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The Effect of Spatial Structure of Pasture Tree Cover on Avian Frugivores in Eastern Amazonia

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ABSTRACT

The movement of frugivores between remnant forests and successional areas is vital for tropical forest tree species to colonize successional habitats. The response of these species to the spatial structure of pasture tree cover is largely unknown. We studied avian frugivores that were found in primary forest edges and large pastures in eastern Amazonia, Brazil. We determined how the small-scale spatial structure of pasture trees at forest edges affects five response variables: bird presence, visitation rate, duration of visit, species richness, and an index accounting for species' level of frugivory and abundance in forests. We used hierarchical linear models to estimate the effect of four predictor variables on response variables: (1) clustering of pasture trees; (2) percent canopy cover of pasture trees; (3) distance of pasture tree to forest edge; and (4) tree crown area. The study species, many of which are widely distributed in the Neotropics, were generally insensitive to percent cover and clustering of trees. Frugivore visitation to individual trees remained constant as cover increased. Visitation was positively correlated with focal tree distance to forest edge and crown area. The positive relationship between distance and visitation rates may be due to the increased abundance of some resource further from forests. If pastures were abandoned the distance from forest edges would not likely limit frugivore visitation and seed deposition under large pasture trees in our study (*i.e.*, up to 200 m distant).

Abstract in Portuguese is available in the online version of this article.

Key words: agroecosystems; average nearest neighbor; distance-sampling; landscape structure; Pará; seed dispersal; Thraupidae; Tyrannidae.

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Secondary forests will dominate many future tropical landscapes, but it is unclear if and how quickly they will return to pre-deforestation composition (Wright & Muller-Landau 2006). The movement of frugivores between remnant forests and successional areas is vital for tropical forest tree species to recolonize secondary habitats (Nepstad *et al.* 1996, Harvey 2000, Hooper *et al.* 2005). The spatial structure of a landscape, meaning the composition and configuration of environmental conditions across an area (as opposed to at a point), can generate nonrandom patterns of animal movements and distribution (McIntyre & Wiens 1999, Levey *et al.* 2005). Isolated patches of tree cover in human-dominated landscapes are used by many native animal species and can be important in maintaining animal diversity (Hughes *et al.* 2002, Harvey *et al.* 2006, Manning *et al.* 2006). Little is known, however, about how the spatial structure of pasture tree cover affects the movements of frugivores.

Animals moving across patchy landscapes face many boundary-crossing decisions, which affect their spatial distributions (Turchin 1991, McIntyre & Wiens 1999). Animals move limited distances to locate appropriate foraging substrate (Fitzpatrick 1980, Robinson & Holmes 1982), and can prefer locations where foraging substrate is clustered (Edwards *et al.* 1994). Species inhabiting edges often move limited distances away from edges in either habitat (da Silva *et al.* 1996, Laurance *et al.* 2004) and cross gaps of limited size (Lees & Peres 2009). Edge and forest species may avoid large open habitats because of increased vulnerability to predation (Rodriguez *et al.* 2001).

Frugivores frequent pasture trees but avoid the large expanses of pasture that are common in eastern Amazonia (da Silva *et al.* 1996, Estrada *et al.* 1997, Sekercioglu *et al.* 2007). Seed deposition is therefore often high around pasture trees, which also ameliorate microclimate (Belsky & Canham 1994, Vieira *et al.* 1994) and generate nuclei of woody successional growth (Guevara & Laborde 1993, Nepstad *et al.* 1996). Non-fruiting pasture trees may attract as much outside seed rain as fruiting trees and are important facilitators of succession (Carriere *et al.* 2002a, Zahawi & Augspurger 2006). We focus on frugivore visitation to non-fruiting trees, avoiding variation in crop size that could obscure spatial effects (Howe & De Steven 1979).

Frugivore visitation to pasture trees has been explored with respect to distance from forests edges (da Silva *et al.* 1996, Luck & Daily 2003, Eshiamwata *et al.* 2006, Zahawi & Augspurger 2006, Berens *et al.* 2008), but the explicit spatial arrangement or percent cover of pasture trees in the landscape has mostly been overlooked. The clustering of pasture trees (*i.e.*, shorter average distance between trees) might promote visitation because many species move limited distances across pasture between trees (da Silva *et al.* 1996).

We determined how visitation of avian frugivores to pasture trees is correlated to small-scale tree cover structure in eastern Amazonia at the edge of primary forest fragments and extensive pastures. We focused on five variables of frugivore visitation that might positively correlate to the intensity and diversity of local

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seed deposition: (1) frugivore presence; (2) frequency of frugivore visits; (3) duration of visit; (4) species richness of frugivores; and (5) an index weighting frugivore visits by their seed dispersal potential. We studied the relationship between the five response variables and four measures of the spatial context of pasture trees and tree size: (1) percent pasture tree cover; (2) clustering of pasture tree patches; (3) distance between tree and primary forest edge; and (4) tree crown area. A fifth covariate, tree height, was measured but not included in analyses because it was strongly correlated with crown area.

