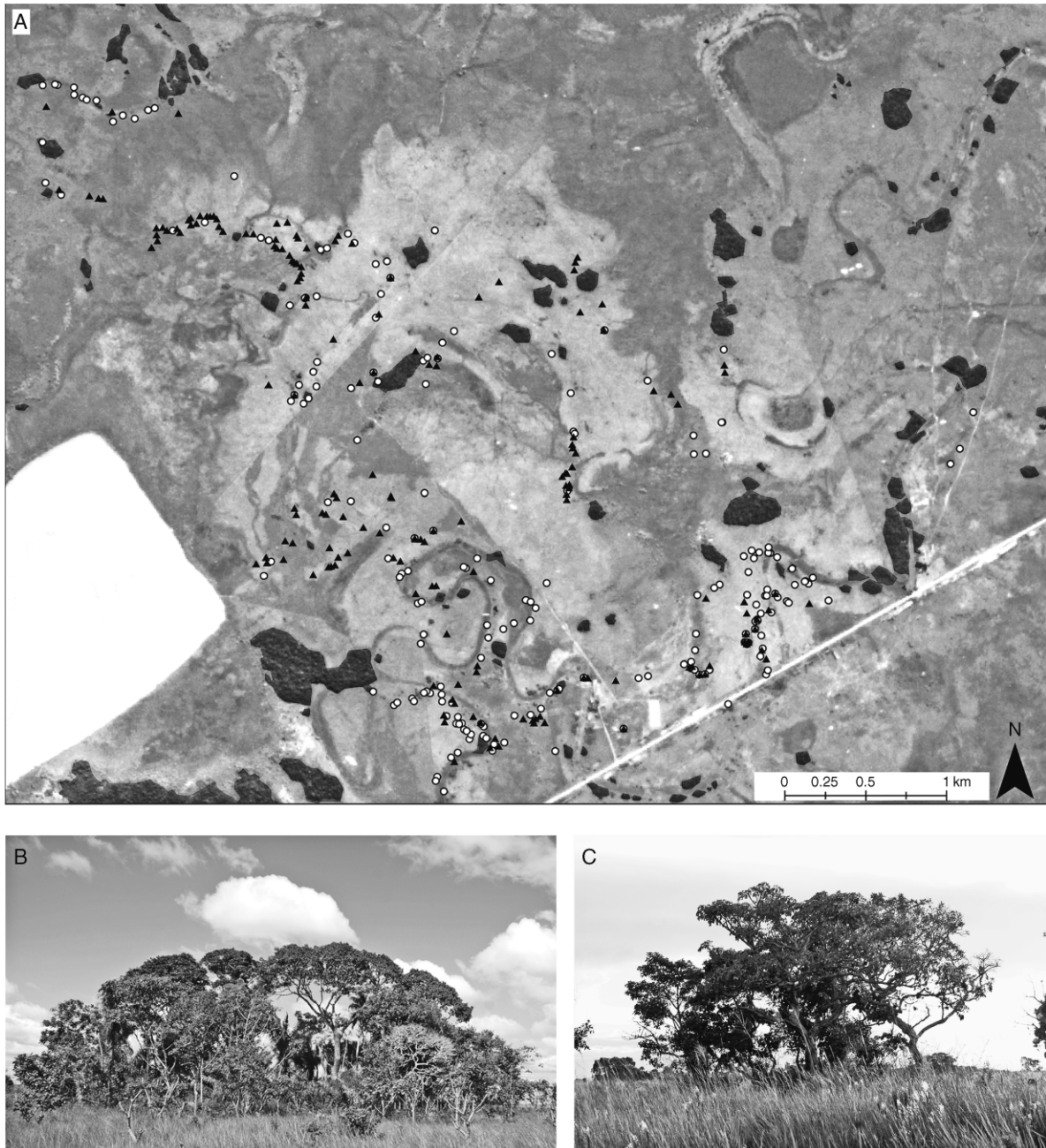


FIG. 1. (A) Map of the study area at Beni Biological Station-Biosphere Reserve in northeastern Bolivia. White circles and black triangles show the location of woody patches with and without the small tree *Guettarda viburnoides* (Rubiaceae), respectively. Dark gray areas are forest islands. The light gray background is the savanna matrix. (B) Forest island. (C) Woody patch. Photo credits: A. P. Loayza.

