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RESEARCH ARTICLE

Scale-dependent effects of forest restoration on Neotropical fruit bats

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Neotropical fruit bats (family Phyllostomidae) facilitate forest regeneration on degraded lands by dispersing shrub and tree seeds. Accordingly, if fruit bats can be attracted to restoration sites, seed dispersal could be enhanced. We surveyed bat communities at 10 sites in southern Costa Rica to evaluate whether restoration treatments attracted more fruit bats if trees were planted on degraded farmlands in plantations or island configurations versus natural regeneration. We also compared the relative influence of tree cover at local and landscape spatial scales on bat abundances. We captured 68% more fruit bat individuals in tree plantations as in controls, whereas tree island plots were intermediate. Bat activity also responded to landscape tree cover within a 200-m radius of restoration plots, with greater abundance but lower species richness in deforested landscapes. Fruit bat captures in controls and tree island plots declined with increasing landscape tree cover, but captures in plantations were relatively constant. Individual species responded differentially to tree cover measured at different spatial scales. We attribute restoration effects primarily to habitat structure rather than food resources because no planted trees produced fruits regularly eaten by bats. The magnitude of tree planting effects on fruit bats was less than previous studies have found for frugivorous birds, suggesting that bats may play a particularly important role in dispersing seeds in heavily deforested and naturally regenerating areas. Nonetheless, our results show that larger tree plantations in more intact landscapes are more likely to attract diverse fruit bats, potentially enhancing seed dispersal.

Key words: ***Artibeus jamaicensis*, *Carollia* species, landscape tree cover, Phyllostomidae, *Sturnira lilium*, tropical forest restoration**

Implications for Practice

- To attract the full complement of seed-dispersing fruit bats, mixed-species tree plantations should be established near existing forests.
- Planting tree islands is not as effective as larger tree plantations for attracting fruit bats.
- Testing tree plantings that include species that produce fruits eaten by bats is needed to determine whether it would increase fruit bat visitation and associated seed dispersal.

Introduction

Tropical forest regeneration is limited, among other factors, by reduced seed dispersal and poor plant establishment (Holl 2012; Chazdon 2014), both of which can be improved by bats. Neotropical fruit bats (family Phyllostomidae) facilitate forest development by dispersing early- and late-successional tree and shrub seeds into disturbed sites (Muscarella & Fleming 2007; Melo et al. 2009), including unique species not often dispersed by birds (Galindo-González et al. 2000). Passage through fruit bats' guts increases germination for some seed species by removing the seed coat (Traveset & Verdú 2002; Heer et al. 2010), and insectivorous bats can reduce arthropod herbivory on tree seedlings (Kalka et al. 2008). Bats may also distribute limiting nutrients via guano (Kunz et al. 2011). Given this range of benefits, there is substantial interest in devising restoration methods that could attract bats to degraded sites in need of restoration.

Several studies have tested novel, bat-attraction techniques, primarily focused on odiferous fruit oils (Bianconi et al. 2007, 2012) and artificial tree cavity roosts (Kelm et al. 2008; Reid et al. 2013). Yet neither of these methods has demonstrably accelerated forest succession (Reid & Holl 2012). Other studies have indirectly evaluated bat activity in restoration sites by comparing the relative contributions of birds and bats to seed rain (Cole et al. 2010), seedling recruitment (de la Peña-Domene et al. 2014), and arthropod reduction (Morrison & Lindell 2012). But it is still an open question whether the most

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widespread active tropical forest restoration practice, planting trees, can attract fruit bats when compared with passive forest regeneration (Mendes et al. 2014). Moreover, it is unclear whether conventional tree plantations are more or less effective than planting trees in patches or islands (i.e. applied nucleation sensu Corbin & Holl 2012).

Tree planting could influence fruit bat behavior at multiple spatial and temporal scales. Locally, tree plantings could provide foraging or roosting sites, both of which are essential to bat populations (Fenton 1997). Roost sites over the short term might include branches and foliage (Morrison 1980; Evelyn & Stiles 2003); over several decades planted trees could also provision cavities (Vesk et al. 2008). Due to heterogeneous, species-specific responses to landscape composition and configuration (Meyer & Kalko 2008; Klingbeil & Willig 2009; Henry et al. 2010; Mendenhall et al. 2014), tree plantings may attract different suites of fruit bat species depending on their broader landscape context (Avila-Cabadilla et al. 2012; Vleut et al. 2012).