We predicted that some avian frugivores would prefer forest edge habitat and respond negatively as pasture tree cover became more sparse and isolated. We expected that for sensitive species response variables would exhibit three patterns: (1) positive correlation to increasing pasture tree cover; (2) positive correlation to more clumped tree distribution; and (3) negative correlation to distance to forest edges. We predicted that our index would show stronger responses to spatial structure than raw frugivore counts, because we expected species with the highest potential to disperse forest seeds (*i.e.*, highly frugivorous forest species) to be more sensitive to structure. Finally, we expected more and longer visitations to larger trees, which presumably contain more resources.

METHODS

STUDY SITE.—The study site was the Fazenda São Marcos (2°11′ 54″ S, 47°20′58″ W). The site is a ranch located at an elevation of 90 m asl in the Capitão Poço municipality of the state of Pará, Brazil, in eastern Amazonia. Rainfall at the site is ~2000–2500 mm/yr (Oliveira *et al.* 2002), with a dry season lasting on average from June to November (Uhl *et al.* 1988). Soil at the study site is yellow latosol (Sistema de Proteção da Amazônia [SIPAM] 2006). Sampling occurred along the edges of two evergreen, terra firme primary forest fragments (3800 and 900 ha) that were surrounded by actively grazed pastures. Successional habitats in the region are described in detail by Uhl *et al.* (1988). Fazenda São Marcos pastures extended at least 500 m from the forest edge. Narrow (<20 m) strips of riparian tree cover were present at sites and were included in tree cover surveys. The study was conducted throughout October–December 2007, in the late dry season. Although fruiting of woody species is greater in the rainy season, about one-third of frugivore individuals in pastures had such seeds in their feces in the dry season, indicating a significant potential for dispersal even in the dry season (da Silva *et al.* 1996).

TREE COVER SURVEYS.—Sampling was conducted at 20 forest edge sites with ~1 km between each site. For use in subsequent bird surveys, three non-fruiting focal trees in the pasture were selected at each site. Focal trees did not have fruiting epiphytes during the study. Trees were selected to capture variation in distance to forest edge within plots at each site. Trees were a mix of remnants predating deforestation (*ca* 1975) and younger pioneers. Trees were not completely identified as part of this study. At each site, a semicircular plot was formed to measure spatial structure of tree cover in the local landscape (Fig. S1). The center point of each of the 20 plots was located using the following method. Using a GPS unit (Brunton MNS, typically less than 15 m RMS error), three edge points were located where a line from each focal tree met the forest edge perpendicularly. The mean of the three edge points was then taken as the center of a semicircle.

The plots had a radius of 200 m, resulting in semicircles of ~ 6.5 ha, and were centered at the forest edge. The 200 m radius encompassed the distance of most movements of the study species, based on published results for three of our study tanager species (da Silva *et al.* 1996) and on our personal experience. Expanding the size of plots beyond 6.5 ha was limited by the time and resources available to conduct our detailed mapping of tree cover.

In each plot, all pasture trees of height ≥ 2 m were mapped with a GPS unit and had two perpendicular diameters of their crown measured. Calculations of tree crown area assumed elliptical shapes. The height of trees was determined using a clinometer. The boundaries of continuous canopy patches of pasture trees were recorded with GPS.

We calculated three spatial metrics potentially important to frugivore visitation: (1) 'cover' as the percentage of the 200 m radius pasture plot covered by tree canopy; (2) 'clustering' as the average nearest neighbor (ANN) index of the plot; and (3) distance from each focal pasture tree to the forest edge. The ANN index is computed by dividing the observed mean nearest neighbor distance between tree patch centroids by the expected distance based on random placement (expected = $0.5/(n/A)^{1/2}$, where n is the number of patches and A is the area surveyed). Calculations were done with ARCGIS v. 9.2 (ESRI).

AVIAN FRUGIVORE SURVEYS.—We assumed that avian frugivores found in the forest were potential dispersers of forest seeds. We estimated species abundances in the forest edge to assess species potential to serve as vectors of primary forest tree seeds. An experienced observer (J.R. Lasky) conducted point counts of frugivores in the forest edge. One 10 min point count was conducted at each site, occurring between sunrise and 3 h 15 min later. Point counts were based at the center point of each of the 20 semicircular plots, which were at the forest edge. Only birds located in the forest were recorded. The distance to each individual detected within 100 m was estimated to model the decay in detection probability with distance (Buckland *et al.* 2001). Distances were divided into four 25-m wide bins. Abundances were estimated with the distance-sampling model of Royle *et al.* (2004) that considers local counts as a Poisson or negative binomial-distributed random variable (see Appendix S1).