years in forest islands. For the purposes of this study, we explicitly consider three habitats that correspond to differences in demographic vital rates for *G. viburnoides*: forest islands (ISL), woody patches with an adult *G. viburnoides* tree (GV), and woody patches without an adult *G. viburnoides* tree (No GV). We note that woody patches without an adult *G. viburnoides* often contain seedlings, saplings, or small trees of this species.

Bird dispersal of Guettarda viburnoides

At our study site, fruits of this species are consumed nonexclusively by 10 species of birds, but >80% of the seed dispersal is due to only two species that we consider the quantitatively important dispersers of *G. viburnoides* (Loayza 2009): *Cyanocorax cyanomelas* (Veillot) (Purplish Jay) and *Pteroglossus castanotis* (Gould) (Chestnut-eared Araçari). Hence, for the

purposes of our model, we consider that fruits of *G. viburnoides* in our study area are consumed and dispersed solely by these two species. *Cyanocorax cyanomelas* are pulp consumers; once they remove the fruit's skin and consume the pulp, they discard the endocarp, usually under the parent tree. Conversely, *P. castanotis* are "legitimate seed dispersers" (sensu Traveset 1994); they swallow the fruit whole and pass the intact endocarp. Although the other species of birds observed eating the fruits of *G. viburnoides* certainly contribute to the overall recruitment pattern of this tree in the landscape, it is unlikely that they have disproportionately important consequences for recruitment, for several reasons. In some cases, these species were only observed once during the three years (e.g., *Pipile pipile*, *Ortalis motmot*), whereas in others, the species were likely to destroy the endocarp (*Columba cayannensis*, *Ara severa*). Additionally, some of the birds observed feeding on the fruits were either primarily insectivorous (*Tyrannus melancholicus*) or nectarivorous (*Psarocolius decumanus*), and thus it is unlikely that fruits, in general, are a significant component of their diet. The last two infrequent visitors of *G. viburnoides* (*Cyanocorax chrysops* and *Ramphastos toco*) are likely to impact the recruitment pattern in much the same way as the quantitatively important dispersers, given that they process the fruit in a similar manner and disperse the seeds to the same habitats.

Cyanocorax cyanomelas consumes 56% of fruits produced by a *G. viburnoides* tree (190 dispersal events recorded during 402 hours of observation from 2006 to 2008; Loayza 2009). *C. cyanomelas* individuals feeding within woody patches with *G. viburnoides* drop 97.9% of the endocarps below or near the parent tree (i.e., no dispersal), and disperse 1.0% and 1.1% of the endocarps to other woody patches, either with or without *G. viburnoides*, respectively (the minimum distance between any two woody patches where the observations were conducted ranged from 50–100 m). Therefore, in total, 98.9% of the endocarps processed by *C. cyanomelas* remain in woody patches with *G. viburnoides*. No observations of *C. cyanomelas* feeding within forest islands were carried out; for our model we assumed 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 that 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 100–200 m over open savanna to feed in a woody patch.

Pteroglossus castanotis consumes 21% of the fruits produced by a *G. viburnoides* tree. Feeding in woody patches with *G. viburnoides*, *P. castanotis* individuals disperse 100% of the endocarps to forest islands (17 dispersal events recorded during 402 hours of observation of the feeding behavior of *P. castanotis* in woody 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 in our model 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 (>95%) of the endocarps collected had been defecated. In contrast, the endocarps collected in woody patches had only the pulp removed.

