

Disentangling the drivers of reduced long-distance seed dispersal by birds in an experimentally fragmented landscape

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Abstract. Seed dispersal is a crucial component of plant population dynamics. Human landscape modifications, such as habitat destruction and fragmentation, can alter the abundance of fruiting plants and animal dispersers, foraging rates, vector movement, and the composition of the disperser community, all of which can singly or in concert affect seed dispersal. Here, we quantify and tease apart the effects of landscape configuration, namely, fragmentation of primary forest and the composition of the surrounding forest matrix, on individual components of seed dispersal of *Heliconia acuminata*, an Amazonian understory herb. First we identified the effects of landscape configuration on the abundance of fruiting plants and six bird disperser species. Although highly variable in space and time, densities of fruiting plants were similar in continuous forest and fragments. However, the two largest-bodied avian dispersers were less common or absent in small fragments. Second, we determined whether fragmentation affected foraging rates. Fruit removal rates were similar and very high across the landscape, suggesting that *Heliconia* fruits are a key resource for small frugivores in this landscape. Third, we used radiotelemetry and statistical models to quantify how landscape configuration influences vector movement patterns. Bird dispersers flew farther and faster, and perched longer in primary relative to secondary forests. One species also altered its movement direction in response to habitat boundaries between primary and secondary forests. Finally, we parameterized a simulation model linking data on fruit density and disperser abundance and behavior with empirical estimates of seed retention times to generate seed dispersal patterns in two hypothetical landscapes. Despite clear changes in bird movement in response to landscape configuration, our simulations demonstrate that these differences had negligible effects on dispersal distances. However, small fragments had reduced densities of *Turdus albicollis*, the largest-bodied disperser and the only one to both regurgitate and defecate seeds. This change in *Turdus* abundance acted together with lower numbers of fruiting plants in small fragments to decrease the probability of long-distance dispersal events from small patches. These findings emphasize the importance of foraging style for seed dispersal and highlight the primacy of habitat size relative to spatial configuration in preserving biotic interactions.

Key words: Amazonian rain forest; dispersal kernels; frugivory; habitat fragmentation; *Heliconia acuminata*; manakins; Manaus, Brazil; patch size; spatially explicit model; thrush; tropical forest; *Turdus albicollis*.

INTRODUCTION

Seed dispersal is a crucial component of plant population dynamics (Levine and Murrell 2003). In the temperate zone, 25–40% of plant species depend on frugivores for seed dispersal, whereas in tropical rain forests, up to 90% of woody species do (Gentry 1982,

Willson et al. 1989, Jordano 1992, Tiffney and Mazer 1995). Despite the critical role frugivores play in the organization of plant communities, general principles about the effects of animal disperser agents on plant populations and communities remain elusive (Carlo and Morales 2008). In part, this is because patterns of seed deposition are an emergent property of disperser–plant interactions resulting from individual- and species-level frugivore behavior (Schupp et al. 2002), the composition of the disperser community (Clark et al. 2005), the spatial distribution of food resources (Morales and Carlo 2006, Carlo and Morales 2008), and landscape

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structure (Levey et al. 2005). All of these factors can vary over space and time, often in unexpected ways.

Frugivore behavior can shape plant populations in myriad ways. Individuals often track the location of fruit resources in space and time (Levey et al. 1984; but see Lehouck et al. 2009a), responding to crop size and the spatial distribution of resources at the landscape level (Farwig et al. 2006, Morales and Carlo 2006). Frugivores may move shorter distances when resources are spatially clustered (Carlo and Morales 2008). In addition, forager density (Carlo and Morales 2008), interactions among dispersers (Schupp et al. 2002), and their nonrandom use of space (Russo et al. 2006) could influence the quantity of seeds dispersed at different distances from parent plants and the shape of the dispersal kernel (Schupp et al. 2002). For example, certain vertebrate vectors may prefer particular microhabitats (e.g., lekking sites), or defecate or consume fruits at specific locations such as roosts (e.g., Russo et al. 2006). These behaviors can shape the spatial configuration of fruit removal (Carlo and Morales 2008) and dispersal-related gene flow (Loiselle et al. 1995).

Plants are commonly visited by several dispersal vectors (Wheelwright et al. 1984, Jordano et al. 2007). Analyses of frugivore communities have demonstrated species-specific differences in visitation rates, fruit removal, and post-feeding behavior, which can result in distinct spatial signatures for different dispersal vectors (Schupp et al. 2002, Clark et al. 2005, Jordano et al. 2007, Lehouck et al. 2009b). In general, large vertebrates (e.g., monkeys) can ingest large numbers of seeds and disperse them over long distances. In contrast, smaller animals (e.g., small birds, ants) typically deposit seeds next to the source plants and, for animals ingesting seeds, have faster regurgitation or defecation times (Clark et al. 2005, Jordano et al. 2007).

Theoretical and empirical studies have demonstrated that landscape heterogeneity such as fragmentation and habitat loss can reduce long-distance dispersal for wind-dispersed species (Higgins et al. 2003, Soons et al. 2005). Landscape heterogeneity can also alter fruit availability (Soons et al. 2005, Farwig et al. 2006, Cordeiro et al. 2009), disperser abundance (Bierregaard and Lovejoy 1989, Moran et al. 2009), disperser behavior (Jordano and Schupp 2000, Clark et al. 2005, Lehouck et al. 2009c), and interspecific interactions (Gonzalez-Varo 2010); these changes can act singly or in concert to influence patterns of seed deposition and seedling establishment for animal-dispersed species (Lehouck et al. 2009a, b), often in unexpected ways. For instance, fragmentation increased fruit availability, frugivore visitation rates, and seed removal in a number of studies (Cordeiro and Howe 2003, Farwig et al. 2006, Valdivia and Simonetti 2007) but can also lead to reduced dispersal (Lehouck et al. 2009a). Given the percentage of tropical plant species disseminated by animal vectors, and the rate at which tropical landscapes are undergoing

deforestation and fragmentation, understanding disperser responses to landscape features is particularly critical in tropical ecosystems. The maintenance of plant populations in habitat fragments and other altered tropical landscapes will require evaluation of the factors that shape animal-plant interactions and the role of animal movement and foraging behavior on seed dispersal and seedling recruitment (Morales and Carlo 2006).

Research on the mechanistic basis of seed dispersal has often relied on simulation models that vary considerably in the amount of field-based data used for calibration (e.g., Higgins et al. 2003, Carlo 2005, Levey et al. 2005, Russo et al. 2006). However, few of these studies have addressed how anthropogenic habitat modification alters seed dispersal; those that have done so limit themselves to examining how a single landscape feature (e.g., the presence of corridors) influences dispersal (e.g., Levey et al. 2005). Other studies have quantified the ultimate effects of landscape configuration on seedling recruitment without attempting to disentangle the relative contributions of different components of dispersal (e.g., fruit abundance, disperser abundance, disperser behavior) to the observed decline in establishment (e.g., Bruna 2002; but see Cordeiro et al. 2009, Lehouck et al. 2009b). Yet, understanding how landscape modifications influence different components of disperser-plant interactions is critical to the development of effective management or conservation schemes.

Here, we examine how anthropogenic landscape modifications influence the dispersal of seeds of the Amazonian herb *Heliconia acuminata* (Heliconiaceae). To do so, we collect data on plant distribution, fruit abundance, and the composition, abundance, foraging behavior, and movement of bird dispersers of *H. acuminata* in an experimentally fragmented Amazonian landscape. Using these data, we develop an individual-based, spatially explicit mechanistic model to estimate seed dispersal kernels and to simulate vector movement and seed dissemination in heterogeneous landscapes. We address the following questions: (1) How does landscape configuration, namely the size of isolated primary forest fragments and the composition of the surrounding forest matrix, affect fruit availability and bird disperser diversity, abundance, and behavior? (2) What are the implications of these effects for the dispersal of *H. acuminata* seeds at the landscape scale?

MATERIALS AND METHODS

Study site and data collection

The study was conducted at the Biological Dynamics of Forest Fragments Project (BDFFP; Laurance et al. 2002), located ~80 km north of Manaus, Brazil (2°30' S, 60° W). The BDFFP is composed of replicated forest fragments of 1, 10, and 100 ha that were originally isolated in the early to mid-1980s by the establishment of cattle pastures on three farms (Appendix A: Fig. A1). For this study we used the 1-, 10-, and 100-ha fragments

at Dimona and Porto Alegre farms and continuous forest sites at all three farms. Structurally, the interiors of 100-ha fragments are similar to those of continuous forest sites away from forest edges. Since isolation, 1-ha and 10-ha fragments have undergone structural deterioration, and secondary forests have colonized the abandoned pastures surrounding fragments (Laurance et al. 2002). The BDFFP landscape is now a mosaic of primary forest and secondary regrowth, with marked habitat boundaries between adjacent cover types.