Each of the three non-fruiting pasture focal trees at each sampling site (N = 55 trees, 5 were excluded after they began fruiting) were observed for a 30 min period from sunrise to 3 h 15 min later, the peak period of bird activity. During each 30 min observation period the time of entry and exit and species identity of each bird landing on the tree was recorded from a distance of ~50 m away, using 8.5 × 44 binoculars. The observer was positioned so as to obscure himself in pasture vegetation, and birds in the vicinity of the focal tree did not visibly respond to the observer's presence. Sallying flights to catch aerial insects or to glean insects from the focal tree were not recorded as exits if the bird returned. We only included duration of visit observations if both the entry and exit of the bird were observed. Species mean duration of visit to a single focal tree was used as an individual observation in statistical analyses. The observations at the focal trees at each of the 20 sites were conducted across at least two different days for each site.

We modeled visitation (*i.e.*, presence, visitation rate, and duration of visit) of individual frugivore species and the aggregated visitation of frugivore species. Species were considered frugivores based on reports in the literature (Moojen *et al.* 1941, Morton 1977, Fitzpatrick 1980, Karr *et al.* 1990, Poulin *et al.* 1994, Arteaga *et al.* 2006, da Mota Gomes *et al.* 2008). We aggregated species in several ways, based on taxonomy, level of frugivory, and abundance in pasture trees, to determine if groups showed distinct relationships to spatial structure. At the broadest level, we aggregated visitation of all frugivore species for analysis. We also aggregated into two separate groups the visitation of Tyrannidae and Thraupidae species, the two most important taxa of pasture-edge frugivores in the region (da Silva *et al.* 1996). In addition, we aggregated movements of species of similar levels of frugivory. We reviewed available literature and divided species into three groups of low (*i.e.*, species where <10% of individuals had fruit in gut), medium, and high frugivory (*i.e.*, where >80% of individuals had fruit in gut) based on diet data (see previously cited references; Table 1). We aggregated visitation of frugivores uncommon in pastures, to determine if relatively rare species showed distinct patterns (Summerville & Crist 2001, Lasky & Keitt 2010). This group consisted of species detected five or fewer times in pasture trees (too few to model their species-specific movement) and is referred to below as the 'group of uncommon frugivores'.

We computed an index to estimate differences among pasture trees in expected seed dispersal from forest sources. The index is a modified version of an index that estimated the importance of dispersers based on abundance and level of frugivory (Galindo-González *et al.* 2000, Arteaga *et al.* 2006). The index was calculated for each species at each pasture tree as the product of three quantities: (1) number of visits; (2) species abundance in the forest edge (as estimated from the above described 100 m radius point counts); and (3) the rank of the species level of frugivory. The index was then summed across all species observed at each tree. We refer to this as the forest-frugivory index. Species of low frugivory received a rank value of 1, species of medium frugivory received a 2, and species of high frugivory received a 3. The results we report below were qualitatively consistent and nearly identical using a wide range of rank values for the three level of frugivory groups (an example of an alternative quantification of ranks giving similar results: low frugivory = 1, medium frugivory = 2, high frugivory = 5).

MODELING FRUGIVORE VISITATION.—Presence, visitation rate, and duration of visit were analyzed with hierarchical linear mixed-models. Plot-level intercept and covariate terms were included because landscape factors could affect visitation to the three focal trees in each plot (Appendix S1). We modeled the effects of two plot-level covariates (γ_1) of spatial structure: percent pasture canopy cover and ANN index, and two tree-level covariates (β_1): distance from tree to forest edge and crown area of the pasture tree. Distance and crown area were log transformed while canopy cover was logit transformed to generate approximately normally distributed covariates. All covariates were scaled to have mean zero and unit standard deviation.

We modeled the effect of the covariates on five response variables of bird visitation: (1) presence of bird in focal tree; (2) number of visits to focal tree; (3) duration of visit to focal tree; (4) species richness in the focal tree; and (5) our forest-frugivory index. We modeled presence in addition to visitation rate because we wanted to model a variable independent of rapid repeated visits by the same bird. Presence was modeled as a Bernoulli response with the logistic link function. Number of visits and species richness were modeled as a negative binomial response with a log link function, appropriate for count data where observations are over-dispersed and non-independent. Duration of bird visits were modeled as the mean of a beta distribution, which is appropriate for responses that are restricted to an interval (duration was limited by 30 min observation periods). In this regression, we used a recently developed link function that allows one to model the mean of the beta distribution, a technique yet to be used extensively in ecology (Ferrari & Cribari-Neto 2004). Finally we modeled the forest-frugivory index using a two-part model, because the data followed a zero-inflated log-normal distribution. We used the two-part regression model of Li *et al.* (2008), with a slight modification suggested by Su *et al.* (2009). The model combines a logistic function modeling presence with a log-normal function modeling the forest-frugivory index, where covariate terms are included in both functions and plot-level error terms are correlated between functions. We also used the two-part model to estimate covariate effects on the number of visits of all frugivores, to compare parameter estimates from the same model when considering raw count data of number of visits vs. the forest-frugivory index.