Our greenhouse experiments indicate that endocarps processed by *C. cyanomelas* have higher emergence (25.2%) than those processed by *P. castanotis* (5.3%) and those not processed by any birds, i.e., endocarps in intact fruits (9.4%) (Loayza 2009). At the end of the fruiting season ~23% of the fruits in each tree are not removed by either disperser (nondispersed fruits, hereafter); 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 earlier. Specifically, in 2005 we selected and permanently tagged 248 individuals in the study area, of which 164 were adult trees. In 2006 and 2007 we added an additional 84 and 148 new non-adult plants, respectively. Therefore, a total of 480 individuals across all habitat types were followed during the study ($N = 383, 44, \text{ and } 53$ for woody patches with adult *G. viburnoides*, woody patches without adult *G. viburnoides*, and forest islands, respectively).

Plants were classified into five relatively discrete stage classes: seedling, sapling, small tree, sprout, and adult. Seedlings are small (<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 nonreproductive individuals that can be up to 2 m 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 have branches. Adult plants (defined as reproductive) are generally >2 m in height and have a nonzero 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 resprout in 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 (results presented in Fig. 2). 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

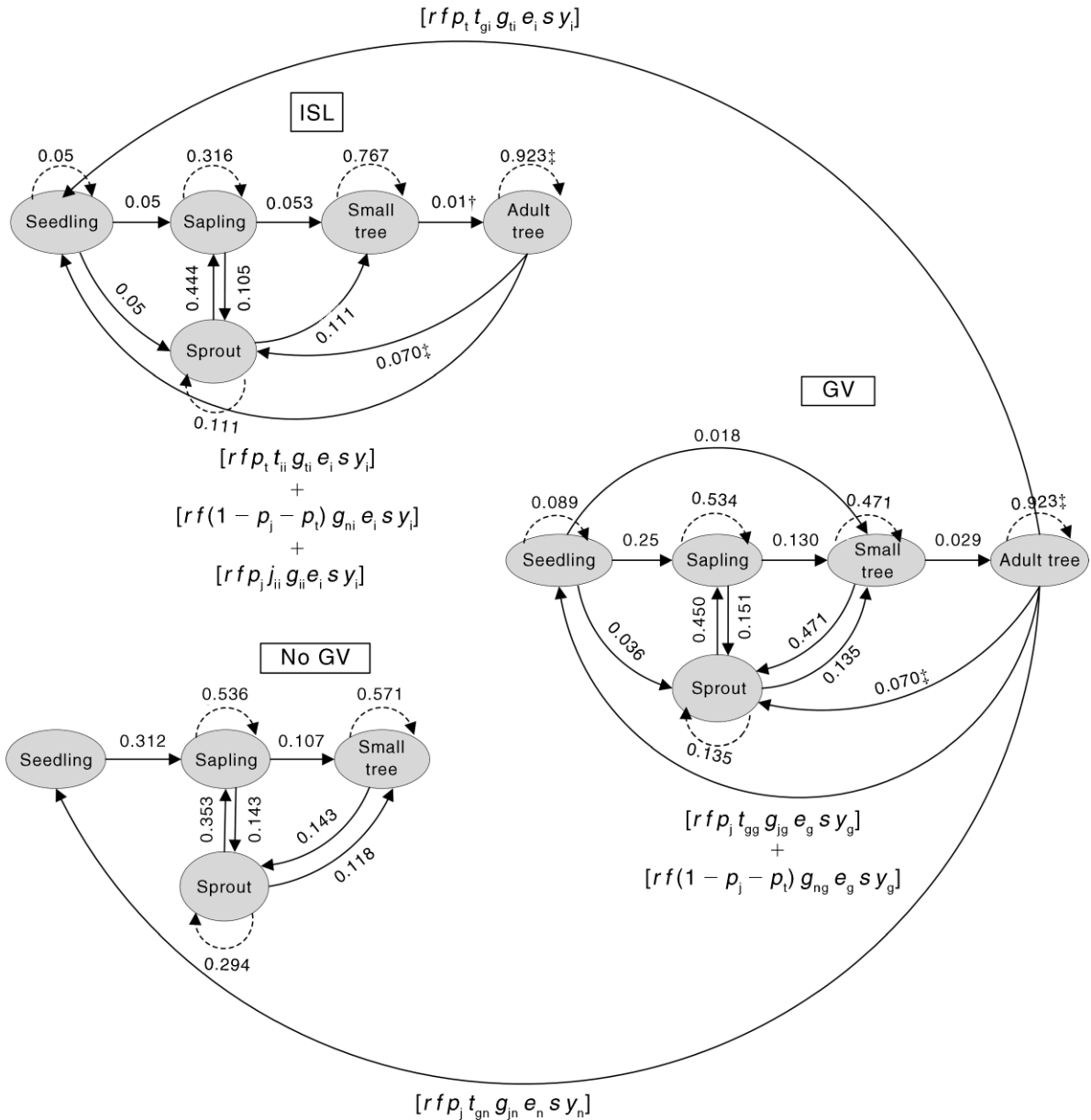


FIG. 2. Life cycle transitions of *G. viburnoides* in three habitats (parameters defined in Appendix A: Table A1): (1) woody patches with an adult *G. viburnoides* (GV); (2) woody patches without an adult *G. viburnoides* (No GV); and (3) forest islands (ISL). Ovals represent five demographic stages. Numbers with the arrows represent the mean probability that plants transition to different stages (solid lines) or remain in the same stage (dashed lines) from one year to the next. Seed dispersal in the landscape is represented by modifying the fecundity values. In brackets are the multiplied parameters used to calculate fecundity: *r*, the proportion of trees fruiting; *f* (fertility), the number of endocarps per adult plant; *s*, the number of seeds per endocarp; *y*, habitat-specific seedling establishment; and the probabilities, respectively, of being consumed (*p*) by the Chestnut-eared Araçari *Pteroglossus castanotis* (subscript *t*) or the Purplish Jay *Cyanocorax cyanomelas* (subscript *j*); of transitioning between habitats after being processed by *Pteroglossus* (*t*) or the jay (*j*); of escaping predation (*e*); and of germinating after being processed by *Pteroglossus* or the jay (*g*). Subscripts *i*, *g*, and *n* denote, respectively, forest islands, patches with *G. viburnoides*, and patches with no *G. viburnoides*. For more details, see Appendix A: Table A1.

† Estimated transition (see *Methods: Stage- and habitat-specific demography*).

‡ Transition estimated at the landscape level, rather than habitat level.

never observed a small tree-to-adult transition in forest islands during the study (two small trees were present in forest islands from 2005 to 2008), the value we used for our model is approximately one-third of the probability

of the same transition in patches with adult *G. viburnoides* (0.01).

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 fruits produced per tree at the beginning of the fruiting season before the fruits ripened and were removed (results are in Appendix A).

From 2006 to 2008, we conducted two different experiments to quantify the proportion of endocarps that escape predation by ants, and the proportion of endocarps that germinate (i.e., emergence of at least one aboveground seedling) and produce an established seedling in all three habitats (results in Appendix A). For the predation experiment, we monitored 3150 endocarps across all three years and habitats to create an average level of ant predation for each habitat. Ant predation resulted in a loss of most seeds within the endocarp. For the germination and seedling survival experiment, in 2006 we sowed 40 endocarps per habitat in three habitats, with 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 with 25 replicates for each habitat). All of the sown endocarps were processed by *C. cyanomelas* (Loayza 2009).

To compare the demography and population growth rate between forest islands and woody patches, we conducted prospective (elasticities) and retrospective (life table response experiment) analyses (Appendix B).

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 (based on our observational data of the dispersers of *G. viburnoides*), and differential emergence of seeds based on whether endocarps were processed by birds and by which species (based on the greenhouse experiments previously described).