Focal species.—*Heliconia acuminata* (Heliconiaceae) is a perennial, understory monocot native to central Amazonia and the Guyanas (Berry and Kress 1991). Flowering begins in late January and fruit production continues through April; during this time it is the most abundant fruiting plant in the understory (Bruna and Kress 2002). Most reproductive plants have one inflorescence with 20–25 flowers. Each flower produces a maximum of three seeds $\sim 7 \times 5$ mm in size. The seeds germinate 6–7 months later at the onset of the rainy season, and seeds rarely germinate beyond the first rainy season (Bruna 2002). The nutritional content (protein and lipid) of *H. acuminata* fruits is 2–3 times that of other fruits consumed by this plant's avian dispersers (S. Hashimoto, *unpublished data*); their superior nutritional content and abundance make them a key resource for the community of understory avian frugivores. Although *H. acuminata* can germinate and grow in regenerating secondary forests, densities in this habitat are an order of magnitude lower than in adjacent primary forests (Bruna and Nogueira Ribeiro 2005). More importantly, adult plants rarely become reproductive in secondary forests and are unlikely to be a seed source for the disperser community (E. M. Bruna and A. Segalín de Andrade, *unpublished data*).

The seeds of all *Heliconia* species are exclusively dispersed by birds (Berry and Kress 1991). In our study sites, the primary dispersers are the White-necked Thrush (*Turdus albicollis*), the Thrush-like-Manakin (*Schiffornis turdinus*), and several species of manakin (*Pipra erythrocephala*, *Pipra pipra*, *Lepidothrix serena*, *Corapipo gutturalis*). The mating season of the dispersers does not overlap the period over which *H. acuminata* flowers and fruits (M. Anciães, *personal observation*).

Data collection.—Characterizing the effects of landscape configuration (i.e., the size of forest fragments and composition of the surrounding matrix habitat) on dispersal of *H. acuminata* seeds requires four distinct steps: first, identifying the effects of fragmentation on the abundance of bird dispersers and fruiting plants; second, determining how fragmentation affects rates of seed removal; third, quantifying how landscape structure influences bird movement, and finally, linking movement with empirical estimates of seed retention times to estimate a mechanism-based seed dispersal distribution. The fieldwork, observations, and experiments used to complete these four steps were conducted during 2007 and 2008.

1. *Effect of fragmentation on frugivore and fruiting plant abundance.*—We estimated bird abundance using both point-count censuses and mist-net sampling. Counts for a 30 m radius were conducted from 05:30 to 09:30 hours, a period of high bird activity, in transect lines with points 200 m apart. Each point was sampled for 5 min using the double-observer dependent design; we estimated species abundance using the software package DOBSEV (Nichols et al. 2000), which accounts for the probability of detection. Mist-net data were collected from June through December 2007 using the BDFFP bird-sampling protocol (Bierregaard and Lovejoy 1989). Estimates of abundance from mist-net data were based on capture rates (i.e., number of birds captured/100 mist-net-hours).

Our questions focus on the functional aspects of habitat use, i.e., characterizing the number of individuals and the frequency at which they use an area. Capture rates represent a more reliable indicator of bird activity than point-count censuses, which focus on the number of individuals present in an area. To describe the functional aspects of bird movement while retaining information about bird densities in our experimental landscapes, we calculated the ratio of capture rates to the number of individuals captured by species (captures : individuals) in mist nets at each area, and then corrected the point-count estimates for each species at each study area. This approach could be problematic if our goal was to quantify capture rates across species. However, our goal here is to compare differences within species in the scale and frequency of movement across habitats (e.g., primary forest and secondary matrix). Moreover, we are dealing with only a few passerine species, mostly from the same family, and therefore with quite similar behaviors and spatial and temporal habitat use patterns.

Fruit abundance at our study sites was quantified using data collected between 1998 and 2007 from a long-term demographic study of *H. acuminata* at the BDFFP (described in Bruna and Kress 2002). In January 1998, a series of permanent demographic plots (each 50×100 m) were established in 13 of the BDFFP reserves: $n = 6$ plots in continuous forest, $n = 3$ in 10-ha fragments, and $n = 4$ in 1-ha fragments (Appendix A: Fig. A1). All *H. acuminata* were measured (i.e., height and number of stems) and were permanently marked with an aluminum tag; since their establishment, the plots have been surveyed annually, and the number and size of flowering plants has been recorded for all plots.

2. *Effect of fragmentation on rates of fruit removal.*—To estimate fruit removal rates in the BDFFP landscape, we marked and monitored *H. acuminata* fruiting plants from January through June of 2008 in a subset of the study sites (Table 1). We randomly chose trails from a grid system in the study areas along which we searched for *H. acuminata* plants. All plants found along the trail were marked and mapped. Depending on the availability of fruiting plants, we marked 4–40 plants per reserve, for a total of 125 plants across the six sampled areas

TABLE 1. Fruit production and removal rates of *Heliconia acuminata* in 2008 throughout the study landscape in the Biological Dynamics of Forest Fragments Project (BDFFP), near Manaus, Brazil.

Farm	Area (ha)	Area code	No. plants monitored	Fruit production		Removal rates (% removed)	
				No. fruits	Ripe fruits (%)	Total fruits	Ripe fruits
Dimona	1	2107	7	89	86.2	45.5	88
Dimona	1	2108	NA	76	NA	NA	NA
Dimona	10	2206	14	125	69.6	68.8	98.9
Dimona	100	2303	40	569	11.8	9.7	82.1
Dimona	CF	CF-4	NA	NA	NA	NA	NA
Esteio (km41)	CF	1501	40	943	13.2	12.6	95.2
Porto Alegre	1	3114	4	77	82	48.1	92.5
Porto Alegre	10	3209	20	414	40.1	38.6	97
Porto Alegre	100	3304	NA	158	NA	NA	NA
Porto Alegre	CF	CF-5	NA	NA	NA	NA	NA

Notes: Plant abundance refers the overall density estimated from 0.5-ha and 0.2-ha plots sampled in each forest for 2008 (Fig. 1); NA indicates that data were not available. Fruit production indices (percentage ripe fruits) were estimated from plots established and sampled in 2008 as part of this analysis. See *Methods: Effect of fragmentation on frugivore and fruiting plant abundance* for methodological details. Area codes are the identification numbers assigned by the BDFFP to each reserve (for additional details, see Bruna and Kress [2002]).

(Table 1). Plants were monitored every 15–20 days, at which time we recorded phenological status, the number of fruits at each stage of development (e.g., green, ripe), and the number of undeveloped ovaries and rotten or destroyed fruits. Total ripe fruit production was estimated as the number of ripe fruits at the last visit plus the number of removed fruits, which we determined by using the characteristic cleaving pattern that results from bird foraging.

3. *Quantifying how landscape structure influences bird movement.*—To quantify the movement patterns of birds in the BDFFP landscape, we radio-tracked birds in continuous forest sites on Esteio farm and in fragments of 1-, 10- and 100-ha at both Dimona and Porto Alegre (Appendix A: Table A1). We captured birds with mist nets and attached radios (0.60 or 0.72 g, based on body mass of birds; Holohil Systems B and BX models, Holohil, Carp, Ontario, Canada) around the birds' legs and back using a harness of 0.1-mm organic surgical string. Birds were released where they were captured, tracked with a receiver (R-100FM ATS, Advanced Telemetry Systems, Isanti, Minnesota, USA) and a three-foldable antenna (ATS Inc.), and their locations recorded with a Global Positioning System (Garmin Etrex Vista HCx; Garmin International, Olathe, Kansas, USA) at 5-min intervals. We followed three birds each day; each was tracked for two consecutive hours per day. We gave priority to time periods of known high bird activity (e.g., early-mid morning, mid-afternoon), and alternated survey periods among tracked individuals to cover the entire day for each individual. Birds were not tracked on rainy days. We radio-tracked 16 individuals; we followed each bird for an average of 15 days (range 1–17 days; Appendix A: Table A1). When birds were not visible to observers, we assumed that they were perched as long as the direction of the antenna reception did not change over time. Because signal reception does not vary with antenna direction below a threshold distance, for a constant receiver gain intensity

(e.g., less than ~20 linear m with receiver gain set to 8 units), we decreased receiver gain (down to 2) in order to allow for variation in signal intensity while changing antenna angle, so that we could detect slight, slow-speed changes in bird location within sampling periods and among close point locations. We spent every 5 min between consecutive registers trying to locate the focal individual. If the bird was sally-gleaning or flying from perch to perch, the signal was stable and we assumed that the bird was moving around a perching site. If the bird was flying, we ran after it so that we could find it in the subsequent 5 min to record its next location, or where it was stable. On a few occasions, we lost individuals that were moving fast, but most of the time we were able to locate them. We calculated perching times using consecutive location registers (multiples of 5-min intervals). We assigned habitat type (primary forest or secondary forest matrix, as well as fragment size when relevant) to each bird location point. We were unable to track *C. gutturalis* individuals. For our simulations, we assumed that their movement patterns paralleled those of other manakins.

