

Frugivory, Post-feeding Flights of Frugivorous Birds and the Movement of Seeds in a Brazilian Fragmented Landscape

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ABSTRACT

Habitat fragmentation can break down the movement processes of frugivorous animals, thus influencing the relationship between plants and their seed dispersers by altering the number and identity of seed dispersers, and their relative contribution to seed dispersal. We studied the assemblages of frugivorous birds, their composition, species richness, and visitation rates to fruiting plants growing in the different landscape elements (forest fragments, live fences, and trees isolated in pastures) embedded in a Brazilian fragmented, agricultural landscape. By following the post-feeding movements of frugivorous birds, we inferred the direction of seed movement from and to each of these landscape elements. Fruiting trees growing at different landscape elements were visited by frugivorous birds at similar rates. Isolated trees attracted a greater and distinct bird assemblage than trees in forest fragments or live fences. Judging by the post-feeding flights of birds, the seeds of isolated trees were the most likely to reach all the landscape elements considered, but the contribution of isolated trees to the seeds falling in forested habitats or pastures depended on their degree of isolation. A few bird species were able to move widely, visiting fruiting plants in all landscape elements, and promoting long-distance dispersal for plants. These few birds are of special interest because they are mobile links that connect habitats in fragmented landscapes with their seed dispersal services.

Abstract in Spanish is available at <http://www.blackwell-synergy.com/loi/btp>.

Key words: Atlantic forest; bird movements; forest fragments; isolated trees; live fences; pastures.

A GROWING BODY OF STUDIES shows that habitat fragmentation influences the relationship between plants and their seed dispersers in different ways, with important consequences for the structure and dynamics of plant populations thriving in fragmented landscapes (Cordeiro & Howe 2003). For instance, the number and identity of seed dispersers may be altered, together with their relative contribution to the seed dispersal process (Pizo 1997, Cordeiro & Howe 2003). In addition, the fragmentation of natural habitats can break down movement processes of seed dispersers because the matrix between patches often impedes movement (Ricketts 2001).

The frequency, distance, and direction of post-feeding movements of seed dispersers determine the spatial patterns of gene movement within and between plant populations (García *et al.* 2007). In fragmented landscapes, such movements, together with the movements of pollinators, are essential to allow gene flow among isolated plant populations, otherwise threatened with extinction due to demographic, genetic, and microsite stochasticity (Trakhtenbrot *et al.* 2005). Movements of seeds between isolated plant populations is achieved through long-distance dispersal (LDD), which may be defined as the dispersal occurring beyond the distance separating populations (Trakhtenbrot *et al.* 2005). LDD helps to biologically connect habitat patches that are no longer physically linked in a fragmented landscape, and its importance is expected to increase because the distance separating fragments tends to increase with the ongoing loss of natural habitats (Ribeiro *et al.* 2009). The number of seed dispersers that are able to promote LDD for seed plants are expected to be reduced in fragmented landscapes, and identifying such dispersal agents, their movement patterns, and effectiveness as seed dispersers (*sensu* Schupp 1993) is important for

predicting plant population dynamics in fragmented landscapes, including the ability of plant populations to migrate in response to anthropogenic climate change (Corlett 2009).

Fragmented landscapes often occur as a mosaic of landscape elements differing in composition and attractiveness to seed dispersers. Three of these elements are of special interest because of their role in the maintenance of biodiversity in forested fragmented landscapes: forest patches remnant of the fragmentation process or resultant of natural regeneration, live fences, and isolated trees. Forest patches, although biologically impoverished, are important repositories of the biodiversity thriving in human-modified landscapes (Turner & Corlett 1996). Live fences may function as movement corridors for plants and animals, frequently connecting forest fragments (Estrada *et al.* 2000). As such, the implementation of live fences in rural properties has been used as a conservation strategy in temperate and tropical landscapes (Nielsen & DeRosier 2000, Forman 2001). Recent studies revealed that trees isolated in pastures are not the 'living dead' that they appear to be. They may play important roles in population dynamics, serving as donors of genes to nearby forests, either via pollination (Dick 2001, White *et al.* 2002) or seeds (Aldrich & Hamrick 1998). For instance, Aldrich and Hamrick (1998) demonstrated that isolated trees in pastures contribute disproportionately to the population recruitment of *Symphonia globulifera* (Clusiaceae) occurring in nearby forest fragments in Costa Rica. From the restoration perspective, isolated trees may attract seed dispersers from nearby forest patches, thus acting as recruitment foci for forest plants and contributing to the expansion of forest into abandoned pastures (Guevara & Laborde 1993, Slocum & Horvitz 2000, Herrera & García 2009). In addition, isolated trees may serve as stepping stones, facilitating the movement of animals through the inhospitable matrix (Fischer & Lindenmayer 2002). For instance, a radio-tracking study showed

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the disproportionate importance of isolated and riparian trees for avian frugivores and their long-distance movements in a Costa Rican agricultural landscape (Sekercioglu *et al.* 2007). With so many important ecological functions, isolated trees have been considered to be keystone elements of special conservation concern in natural and human-modified landscapes (Manning *et al.* 2006).