We used hierarchical Bayesian inference to estimate model parameters. We attempted maximum likelihood techniques but resulting parameter estimates were unrealistic. Hierarchical Bayes methods allow complex multi-level models (*e.g.*, tree and plot-level effects) to be decomposed into smaller problems (Clark 2005). Bayesian sampling methods use the likelihood of the data and the prior probability of the parameters to sample from the posterior probability distribution of parameters, defined as the probability of parameter values given the observed data. Here, we report 95% credible intervals (CI) of covariate effects β_1 and γ_1, which mean that given the data there is a 95% probability that the true parameter value lies within the interval. We highlight covariate effects where their 95% CI excludes zero, but we also note some covariates where effects have marginal support. We note this range of results to avoid simple null hypothesis testing, which can be relatively uninformative and oversimplify results (Anderson *et al.* 2000). We estimated Bayesian posterior distributions of

TABLE 1. *Species recorded in observations of focal pasture trees (*N = 55*). The total visits made during all observation periods is given, along with species abundances in the forest edge as estimated from Poisson or negative binomial models of abundance. Species with five or fewer visits to pasture trees were aggregated as uncommon frugivores in visitation models. Species with 'n/a' reported for edge abundance were not recorded during forest edge point counts but were recorded in the forest edge at other times in this study. Frugivory level is divided into three categories:* L = *Low,* M = *Medium, and* H = *High.*

Family	Species	Visits	Abundance in forest edge (birds ha-1)	Abundance model	Frugivory level	English name
Picidae	*Dryocopus lineatus*	2	0.43	Poisson	M	Lineated Woodpecker
Tyrannidae	*Camptostoma obsoletum*	10	1.7	Poisson	L	Southern Beardless-Tyrannulet
Tyrannidae	*Elaenia flavogaster*	23	2.92	neg. bin.	M	Yellow-bellied Eleania
Tyrannidae	*Empidonomus varius*	3	n/a		M	Variegated Flycatcher
Tyrannidae	*Legatus leucophaius*	1	0.85	Poisson	H	Piratic Flycatcher
Tyrannidae	*Myiarchus ferox*	1	n/a*		M	Short-crested Flycatcher
Tyrannidae	*Myiophobus fasciatus*	2	0.43	Poisson	L	Bran-colored flycatcher
Tyrannidae	*Myiozetetes similis*	15	0.72	Poisson	M	Social flycatcher
Tyrannidae	*Phaeomyias murina*	12	n/a*		M	Mouse-colored Tyrannulet
Tyrannidae	*Pitangus sulphuratus*	5	0.46	Poisson	M	Great Kiskadee
Tyrannidae	*Todirostrum cinereum*	2	n/a		L	Common Tody-flycatcher
Tyrannidae	*Tolmomyias sulphurescens*	2	0.85	Poisson	L	Yellow-olive Flycatcher
Tyrannidae	*Tyrannulus elatus*	4	1.1	Poisson	M	Yellow-crowned Tyrannulet
Tyrannidae	*Tyrannus melancholicus*	24	0.52	Poisson	M	Tropical Kingbird
Thraupidae	*Ramphocelus carbo*	9	4.32	Poisson	M	Silver-beaked Tanager
Thraupidae	*Schistochlamys melanopis*	2	n/a*		M	Black-faced Tanager
Thraupidae	*Tachyphonus rufus*	11	2.35	neg. bin.	H	White-lined Tanager
Thraupidae	*Thraupis episcopus*	46	2.66	neg. bin.	M	Blue gray Tanager
Thraupidae	*Thraupis palmarum*	19	1.89	neg. bin.	M	Palm Tanager
Fringillidae	*Euphonia minuta*	1	n/a*		H	White-vented Euphonia
Incertae sedis	*Saltator maximus*	3	2.19	neg. bin.	M	Buff-throated Saltator

*indicates species not observed in the forest edge during this study, but that could occur there based on the literature.

model parameters using a Gibbs sampler to generate Markov Chain Monte Carlo (MCMC) samples (see Appendix S1).

RESULTS

TREE COVER SURVEYS.—We mapped cover of pasture trees across a total of 129.6 ha of pasture at the 20 sample sites, with each plot covering a mean of 6.5 ha (range = 5.7, 7.6; SD = 0.4). Mean canopy coverage in plots was 5.4 percent (range = 0.1, 31.2; SD = 8.1). Plots had a mean ANN index of 0.9 (range = 0.4, 1.4; SD = 0.3). The 55 focal pasture trees were on average 10.8 m tall (range = 5.0, 22.7; SD = 3.6) with a crown area of 62.6 m^2 (range = 3.8, 296.6; SD = 56.0). The mean distance between focal pasture trees and the primary forest edge was 84.6 m (range = 1.6, 183.8; SD = 58.6).