4. *Estimating a mechanism-based seed dispersal distribution.*—A distribution of seed retention times was obtained experimentally for 39 birds representing five species (*C. gutturalis*, *P. erythrocephala*, *P. pipra*, *L. serena*, and *T. albicollis*) using a modification of Levey's (1987) method (Appendix B). Birds were captured using mist nets and were maintained in 1 × 1 × 1 m cages on a diet of mashed bananas, protein, and water until acclimated. Cages ($n = 4$) were isolated from neighboring cages by shade cloth. Paper sheets were placed at the bottom to recover regurgitated or defecated seeds. Following acclimation, each bird was initially presented with 6–10 *H. acuminata* fruits as well as other fruits with overlapping phenologies that make up their diet (e.g., Melastomataceae, Rubiaceae). One observer per cage began continuous observations at the moment the bird was placed in the cage and recorded changes in

behavioral states (i.e., stopped moving, started moving) or non-instantaneous behaviors (e.g., fruit consumption, defecation, regurgitation). We were unable to capture *S. turdinus* individuals for these experiments so we assumed that their seed passage rates resembled those of manakins. Given that the potential for long-distance dispersal is often associated with larger body sizes, this assumption would provide a conservative estimate for *H. acuminata* long-distance dispersal in the simulations.

We recorded the time elapsed from ingestion of the fruit to its regurgitation or defecation on the cage floor. Because *H. acuminata* fruits have multiple seeds (1.9 ± 0.02 seeds/fruit, mean \pm SE; $n = 873$ fruits), and birds regurgitated or defecated one seed at a time, we estimated the time for each seed to drop after a fruit was ingested. Experimental trials in which birds did not forage on *H. acuminata* fruits (25% of the individuals) were not included in our estimates. We assessed goodness of fit for the distributions of retention times using two metrics. First, we generated contingency tables of observed vs. predicted retention times by grouping predictions and observations into 5-min categories (i.e., 0–4.99, 5–9.99 min, and so on) and calculated χ^2 using these values. However, χ^2 is really a “badness-of-fit” statistic, and as such is unsatisfying. To address fit to the actual observed distribution, we also calculated R^2 for observed frequency of categories (e.g., regurgitation times) and to the fitted distributions.

Model construction

Our approach was to use fruit abundance and bird data together with seed retention times to parameterize a mechanistic seed dispersal model with the goal of simulating dispersal for *H. acuminata* in hypothetical landscapes. Here we describe the fitting procedures.

Parameter estimation.—To quantify the effects of forest fragmentation on bird movement, we developed statistical models that describe perching time between movements, movement length and speed, and movement direction as a function of the habitat that the bird was occupying (primary forest or second-growth matrix), and distance to the nearest habitat boundary in the nearest plant census plot (see *Data collection: Step 1*) (Levey et al. 2005). Habitat and distance to habitat boundary were correlated: birds inside primary forests were generally farther from forest–matrix boundary than birds in the matrix, so we removed distance to the boundary from the analyses. For all variables, we used AIC_c for model selection (Burnham and Anderson 2002). Following the principle of parsimony, we dropped covariates if the added complexity did not improve the likelihood of the model.

Perch times (in seconds) were initially calculated as the cumulative time that birds remained on a perch without detectable movement by the radio receiver device; perch times were exponentially distributed, $P(t) = 1/\lambda e^{[-t/\lambda]}$, where $1/\lambda$ is the perch time in seconds. However, birds often changed direction in flight without

perching (i.e., sally-gleaning foraging behavior). In our simulations, we needed to account for how these changes in direction might vary in response to habitat variation (e.g., habitat boundary proximity). For this reason, we included these zero values, which led to zero-inflated negative exponential distributions of perching times. We used maximum likelihood estimation to test for effects of habitat type (primary forest vs. secondary growth) and bird species on perch times.

The distance and speed of bird movements between perching points was calculated using Spatial Analyst 3.0 in ArcView 3.2 (ESRI 2000). To avoid biases in path length, we disregarded the distance between the points marked on different days, or when data collection was interrupted by more than 1 hour. Movement distance and speed data were fitted assuming lognormal distributions. We tested for dependence of path length and movement speed on habitat and bird species, both individual species and species guilds, using a generalized linear mixed model with individual as a random effect. *S. turdinus* has traditionally been placed in the manakin family. However, evidence strongly suggests that it is better placed in Tityridae; its body size is in between that of *T. albicollis* and the manakins. For our analyses, we relied on model comparison to assess the grouping for *S. turdinus* that was more consistent with the movement data.

We estimated two metrics of bird movement direction: change in direction between consecutive paths (i.e., turning angles) and path direction relative to the closest habitat boundary between forest and surrounding matrix. We calculated path direction (standard azimuth) and change in direction between consecutive moves as the minimum angular difference (in degrees) between bearings of consecutive paths.

To assess path direction relative to forest–matrix boundary, we used a 2006 Landsat satellite image (30-m resolution). We drew closed-shapes polygons to represent forests and open-shape polygons to represent the matrix, and then estimated bearings for each forest–matrix boundary. Direction of a path to the closest habitat boundary was determined for each path using bearing of the closest forest boundary in the landscape.

We used Von Mises (circular normal) distributions to describe the probability of movement direction x for a bird of a given species in a given habitat (primary forest vs. second-growth matrix) as

$$f(x|\mu, \kappa) = \frac{e^{\kappa \cos(x-\mu)}}{2\pi I_0(\kappa)} \quad (1)$$

where x are observed movement angles, μ determines the change in the modal or primary move direction (angle θ , 0–360°), and κ (0–Inf) controls dispersion. $I_0(\kappa)$ is the modified Bessel function of order 0. Low values of κ indicate random movement, while higher values indicate increased concentration of movement in the primary direction. As per Levey et al. (2005) and Schultz and

Crone (2001), we modified these two parameters for our analyses as follows.

A bird's change in primary move direction (μ) could depend on its previous move direction (θ_{t-1}), the bird's response to the habitat boundary, or some combination of both factors. We assessed the relative importance of these factors by testing five possible cases: (1) μ depends only on the previous move direction (i.e., the bird tends to keep traveling in the same direction it has been traveling) ($\mu = \theta_t - \theta_{t-1}$); (2) μ is parallel to the nearest habitat boundary (with azimuth α) in a direction consistent with the previous move (i.e., the bird tends to follow along edges $\mu = \theta_t - \alpha$); (3) μ is perpendicular to the nearest habitat boundary in a direction consistent with the previous move (the bird tends to cross edges: $\mu = \theta_t - (\alpha + 90)$); (4) μ depends on both previous move direction and the nearest habitat boundary, moving parallel to that boundary or edge (a mix of cases 1 and 2, with μ_1 and μ_2 representing cases 1 and 2, respectively):

$$f(x|\mu_1, \mu_2, \kappa) = \beta \exp\left(\kappa \cos[\theta_{(t-1)} - \theta_t]\right) / (2\pi I_0(\kappa)) + (1 - \beta) \exp\left(\kappa \cos[x - \theta_t - \alpha]\right) / (2\pi I_0(\kappa)) \quad (2)$$

and (5) μ depends on both previous move direction and the nearest habitat boundary, moving perpendicular to that edge (a mix of cases 1 and 3, with μ_1 and μ_2 representing cases 1 and 3):

$$f(x|\mu_1, \mu_2, \kappa) = \beta \exp\left(\kappa \cos[\theta_{(t-1)} - \theta_t]\right) / (2\pi I_0(\kappa)) + (1 - \beta) \exp\left(\kappa \cos[x - \theta_t - (\alpha + 90)]\right) / (2\pi I_0(\kappa)). \quad (3)$$

In cases 4 and 5, the movement probability is a weighted average of the direction vectors produced by the two cases being mixed, with the weighting factor β being an estimated parameter ranging from 0 to 1. If $\beta = 1$, the mixed case collapses to case 1; if $\beta = 0$, the mixed case collapses to either case 2 or case 3.

Simulations.—In the *Introduction*, we posed two questions. The first one focuses on differences among primary and secondary forests in fruit density and the abundance, behavior, and movement of birds. We answer this question by analyzing data collected at the site using statistical modeling tools. In some cases, response variables responded to fragment size (e.g., fruit abundance), whereas in others (e.g., movement direction or distance), the critical landscape driver was habitat (i.e., primary vs. secondary forest). To address the importance of these differences in seed dispersal, the response variables of interest, we employed landscape configurations that varied both in fragment size and in the surrounding matrix. We then used estimated

parameters from the most parsimonious model to conduct the simulations.

