Conventional and genetic measures of seed dispersal for *Dipteryx panamensis* (Fabaceae) in continuous and fragmented Costa Rican rain forest

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Abstract: The effects of habitat fragmentation on seed dispersal can strongly influence the evolutionary potential of tropical forest plant communities. Few studies have combined traditional methods and molecular tools for the analysis of dispersal in fragmented landscapes. Here seed dispersal distances were documented for the tree *Dipteryx panamensis* in continuous forest and two forest fragments in Costa Rica, Central America. Distance matrices were calculated between adult trees (n = 283) and the locations of seeds (n = 3016) encountered along 100 × 4-m transects (n = 77). There was no significant difference in the density of seeds dispersed > 25 m from the nearest adult (n = 253) among sites. There was a strong correlation between the locations of dispersed seeds and the locations of overstorey palms favoured as bat feeding roosts in continuous forest and both fragments. Exact dispersal distances were determined for a subset of seeds (n = 14) from which maternal endocarp DNA could be extracted and matched to maternal trees using microsatellite analysis. Dispersal within fragments and from pasture trees into adjacent fragments was documented, at a maximum distance of 853 m. Results show no evidence of a fragmentation effect on *D. panamensis* seed dispersal in this landscape and strongly suggest bat-mediated dispersal at all sites.

Key Words: bats, gene flow, habitat fragmentation, microsatellites, tropical trees

INTRODUCTION

Animal-mediated seed dispersal exerts a strong influence on the distribution and dynamics of tropical forest tree communities (reviewed in Nathan & Muller-Landau 2000, Wright 2002). Dispersal limitation can promote species diversity by reducing competition and competitive advantage at recruitment sites (Hubbell *et al.* 1999), while high mortality near parent trees creates selection pressure for long-distance dispersal (Connell 1971, Janzen 1970). In terms of gene flow, dispersed seeds carry both maternal and paternal genetic information, giving seed dispersal twice the evolutionary weight as pollination (Hamilton 1999).

Disruption of seed dispersal mutualisms is predicted to alter recruitment patterns and reduce plant diversity in fragmented tropical forests (Cordeiro & Howe 2003). For individual species, evolutionary potential may erode as the loss of gene flow partitions genetic variation among increasingly isolated, inbred and vulnerable populations (Young *et al.* 1996). Low population density and high dependence on animal-vectored dispersal makes many tropical trees particularly vulnerable to these effects (Nason *et al.* 1997). With deforestation rates reaching 12 million ha annually in the tropics (FAO 2000), the degree to which forest remnants maintain seed dispersal and other ecological processes has far-reaching implications for biodiversity conservation (Laurance & Bierregaard 1997).

Although widely recognized as critical, documenting seed dispersal distances in the field has proven challenging, particularly for long-distance dispersal events (Cain *et al.* 2000, Sork & Smouse 2006). Studies of tropical trees have modelled dispersal curves based on seed rain data (Harms *et al.* 2000), the composition of progeny cohorts (Webb & Peart 2001), and estimates of frugivore movements and gut-passage time for seeds (Westcott & Graham 2000). Idiosyncratic disperser behaviours, however, and a lack of species-specific data

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have hampered accurate modelling of the narrow, long-distance tail of the dispersal curve (Cain *et al.* 2000). Innovations in molecular genetics offer new tools for measuring exact dispersal distances (reviewed in Cain *et al.* 2000, Sork & Smouse 2006, Wang & Smith 2002) and estimating seed pool contributions (Grivet *et al.* 2005). Initial research suggests extensive dispersal from pasture trees into adjacent fragments (Aldrich & Hamrick 1998) and from continuous forest into regenerating pasture (Sezen *et al.* 2005). There is also evidence that long-distance dispersal events may be more frequent than previously expected (Hardesty *et al.* 2006).