BIRD SURVEYS.—The 20 forest edge point counts yielded 101 individuals of 16 species of frugivores that we also observed in pasture trees. These species can potentially transport seeds from forest to pasture. The most abundant frugivore in the forest counts that also visited pastures was *Ramphocelus carbo* (Table 1).

In focal observations of 55 pasture trees, we detected 21 species of avian frugivores that occur within primary forest edges (Ridgely & Tudor 1989, Table 1). These species had 197 visits to pasture trees during surveys. Both the birds' entrance and exit were observed for 124 visits (observations used to model duration). *Thraupis episcopus*, a species widespread and abundant throughout the Neotropics, was the most observed frugivore in pasture trees (46 visits to 13 pasture trees). We modeled the presence of seven species, the visitation rate of seven species and the duration of visit of two species.

In general frugivores showed increased visitation to trees more distant from the forest edge and to larger crowned trees (Table S1). No species or groups were less likely to be present at more distant trees (based on 95% CIs). We focus on models of visitation frequency, because logistic models of frugivore presence were largely consistent but provide less information.

Frequency of visits to pasture trees increased in pasture trees more distant from the forest edge for three species and one family, Tyrannidae, based on 95% CIs (Table 2; Fig. 1). The aggregated visits of medium-frugivory and of all frugivores increased with distance from forest edge (Fig. 2). No species had strong negative effects for the distance parameter (all 95% CIs included zero or were positive). Visits mostly increased with increasing crown area, and one species and three groups, including total frugivores, had positive responses to crown area. All 95% CIs of posterior distributions for AVNN index and tree cover effects on the number of visits included zero. *Tyrannus melancholicus*, however, had a negative estimated response to percent tree cover (96% of posterior <0), and *Tachyphonus rufus* had a positive posterior (93% of posterior >0), although 95% CIs included zero.

The two-part model indicated that distance to forest edge and crown area again had positive effects on total frugivore visitation (Table 3), as in the negative binomial model (Table 2). When analyzing the forest-frugivory index, the same two covariates had mostly positive posterior estimates. Note however, that the distance to forest covariate had a lower CI for the forest-frugivory index than for total raw visits, indicating that the distance effect was diminished when accounting for level of frugivory and forest edge abundance (Fig. 2D; Table 3). Species richness of frugivores in pasture trees increased with increasing distance from the forest edge (Fig. 2C) and increasing tree crown area, while AVNN index and tree cover had apparently no effect (Table 2).

TABLE 2. *Posterior estimates for covariate parameters from negative binomial models of number of frugivore visits to pasture trees, as well as parameters from a negative binomial model of frugivore species richness in pasture trees. 95% credibility intervals are shown; intervals in bold are those that exclude zero.*

Species or group	AVNN	% Cover	Crown area	Distance
Camptostoma obsoletum	−5.4, 8.9	−6.6, 9.8	−9.2, 8.7	−5.9, 10.2
Elaenia flavogaster	−3.4, 1.2	−2.5, 1.5	−0.0, 3.4	−0.6, 3.7
Tyrannus melancholicus	−0.6, 0.9	−1.9, 0.1	−0.2, 1.5	**0.6, 3.6**
Tachyphonus rufus	−2.9, 3.4	−0.5, 5.4	−2.2, 1.8	**0.0, 7.1**
Ramphocelus carbo	−3.1, 7.5	−7.5, 6.1	−2.4, 7.9	−5.8, 3.5
Thraupis episcopus	−2.3, 0.4	−2.0, 1.5	−1.0, 1.2	**0.3, 5.8**
Thraupis palmarum	−6.9, 1.6	−3.3, 4.6	**1.0, 12.0**	−4.8, 1.0
Tyrannidae	−0.5, 0.9	−0.8, 0.7	**0.0, 1.4**	**0.5, 2.1**
Thraupidae	−0.6, 0.5	−0.5, 0.9	−0.1, 1.0	−0.1, 1.1
Low frugivory	−1.4, 1.5	−0.8, 2.3	−0.8, 2.7	−0.8, 3.0
Med. frugivory	−0.5, 0.4	−0.6, 0.6	**0.1, 1.1**	**0.2, 1.3**
High frugivory	−1.2, 4.1	−1.5, 3.6	−0.6, 2.0	−0.2, 2.4
Uncommon spp.	−1.1, 1.1	−0.3, 2.0	−0.0, 2.1	−0.2, 2.3
All spp.	−0.4, 0.5	−0.3, 0.6	**0.1, 0.9**	**0.3, 1.2**
Species richness	−0.4, 0.4	−0.3, 0.5	**0.1, 0.8**	**0.2, 1.1**

Tyrannus melancholicus spent longer time periods in pasture trees as distance increased (Table 4; Fig. 3). *Thraupis episcopus* had shorter visits as distance increased, although the 95% CI of the distance covariate included zero. Other covariate parameters did not show strong effects on duration of visit for these species and the aggregated visits of groups of species (Table 4).