To assess the implications of the effects of fragmentation on fruiting plant abundance and on frugivore composition, abundance, and behavior, we used the results of the models to simulate *H. acuminata* seed dispersal as follows. Initial *H. acuminata* flowering plant abundance for 1-ha and 10-ha fragments and continuous forest were assigned from normal distributions derived from actual density data collected in long-term censuses (1998–2008) of the 13 0.5-ha permanent plots (See *Data collection: Step 1*). Most reproductive plants have one inflorescence with a total of 20–25 flowers (Bruna and Kress 2002); for the simulations we used 25 flowers per inflorescence. Although the number of flowers produced per plant did not vary with fragment size, fruit maturation rates declined with increasing fragment size, possibly due to differences in resource availability or pollination limitation, so we calculated separate fruit maturation rates for inflorescences in 1-ha and 10-ha fragments and continuous forest, CF (10-ha fragments are indistinguishable from CF) (CF mean = 25% of fruits ripened, $n = 2$ plots; 1-ha mean = 85% of fruits ripened, $n = 2$ plots; 10-ha mean = 55% of fruits ripened, $n = 2$ plots; Table 1). We assumed that each mature fruit produces a maximum of three seeds, based on the actual data (1.9 ± 0.02 seeds/fruit, mean \pm SE, $n = 873$ fruits). We used observed fruit removal rates for the simulations. Only ripe fruits were distributed.

Flowering plants were dispersed randomly across the simulated area. Although this could bias dispersal distances if fruit removal rates were affected by aggregation patterns, our analyses showed that fruit removal rates were independent of spatial aggregation of fruiting plants (data not shown). Initial bird abundances for each species were taken from point-count data adjusted by the activity ratio (Table 2), as described in *Data collection: Step 1*. Species identity for each individual was chosen using a random draw and observed proportional species abundance (Table 2). After each draw, relative species abundances were adjusted. Each fruit provided the starting location for one individual bird and simulations were conducted separately for each individual. We chose an initial move direction for each individual at random. Initial move length and speed were drawn from estimated lognormal distributions and were used to calculate flight time; initial perch times were drawn from the estimated zero-inflated distribution. Because the simulations started at the point when the individual eats a seed, we randomly chose whether or not the seed would be dropped through regurgitation or defecation, according to species-specific probability distribution of retention times. Seed retention times were calculated according to the seed drop event type and disperser. Bird location and seed retention times were then

TABLE 2. Bird abundances (means, with SE in parentheses) estimated by point-count (PC) census, mist-net capture-rate data (CR), and point-count data adjusted by capture rates (PC-adj.) in 1-, 10-, and 100-ha forest fragments and continuous forests (CF).

Forest size	Metric	<i>C. gutturalis</i>	<i>L. serena</i>	<i>P. erythrocephala</i>	<i>P. pipra</i>	<i>S. turdinus</i>	<i>T. albicollis</i>
1-ha ($n = 2$)	PC	4.86 (3)	0.97 (0.06)	3.53 (1.1)	1.94 (0.9)	0	0.1 (0.1)
	CR	0.05 (0.03)	0.95 (0.2)	0.86 (0.1)	1.9 (0.5)	0	0.06 (0.02)
	PC-adj.	4.86 (3)	4.09 (0.9)	5.88 (0.8)	8.18 (2.1)	0	0.39 (0.2)
10-ha ($n = 2$)	PC	0.94 (0.04)	0.44 (0.2)	0	0.5 (0.03)	0	0.1 (0.02)
	CR	0	0.57 (0.15)	0.35 (0.01)	2.67 (0.06)	0	0.12 (0.03)
	PC-adj.	0.49 (0.2)	2.11 (0.08)	1.49 (0.03)	11.47 (2.01)	0	0.9 (0.03)
100-ha ($n = 2$)	PC	0.42 (0.1)	0.208 (0.1)	0.42 (0.15)	0.21 (0.1)	0.21 (0.1)	0.21 (0.1)
	CR	0.04 (0.01)	0.34 (0.01)	0.14 (0.04)	0.73 (0.1)	0.08 (0.02)	0.11 (0.06)
	PC-adj.	0.26 (0.1)	0.95 (0.2)	0.4 (0.03)	3.1 (0.5)	0.34 (0.1)	0.21 (0.06)
CF ($n = 3$)	PC	0.48 (0.2)	0.58 (0.2)	0.63 (0.02)	0.29 (0.02)	0.23 (0.02)	0.48 (0.2)
	CR	0.07 (0.01)	0.41 (0.04)	0.19 (0.03)	1 (0.08)	0.19 (0.04)	0.25 (0.07)
	PC-adj.	0.55 (0.12)	1.59 (0.17)	1.29 (0.3)	4.29 (0.3)	0.98 (0.3)	0.78 (0.2)

Notes: Sample size ($n = 2$ or 3) is the number of permanent demographic plots (each 50×100 m). Capture rate is the number of captures per 100 mist-net-hours, approximately 12 days of bird activity at one net. Point-count adjusted abundance is the number of individuals/ha adjusted by the ratio of captures : individuals from mist-net data; see *Methods: Step 1: Effects of fragmentation on frugivore bird abundance*.

updated and the individual's movement continued until the seed retention time had been reached. We continued the simulations until we reached the rates of observed fruit removal for *H. acuminata* in each habitat.

We conducted the simulations in two hypothetical landscapes: (1) dispersal from 1-ha and 10-ha primary forest patches embedded within a primary forest matrix; and (2) dispersal from 1-ha and 10-ha primary forest patches surrounded by a secondary forest matrix. We chose these hypothetical landscapes because they allow us to separate area effects on the population size of fruiting plants, and therefore on seed dispersal, from effects resulting from changes in disperser relative abundance or behavior among habitats. Each simulation was replicated 20 times. Average mean and maximum dispersal distances for the 20 replicate runs were calculated and compared using disperser identity or guild (e.g., small vs. larger birds) and landscape configuration (the two hypothetical landscapes) as fixed covariates.

To tease apart the effects of differences in fruit availability, and the abundance, activity and behavior of the bird disperser on mean and maximum seed dispersal, we conducted sensitivity analyses of simulation results. If simulated dispersal distances differed among the hypothetical landscapes, we conducted sensitivity analyses by equalizing one set of parameters for primary and secondary forest (e.g., movement distance, relative abundance of one of the bird dispersers) at a time. For instance, we could determine whether differences in mean and maximum dispersal distance were the result of differences between hypothetical landscapes in the relative abundance of *Turdus albicollis*. This approach allowed us to identify the critical drivers of differences in dispersal between experimental landscapes. All analyses and simulations were conducted using R statistical software (R Development Core Team 2008).

RESULTS

Effects of landscape configuration on plant and disperser abundance, foraging behavior, and movement

Flowering plant abundance.—We used data collected in censuses of 13 permanent plots (each 50×100 m) from 1998 to 2007 to estimate the density of *Heliconia acuminata* flowering plants in the landscape. There was considerable variation in the average abundance of flowering plants between plots in continuous forest and 1- and 10-ha fragments (for CF, 32.54 ± 32.22 flowering *H. acuminata* plants/plot, mean \pm SD, $n = 6$ plots; for 10-ha, 19.79 ± 22.71 flowering plants/plot, $n = 3$ plots; for 1-ha, 8.6 ± 7.87 flowering plants/plot, $n = 4$ plots) but means were not significantly different at $\alpha = 0.05$. Nevertheless, we used these estimates to draw initial plant abundance in the simulations.

Frugivore bird abundance.—Mist-net capture rates and point-count values are not directly comparable because effective survey areas differ between methods; however, both methods provided consistent results, indicating increased abundance of manakins in forest fragments (Table 2). In contrast, mist-net capture rates for the thrush *T. albicollis* were higher in continuous forest and the Thrush-like-manakin (*S. turdinus*) was only detected in continuous forest. For the simulations, we used mean values of point-count data adjusted by mist-net captures (Table 2; see *Data collection: Step 2* for details).

Foraging rates.—We quantified fruit removal rates for 141 *H. acuminata* plants across the six sampled areas (Table 1). In total we tracked 2717 *H. acuminata* fruits in the field, of which approximately one-third were estimated to mature. Fruit removal rates were not affected by fragment size, so we averaged data for all plots ($92.28\% \pm 6.27\%$ fruits removed, mean \pm SD, $n = 8$ plots).

Bird movement.—To quantify the effects of landscape configuration on bird movement, we developed statisti-

cal models that describe perching time between movements, movement length, speed, and direction as a function of disperser position in primary vs. secondary forest and distance to the habitat boundary, and we used model comparison to identify the most parsimonious model. Here we provide results for each of these components of movement.

1. *Perch times*.—Best models included species groups (thrush vs. all other species) and habitat type, indicating a substantial increase in perch time in primary forest habitats relative to secondary growth (primary, 20.4 ± 3.99 s, mean \pm SE; secondary, 9.3 ± 1.47 s; when zeroes were excluded, 453 ± 77.34 s vs. 350 ± 23.92 s, respectively), and longer perch times for the thrush, but only when zeroes were included (with zeroes, 20 ± 3.61 s, mean \pm SE; without zeroes, 360 ± 23.35 s) relative to other dispersers (with zeroes, 13 ± 4.3 s; without zeroes, 453 ± 59.83 s) (Appendix C: Table C1). To capture these patterns, we fitted zero-inflated negative exponential distributions to the data (Appendix C: Table C1).