Here we examine the effects of habitat fragmentation on seed dispersal of *Dipteryx panamensis* (Fabaceae), a canopy emergent tree endemic to the Caribbean lowlands of Mesoamerica (Flores 1992). Seed dispersal distances are documented in continuous forest and two forest fragments in Cantón Sarapiqui, Costa Rica. We expect fragmentation impacts on disperser communities to lead to different quantities and spatial patterns of dispersed seeds. Transect-based dispersal data are augmented with genetic analysis to compare minimum and exact dispersal distances, and to look for the movement of seeds between pasture trees and forest fragments. Finally, we document the relationship of dispersed seed locations to the distribution of large, pinnate palms favoured as feeding roost sites by fruit bats of the genus *Artibeus*, the putative primary medium-to-long-distance dispersal agents for *D. panamensis* (Bonaccorso *et al.* 1980).

METHODS

Study sites

One continuous forest and two forest fragments in Cantón Sarapiqui, Costa Rica, served as study sites for this project. La Selva Biological Station is a 2500-ha private reserve that includes 700 ha of lowland rain forest protected from logging and hunting for at least the last 20–30 y. It adjoins Braulio Carrillo National Park, forming the largest tract of continuous habitat in the region (McDade *et al.* 1994). Pineda (40 ha) and Ladrillera 3 (52 ha) are privately held remnants surrounded by pastures and managed under sustainable forestry principles in partnership with the Fundación para el Desarrollo y Conservación de la Cordillera Volcánica Central (FUNDECOR), a local non-governmental organization. The fragment sites are separated from the focal area at La Selva by 7.4 km (Ladrillera 3) and 24.0 km (Pineda) and from one another by 24.5 km. All sites lie in primary wet tropical forest at elevations of 40–75 m, with annual rainfall of ~4000 mm (McDade & Hartshorn 1994). Forest cover in the area is estimated at 55.0% and the matrix includes banana and pineapple plantations and pastures with remnant trees

(Ramos & Finegan 2005). Ladrillera 3 and Pineda have been selectively logged, but maintain diverse canopies with populations of adult (> 30 cm dbh) *D. panamensis* at $0.21 \, ha^{-1}$ and $0.58 \, ha^{-1}$ respectively. The core La Selva study area (~85 ha) is in unlogged, interior forest with adult *D. panamensis* at $0.45 \, ha^{-1}$.

Study species

Dipteryx panamensis (Pittier) Record & Mell (Fabaceae; Papilionoideae) is a large canopy emergent tree occurring in lowland wet tropical forests of the Caribbean slope, from Colombia to Nicaragua (Flores 1992). Initial genetic analysis suggests a polyploid origin for the species, with eight of nine microsatellite markers behaving in a tetraploid fashion (Hanson 2006). *Dipteryx panamensis* bears single-seeded drupes averaging 6.0–8.0 cm in length, 4.0–5.0 cm in width and weighing 18.0–26.3 g (Bonaccorso *et al.* 1980, Flores 1992). Sixteen species of mammal (Bonaccorso *et al.* 1980) and approximately 100 species of bird (Flores 1992) have been observed in and around fruiting trees. No animals are known to consume the fruit whole, but many species will eat the fleshy mesocarp and discard the endocarp with the intact seed inside (Bonaccorso *et al.* 1980). This activity is usually carried out in or around fruiting trees, however, with the exception of large fruit bats that carry whole fruits away to feeding roosts. The bat *Artibeus lituratus* is thought to be the major medium- and long-distance disperser, with occasional short-distance dispersal by primates, coatis (*Nasua narica*), kinkajous (*Potus flavus*) and taryas (*Eira barbara*) (Bonaccorso *et al.* 1980). Agoutis (*Dasyprocta punctata*), squirrels (*Sciurus* spp.) and other small mammals are primarily seed predators, but also carry out important secondary and short-distance dispersal, particularly through scatterhoarding (Bonaccorso *et al.* 1980, Forget 1993). Recruitment patterns appear to follow the inverse relationship between progeny mortality and dispersal distance predicted by Janzen (1970) and Connell (1971) (Clark & Clark 1984), although high seedling densities near reproductive adults in fragments suggest that this relationship may be disrupted by forest disturbance (Hanson *et al.* 2006). Individual trees mature and begin bearing fruit at approximately 30 cm dbh (T. Hanson, pers. obs.) and the population structure is bimodal, with few individuals in intermediate (10–30 cm dbh) size classes (Clark & Clark 1987).