We studied the assemblages of frugivorous birds, their composition, species richness, and visitation rates to fruiting plants growing in the different landscape elements described above embedded in a fragmented, agricultural landscape in the Brazilian Atlantic forest. By following the post-feeding movements of frugivorous birds, we inferred the direction of seed movement from and to each of the landscape elements. Indeed, for animal-dispersed plants, the spatial heterogeneity of seedfall is influenced by the post-foraging behavior of frugivores. More specifically, it depends on the kinds of habitats the frugivores frequent after eating a fruit (Jordano & Schupp 2000). In addition, we could weigh the relative contribution of each bird species to the putative seed rain occurring at the different landscape elements. This is particularly important because habitats differ in suitability to plant recruitment; thus, different birds may exert different effects on the demography and population genetic structure of plant species by dispersing seeds to particular habitats (Wenny & Levey 1998). Focusing specifically on isolated trees, we evaluated the influence of the degree of isolation (*i.e.*, the distance separating a given tree isolated in pasture from the nearest forested landscape element) on the composition and post-feeding movements of the assemblage of frugivorous birds.

METHODS

The study was conducted in private lands located in the rural zone of Itatiba (22°57' S, 46°44' W; 800 m asl), state of São Paulo, SE Brazil, in an area of ca 80 ha. The region was originally covered by semideciduous Atlantic Forest (*sensu* Morellato & Haddad 2000), which was fragmented several decades ago to give place to pastures and agricultural fields. Embedded in this human-derived matrix, one can find three distinct habitats: (i) small forest fragments (1–30 ha) in different successional stages, (ii) live fences (140–450 m long, 6–12 m wide) composed of native vegetation usually located along the boundaries of properties, and (iii) trees isolated in active pastures, separated by 5–320 m from the nearest forest fragment or live fence. The coverage of forest fragments, live fences, isolated trees, and pastures, as estimated from an aerial photograph, is 13.6, 1.0, 0.3, and 85.1 percent, respectively. Climate is seasonal, with a hot-wet season from September to March and a dry-cold season from April to August. An ongoing bird survey recorded 165 bird species in the area (M. A. Pizo, unpubl. data).

From September 2002 to December 2004, we made a total of 262.7 h of observations on two fleshy-fruited plant species: *Casearia sylvestris* Sw. (Salicaceae; 38 trees observed in 2002 and 2003 on average [\pm SD] for 3.7 ± 1.5 h, totaling 163.1 h) and *Erythroxylum deciduum* A. St.-Hil. (Erythroxylaceae; 32 trees observed in 2002 and 2004 on average for 3.0 ± 1.7 h, totaling 99.6 h; hereafter referred only by their generic names). We choose these species because they are abundant in the study area, occurring in all landscape

elements of interest (see Table S1 for the observation effort in each habitat), they fruit abundantly every year (each individual produces thousands of fruits containing one to four seeds in *Casearia*, and one seed in *Erythroxylum*), and bear small fruits (mean diam \pm SD: *Casearia* 3.2 ± 0.4 mm; *Erythroxylum* 7.0 ± 0.4 mm, $N = 10$ for both species), able to be swallowed whole by most of the frugivorous birds in the study area (Pizo 2004). *Casearia sylvestris* is one of the most abundant plants in secondary forests of south-southeast Brazil, being an important invasive species elsewhere (Aide *et al.* 2000).

Observations were conducted in the morning (0600–1000 h) and late afternoon (1600–1800 h) from observation points, concealed whenever possible, located at least 15 m from focal plants. Upon each feeding visit by a bird (*i.e.*, when we were minimally confident that the bird indeed ate fruits), we recorded the bird species, the first landscape element the bird landed after leaving the focal plant, and the distance separating the focal plant from the first perch it landed. The landscape element faced by a bird after leaving the focal tree was assumed to be a likely place for the deposition of seeds (see, Jordano & Schupp 2000 for the same rationale). Flight distances were estimated visually to a maximum of 100 m, a procedure that underestimates actual displacement distances, but allow ranking the different bird species in relation to each other. Given the current distribution of Atlantic forest fragments (Ribeiro *et al.* 2009), flights > 100 m potentially provide LDD for dispersed seeds.