We surveyed fruit bats in a replicated, controlled restoration experiment spanning a landscape deforestation gradient. We aimed to determine whether small-scale tree planting attracts fruit bats to a greater degree than natural regeneration, and to compare the relative influence of tree cover at local versus landscape scales. We expected to find more fruit bats in planted restoration plots and in sites with higher landscape tree cover due to increased foraging and roosting opportunities. A positive result would suggest that contemporary restoration methods are already attracting fruit bats, whereas a negative result could provide insight on how and where to improve practices to increase visitation, and possibly seed dispersal, by these important frugivores.

Methods

Study Area

We captured fruit bats at 10, approximately 1 ha, restoration sites between Las Cruces Biological Station (8°47′ N, 82°57′ W) and the town of Agua Buena (8°44′ N, 82°56′ W) in southern Costa Rica (Fig. S1, Supporting Information). Site elevations ranged from 1,100 to 1,300 m above sea level. Prior to extensive deforestation beginning in the 1950s, the dominant regional ecosystem was premontane moist forest (Holdridge et al. 1971). Today approximately 35% of the region retains tree cover (Mendenhall et al. 2011). The remainder of study area is a heterogeneous mixture of coffee plantations, cattle pastures, a small number of other crop types, small forest fragments, second-growth areas, and rural towns. Precipitation across the study area varies with microtopography; Las Cruces receives 3,600 mm of rainfall annually and average temperatures range from 17 to 24°C. There is a distinct dry season from December to March. Sixty one bat species have been recorded from Las Cruces and the surrounding landscape; 23 of these are primarily frugivorous (LCBS 2014).

Experimental Design

Each of the 10 restoration sites contained three 50 × 50 m treatment plots of degraded farmland (mostly former pastures) surrounded by forests and farmlands. Within a site, each treatment plot was separated by 5–200 m, and sites were separated by ≥ 650 m. Plots were randomly assigned one of three treatments (Fig. S2). *Controls* were allowed to regenerate naturally; *islands* were planted with six clusters of tree seedlings (two each with initial planting dimensions of 4 × 4, 8 × 8, and 12 × 12 m; 86 tree seedlings planted); and *plantations* were planted with tree seedlings over the entire area of the plot (313 seedlings). Plantings consisted of four tree species planted in alternating rows. Species included two naturalized, nitrogen-fixing trees (*Erythrina poeppigiana* (Walp.) Skeels and *Inga edulis* Mart. [Fabaceae]) and two native trees (*Terminalia amazonia* (J.F. Gmel) Exell [Combretaceae] and *Vochysia guatemalensis* Donn. Sm. [Vochysiaceae]). *Inga edulis* produces fleshy pulp encased within a hard fruit, which probably prevents bats from consuming it except when fruits are opened first by other animals (Lobova et al. 2009). The other species have dry, wind-dispersed seeds. Five of the sites were established in 2004, four in 2005, and one in 2006. One island plot had a non-standard design and was excluded from sampling. See Holl et al. (2011) for a detailed description of the restoration planting.

At the time of bat community sampling (2009, 2012) sites had been established for 3–8 years. By 2012, plantations had developed closed canopies and planted trees were typically greater than 9 m tall (Holl et al. 2013). Vegetation in control plots was variable, but mostly was characterized by dense early-successional shrubs (e.g. *Vernonia arborescens* (L.) Sw., *V. patens* Kunth [Asteraceae]), forbs (*Heterocondylus vitalbae* (DC.) R.M. King & H. Rob., *Ageratum conyzoides* L. [Asteraceae]), and grasses (e.g. *Axonopus scoparius* Flüggé Kuhlm, *Pennisetum purpureum* Schumach., *Urochloa brizantha* (Hochst. ex A. Rich.) R.D. Webster [Poaceae]) with little bare ground. Several common, naturally recruiting trees (e.g. *Cecropia peltata* L. [Urticaceae]) and shrubs (e.g. *Piper hispidum* Sw. [Piperaceae], *Solanum umbellatum* Mill. [Solanaceae]) produced fruits eaten by bats. Vegetation in control plots was typically less than 2 m high, but one plot was densely covered in approximately 5-m tall trees of *Conostegia xalapensis* (Bonpl.) D. Don ex. DC. [Melastomataceae]. Island plots had greater within-plot variability in canopy cover than the other treatments (Holl et al. 2013). Tree height in the planted tree islands was similar to the plantations, although tree cover varied greatly (2012 mean: 42%, range: 15–65%) due to differential expansion of tree islands into the unplanted portions of the plots via branching and seedling recruitment at the edges. Unplanted portions of island plots ranged from low, early-successional scrub with similar composition to control plots, to vine tangles as tree islands began to coalesce.