Transect sampling and analyses

We searched for seeds along 100×4-m transects (seed transects) with pre-selected start points and directions

inside the La Selva Grid System (described in Clark 1998) (n = 42) and along GPS-referenced transects in the fragments (Ladrillera 3, n = 19; Pineda, n = 16). Transects were spatially arranged for a systematic sample of each site and their numbers reflect the relative size and shape of sites. Within each transect we located, mapped and gathered all fresh *D. panamensis* fruits, as well as their distinctive woody endocarps, which can persist on the forest floor through at least two fruiting seasons (T. Hanson, pers. obs.). Seedlings in the transects were also noted and included in dispersal estimates. For simplicity in the descriptions and discussion below, we use the term 'seeds' in reference to both dispersed endocarps and fruits. All seed transects were completed between January and April 2005.

To determine the minimum dispersal distance, i.e. the distance from a dispersed seed to the nearest adult tree, we calculated distance matrices between all mapped seeds and all adult *D. panamensis* at each site. All adult trees (> 30 cm dbh) in the forest and adjacent pastures at Pineda and Ladrillera 3 were located and GPS-mapped as part of a parallel study of pollen dispersal (described in Hanson 2006). Trees at La Selva had been mapped as part of an ongoing, long-term demographic study (Clark & Clark 1999, 2001).

For this study we defined seed dispersal as the transport of diaspores away from the adult plant (Begon *et al.* 2005) and therefore restricted our analyses and discussion to seeds > 25 m from the trunk of the nearest mature tree. (Crowns of *D. panamensis* can be extremely large, and the area < 25 m from the base of the tree is usually carpeted with fruits and seeds that have fallen directly from the crown.) Dispersed seeds were sorted into five distance classes to capture the expected leptokurtic distribution pattern (number of seeds rapidly diminishing with distance): 25–50 m, 50–75 m, 75–100 m, 100–150 m and > 150 m. We compared seed density (dispersed seeds m^{-2}) between all sites using t-tests (two-tailed). We also compared the density of seeds in distance classes among sites using chi-square tests for independence, with the longest two distance classes collapsed to account for small sample sizes. All statistical analyses were performed using SAS version 9.1 (©2002–2003, SAS Institute Inc.).

Genetic sampling and analyses

Endocarps and fruits gathered in the seed transects were dried immediately and stored in silica gel for later DNA extraction. For genotyping adult trees and endocarps, we used nine microsatellites designed from markers for the Amazonian congener *Dipteryx odorata* (Vinson 2004). The primers, PCR characteristics and results from adult genotyping are described in detail elsewhere (Hanson 2006). In this study we used the same extraction

procedures and PCR protocols to genotype endocarps and endocarp material from whole fruits. Due to the low yields and poor quality of DNA from endocarp tissue, amplification success was extremely low (< 7% of 340 trials). The addition of a pre-amplification step designed to increase template quality (Piggott *et al.* 2004) had no effect, nor did additional sample purification through alcohol precipitation. To verify the accuracy of our limited results, we repeated the extraction process and up to four duplicate PCR runs for each sample. Only unambiguously repeatable genotypes (23 samples) were used for further analyses.

Because *D. panamensis* is a polyploid, partial heterozygotes cannot be accurately discerned from microsatellite data (Markwith *et al.* 2006). We therefore treated our microsatellite alleles as dominant loci, creating binary genotypes following the methods of Rodzen *et al.* (2004). The dominant error rate (percentage of miscalled loci for full dominant genotypes) was calculated from duplicate PCR runs for all loci, using the 23 successful samples.

Since endocarp material is maternally derived, its DNA provides an exact match with the maternal tree of origin and can be used to trace dispersed seeds directly to their source (Godoy & Jordano 2001). We conducted a maternity analysis on the 23 successful endocarp amplifications by visual inspection of the genotypes and simple exclusion, comparing each endocarp to the genotypes for all adults at each site (La Selva, n = 181; Pineda, n = 52; Ladrillera 3, n = 50). Adult trees, including those in pastures surrounding Pineda and Ladrillera 3, had been exhaustively mapped and thoroughly genotyped for a concurrent study of pollen dispersal, and all of them had unique genotypes (Hanson 2006). When an exact endocarp-adult match was obtained, we determined precise seed dispersal distances from our distance matrices of dispersed seeds and adult trees. Endocarps with no matching adult were assumed to have originated from outside of the sampled area at each site.