DATA ANALYSES.—Because of the difficulties in following birds amidst the dense foliage of focal trees to evaluate the number of fruits removed (especially for *Casearia*), we used total number of visits to fruiting plants rather than the number of fruits removed as a proxy to the contribution of each bird species to seed dispersal. Indeed, for the few bird species with sufficient data, we found a positive correlation between number of visits to fruiting plants and number of fruits removed (Pearson's correlations on log-transformed data: *Casearia* $r = 0.87$, $P < 0.001$, $N = 11$; *Erythroxylum* $r = 0.87$, $P = 0.02$, $N = 6$).

We compared the three landscape elements (forest fragments, live fences, and trees isolated in pastures) in relation to the number of visiting bird species, the number of visits, and the visitation rates to focal plants. Additional comparison was made considering the degree of isolation of trees in pastures defined as the distance separating them from the nearest forested element (*i.e.*, forest fragment or live fence). Based on the distance distribution of isolated trees, we defined two categories of isolation: trees near (< 20 m) and far (70–250 m) from the forested elements.

Rarefaction analyses based on confidence intervals (CI) derived from 1000 iterations implemented in EcoSim 7.0 (Gotelli & Entsminger 2001) were used to compare the total number of visiting bird species among the three landscape elements and between near and far isolated trees. For rarefaction analyses, we report average rarefied means plus 95% CIs.

An analysis of similarity (ANOSIM) was performed to compare the three landscape elements, and also near and far isolated trees, in relation to the similarity in the composition of the

assemblages of birds that visited focal trees. ANOSIM is a nonparametric permutation procedure that uses a test statistic (R) to compare the level of similarity between and within groups (landscape elements in our case; Clarke 1993, Clarke & Warwick 1998). R ranges from -1 to $+1$. Differences between groups would be suggested by R values > 0 , indicating that the bird assemblages were more dissimilar between groups than within groups. For each plant species, ANOSIM was performed upon a matrix of bird visits among focal trees. We used the Morisita index as a measure of similarity among trees. The significance of R was determined by comparison with the values obtained by 10,000 randomizations implemented in the software PAST (version 1.81; Hammer *et al.* 2001).

Visiting birds were classified according to the diet and dependence on forested habitats. Because of the lack of precise diet studies for most species, we used broad diet categories to lessen the probability of erroneous diet assignment. The following diet categories were then considered: frugivores (species eating predominantly fruits), insectivores (species eating predominantly arthropods), granivores (species for which seeds form an important part of the diet), and omnivores (species frequently eating more than two food categories). The classification was based on the literature (Moojen *et al.* 1941, Schubart *et al.* 1965) and the experience of the authors. Forest dependence was based mostly on Silva (1995), with a few modifications based on the experience of the authors in the study area. The following forest dependence categories were considered: dependent (species found mainly in forest habitats), semi-dependent (species that occur in forest but also found frequently in open habitats, usually with scattered trees), and independent (species that occur in open vegetation like pastures, grasslands, and marshes). The number of visits and number of bird species visiting plants classified according to the diet and forest dependence categories were compared using χ^2 -tests followed by residual analyses (not reported here) to highlight the most extreme deviances from expected values.

We used a two-factor analysis of variance (ANOVA) to test for the effects of space and time on the visitation rate of birds. The spatial component was represented by the different landscape elements where plants were observed, while the temporal component was represented by the 2 yr of study. Because of the unbalanced design given by different number of plants observed in each year \times landscape element combination, we run the ANOVA with the Type III sums of squares (Shaw & Mitchell-Olds 1993). Because of sample size constraints, we restricted the comparison between near and far trees to the first year of study. Only trees observed for at least 1 h were included in these analyses. Data were transformed to $\log(x+1)$ to improve normality and homocedasticity of variances.

To evaluate whether the destinies of birds after leaving the focal plants occurred at random with respect to the availability of the different landscape elements, we used the technique proposed by Neu *et al.* (1974) (see also Byers *et al.* 1984). This technique involves the use of a Bonferroni z statistic to calculate simultaneous CI based on observed frequencies of flight destinies that were contrasted with expected frequencies based on the availability of the landscape elements. The availability of each landscape element was

based on the area covered by it, which was measured from an aerial photograph scanned with a resolution of 500 dpi and exported to the SIG IDRISI 3.2 to classify and quantify the area of each landscape element, as recognized previously in the field.