DISCUSSION

The patterns we observed may occur beyond the study site, as most of the species are widely distributed in the Neotropics (Ridgely & Tudor 1989, Souza 2006). Nearly all species and groups were insensitive to percent cover, configuration of pasture canopy cover, and distance to forest edge of focal trees, though we expected at least some sensitivity among species that are abundant in forest edges or uncommon in open pasture. This is the first Neotropical finding of a positive relationship between distance to forest edge and the visitation of multiple species of frugivores to pasture trees. Previous researchers have found both positive and negative relationships between frugivore movements and distance to forest edge, though the sign of the relationship is not clearly related to spatial scale. da Silva *et al.* (1996) found a negative relationship at distances up to 0.25 km, Luck and Daily (2003) found negative and positive relationships (depending on the species) at distances up to 8 km, Eshiamwata *et al.* (2006) found no relationship for all frugivores combined and a negative relationship for forest-dependent frugivores at distances up to 1.3 km, and Berens *et al.* (2008) found a positive relationship for distances up to 2 km. These previous studies also vary from lowland to ~1700 m elevation and were conducted in both the neo- and paleotropics, making it difficult to generalize results.

We did not observe declining visitation of species with distance, reduced cover, or clustering, possibly because the distribution of resources (Johnson & Sherry 2001) over-rode any spatial

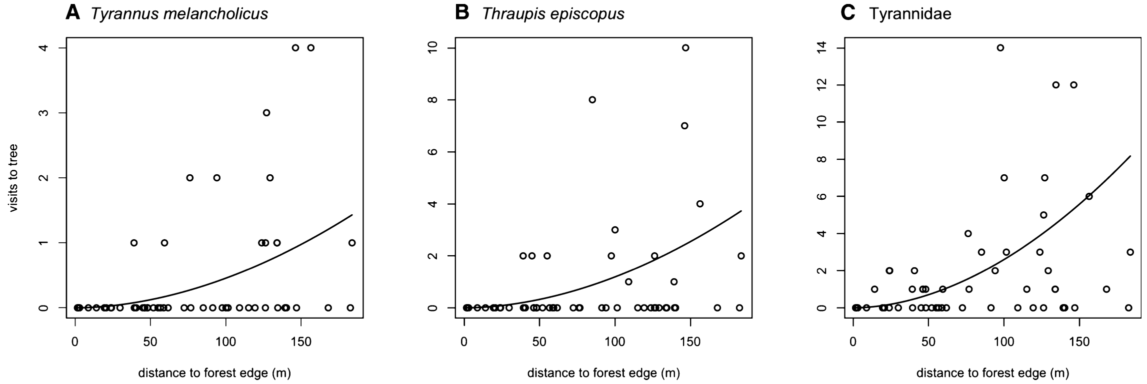

FIGURE 1. Number of visits of frugivores to focal trees vs. tree distance from forest edge for three taxa. Circles indicate observations of individual focal trees (N = 55). The curve shows the expected visits vs. distance taken from negative binomial regression, using the medians of posterior parameter distributions.

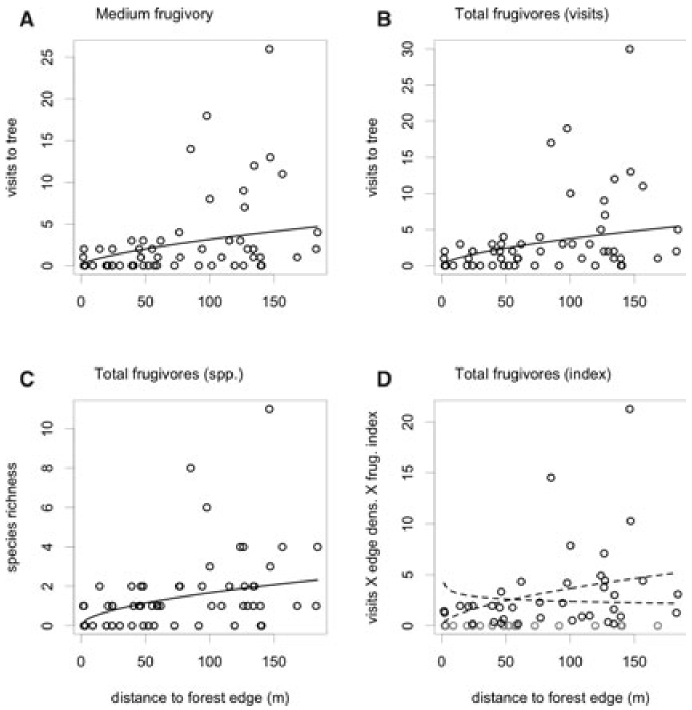

FIGURE 2. Aggregated frugivore response variables vs. tree distance from forest edge. (A) Number of visits by species of medium frugivory; (B) number of visits by frugivores of all species; (C) species richness of all frugivores at pasture trees; and (D) forest-frugivory index (visits × edge density × frugivory level) for all frugivores. The curves show the expected response vs. distance taken from negative binomial regression (A–C), using the medians of posterior parameter distributions. Circles indicate observations of individual focal trees ($N = 55$). In (D) the curves represent the log-normal portion of a two part model; the two dotted curves show the 95% CI values for the distance covariate, which included zero. Gray circles (D) indicate trees where no frugivores were observed and trees that are not included in the log-normal part of the model.