We began the model with 1000 *G. viburnoides* individuals in the population, distributed unequally between habitats and stage classes based on the relative abundances of individuals found naturally at our study site when we subsampled the population for the demographic data collection (we note, however, that reasonable deviations in the starting number of individuals and stage and habitat distributions do not influence the qualitative results of the study). Specifically, the initial population size can be described by the following matrix:

$$\begin{bmatrix} 27 & 360 & 28 \\ 26 & 249 & 50 \\ 9 & 98 & 30 \\ 3 & 86 & 12 \\ 5 & 17 & 0 \end{bmatrix}$$

where columns represent the three habitat types (forest islands, woody patches with *G. viburnoides*, and woody 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 are modeled to 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. 2). Adult plants reproduce with probability r . All reproductive adult plants produce 1981 endocarps (see Appendix A). 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 in this model depends on the species of seed disperser and the habitat, and these parameters are described in Appendix A (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 five 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: emergence probabilities of seeds in endocarps processed by *P. castanotis*/emergence probabilities of seeds in endocarps processed by *C. cyanomelas* \times emergence probabilities of seeds in forest islands. Germination parameters are presented in Appendix A (parameters g_{ii} , g_{ji} , g_{ni} , g_{ig} , 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, woody patches without *G. viburnoides* are likely to transition into woody 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 woody 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.

To project the population size of *G. viburnoides* into the future in the presence of normal seed disperser dynamics (both quantitatively important dispersers 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 time 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 $p_t = 0$), absence of only *C. cyanomelas* ($p_j = 0$), and absence of both quantitatively important dispersers ($p_t = p_j = 0$). Thus, in our model we assumed that when one of the dispersers was absent, the proportion of fruits that this species removed was not removed by the remaining species; instead those fruits remained as nondispersed. This assumption was based on the fact that 23% of the fruits remained nondispersed at the end of the fruiting season, with all dispersers present, suggesting that 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

Field survivorship patterns revealed that, 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 5–6 times more likely to transition to saplings in woody patches with and without *G. viburnoides*, respectively, than in forest islands (Fig. 2). Seedlings were also more likely to lose all their foliage and resprout the next year in forest islands than in the other two habitats, which suggests a higher probability of aboveground 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 2.0 times lower, respectively, in forest islands than in woody patches. In the absence of dispersal, modeled population growth rate is 0.93 in forest islands and 1.07 in woody patches (Appendix B). Life table response experiments indicate that this difference is primarily due to higher growth of seedlings and small trees in woody patches, as well as higher fertility of adult trees (Appendix B). These results strongly indicate that, compared to woody 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 woody patches with and without *G. viburnoides*, with two exceptions. First, the probability that small trees would die aboveground and resprout the

next year was three times higher in woody patches with *G. viburnoides* than without it. Second, sprouts were twice as likely to die and resprout the following year in woody patches without *G. viburnoides* than with it. Except for those differences, woody patches with and without *G. viburnoides* had comparable demographic vital rates.

Individual-based model

The values for the parameters that we used for the model (Appendix A) are developed 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 quantitatively important dispersers (QID) in the next 10 years (Fig. 3). Interestingly, the population can grow even in the scenario for which neither of the quantitatively important dispersers is present (i.e., no seed dispersal). Highest population growth (almost a fourfold increase) is predicted to occur in the scenario in which only *C. cyanomelas* consumes the fruits and disperses the seeds, whereas negative growth is predicted to occur if the fruits of *G. viburnoides* are solely consumed by *P. castanotis* (Fig. 3).

When we examined the effects of seed dispersal for each habitat separately, the population trajectories varied among habitats for each scenario (Fig. 4). Predicted population trajectories in woody patches with *G. viburnoides* paralleled those at the landscape level; the population was projected to grow under all scenarios, except if seeds were dispersed only by *P. castanotis*. After 10 years, modeled 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. 4A). In woody patches without *G. viburnoides*, seed dispersal was not sufficient to sustain modeled population size. Therefore, over time the model projected that the total number of individuals would decline in all scenarios (Fig. 4B); this result suggests severe dissemination limitation into woody patches without *G. viburnoides*. The modeled population declines toward zero if no quantitatively important dispersers are present or if fruits are solely consumed by *P. castanotis*, because in this habitat all *G. viburnoides* are small, nonreproductive plants, and the only influx of seeds is provided by *C. cyanomelas*. Seed dispersal by *C. cyanomelas* into woody patches without *G. viburnoides*, however, is so low that the model does not project any positive population growth. Nonetheless, if seeds are dispersed only by *C. cyanomelas*, following an initial decrease in the number of individuals occurring in this habitat, modeled population size appears to stabilize (Fig. 4B). 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 quantitatively important dispersers (Fig. 4C).