Because the overall assemblage of birds visiting the two plant species did not differ from each other (ANOSIM: $R=0.00$, $P=0.59$), and we were not interested in comparing their dispersal system, data from both species were pooled for the analyses unless otherwise noted.

RESULTS

We recorded a total of 723 feeding visits to fruiting plants involving 38 bird species (12 families; Table S1). A greater number of bird species was recorded in isolated trees (34) than in forest fragments (24) or live fences (25), which did not differ from each other (estimated bird species richness 'rarefied' down to the smallest sample size obtained in forest fragments: live fences mean = 24.5, CI = 23–25 species; isolated trees mean = 28.4, CI = 25–32 species). Among isolated trees, near trees were visited by more species (29) than far trees (18 species; bird species richness of near trees rarefied down to the sample size obtained for far trees: mean = 28.6, CI = 26–30 species).

The bird assemblage visiting the focal trees differed among landscape elements for the two plant species (*Casearia*: $R=0.25$, $P=0.001$; *Erythroxylum*: $R=0.17$, $P=0.02$) due to the particular assemblage recorded in isolated trees, which differed both from trees growing in forest fragments (*Casearia*: $R=0.42$, $P < 0.001$; *Erythroxylum*: $R=0.15$, $P=0.08$, a marginally significant difference) and live fences (*Casearia*: $R=0.32$, $P < 0.001$; *Erythroxylum*: $R=0.28$, $P=0.02$). Fragments and live fences did not differ from each other for any species (*Casearia*: $R=0.06$, $P=0.75$; *Erythroxylum*: $R=0.08$, $P=0.18$). The degree of isolation influenced the composition of the bird assemblage visiting isolated trees (*Casearia*: $R=0.65$, $P=0.002$; *Erythroxylum*: $R=0.85$, $P=0.04$). In sum, isolated trees of both plant species were visited by a bird assemblage reasonably distinct from that recorded in forest fragments or live fences, but the great distinction (greater R values) occurred between near and far isolated trees.

Comparing the landscape elements in relation to the contribution of each bird species to the visits made to focal plants, we noted that while in live fences and isolated trees, two to three bird species accounted for a great part of the visits, in forest fragments, the visits were more evenly distributed, with several bird species likely making a relatively small contribution to seed removal (Table S1; Fig. 1A). Such a distinction is still more pronounced when we compared isolated trees according to the degree of isolation. For near trees, the most frequent visitors were responsible for a relatively low proportion of the total number of visits, while the most frequent visitor of far trees (the insectivorous *Tyrannus savana*) comprised the bulk (52.7%) of visits (Table S1; Fig. 1B).

Most (18 species or 52.6% of total species richness) of the bird species were insectivorous, followed by omnivores, granivores, and frugivores with similar species numbers (seven, six, and five species, respectively). The relative contribution of diet categories to species

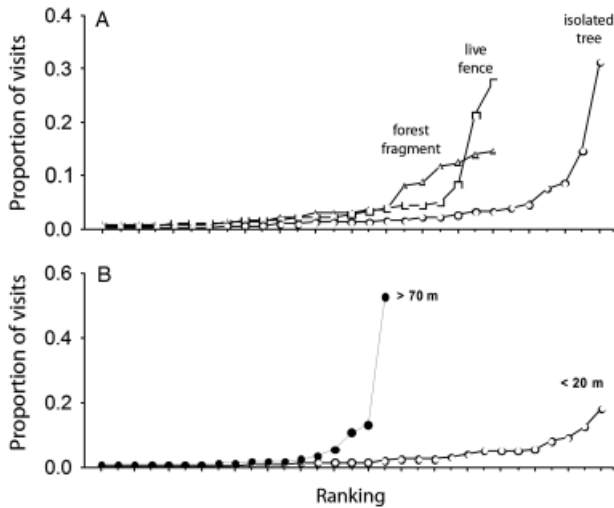


FIGURE 1. Proportion of feeding visits made by frugivorous birds to fruiting plants growing in (A) forest fragments, live fences, and as isolated trees in pastures, and (B) isolated trees in pastures located near (< 20 m) and far (> 70 m) from the nearest forest fragment or live fence. Bird species are ranked in the horizontal axis from the least to the most frequent visitor.

richness did not differ among landscape elements ($\chi^2 = 1.25$, $df = 6$, $P = 0.97$) or between near and far isolated trees ($\chi^2 = 2.70$, $df = 3$, $P = 0.44$). The number of visits by birds in the different diet categories differed among landscape elements, especially due to the high number of visits by insectivorous birds to isolated trees. Insectivorous birds also visited far isolated trees more frequently than near isolated trees (Fig. 2A).