effects. Frugivores can be attracted to safer nesting sites farther from the forest (Skutch 1966, Sekercioglu *et al.* 2007), though we do not have data for our study site to test this possibility. Insect densities can vary with distance from forest (Landis *et al.* 2000, Rand *et al.* 2006). Many of our study species consume insects (Fitzpatrick 1980, Ridgely & Tudor 1989) and their visitation could have been affected by spatial variation in insect density (Berens *et al.* 2008). Another possible cause of the visitation-distance relationship is flocking behavior. Birds may be more willing to cross into open habitat when in larger groups and groups may become more cohesive at more distant sites if predation risk increases (Rodriguez *et al.* 2001).

Species that showed the strongest marginal responses to forest cover (although 95% CIs included zero) did so in the direction expected based on reported habitat associations. The visitation of *Tyrannus melancholicus*, a common species of open and canopy habitats, was negatively correlated, while visitation by *Tachyphonus rufus*, a species typical of forest edge habitats (Ridgely & Tudor 1989, Souza 2006), was positively correlated to cover.

For most species, however, visitation to individual trees was largely unchanged as tree cover increased. A previous study found that frugivore species richness increased while abundance did not vary with greater pasture tree cover levels in Nicaraguan dry forest landscapes (Harvey *et al.* 2006). Species' insensitivity to clustering of pasture trees indicates that study species utilized even relatively isolated trees. Species may have foraged in short movements while at isolated trees but were apparently not averse to traveling distances on the order of 100 m between trees (Robinson & Holmes 1982). Our sampling, however, was limited to 20 ~6.5 ha plots, and it is likely that large scale, extreme isolation and scarcity of tree cover lead to decreased visitation by frugivores. One of our study species, *Dryocopus lineatus,* can cross forest gaps up to 425 m (Lees & Peres 2009), and facultative frugivores of similar body size to our study species in Costa Rica moved distances of several kilometers across the landscape, albeit in a matrix with greater tree cover than our site (Sekercioglu *et al.* 2007). Most movements by our study species, however, approach the scale we studied (da Silva *et al.* 1996). Thus the visitation patterns we observed are the outcome of daily interactions between study species and spatial vegetation structure we studied.

Our finding that large-crowned trees were more attractive to frugivores is consistent with previous studies (Carlo & Aukema 2005, Zahawi & Augspurger 2006, Fink *et al.* 2009). Note that none of the 55 focal trees were fruiting during the study, so that fruit abundance did not vary with tree size. Larger focal trees, however, might have contained more insects. Species composition of pasture trees could have been an additional source of unattributed variation in visitation (Fink *et al.* 2009).

TABLE 3. *Posterior estimates for covariate parameters from two-part models of number of frugivore visits to pasture trees and of forest-frugivory index (visits × edge density × frugivory level). Column headings give covariate names followed by abbreviations indicating whether the covariate is from the logistic or log-normal portion of the model (L = logistic, LN = log-normal). 95% credibility intervals are shown; intervals in bold are those that exclude zero.*

Metric	AVNN – L	AVNN – LN	% Cover – L	% Cover – LN	Crown area – L	Crown area – LN	Distance – L	Distance – LN
Visits	−1.2, 0.4	−0.2, 0.5	−0.4, 1.4	−0.5, 0.3	−0.6, 0.9	**0.0, 0.6**	−0.0, 1.6	−0.0, 0.6
Forest-frugivory index	−1.0, 0.4	−0.3, 0.7	−0.3, 1.2	−0.5, 0.7	−0.4, 0.9	−0.2, 0.7	−0.1, 1.4	−0.2, 0.8

TABLE 4. *Posterior estimates for covariate parameters from beta-distributed models of duration of frugivore visits to pasture trees. 95% credibility intervals are shown; intervals in bold are those that exclude zero.*