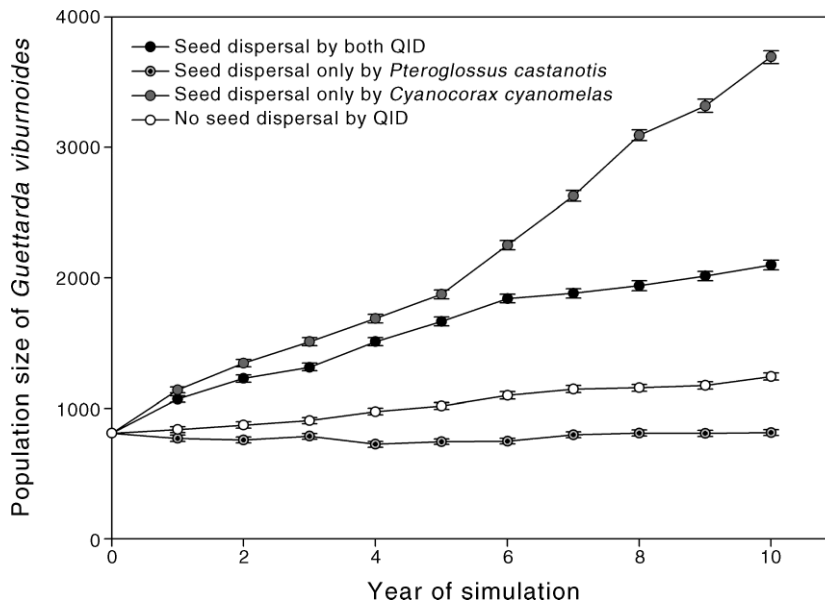


FIG. 3. Projected population trajectories of *G. viburnoides* at the landscape level in four seed disperser scenarios. In each year, the mean and 95% confidence intervals are shown from 1000 runs of our individual-based model. Purplish Jays (*Cyanocorax cyanomelas*) are pulp consumers; the Chestnut-eared Araçari (*Pteroglossus castanotis*) is a “legitimate” seed disperser; both are considered quantitatively important dispersers (QID).

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 projected population growth of this species. To our knowledge, this is the first study to report negative effects of a “legitimate seed disperser” (sensu Traveset 1994) 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*. *Cyanocorax cyanomelas* is a pulp consumer that deposits 99% of the endocarps in woody patches with a fruiting adult (Loayza 2009). Therefore, to the extent that one of the advantages of seed dispersal is hypothesized to be 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 can be

regarded as a noneffective disperser. *Pteroglossus castanotis*, in contrast, is typically regarded as an effective disperser because it swallows and defecates 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 et al. 1985, Howe 1993, 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 these expectations; the success of seeds taken by *C. cyanomelas* is ultimately higher than those taken by *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 germination in other species may be enhanced after a seed has passed through a vertebrate’s gut (Traveset 1998, Bas et al. 2006, Traveset et al. 2007), this was not the case in our system. Our results concur with the results of Domínguez-Domínguez et al. (2006), who show that seed ingestion by another species of toucan also lowers germination in the Neotropical tree *Ficus insipida*. Conversely, pulp removal by *C. cyanomelas* leads to higher emergence rates than for endocarps processed by *P. castanotis* or not processed by frugivores. Second, in our system, *P. castanotis* disperses 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 woody patches. Additionally, even though *C. cyanomelas* deposits the vast majority of the endocarps under the parent or a conspecific tree, the remaining 1%