In relation to forest dependence, 15 species of semi-dependent and independent birds were recorded, followed by eight dependent species (Table S1). Similarly to diet categories, no difference occurred among landscape elements ($\chi^2 = 1.53$, $df = 4$, $P = 0.82$) or between near and far isolated trees ($\chi^2 = 2.01$, $df = 1$, $P = 0.37$) in terms of the relative contribution of each forest dependence category to species richness. Isolated trees in general, and far trees in particular, were visited more frequently by independent species and less frequently by forest-dependent species (Fig. 2B).

Visitation rates varied widely for both plant species in all years of study (coefficients of variation for *Casearia*: $CV_{2002} = 122.3\%$, $CV_{2003} = 168.9\%$; *Erythroxylum*: $CV_{2002} = 106.2\%$, $CV_{2004} = 228.1\%$). For *Casearia*, visitation rates did not differ among landscape elements ($F_{2,38} = 0.43$, $P = 0.63$) or study years ($F_{1,38} = 1.74$, $P = 0.19$), but the interaction effect was significant ($F_{2,38} = 14.8$, $P < 0.001$), especially due to the high temporal variation observed in forest fragments (Fig. 3A). The degree of isolation did not influence the visitation rate in *Casearia* trees ($F_{1,8} = 0.52$, $P = 0.25$). Similarly, for *Erythroxylum*, visitation rates did not differ among landscape elements ($F_{2,27} = 0.38$, $P = 0.69$), but was lower in the second year of study ($F_{1,27} = 8.19$, $P = 0.008$; Fig. 3B). The interaction effect was not significant ($F_{2,27} = 1.28$, $P = 0.29$). Near and far isolated *Erythroxylum* trees had similar visitation rates ($F_{1,9} = 0.41$, $P = 0.54$).

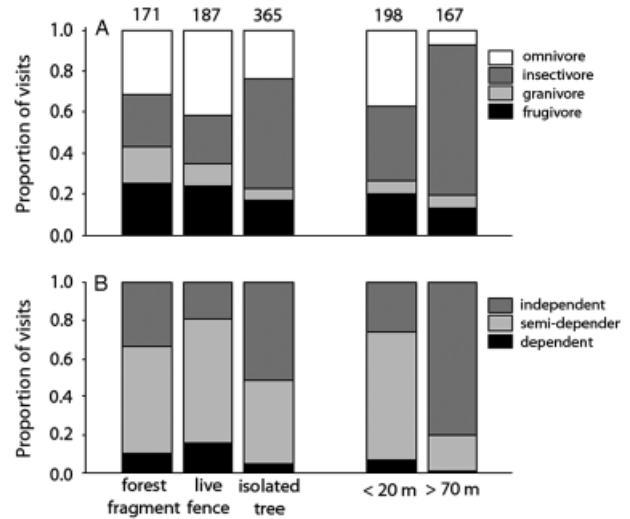


FIGURE 2. Proportion of feeding visits made by frugivorous birds to fruiting plants growing in forest fragments, live fences, and as isolated trees in pastures. Isolated trees were further split into trees growing near (< 20 m) and far (> 70 m) from the nearest forest fragment or live fence. Birds were classified according to diet (A) and dependence on forested habitats (B; see text for definition of categories). Numbers above bars refer to sample sizes. The relative contribution of diet and forest dependence categories differed among the landscape elements (diet: $\chi^2 = 73.9$, $df = 6$, $P < 0.001$; forest dependence: $\chi^2 = 61.2$, $df = 4$, $P < 0.001$) and between near and far trees (diet: $\chi^2 = 58.3$, $df = 3$, $P < 0.001$; forest dependence: $\chi^2 = 106$, $df = 2$, $P < 0.001$).

POST-FEEDING FLIGHTS.—Birds that visited trees in fragments typically remained in the fragment after leaving the focal tree (93.9%, $N = 98$; Table 1). In only six instances, a bird left a forest fragment toward a different fragment. Likewise, when birds fed on trees in live fences, their destinies were predominantly live fences, invariably the same live fence where they fed (Table 1). Although the