To determine the veracity of maternity assignments, we calculated the probability of identity ($P_{(ID)}$) for each match, based on the loci used and their frequency in the adult population (Waits *et al.* 2001). In maternity analysis, $P_{(ID)}$ represents the likelihood of a mismatch. It calculates the probability that a given genotype will equal one drawn at random from the population, using the equation $P_{(ID)} = (p^2)^2 + (2pq)^2 + (q^2)^2$, multiplied across all loci (Waits *et al.* 2001). This theoretical $P_{(ID)}$ can underestimate observed $P_{(ID)}$ in natural populations that deviate from random mating, so we also calculated a stricter measure based on the $P_{(ID)}$ equation for full siblings ($P_{(ID)sib} = 1 - \{(3/2p)(q^2)\}$) (Waits *et al.* 2001). Maternity assignments with no genotypic mismatches and $P_{(ID)}$ scores of < 0.001 were assigned with confidence. $P_{(ID)sib}$

scores are also reported as a guideline in the unlikely event that adult populations were made up of closely related individuals (i.e. full siblings).

Bat-mediated dispersal

To evaluate the role of fruit bats in seed dispersal, we studied the spatial relationship between dispersed seeds and the canopy or sub-canopy palms often used as roosting sites by the genus *Artibeus* (Evelyn & Stiles 2003, Morrison 1978). At the location of each dispersed seed or group of seeds (those found within a 100-cm radius), we assessed the overstorey directly ($90°$) above with a clinometer, noting the presence or absence of large pinnate palms, including the genera *Welfia*, *Iriartea*, *Socratea*, *Bactris* and *Euterpe*. This protocol was also repeated from survey points located at 5-m intervals along all seed transects to generate a systematic estimate of palm distribution for each site. To test the relationship between seed location and overstorey palms, we compared the frequency of palms above seed locations to the frequency of palms in the canopy at each site using chi-square tests. Finally, we used chi-square tests to examine the occurrence of grouped seeds (typical when bats re-use foraging roosts) vs. single seeds among sites.

RESULTS

Transect dispersal estimates

Of the total seed transect area, 88.0% was located > 25 m from the nearest adult *D. panamensis*. A total of 3016 seeds was recovered from the transects, of which 253 (8.4%) were located > 25 m from the nearest adult and therefore considered dispersed (La Selva $n = 143$; Ladrillera 3 $n = 68$; Pineda $n = 42$). We found no significant difference in the seed density between Ladrillera 3 and Pineda ($t = 0.589$; $P = 0.588$), Ladrillera 3 and La Selva ($t = 0.149$; $P = 0.889$), or Pineda and La Selva ($t = 1.54$; $P = 0.199$). The distribution of seeds in distance classes varied significantly among all sites ($\chi^2 = 52.5$; $P < 0.0001$), though this may have been influenced by a sampling artifact: the close spacing of trees at Pineda allowed very little sampling (6.6%) in the 100–150 and > 150 distance classes at that site. The longest minimum dispersal distances from our transect data were 243 m at La Selva, 251 m at Ladrillera 3 and 87.6 m at Pineda.

Genetic dispersal estimates

Of the nine microsatellite markers used in genotyping, two failed to amplify for endocarp DNA and were
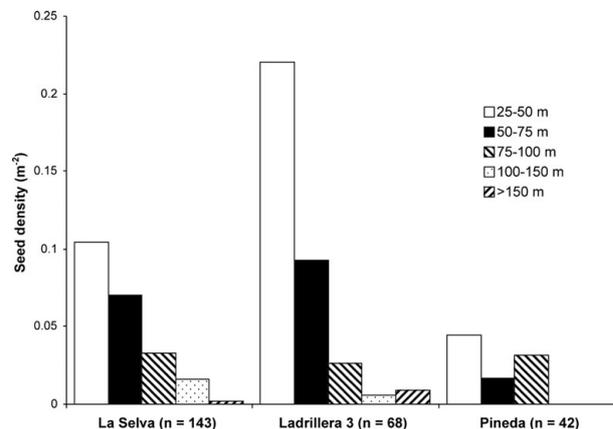