2. *Movement distance and speed*.—The best models included only habitat (primary vs. secondary forest) as a predictor of bird movement distance and speed (Appendix C: Tables C2 and C3). Birds flew longer distances in primary forest relative to the surrounding secondary forest matrix. To account for these differences, we fitted separate lognormal distributions for movement distance (originally measured in meters) in each habitat: $\log(\text{distance})$ mean = 2.95 (0.13 SD) and $\log(\text{distance})$ mean = 2.34 (0.13 SD), respectively. Birds also flew faster in primary forest relative to the surrounding secondary forest matrix (4.4 ± 0.18 m/min, mean \pm SE (primary forest) vs. 3.5 ± 0.19 m/min (secondary matrix), although maximum speed tended to be higher in secondary forests. To capture this variation, we fitted separate lognormal distributions for primary and secondary forest data: $\log(\text{flight speed})$ mean = 1.01 (0.93 SD) and $\log(\text{flight speed})$ mean = 0.54 (1.05 SD), respectively.

3. *Movement direction*.—We estimated three metrics of bird direction: path direction; change in direction between consecutive paths, and path direction relative to the closest boundary between forest and surrounding matrix. Most species followed a simple correlated random walk model of movement (Fig. 1 and Appendix C: Table C4). The only exception was the manakin *Lepidothrix serena*, which displayed greater propensity to move forward relative to the previous move and to cross into secondary forests in a direction perpendicular to the habitat boundary. Movement for this species was also more concentrated along the primary direction of movement in primary relative to secondary forest (Appendix D).

Implications of effects of landscape configuration on bird abundance and behavior for the dispersal of H. acuminata seeds

Estimation of seed retention times.—Most species regurgitated all seeds offered during feeding trials. In

all cases, seed regurgitation times followed a lognormal distribution (Appendix B). Model selection results indicated no differences among manakin species in seed regurgitation times (Appendix C: Table C5), so we fitted a single lognormal distribution to estimate seed retention times for this group (Appendix B and Fig. 2). Goodness of fit for observed and predicted frequencies of seed retention times for manakins was high ($\chi^2 = 3.39$, $df = 7$, $P = 0.84$, $R^2 = 0.89$). However, the thrush *T. albicollis* regurgitated and defecated seeds, resulting in a bimodal distribution of seed retention times, with longer intervals for defecation relative to regurgitation events. To account for this pattern, we fitted a mixture of a lognormal distribution for regurgitation events and a truncated normal distribution for defecations (Appendix B and Fig. 2). The longest retention time for *T. albicollis* was 37 min, so we truncated the distribution at 40 min. Goodness of fit for *T. albicollis* seed retention data was lower than for manakins ($\chi^2 = 8.84$, $df = 7$, $P = 0.26$, $R^2 = 0.65$). We were unable to capture *S. turdinus* individuals for our feeding experiments. In our seed dispersal simulations, we assumed that this species only regurgitated seeds, with retentions times similar to those of manakins. In the face of uncertainty, this assumption ensures that our estimates of long-distance dispersal are conservative.

Simulation results.—To assess the effects of bird abundance, behavior, and foraging on dispersal of *H. acuminata* seeds, we used the results of our statistical analyses to simulate seed dispersal in two hypothetical landscapes: (1) a homogeneous landscape composed of 100% primary forest; and (2) 1-ha and 10-ha fragments embedded in a secondary forest matrix. As expected, the shape of the resulting dispersal kernel was the result of interactions between the identity and relative abundance of dispersers with landscape configuration, specifically fragment size (Table 3). On average, seeds dispersed by the thrush traveled ~ 5 m farther than those dispersed by all other birds, but the variation around the mean was extremely large ($F = 3538$, $df = 1, 19$, $P < 0.00001$; Table 3). In addition, maximum dispersal distance for thrush-dispersed seeds was almost three times as high as that of seeds dispersed by all other species ($F = 3538$, $df = 1, 19$, $P < 0.00001$), not a surprising result, given that this was the only species that swallowed and defecated seeds.

The effect of landscape configuration on dispersal distances was subtle, mediated by fragment size, and only evident for seeds dispersed by the thrush. Although average dispersal distances were largely uniform across the chosen landscape configurations, maximum dispersal distances were shortest for thrush-dispersed seeds from 1-ha fragments relative to both continuous forest and 10-ha fragments (Table 3). Sensitivity analyses of these results indicated that lower thrush abundance was largely responsible for the short maximum distances in 1-ha fragments surrounded by secondary forests (Appendix E). Thrush-dispersed seeds also traveled longer maximum distances from larger (10-ha) patches regard-

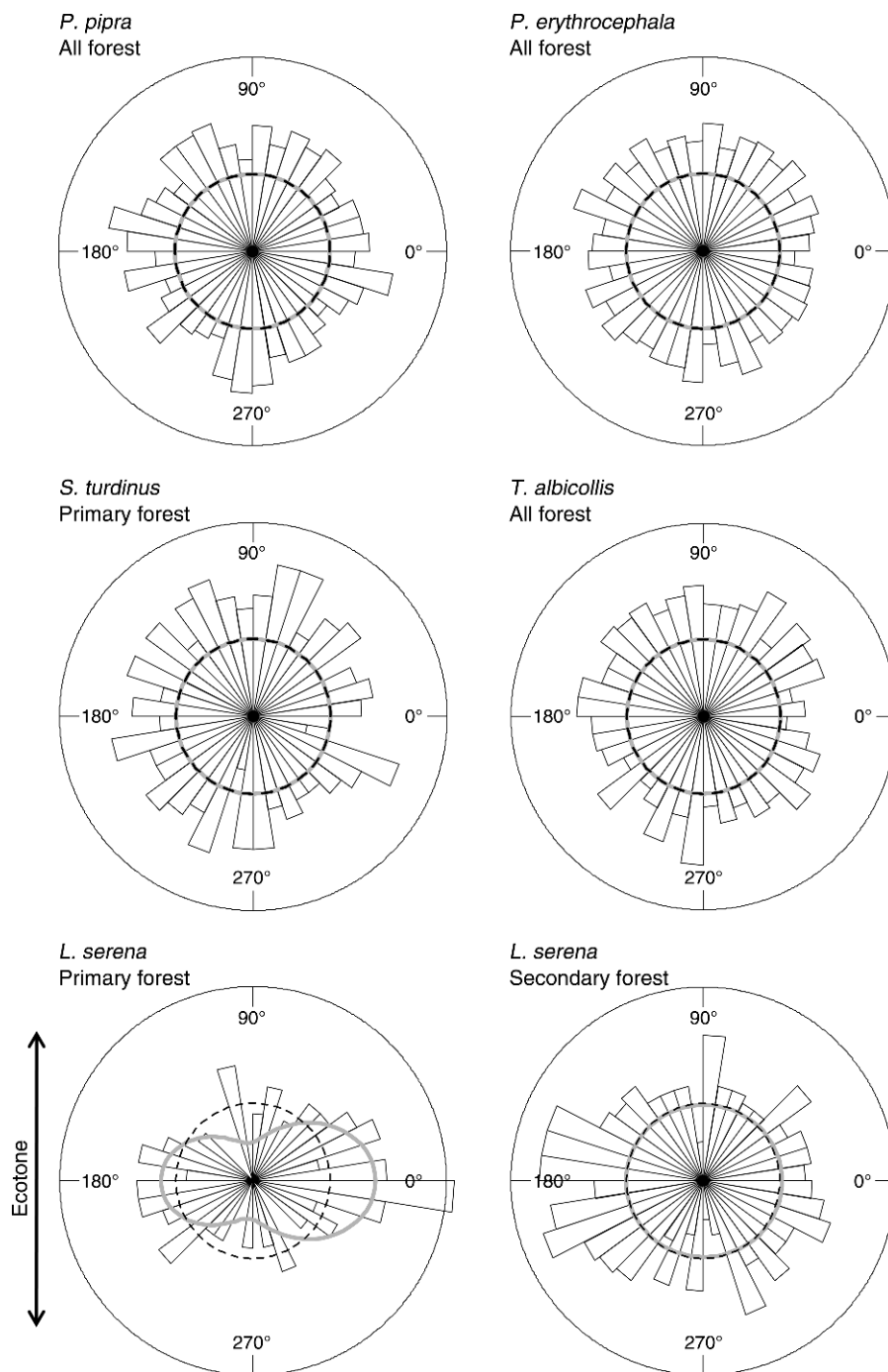


FIG. 1. Distributions of movement directions (angles, in degrees) of each bird species that disperses *Heliconia acuminata*, an Amazonian understory herb, based on fieldwork in the Biological Dynamics of Forest Fragments Project (BDFFP), near Manaus, Brazil. Data and fitted parameters are shown for the model supported by movement data for each species. *Pipra pipra*, *P. erythrocephala*, and *Turdus albicollis* did not change movement direction in response to the habitat boundary, so we show data for all forest types together. We only show movement angle data for *Schiffornis turdinus* in primary forest, because this species was restricted to this habitat. *Lepidothrix serena* changed movement direction patterns in response to the habitat boundary between primary and secondary forest. We show the distribution of movement angles in both habitats. Wedges show observed data; dashed black lines show a simple correlated random walk; solid gray lines show the best-fit movement direction model. All directions are relative to a vector parallel to the nearest edge, oriented in the same 180° arc as the previous movement. Parameter estimates and associated support intervals for movement direction models are provided in Appendix D.