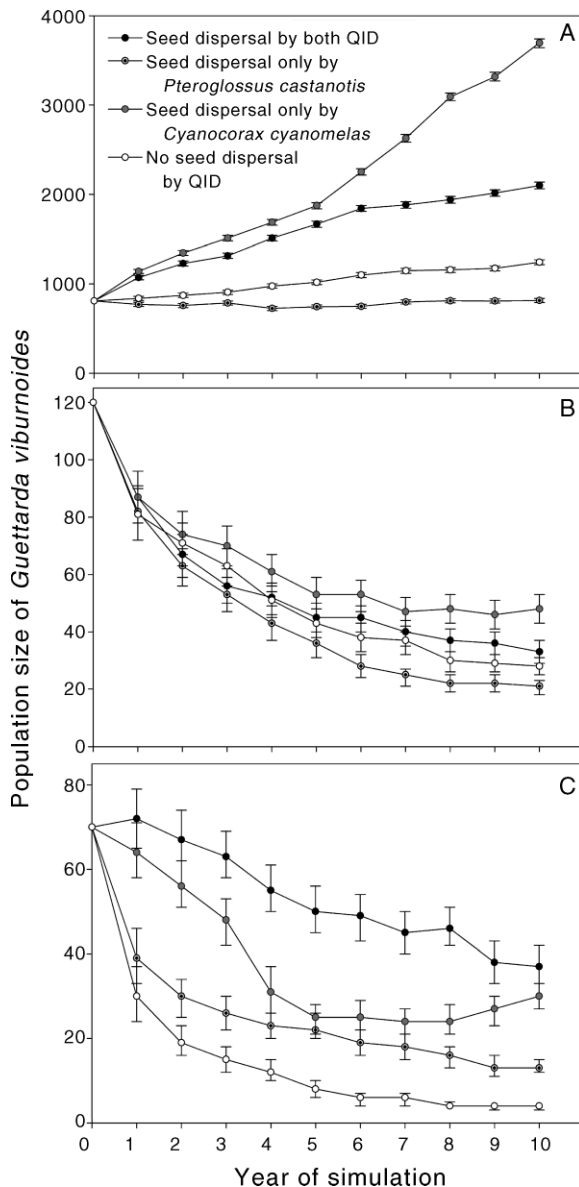


FIG. 4. Projected population trajectories of *G. viburnoides* under four seed dispersal scenarios in three habitats: (A) woody patches with an adult *G. viburnoides*; (B) woody patches without an adult *G. viburnoides*; and (C) forest islands. In each year, the mean and 95% confidence intervals are shown from 1000 runs of our individual-based model. QID refers to the two quantitatively important dispersers.

are dispersed to woody 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 suggests that rare dispersal events, which are often accidentally neglected in empirical studies, may have critical consequences for plant population dynamics. However, the effects of these rare dispersal events might be best examined in a model that includes longer time intervals and takes into account extinction and colonization dynamics.

Dissemination limitation and the spatial distribution of G. viburnoides.—Our individual-based model projects that, at the landscape level, the population of *G. viburnoides* grows 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 for the spatial distribution of this species.

First, even with the dispersal services provided by both quantitatively important dispersers, the population of *G. viburnoides* is strongly dispersal limited (Jordano and Godoy 2002); 98% of 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 woody patch with an adult tree present could eventually be the offspring of the resident maternal tree, and would result in spatial isolation of close relatives, eventually leading to within-patch reduction of genetic diversity (Jordano and Godoy 2002, Holbrook 2006). *Guettarda viburnoides* is an outcrossing species, presumably pollinated by night-active moths (Charlotte Taylor, Missouri Botanical Gardens, *personal communication*); 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, *G. viburnoides* plants of all stage classes frequently die in woody patches due to the yearly fire regime in the study area; therefore, without seed dispersal, and specifically without seed dispersal by *C. cyanomelas* to woody patches without *G. viburnoides* as they become available, eventually the population size of this species may be significantly reduced.