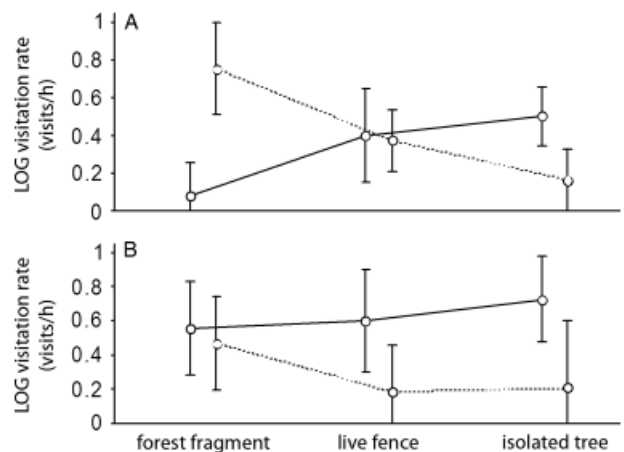


FIGURE 3. Visitation rates of birds visiting fruiting plants of (A) *Casearia sylvestris* and (B) *Erythroxylum deciduum* growing in forest fragments, live fences, and as isolated trees in pastures. Continuous lines refer to 2002, interrupted lines refer to 2003 (*Casearia*) or 2004 (*Erythroxylum*), and vertical lines denote 95% CIs.

TABLE 1. *Destiny of frugivorous birds after feeding on fruiting plants in a fragmented landscape in southeast Brazil. The origin of the bird (i.e., the location of its feeding plant) and its destiny (i.e., the landscape element where the bird perched after feeding) are shown. Isolated trees were divided according to their distance to the nearest forest fragment or live fence. The most frequent flight directions from each origin are bold. Within each origin, the signs between parentheses indicate if a given destiny is more (+), equal to (0), or less (-) frequent than expected based on the area covered by each landscape element.*

Origin	Number of flights	Destiny (proportion of flights)			
		Forest fragment	Live fence	Isolated tree	Pasture
Forest fragment	101	0.83 (+)	0 (-)	0.06 (0)	0.11 (-)
Live fence	132	0.07 (-)	0.90 (+)	0.03 (0)	0 (-)
Isolated tree					
< 20 m	121	0.74 (+)	0.19 (+)	0.05 (0)	0.02 (-)
> 70 m	89	0.17 (0)	0.06 (0)	0.56 (+)	0.21 (-)
Total	210	0.50 (+)	0.13 (+)	0.27 (+)	0.10 (-)

predominant direction faced by birds feeding on isolated trees was a forest fragment, their destinations were more evenly distributed through the different landscape elements and varied with the distance separating the focal tree from the nearest forested element ($\chi^2 = 111$, $df = 3$, $P < 0.001$; Table 1). For near trees, birds flew to the nearest fragment or live fence in most cases (74.4%, $N = 121$), but for far trees, other isolated trees were the most frequent destiny, seconded by pasture (Fig. 4). In pastures, birds perched on small herbaceous plants (grasses and other ruderal species) rather than on

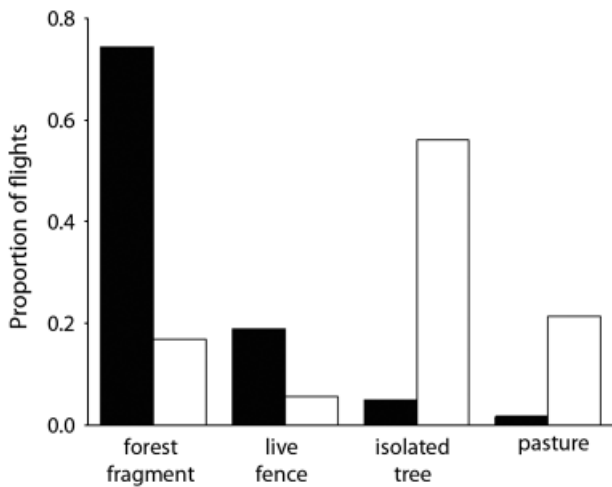


FIGURE 4. Destinies of birds after feeding on fruiting trees isolated in pastures located < 20 m (black bars, $N = 105$) and > 70 m (white bars, $N = 89$) from the nearest forest fragment or live fence.

the ground. In summary, birds feeding in forested elements tended to stay on them after feeding, while birds feeding on isolated trees faced toward other isolated trees or forested elements depending on the isolation of the feeding tree. Pastures were used as a post-feeding destiny much less frequently than expected based on their availability (Table 1).

Post-feeding flight distances ranged widely, from 1 to > 100 m (mean \pm SD = 30.9 \pm 35.1 m, median = 15.0 m, $N = 266$), with only 17.3 percent of the flights > 100 m. Not surprisingly, the highest mean flight distances are associated with the species visiting isolated trees, especially far trees (Table S1). For species with a mean flight distance > 40 m, at least 20 percent of the flights were > 100 m long.