Figure 1. Density of 253 dispersed seeds of *Dipteryx panamensis* in distance classes from the closest reproductive adult trees. Data are from surveys of continuous forest (La Selva) and two forest fragments (Ladrillera 3 and Pineda) in Cantón Sarapiquí, Costa Rica. Seed density in distance classes varies significantly among sites ($\chi^2 = 52.5$, P < 0.0001).

discarded from the analysis (Do18, Do39). The seven remaining markers (Do3, Do5, Do8, Do17, Do20, Do24, Do25) produced dominant genotypes of up to 57 loci (microsatellite alleles) with an overall PCR amplification error rate of 6.1%. Endocarps from fresh fruit provided the most reliable DNA, constituting 89.5% of successful, reproducible amplifications. DNA from older endocarps performed inconsistently or not at all. Maternity was unambiguously assigned to 14 of the 23 genotyped endocarps (Table 1). The majority of successful assignments were to one tree within the Ladrillera 3 forest fragment, although we also documented three cases of seed dispersal from adjacent pastures into fragments (Table 1, Figure 2). No dispersal events were assigned at La Selva, probably as a result of the lack of fresh fruit recovered at that site (< 1.0% of dispersed seeds). Maximum dispersal distances from the maternity analysis were 356 m at Pineda and 853 m at Ladrillera 3, and the closest adult tree was the true maternal tree in six (42.9%) of the assignments.

Among the unassigned endocarps, eight individuals lacked enough genotypic resolution to assign maternity while one from the Pineda site contained combinations of alleles not found in any potential source tree, suggesting dispersal from outside the known adult population (minimum distance to edge of sampled area $= c.$ 550 m).

Bat-mediated dispersal

We completed 1426 systematic point surveys for pinnate palm coverage in the overstorey (La Selva, $n = 684$; Ladrillera 3, $n = 379$; Pineda, $n = 363$) and compared the results with palm occurrence above dispersed seeds

Table 1. Exact genotype matches between maternal endocarp tissue and adult source trees for *Dipteryx panamensis* in two forest fragments, Canton Sarapiqui, Costa Rica. Loci are microsatellite alleles used in dominant fashion for polyploid analysis (Rodzen *et al.* 2004). $P_{(ID)}$ − probability of identity (Waits *et al.* 2001). $P_{(ID)sib}$ − probability of identity for full siblings (Waits *et al.* 2001).

| Seed ID	Site (habitat)	Maternal tree (habitat)	Dispersal distance (m)	Number of loci	Number of genotype mismatches	$P_{(ID)}$	$P_{(ID)sib}$
PSD15	Pineda (fragment)	P38 (pasture)	356	25	0	0.0003	0.080
L3SD3	Ladrillera 3 (fragment)	L31 (fragment)	176	46	0	< 0.0001	0.004
L3SD4	Ladrillera 3 (fragment)	L31 (fragment)	178	46	0	< 0.0001	0.004
L3SD6B	Ladrillera 3 (fragment)	L31 (fragment)	70.6	46	0	< 0.0001	0.004
L3SD6C	Ladrillera 3 (fragment)	L31 (fragment)	70.6	38	0	< 0.0001	0.007
L3SD6E	Ladrillera 3 (fragment)	L31 (fragment)	70.6	38	0	< 0.0001	0.007
L3SD6H	Ladrillera 3 (fragment)	L31 (fragment)	70.6	46	0	< 0.0001	0.004
L3SD10	Ladrillera 3 (fragment)	L31 (fragment)	38.3	46	0	< 0.0001	0.004
L3SD15A	Ladrillera 3 (fragment)	L31 (fragment)	38.7	34	0	< 0.0001	0.007
L3SD15B	Ladrillera 3 (fragment)	L341 (pasture)	853	29	0	0.00019	0.044
L3SD18C	Ladrillera 3 (fragment)	L31 (fragment)	69.0	38	0	< 0.0001	0.007
L3SD19C	Ladrillera 3 (fragment)	L31 (fragment)	74.1	46	0	< 0.0001	0.004
L3SD20	Ladrillera 3 (fragment)	L31 (fragment)	142	46	0	< 0.0001	0.004
L3SD21	Ladrillera 3 (fragment)	L349 (pasture)	567	26	0	0.00014	0.041
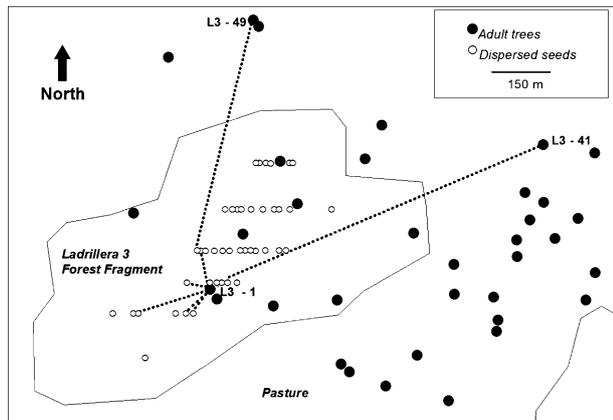
Figure 2. Location of adults and dispersed seeds of *Dipteryx panamensis* in the Ladrillera 3 forest fragment and adjacent pasture. Dispersal events confirmed by maternity analysis are indicated by dashed lines.