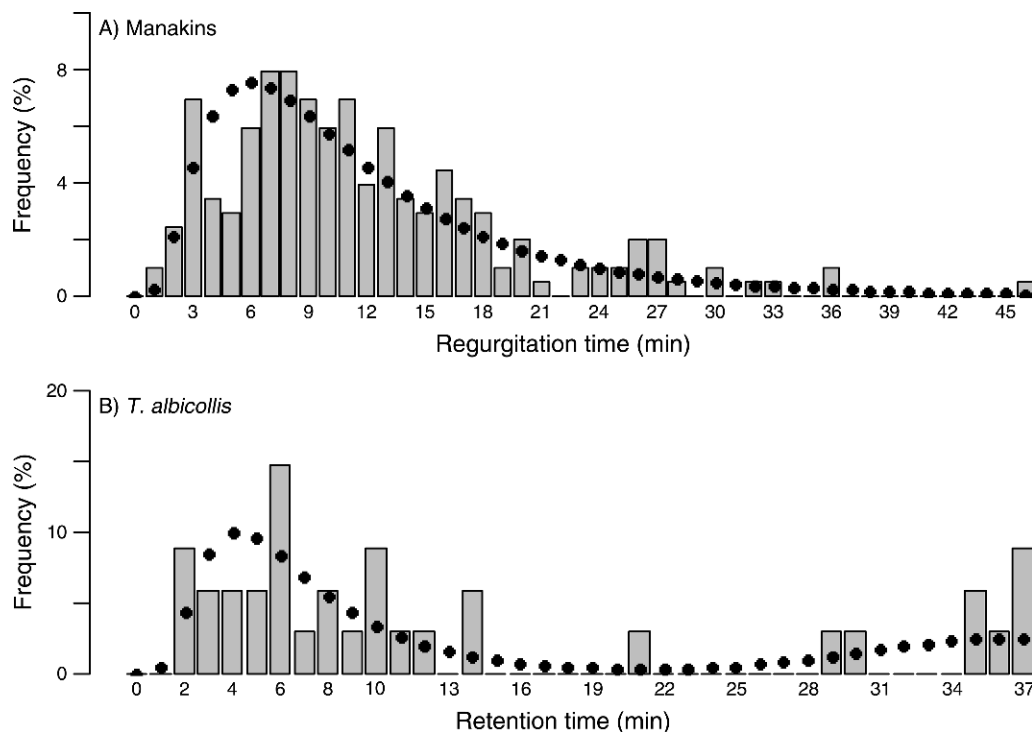


FIG. 2. Frequency distributions of regurgitation and seed retention (=gut passage) times for (A) manakin species (*P. erythrocephala*, *P. pipra*, *L. serena*, and *Corapipo gutturalis*), and (B) the thrush *T. albicollis*. Black dots indicate a fitted lognormal distribution for manakins and a mixture distribution of lognormal and truncated normal for *T. albicollis*.

less of the surrounding matrix. Sensitivity analyses indicated that the high maximum dispersal distances observed for seeds produced in 10-ha fragments resulted from greater population sizes of fruiting plants in these patches, which increased the probability of rare, long-distance dispersal events (Appendix E).

DISCUSSION

Because most species of tropical plants are dispersed by animals, it has been widely hypothesized that forest fragmentation could result in a cascade of plant extinctions resulting from fragmentation-induced changes in seed dispersal. Nevertheless, studies investigating the consequences of fragmentation-induced changes in

disperser diversity, abundance, and behavior for seed dispersal remain rare (Levey et al. 2005, Cordeiro et al. 2009, Lehouck et al. 2009a, b, c). The results from our central Amazonian sites suggest that the most important effects of landscape configuration on seed dispersal are (1) changes in the composition of the disperser community, specifically, the abundance of the largest-bodied bird disperser, and (2) shifts in the population size of fruiting plants, driven by fragment size. As a consequence of these changes, the probability of seeds dispersing greater distances from larger fragments increased. Our results illustrate the difficulty in predicting how forest fragmentation influences seed dispersal without a comprehensive understanding the synergistic

TABLE 3. Percentage of *Heliconia acuminata* seeds dispersed by the thrush *T. albicollis*, dispersal distances of foraging thrushes and other species, and percentage of seeds deposited in primary forest fragments (CF).

Landscape configuration	Dispersed by <i>T. albicollis</i>				Dispersed by all other birds			Seeds deposited in CF (%)
	Seeds dispersed (%)	Dispersal distance (m)			Dispersal distance (m)			
		Mean	SD	Maximum	Mean	SD	Maximum	
1-ha continuous forest	8	24.84	0.64	95.01 ^a	19.25	0.04	30.49	100
10-ha continuous forest	8	24.60	0.25	114.6 ^b	19.26	0.01	32.73	100
1-ha fragment in secondary matrix	2	24.56	1.82	72.39 ^c	19.27	0.03	30.59	77
10-ha fragment in secondary matrix	6	24.26	0.18	115.4 ^b	19.26	0.01	32.88	92

Notes: Different superscript letters indicate that mean statistics for the 20 simulations were significantly different ($P \leq 0.05$) between landscape configurations within a species. Percentage of seeds deposited in primary forest fragments surrounded by either primary or secondary forests refers to dispersal by all species (manakins and thrush).

effects of disperser behavior, the pool of species in the disperser community, the various components of landscape structure, and the distribution of plant populations.

Most plant species are dispersed by several frugivores (Clark et al. 2005, Jordano et al. 2007), and previous research has demonstrated species-specific differences in visitation rates, fruit removal, seed germination, and long-distance dispersal (Jordano et al. 2007, Lehouck et al. 2009b). For instance, large-sized birds and mammals often carry seeds farther from the source tree than small birds (Clark et al. 2005), and in diverse frugivore communities it is likely that a limited number of disperser species contributes disproportionately to long-distance dispersal (Jordano et al. 2007, Lehouck et al. 2009b). In addition, maximum dispersal distances depend not only on the distance that dispersers travel, but also on the size of seeds relative to frugivore body mass, which can affect fruit handling techniques, the likelihood of seed ingestion, and seed passage rates (Levey 1987). In our study system, only one of the bird species we examined, the thrush *Turdus albicollis*, swallowed and defecated *Heliconia acuminata* fruits. This led to only modest increases in the mean distances that thrushes dispersed seeds, but a 3–5 fold increase in the maximum dispersal distances for seeds ingested by thrushes relative to those dispersed by other species. Furthermore, smaller-bodied bird species, responsible for the removal of >90% of *H. acuminata* seeds, dispersed seeds in a spatially clustered pattern because they forage by removing the pulp from seeds and regurgitating seeds near the source plant. These differences in fruit handling may be driven by bird mass relative to that of *H. acuminata* seeds (seeds, mean 0.08 g, 7×5 mm); range in mean body mass for $n = 4$ individuals of each species: manakin species: 8–12 g; size 7–15 cm; *T. albicollis* body mass 40–77 g (E. Johnson, unpublished data). Further elucidating the relationship between seed size and fruit nutritional characteristics and disperser foraging style and movement will greatly enhance our understanding of seed dispersal (Morales and Carlo 2006).

The effects of forest fragment size on bird abundance and habitat use were most dramatic for the largest dispersers, *S. turdinus* and the thrush *T. albicollis*. *S. turdinus* was altogether absent from 1- and 10-ha fragments. Capture rates of the thrush, the primary long-distance disperser of *H. acuminata*, were similar in primary forest and fragments, but its relative abundance (point counts) was significantly lower in fragments. An explanation for the observed declines in the abundance of the largest dispersers in fragments relative to continuous primary forests may be that these species have area or nutritional requirements that cannot be met in small fragments. Data from our study site show that habitat requirements for *T. albicollis* range from 15–20 ha in continuous forests (E. Johnson, unpublished data). Plant species that depend on large-bodied species for

dispersal are predicted to be more affected by landscape modification than those dispersed by small bodied species (Silva and Tabarelli 2000). However, the consistency of this effect is more likely to depend on the total amount of suitable habitat available (Fahrig 2003), which may determine the size and composition of the disperser community (Stouffer et al. 2006, Lehouck et al. 2009b), and habitat fidelity (Lehouck et al. 2009c), and on the spatial and temporal distribution of resources, which will influence the degree to which disperser populations can persist in available habitat patches (Gentry and Emmons 1987). The effects of decreases or losses of large-bodied dispersers on seed dispersal will also depend on the degree to which other functionally redundant species (i.e., generalists) can compensate for this loss (Moran et al. 2009, Lehouck et al. 2009b).