DISCUSSION

The assemblage of birds we recorded was predominantly composed of insectivorous and, to a lesser extent, granivores or omnivorous species, with little dependence on forested habitats, which is typical for human-modified landscapes around the world (Corlett 2002, Pizo 2007, Berens *et al.* 2008). Although not regarded as truly frugivorous, these birds often eat fruits (Skutch 1997 for tyrant flycatchers; Mikich 2002 for woodpeckers), and contribute toward maintaining and enhancing biodiversity in fragmented landscapes by bringing seeds into fragments from elsewhere, dispersing seeds within fragments, and dispersing them away from fragments to other sites (Green 2007). With such a prominent ecological function, it is important to evaluate the effects these predominantly insectivorous or granivorous birds have on the germination success of the seeds they ingest, *i.e.*, if they destroy or pass seeds intact through the gut. Granivorous birds, for instance, are considered seed predators by default, which may not be true always, especially for tiny seeds that usually abound in degraded areas (Schubart *et al.* 1965).

As found elsewhere, isolated trees were visited by a rich bird assemblage (Eshiamwata *et al.* 2006), which shrinks as distance from nearby forest fragments increases (Luck & Daily 2003). As a result, distantly isolated trees depend on a few bird species to keep them genetically alive in the population. These few bird species, notably *Thraupis sayaca*, are able to visit all landscape elements, connecting them through their seed dispersal services, thus constituting in key mobile links that by connecting habitats contributes to ecosystem resilience (Lundberg & Moberg 2003). These mobile links, however, are small birds with small gape widths (< 13 mm) that are unable to eat large fruits (> 15 mm diam) with large seeds (Pizo 2004). Birds large enough to eat such large-seeded fruits are uncommon in the study area, not constituting in good mobile links: the guam *Penelope supercilii* (gape width 19.1 mm; Motta Jr. 1991) is a species restricted to forested habitats, while the jay *Cyanocorax cristatellus* (20.5 mm; Motta Jr. 1991) frequent mainly open habitats (Table S1). The lack of large-seed dispersers is common in human-modified landscapes around the world (Corlett 2002, Pizo 2007), resulting in the absence of true mobile links for large-seed plants among avian seed dispersers.

After pasture abandonment, isolated trees may function as recruitment foci for forest plants, thus acting as nucleation points for

the formation of forest thickets in pastures (Guevara & Laborde 1993, Slocum & Horvitz 2000, Herrera & García 2009). The seed rain arriving at our distantly isolated trees, however, resulted from the contribution of a smaller assemblage of seed dispersers, with a heavy contribution of insectivorous species that, in comparison with frugivorous species, likely consume fruits less frequently and of a smaller variety of plant species. Therefore, the diversity and abundance of the seed rain occurring under such trees are predicted to be lower than trees closer to forest fragments, as observed in pastures bordering riparian forest patches at Los Tuxtlas, Mexico (Martínez-Garza & González-Montagut 1999). In addition, it may be more homogeneous in composition than sites close to forest fragments (Martínez-Garza & González-Montagut 1999, White *et al.* 2004). Thus, everything being equal, it is expected that forest thickets that originated from distantly isolated trees present lesser β diversity in what concerns ornithochorous plant species than forest thickets growing near forest fragments, a prediction awaiting future validation.

Some of the results and predictions above contrast with the findings of studies conducted in Africa, where no distance effect was detected for the abundance and species richness of bird species visiting isolated trees or the seed rain falling under them (Duncan & Chapman 1999, Eshiamwata *et al.* 2006, Berens *et al.* 2008). Similarly, Berens *et al.* (2008) found no distance effect in the richness but a slight increase in the abundance of animal-dispersed seedlings sampled under isolated guava trees (*Psidium guajava*, Myrtaceae) in Kenya. The structural diversity of the African landscapes, however, was clearly higher than that in our study, which was predominantly composed of active pastures with a low density of isolated trees. This distinction highlights the importance of landscape context influencing the interactions between isolated trees and seed dispersal agents and the seed rain they produce (Luck & Daily 2003).

POST-FEEDING FLIGHTS.—We have shown that the post-feeding flights of frugivorous birds are nonrandomly distributed across the different landscape elements forming a fragmented landscape. Most birds avoided active pastures completely, whereas forest fragments and live fences were used more frequently than expected based on the surface they cover. As a consequence, the arrival of bird-dispersed seeds should be concentrated in certain types of habitats in detriment of others, as often observed in fragmented landscapes similar to ours (Martínez-Garza & González-Montagut 1999, Harvey 2000). In such a scenario, special attention should be given to landscape elements used the least by frugivorous birds if a more homogeneous seed rain through the landscape is desirable, for instance, for restoration purposes. Among the habitats least selected by frugivorous birds after feeding on trees, pastures are of special interest because they usually suffer from a lack of seeds, which constitutes a barrier for forest regeneration after pasture abandonment (Nepstad *et al.* 1990, Wijdeven & Kuzee 2000). In the present study, predominantly insectivorous birds (*e.g.*, *Colaptes campestris*, *T. savana*, *Xolmis velatus*) were the most frequent to perch in pastures. These birds may play a key role in forest restoration in abandoned pastures.