(La Selva, n = 143; Ladrillera 3, n = 68; Pineda, n = 42). Dispersed seeds occurred disproportionately more often under palms at La Selva ($\chi^2 = 39.1$, P < 0.0001), Ladrillera 3 ($\chi^2 = 10.4$, P = 0.0013), and Pineda ($\chi^2 = 8.97$, P = 0.0027), suggesting an association with bat dispersal at all three sites. Also, the occurrence of grouped seeds common below bat feeding roosts did not vary among sites (La Selva, 29.2%; Ladrillera 3, 26.5%; Pineda, 24.3%) ($\chi^2 = 0.344$, P = 0.842).

DISCUSSION

Transect dispersal estimates

The majority of seeds recovered in this study (91.6%) had not been dispersed > 25 m from the nearest reproductive adult tree. This probably underestimates the true figure since our sampling design focused on longer distances, but it fits the general prediction that most diaspores fall close to the source (Howe & Smallwood 1982), and sets the stage for the high density-dependent mortality near reproductive adults predicted by Janzen (1970) and Connell (1971), and observed in an earlier study of *D. panamensis* (Clark & Clark 1984). The density of seeds that occurred > 25 m from adult trees did not vary among sites. These results belied our predictions, but complement two earlier studies of dispersal in fragmented landscapes. Aldrich & Hamrick (1998) inferred extensive seed dispersal for the tree *Symphonia globulifera* between pastures and fragments in south-eastern Costa Rica, while Chapman *et al.* (2003) noted evidence of long-distance, inter-fragment dispersal for several tree species dispersed by hornbills (*Ceratogymna subcylindricus*) and chimpanzees (*Pan troglodytes*) in Uganda. On the other hand, Cordeiro & Howe (2003) found lower dispersal and recruitment for the tree *Leptonychia usambarensis* in fragments with low abundance of its avian frugivore dispersers. Clearly, fragmentation effects on seed movement are determined by impacts on the vectors, and the dispersal agents of *D. panamensis* appear to remain active in fragmented landscapes.

Though the total density of dispersed seeds did not vary, we did find differences in the distribution of seeds among distance classes. The pattern of dispersed seeds at La Selva and Ladrillera 3 followed the classic leptokurtic dispersal curve, with the number of seeds dropping rapidly to a 'long tail' in distance classes far from reproductive adults (Cain *et al.* 2000, Howe & Smallwood 1982) (Figure 1). This pattern was more erratic at Pineda, where no long-distance (> 100 m)

events were documented (Figure 1). The close spacing of adult trees at Pineda allowed very little sampling at long distances, but there may also be inherent differences among sites. While we suspect that the main bat dispersers of *D. panamensis* persist in fragmented landscapes, the community of terrestrial dispersers is almost certainly altered by hunting and fragmentation effects (Wright 2003). Working in nearby forest fragments, Guariguata *et al.* (2002) noted few or no signs of squirrels or agoutis, both important scatterhoarders and dispersers of *D. panamensis* (Bonaccorso *et al.* 1980, De Steven & Putz 1984, Forget 1993). Changes in the abundance of such terrestrial dispersers may also contribute to differences in dispersal patterns among sites.