In a study aimed at estimating seed production, dispersal, and recruitment limitation in this study system, Uriarte et al. (2010a) found strong variation in dispersal at the 1×1 m scale, indicating that seed input limitation is strong for *H. acuminata*. This result is not surprising, as forests in Central Amazonia have among the lowest recorded levels of plant fertility in the tropics (Gentry and Emmons 1987). Estimates of dispersal distance using mapped seedling data and inverse modeling methods, however, were much lower (~ 4 m) than those obtained here using radiotelemetry and feeding experiments. This bias may have resulted from the strong effects of light availability on *H. acuminata* establishment, which may lead to hotspots of fruit production and recruitment in recently formed gaps and lower effective dispersal distance (Uriarte et al. 2010a; M. Côrtes, M. Uriarte, E. M. Bruna, and W. J. Kress, unpublished data). Because the spatial distribution of seedlings reflects the effects of multiple filters on recruitment, inverse modeling methods using seedling data are inadequate to capture long-distance dispersal (LLD) events, such as the ones associated with *T. albicollis* seed defecation events, probably overestimating the importance of dispersal limitation (Nathan and Muller-Landau 2000). By underestimating the frequency of LDD, they also underestimate the spatial scales at which dispersal influences population and evolutionary dynamics (Jones et al. 2005).

Habitat type (i.e., primary vs. secondary forest) influenced average movement distances, perching time, and (for *L. serena*) movement direction. Overall, bird dispersers flew farther and faster and perched longer in primary than in secondary forests. The tendency of *L. serena* to cross the forest–matrix edge may have been a response to several fruit-bearing pioneer species that recruit at these sites. However, none of these differences in movement between primary and secondary forest affected either mean or maximum seed dispersal distances in our simulations. Changes in an animal's movement trajectory (i.e., edge-following behavior) in response to landscape features have been shown to alter

seed dispersal patterns in other systems (Levey et al. 2005, Lehouck et al. 2009b). However, to our knowledge the importance of these changes relative to concomitant changes in the composition and abundance of the disperser community have only been addressed in one other system. In a fragmented cloud forest in Kenya, Lehouck et al. (2009b) found that differences in mobility and habitat use among the three avian frugivores of the tree *Xymalos monospora* resulted in complementary seed dispersal, despite the fact that gut passage times were very similar. Although the most sedentary and forest-dependent species were responsible for most short-distance dispersal, two more mobile species dispersed seeds farther away from the source trees. In contrast, the critical driver of long-distance dispersal in our study system was thrush abundance. The absence of *S. turdinus* from fragments had little effect on seed dispersal for *H. acuminata* because we assumed that this species is functionally similar to the manakins: a conservative assumption, but one justified on the basis of movement patterns. Our findings suggest that the composition and functional redundancy of the disperser community are the critical determinants of mean and maximum dispersal distances. Cordeiro et al. (2009) also found that dispersal of *Leptonychia usambarensis* in a fragmented landscape in Tanzania depended critically on the abundance of generalist primary forest species that were not replaced by secondary or edge species. Conservation measures such as the creation of corridors between habitat fragments in degraded landscapes are unlikely to increase the effectiveness of seed dispersal unless accompanied by increases in the effective disperser population (Fahrig 2003).

The abundance and spatial distribution of fruit resources at the landscape scale can also influence seed dispersal patterns (Carlo 2005, Carlo and Morales 2008, Jordano and Schupp 2000). Carlo (2005) found that fruit removal rates and seed dispersal kernels were affected by plant neighborhood density and by the aggregation patterns of plants in the landscape. In contrast, we found that fruit removal rates were almost 100% independent of neighborhood density. It is important to note, however, that the abundance of disperser populations can vary from year to year. In addition, interannual differences in rainfall and other climatic conditions can also lead to variation in seed production (Wright et al. 2005) and in fruit removal rates (Jordano and Schupp 2000). The study area has a pronounced dry season from June through December and soils in the BDFFP reserves are highly weathered oxisols that have poor water retention capacity despite their relatively high clay content (Laurance et al. 1999). In a comparative study of 13 tropical forest understories across 13 sites in six countries, Gentry and Emmons (1987) found that density, fertility, and diversity of understory species was an order of magnitude lower in the BDFFP than at sites where soils are higher in nutrients and rainfall. To the degree that *H. acuminata*

represents a significant and irreplaceable component of frugivore dispersers' diets, we might expect high fruit removal rates. The seeds of *H. acuminata* contain 2–3 times the concentration of lipids and protein relative to seeds from other species with overlapping phenologies, and consequently are probably a critical and preferred resource for species that forage in the understory (S. Hashimoto and M. Anciães, *unpublished data*). To our knowledge, there are no studies that couple spatial variation in abiotic constraints on seed production with foraging rates and dispersal effectiveness; this seems like a promising avenue of research.

Greater populations of fruiting plants in larger (10-ha) primary forest patches relative to smaller patches led to longer maximum dispersal distances, regardless of the type of matrix habitat surrounding them. This result was simply the effect of area on population size, coupled with a greater probability of long-distance dispersal due to an increasing number of simulated movements. This effect overwhelmed differences in fruit maturation rates between continuous primary forest and forest fragments, reinforcing the findings elsewhere for both animal- and wind-dispersed plant species that emphasize the primacy of absolute seed production (e.g., size of the population of reproductive plants in our study) over ecological interactions (e.g., fraction of seeds dispersed) as the major driver of seed dispersal (Jordano and Schupp 2000, Clark et al. 2001, Soons et al. 2005). Given the relationship between size and fecundity in plants (Bruna and Kress 2002) and between habitat size and plant population size (Higgins et al. 2003), this study underscores the conclusion that the physiological responses of plants to conditions in fragmented habitats will play a larger role in their population dynamics than changes in the interspecific interactions that have received the bulk of ecologists' attention (Higgins et al. 2003, Bruna et al. 2009). Our results also highlight the need to conserve large remnant plant populations associated with larger habitat fragments (Soons et al. 2005).

Two important caveats to our conclusions bear discussion. First, remnant forest patches are rarely protected from hunting, fire, or other forms of human disturbance, as those at the BDFFP are, and all of these factors could exacerbate the factors leading to dispersal limitation in fragments and biodiversity loss (Galetti et al. 2009). Second, as a result of the experimental design used in its establishment, the BDFFP landscape mosaic of primary forest and secondary regrowth represents a limited set of landscape context (i.e., land clearing without subsequent land use). In contrast, working fragmented landscapes may contain a mixture of agricultural land uses, secondary regrowth, and primary forest patches with their own transition dynamics (Uriarte et al. 2010b). Despite these shortcomings, the experimental design allows us to examine the effects of fragment size on population dynamics. We believe it is essential to conduct similar studies in a diversity of

fragmented landscapes, as well as with a broader diversity of plant and disperser taxa, to better predict the consequences of fragmentation on plant dynamics.

Although much theoretical work posits that dispersal into fragments from nearby habitat can ameliorate the negative demographic consequences of reduced reproduction, empirical tests to date remain limited (Soons et al. 2005, Bruna et al. 2009) and evidence that source-sink dynamics are operating in plant systems remains largely circumstantial (Lehouck et al. 2009b). Our results suggest that the maintenance of seed dispersal depends critically on the effects of landscape modifications on the composition and size of the disperser community and on the number of seeds available for dispersal. By coupling these results with ongoing demographic surveys and paternity analyses based on microsatellites, we finally may be able to determine the extent to which habitat destruction and fragmentation alter biotic interactions in human-modified landscapes.