Concerning the movement of frugivorous birds through fragmented landscapes, Van Dorp and Kalkhoven (1988) distinguished transversal dispersal agents (*i.e.*, birds that mainly fly across the landscape) and longitudinal dispersal agents (*i.e.*, birds that prefer to stay in the woody vegetation of forest or live fence). Under the framework of mobile links (Lundberg & Moberg 2003), transversal dispersal agents would be especially important to connect isolated forest fragments. Judging by the post-feeding flights of birds, most of the birds we recorded at forest fragments were longitudinal dispersal agents causing the likely dispersal of seeds within fragments, even for plants located in the edge of the smallest (*ca* 1 ha) fragments we studied. Indeed, even frugivorous birds typical of disturbed habitats often use forested patches (*e.g.*, thrushes *Turdus* spp.; Sekercioglu *et al.* 2007, Gasperin & Pizo 2009), possibly resulting in the retention of a great proportion of the seeds within the fragment where they were produced. The predominance of longitudinal dispersal agents in live fences indicates its use as movement corridors by frugivorous birds, which occasionally visit fruiting plants growing in live fences (Estrada *et al.* 2000). Moving along live fences, such birds allow the movement of seeds not only within the fences but also among the forest fragments they connect (Harvey 2000).

The dispersal of seeds of isolated trees provided by the few birds that frequent forested habitats and are able to cross the open spaces separating them from nearby forest remnants may be seen as a form of directed dispersal (*sensu* Wenny 2001) if we consider that forest fragments provide better chances of survival for dispersed seeds than the active pastures where isolated trees were located. These birds not only maintain isolated trees genetically alive in the population through the dispersal of their seeds but also may influence profoundly the structure and genetic profile of the plant populations thriving in nearby forest fragments in tropical landscapes, as Aldrich and Hamrick (1998) demonstrated for *S. globulifera*, and also in temperate regions. For instance, Kollmann and Schneider (1999) found a correlation between fleshy-fruited species diversity along forest edges and the number of nearby isolated trees in Switzerland.

Recently, the concept of functional groups is being applied in tropical forests to reduce the often large number of seed dispersers to a more tractable set of species groups providing similar seed dispersal services (Dennis & Westcott 2006). Morphological and behavioral traits are used to assign a seed disperser to a given functional group (Moran *et al.* 2004, Dennis & Westcott 2006). In fragmented landscapes, the ability to cross open spaces and provide LDD should be features of interest to evaluate properly the role of seed dispersers in promoting the flow of seeds among isolated plant populations. Among a variety of frugivorous birds thriving in fragmented landscapes, a few figure within such functional group in both tropical (this study) and temperate regions (Hewitt & Kellman 2002). Such birds are thus of special importance, because through seed dispersal, they enhance the chance of plant colonization of new habitats, conferring them increased robustness to the fragmentation process (Johst *et al.* 2002), and to anthropogenic climate change (Corlett 2009). The spatial scale of this important ecological service may eventually go far beyond the 100 m limit

considered here. For instance, 3 percent of the movements of radio-tracked Costa Rican tanagers and thrushes were ≥ 500 m, and some birds moved as far as 5809 m (Sekercioglu *et al.* 2007).

In summary, we have shown that fruiting trees growing at different landscape elements that compose a fragmented landscape are visited by frugivorous birds at similar rates. Trees isolated in pastures, however, attract a greater and more distinct bird assemblage than trees in forest fragments or live fences. Judging by the post-feeding flights of birds, the seeds of isolated trees are the most likely to reach all the landscape elements considered, but the contribution of isolated trees to the seeds falling in forested habitats or pastures depends on their degree of isolation. A few bird species were able to move widely, visiting fruiting plants in all landscape elements, and promoting LDD for them. These few birds are of special interest because they are key mobile links that connect habitats in fragmented landscapes by their seed dispersal services, some of them far apart from each other.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. *Diet and forest dependence categories, number of visits, and distances of post-feeding flights of birds after feeding on fruiting plants in forested fragments, live fences, and trees isolated in pastures.*

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