Species or group	AVNN	% Cover	Crown area	Distance
Tyrannus melancholicus	−1.7, 0.7	−1.8, 2.0	−2.4, 0.3	**0.9, 3.9**
Thraupis episcopus	−1.0, 1.8	−1.6, 0.6	−0.3, 2.3	−5.2, 0.4
Tyrannidae	−0.4, 0.5	−0.9, 0.4	−0.6, 0.6	−1.3, 0.4
Thraupidae	−0.4, 0.6	−0.4, 0.6	−0.2, 0.6	−0.2, 0.8
Low frugivory	−2.2, 4.7	−2.7, 2.0	−1.8, 6.4	−8.0, 3.3
Med. frugivory	−0.4, 0.3	−0.6, 0.2	−0.6, 0.3	−0.3, 0.5
High frugivory	−1.5, 2.5	−0.6, 4.0	−0.3, 1.4	−1.1, 0.5
All spp.	−0.5, 0.2	−0.4, 0.3	−0.2, 0.4	−0.2, 0.5

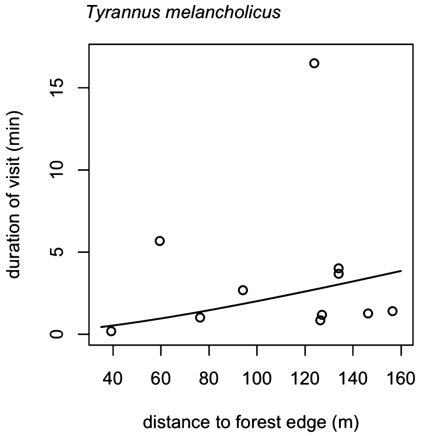

FIGURE 3. Duration of visits by *Tyrannus melancholicus* to pasture trees vs. distance to forest edge. Circles indicate observations of individual focal trees where both the entry and exit of birds were observed (*N* = 11). The curve shows the expected duration of visit vs. distance modeled in beta regression, using the median of the posterior parameter distribution.

We did not find evidence that the spatial structure of pasture trees at the scale we studied affects visitation of our study frugivores to pasture trees at our site. The configuration of pasture trees, whether natural or artificial (*e.g.*, perches installed by managers seeking to attract frugivores and seed rain; Zahawi & Augspurger 2006) might have limited effects on seed rain at this scale. Nevertheless, patterns we observed might affect zoochoric seed rain and pasture succession. First, visitation to individual trees largely stayed constant across increasing levels of pasture tree cover. Thus pastures with greater cover likely received more visitation and possibly more seed rain per unit area of pasture because they contained a higher density of individual trees. Second, our results suggest isolated pasture trees can be important attractors of frugivores and possibly potential nuclei of succession, even up to ~200 m distant from forest edges. Third, species varied in their response to tree size and distance to forest edge. For example, the presence and visitation rates of Tyrannidae were more strongly positively related to distance from forest edge than for the Thraupidae group. This finding may be due to the greater insect preference of Tyrannidae species, and the greater fruit preference of Thraupidae species, fruit that may be of limited abundance in pastures. As a result, seeds of tree species more likely to be consumed by Tyrannidae than other groups might be deposited at greater distances in pastures.

We sampled a larger number of sites relative to some previous studies (Guevara & Laborde 1993, da Silva *et al.* 1996, Fink *et al.* 2009). Further studies could use remote sensing to map the distribution of large pasture trees (*e.g.*, Gibbons & Boak 2002) and model large-scale variation frugivore visitation to pastures (Caillaud *et al.* 2010). Tracking forest-dependent frugivores that infrequently enter extensive pastures is warranted (*e.g.*, Graham 2001), as these species may promote rare but important dispersal events.

The implications of this study are limited by the temporal extent and amount of data we were able to collect in a 3 month window. Frugivory levels are higher when fruits are more abundant in the rainy season (da Silva *et al.* 1996) and it is unclear how this pattern would affect our results. A previous study, however, found no differences between seasons in spatial patterns of movement for three of our study species (da Silva *et al.* 1996). Tree cover and clustering might have non-linear (*e.g.,* threshold) effects on visitation outside the range of conditions we studied. Spatial structure might influence extinction and colonization of local populations of study species over larger areas and longer time periods (Hanski & Ovaskainen 2000). Long-term studies of succession are needed to detect landscape-scale effects of variation in frugivore movements because these effects emerge over many years (Carriere *et al.* 2002b).

Isolated tree cover in human-dominated landscapes provides resources for numerous animal taxa (Harvey *et al.* 2006) and can provide dispersal stepping-stones across the matrix (Graham

2001, Gibbons & Boak 2002). We demonstrated that species most frequently crossing primary forest-pasture edges show little sensitivity to small-scale configuration and cover of pasture trees during our study. Nevertheless, this study has shown that many avian frugivores use and possibly depend on pasture trees. The preservation of such trees in the eastern Amazonian region likely supports the local conservation of these species.

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SUPPORTING INFORMATION

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

APPENDIX S1. Introductory notes.

TABLE S1. *Posterior estimates for covariate parameters from logistic models of frugivore presence in pasture trees.*

FIGURE S1. Simplified aerial representation of a forest edge sample site.

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