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LITERATURE CITED

- Berry, F., and W. J. Kress. 1991. *Heliconia*: an identification guide. Smithsonian Institution Press, Washington, D.C., USA.
- Bierregaard, R. O., and T. E. Lovejoy. 1989. Effects of forest fragmentation on Amazonian understory bird communities. *Acta Amazonica* 19:215–241.
- Bruna, E. M. 2002. Effects of forest fragmentation on *Heliconia acuminata* seedling recruitment in central Amazonia. *Oecologia* 132:235–243.
- Bruna, E. M., I. J. Fiske, and M. D. Trager. 2009. Habitat fragmentation and plant populations: Is what we know demographically irrelevant? *Journal of Vegetation Science* 20:569–576.
- Bruna, E. M., and W. J. Kress. 2002. Habitat fragmentation and the demographic structure of an Amazonian understory herb (*Heliconia acuminata*). *Conservation Biology* 16:1256–1266.
- Bruna, E. M., and M. B. Nogueira Ribeiro. 2005. The compensatory responses of an understory herb to experimental damage are habitat-dependent. *American Journal of Botany* 92:2101–2106.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Springer-Verlag, New York, New York, USA.
- Carlo, T. A. 2005. Interspecific neighbors change seed dispersal pattern of an avian-dispersed plant. *Ecology* 86:2440–2449.
- Carlo, T. A., and J. M. Morales. 2008. Inequalities in fruit-removal and seed dispersal: consequences of bird behaviour, neighbourhood density and landscape aggregation. *Journal of Ecology* 96:609–618.
- Clark, J. S., M. Lewis, and L. Horvath. 2001. Invasion by extremes: population spread with variation in dispersal and reproduction. *American Naturalist* 157:537–554.
- Clark, C. J., J. R. Poulsen, B. M. Bolker, E. F. Connor, and V. T. Parker. 2005. Comparative seed shadows of bird-, monkey-, and wind-dispersed trees. *Ecology* 86:2684–2694.
- 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 USA* 100:14052–14056.
- Cordeiro, N. J., H. J. Ndangalasi, J. P. McEntee, and H. F. Howe. 2009. Disperser limitation and recruitment of an endemic African tree in a fragmented landscape. *Ecology* 90:1030–1041.
- ESRI. 2000. Spatial analyst 3.0 in ArcView 3.2. ESRI, Redlands, California, USA.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology and Systematics* 34:487–515.
- Farwig, N., K. Bohning-Gaese, and B. Bleher. 2006. Enhanced seed dispersal of *Prunus africana* in fragmented and disturbed forests? *Oecologia* 147:238–252.
- Galetti, M., et al. 2009. Priority areas for the conservation of Atlantic forest large mammals. *Biological Conservation* 142:1229–1241.
- Gentry, A. H. 1982. Patterns of neotropical plant species diversity. *Evolutionary Biology* 15:1–84.
- Gentry, A. H., and L. H. Emmons. 1987. Geographical variation in fertility, phenology and composition of the understory of neotropical forests. *Biotropica* 19:216–217.
- González-Varo, J. P. 2010. Fragmentation, habitat composition and the dispersal/predation balance in interactions between the Mediterranean myrtle and avian frugivores. *Ecography* 33:185–197.
- Higgins, S. J., S. Lavorel, and E. Revilla. 2003. Estimating plant migration rates under habitat loss and fragmentation. *Oikos* 101:354–366.
- Jones, F. A., J. Chen, G.-J. Weng, and S. P. Hubbell. 2005. A genetic evaluation of seed dispersal in the Neotropical tree *Jacaranda copaia* (Bignoniaceae). *American Naturalist* 166:543–555.
- Jordano, P. 1992. Fruits and frugivory. Pages 105–156 in M. Fenner, editor. *Seeds: the ecology of regeneration in plant communities*. CABI, Wallingford, UK.
- Jordano, P., C. Garcia, J. A. Godoy, and J. L. Garcia-Castano. 2007. Differential contribution of frugivores to complex seed dispersal patterns. *Proceedings of the National Academy of Sciences USA* 104:3278–3282.
- 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.
- Laurance, W. F., P. M. Fearnside, S. G. Laurance, P. Delamonica, T. E. Lovejoy, J. M. Rankin-de Merona, J. Q. Chambers, and C. Gascon. 1999. Relationship between soils and Amazon forest biomass: a landscape-scale study. *Forest Ecology and Management* 118:127–138.
- Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605–618.
- Lehouck, V., T. Spanhove, L. Colson, A. Adringa-Davis, N. J. Cordeiro, and L. Lens. 2009a. Habitat disturbance reduces seed dispersal of a forest interior tree in a fragmented African cloud forest. *Oikos* 118:1023–1034.
- Lehouck, V., T. Spanhove, S. Demeter, N. E. Groot, and L. Lens. 2009b. Complementary seed dispersal by three avian frugivores in a fragmented Afromontane forest. *Journal of Vegetation Science* 20:1110–1120.
- Lehouck, V., T. Spanhove, C. Vangestel, N. J. Cordeiro, and L. Lens. 2009c. Does landscape structure affect resource

- tracking by avian frugivores in a fragmented Afrotropical forest? *Ecography* 32:789–799.
- Levey, D. J. 1987. Seed size and fruit-handling techniques of avian frugivores. *American Naturalist* 129:471–485.
- Levey, D. J., B. M. Bolker, J. J. Tewksbury, S. Sargent, and N. M. Haddad. 2005. Effects of landscape corridors on seed dispersal by birds. *Science* 309:146–148.
- Levey, D. J., T. C. Moermond, and J. S. Denslow. 1984. Fruit choice in Neotropical birds: the effect of distance between fruits on preference patterns. *Ecology* 65:844–850.
- Levine, J. M., and D. J. Murrell. 2003. The community-level consequences of seed dispersal patterns. *Annual Review of Ecology and Systematics* 34:549–574.
- Loiselle, B. A., V. L. Sork, and C. Graham. 1995. Comparison of genetic variation in bird-dispersed shrubs of a tropical wet forest. *Biotropica* 27:487–494.
- Morales, J. M., and T. S. Carlo. 2006. The effects of plant distribution and frugivore density on the scale and shape of dispersal kernels. *Ecology* 87:1489–1496.
- Moran, C., C. P. Catterall, and J. Kanowski. 2009. Reduced dispersal of native plant species as a consequence of the reduced abundance of frugivore species in fragmented rainforest. *Biological Conservation* 142:541–552.
- Nathan, R., and H. C. Muller-Landau. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. *Trends in Ecology and Evolution* 15:278–285.
- Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon, and P. J. Geglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *Auk* 117:393–408.
- R Development Core Team. 2008. A language and environment for statistical computing. Foundation for Statistical Computing, Vienna, Austria.
- Russo, S. E., S. Portnoy, and C. K. Augspurger. 2006. Incorporating animal behavior into seed dispersal models: implications for seed shadows. *Ecology* 87:3160–3174.
- Schultz, C. B., and E. E. Crone. 2001. Edge-mediated dispersal behavior in a prairie butterfly. *Ecology* 82:1879–1892.
- Schupp, E. W., T. Milleron, and S. Russo. 2002. Dispersal limitation and the origin and maintenance of species rich tropical forests. Pages 19–33 in D. J. Levey, W. R. Silva, and M. Galetti, editors. *Seed dispersal and frugivory: ecology, evolution, and conservation*. CAB International Press, Cambridge, UK.
- Silva, J. M. C., and M. Tabarelli. 2000. Tree species impoverishment and the future flora of the Atlantic forest of northeast Brazil. *Nature* 404:72–74.
- Soons, M. B., J. H. Messelink, E. Jongejans, and W. Heil. 2005. Habitat fragmentation and grassland connectivity for both short-distance and long-distance wind-dispersed forbs. *Journal of Ecology* 93:1214–1225.
- Stouffer, P. C., R. O. Bierregaard, C. Strong, and T. E. Lovejoy. 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20:1212–1223.
- Tiffney, B. H., and S. J. Mazer. 1995. Angiosperm growth habit, dispersal and diversification reconsidered. *Evolutionary Ecology* 9:93–111.
- Uriarte, M., E. M. Bruna, P. Rubim, M. Anciães, and I. Jonckheere. 2010a. Effects of forest fragmentation on seedling recruitment of an understory herb: assessing seed vs. safe-site limitation. *Ecology* 91:1317–1328.
- Uriarte, M., L. Schneider, and T. K. Rudel. 2010b. Synthesis: land use transitions in the tropics. *Biotropica* 42:59–62.
- Valdivia, C. E., and J. A. Simonetti. 2007. Decreased frugivory and seed germination rate does not reduce recruitment rates of *Aristotelia chilensis* in a fragmented forest. *Biodiversity and Conservation* 16:1593–1602.
- Wheelwright, N. T., W. A. Haber, K. G. Murray, and C. Guindon. 1984. Tropical fruit-eating birds and their food plants. A survey of a Costa Rican lower montane forest. *Biotropica* 16:173–192.
- Willson, M. F., and A. K. Irvine, and N. G. Walsh. 1989. Vertebrate dispersal syndromes in some Australian and New Zealand plant communities, with geographic comparisons. *Biotropica* 21:133–147.
- Wright, S. J., H. Muller-Landau, O. Calderon, and A. Hernandez. 2005. Annual and spatial variation in seedfall and seedling recruitment in a Neotropical forest. *Ecology* 86:848–860.

APPENDIX A

Map of the biological dynamics of forest fragments project and summary of radio tracking sample sizes (*Ecological Archives* E092-078-A1).

APPENDIX B

Results of cage feeding experiments (*Ecological Archives* E092-078-A2).

APPENDIX C

Model comparison results for perch times, movement distance, movement speed, movement angle, and seed retention times (*Ecological Archives* E092-078-A3).

APPENDIX D

Parameter estimates and support intervals for most parsimonious models of move direction for each species and habitat (*Ecological Archives* E092-078-A4).

APPENDIX E

Results from sensitivity analyses of simulation results (*Ecological Archives* E092-078-A5).