The effects of dissemination limitation in the landscape can also be determined by examining the projected population trajectory in woody 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 is projected to occur in this habitat with time reveals that new recruitment is limited by seed dispersal. Further exploration of these results (not shown) indicates that small increases in seed dispersal by *C. cyanomelas* to patches without adult *G. viburnoides* (from 1.1% to 4%) 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 woody 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; 3–4% of the dispersed seeds arrive at woody 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 woody patches without *G. viburnoides* may be very important for population growth in the landscape.

Density dependence and projected population growth of G. viburnoides.—Although, at the landscape level, the population is predicted to grow within the first 10 years in all but one scenario, environmental constraints are likely to limit population growth. Specifically, the woody patches where *G. viburnoides* occurs are sites where woody species can establish because they are above the floodwaters during the wet season. These habitats have a limited area, and generally cannot expand because the surrounding savanna is submerged for 4–8 months per year. This suggests that each woody patch probably holds a certain carrying capacity of trees and shrubs, and additional recruits will be unable to establish unless other plants in the woody patch die. Therefore, at the patch level, it is likely that density-dependent processes strongly limit the population size of *G. viburnoides*. Because in our model we did not explicitly consider the effects of density dependence, it is possible that the projected population size in woody patches with *G. viburnoides* may be overestimated, particularly for the smaller stage classes and over longer timescales.

In the scenario where highest population growth occurs (i.e., dispersal only by *C. cyanomelas*), a population of 1000 individuals is projected to increase to ~4000 individuals after 10 years, of which 49 are adults (starting with 22 adults in the population; results not shown). At our study site, the majority of the woody patches with *G. viburnoides* (>95%) have only one adult *G. viburnoides* tree, suggesting that these habitats have a carrying capacity of one adult. Given this, population growth of *G. viburnoides* at the landscape level will occur via colonization events of “empty” available habitats (i.e., woody patches without adult *G. viburnoides*) rather than by the establishment of new adults in already “occupied” woody patches. Therefore, recruitment of adult *G. viburnoides* trees in the landscape will be limited by the availability of woody patches without *G. viburnoides* in the landscape. Currently, more than half of the woody patches at the study site do not have an adult *G. viburnoides* tree, and over three years the turnover rate of patches without *G. viburnoides* to patches with *G. viburnoides*, and vice versa, was approximately equal. Therefore, it is feasible that the study area can sustain the projected increase in the number of adults (122%) over 10 or more years.

Assumptions of the model.—We emphasize caution when interpreting results of models with assumptions that can limit 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 that 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 population growth.

Nonetheless, the strength of this modeling approach lies in its ability to compare the potential effects of different frugivores on the population trajectory of *G. viburnoides*, rather than in accurately predicting the population size of this species over 10 years. In models such as this, the qualitative patterns (i.e., relative rankings of different dispersers) are more useful than the actual values (Godínez-Alvarez and Jordano 2007).

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 about 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 on plant fitness. Considering its disproportionate influence on the recruitment dynamics of *G. viburnoides* in our study area, we conclude that *C. cyanomelas* is a key species for the persistence of this tree. Moreover, the dispersal services provided by *P. castanotis* are not ecologically equivalent to those of *C. cyanomelas*.

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 valuable for plant ecology. Such models enable us

to close the “seed dispersal loop” (Wang and Smith 2002) 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.

ACKNOWLEDGMENTS

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, Eugene Schupp, and two anonymous reviewers helped improve an earlier version of this manuscript.

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APPENDIX A

Parameters used to develop the individual-based model of the consequences of seed dispersal of *Guettarda viburnoides* by *Cyanocorax cyanomelas* and *Pteroglossus castanotis* (*Ecological Archives* E091-192-A1).

APPENDIX B

Demographic matrices, elasticity matrices, and life table response experiments (LTRE) for two habitats of *Guettarda viburnoides* in a neotropical savanna using three years of demographic data, 2005–2008 (*Ecological Archives* E091-192-A2).