Genetic dispersal estimates

The limited amount of viable DNA recovered from endocarps severely restricted this analysis, but our 14 successful assignments augment the transect-based results and hint at the insights possible through maternity analysis. We documented three instances of seeds moving from pasture trees into neighbouring fragments at distances of up to 853 m. Additionally, one seed at Pineda arrived from a pasture or fragment outside of the study area ($>$ *c.* 550 m). These events suggest that seed dispersal for *D. panamensis* persists at least to some degree in a fragmented landscape, and that pasture trees play a role in maintaining gene flow. The Aldrich & Hamrick study (1998) also noted dispersal from pastures into fragments for a bat-dispersed tree. Combined with evidence for pollen flow between pastures and fragments for *D. panamensis* (Hanson 2006) and other tropical trees (Dick *et al.* 2003), it appears that some species can maintain connectivity in fragmented populations, provided their pollen and seed dispersal mechanisms adapt to the new conditions.

In more than half of our maternity assignments, the true source tree was not the nearest tree. Hardesty *et al.* (2006) found a similar but more pronounced pattern for *Simarouba amara* at Barro Colorado Island, Panama, where only 8.2% of seedlings assigned with the highest confidence came from the nearest reproductive adult. The minimum dispersal distances from our transect data should therefore be viewed as an indicator of dispersal patterns that probably underestimates the actual movement of seeds. At Ladrillera 3, for example, the mean dispersal distance from 12 maternity assignments was 154 m (SD $=$ 65 m), more than twice the mean minimum distance from transect data (71.7 m $\pm$ 6.40 m).

Bat-mediated dispersal

Our data on palm and seed distributions show a correlation between seed deposition and the presence of large, pinnate palms in the overstorey at all sites, a strong indication of bat-mediated dispersal. *Artibeus lituratus* has been mist-netted while carrying *D. panamensis* fruit and is assumed to be the major medium-to-long-distance seed disperser (Bonaccorso *et al.* 1980). Though smaller, *A. jamaicensis* also visits *D. panamensis* and may be capable of occasionally carrying its heavy fruit (Bonaccorso *et al.* 1980). Two studies have noted that *Artibeus* bats often choose large pinnate palms as feeding roosts, perching under the midrib of a leaf where they are out of sight from avian predators, and where any terrestrial predator would inadvertently shake the frond in warning as it climbed (Evelyn & Stiles 2003, Morrison 1978). Although many bat species are adversely affected by habitat fragmentation (Cossons *et al.* 1999), both *A. lituratus* and *A. jamaicensis* have been captured repeatedly in highly fragmented landscapes within 25 km of our study sites (Esquetini 2006) and are known from other agriculturally dominated landscapes in the region (Medina *et al.* 2007). *Artibeus* bats often use a feeding roost repeatedly, dropping one or more seeds together before moving on (Morrison 1978). Grouped seeds (deposited within 100-cm radius) were equally prevalent at all of our sites, another likely indicator of bat-mediated dispersal. Because no animals are known to consume and pass *D. panamensis* seeds, the *Artibeus* bats' habit of carrying whole fruits to feeding roosts offers the most plausible means for regular dispersal of *D. panamensis*.

CONCLUSIONS

Our results point to similar densities of dispersed seed for *D. panamensis* in one continuous forest and two forest fragments and suggest that fruit bats are the primary medium- to long-distance dispersal agents at all sites. Though limited in scope, the exact dispersal events from maternity analysis enhanced the data, indicating seed flow from pastures to fragments and pointing out the disparity between minimum estimates from transects and true dispersal distances. These results suggest that this tree species can maintain connectivity and evolutionary potential in a fragmented landscape, provided its dispersers can adapt to the altered conditions. Future seed dispersal efforts should expand the use of maternity analysis to other tropical trees and be extended across longer time frames to better elucidate the full dispersal cycle, from deposition through recruitment.

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