Bat Survey

We surveyed bats during the dry season in 2009 (March–April) and 2012 (January–February) using ground-level mist nets (approximately 2 m height). Our protocol was approved by an animal care and use committee at the University of California Santa Cruz and by the Costa Rican Ministry of the Environment. Nets were opened at sunset in fair weather, checked every 30 min, and closed after 4 hours. Captured bats were identified using a field key (York et al., unpublished data) and temporarily marked by clipping hair in order to prevent recounting individuals that had already been captured. Survey effort in both years was consistent, but some aspects of sampling differed between years. In 2009, we netted for one night per site using nine 12-m nets (three/plot) set along trails. In 2012, we sampled for two nights per site using 6-m nets paired with permanent vegetation transects, and we elevated the bottoms of nets above the level of the grass. In both years, nets in island plots were placed within and between the planted tree islands. Given low capture rates, we combined capture data from 2009 and 2012 for all analyses. Total sampling effort was 16,704 m^2 h, or 576 m^2 h per plot ($n = 29$ plots; Straube & Bianconi 2002).

Landscape Tree Cover and Edge Density

To evaluate landscape effects on fruit bat captures, we calculated landscape tree cover and edge density within concentric buffers around each restoration plot. Because the appropriate landscape scale was unknown, we tested buffer sizes ranging from 50 to 650 m, the minimum distance between any two sites in our sample (Fahrig 2013). Landscape tree cover was determined using digitized, aerial photographs from 2003 and 2005 and included old-growth and regrowth forest fragments, fence rows, and tree plantations measured at a 2-m spatial resolution (Mendenhall et al. 2011).

Data Analysis

We evaluated the thoroughness of our bat sampling by comparing observed species accumulation with estimated species richness (Moreno & Halffter 2000). For estimated species richness, we used the Chao1 estimator (Chao 1984) in EsimateS (Colwell 2013). We performed these analyses separately for each restoration treatment (control, islands, plantation) and for groups of sites with low (14–25%; three sites) versus high (58–77%; three sites) landscape tree cover within a 200-m radius.

We used generalized linear mixed-effects regression to evaluate restoration treatment and landscape effects on the number of fruit bat individuals captured. We separately modeled five fruit bat species with ≥ 20 individuals captured. First, we developed two sets of fully specified candidate models, one using restoration treatment × landscape tree cover and one using restoration treatment × landscape edge density. Models within each set differed only in the buffer radius in which landscape tree cover or edge density was calculated. Selected models from each set were compared to one another, and the best model was then compared to simpler versions including (1) null [intercept only], (2) restoration treatment, and (3) restoration treatment + landscape variable. Candidate models were compared using Akaike Information Criterion scores corrected for small sample sizes (AIC_c; Burnham & Anderson 1998). Models used a Poisson error distribution. To evaluate model fit, we compared deviance in fitted models (dev_{fit}) to deviance in null models that included only the intercept and random site effect (dev_{null}) using the formula: Deviance explained $= 1 - (dev_{fit}/dev_{null})$. One outlier (a plantation plot) was removed that had a particularly high abundance of *Artibeus jamaicensis*, likely due to two large, fruiting trees (a *Ficus caldasiana* Dugand [Moraceae] and a *Calophyllum brasiliense* Cambess. [Calophyllaceae]) in a nearby riparian forest.

We accounted for potential spatial autocorrelation in three ways. First, we performed a Mantel test of the correlation between a Bray–Curtis dissimilarity matrix of bat biodiversity and a site-distance matrix. We found no evidence of spatial autocorrelation ($r = -0.17$, $p = 0.9$, 9,999 permutations). Second, we compared fully specified models using five spatial correlation structures (corSpher, corLin, corRatio, corGaus, corExp); none of these improved model fit (all $\Delta AIC_c > 2$). Third, we included in all models a random, variable intercept term to account for spatial non-independence of the three restoration plots at each site.

Analyses were conducted in R version 3.1.1 (R Core Team 2014). We used the lmer and glmer functions in the lme4 (Bates et al. 2014) and lmerTest (Kuznetsova et al. 2014) packages, and the aictab function in AICcmodavg package (Mazerolle 2014). Data are available at http://n2t.net/ark:/13030/m57w6g68.

Results

During 30 sampling nights, we captured 199 individual fruit bats representing 12 species in restoration treatments that were recently degraded farmlands (Fig. 1, Table S1). Nine species in subfamily Stenodermatinae made up 64% of individuals; three *Carollia* species (subfamily Carolliinae) comprised 36%. Two small *Artibeus* species (*A. phaeotis* and *A. watsoni*) could not always be distinguished and were thus analyzed as a single taxon. Fruit bat communities were thoroughly sampled in plantation and island plots and in sites with low landscape tree cover, but not in control plots or high landscape tree cover sites, where we recorded 78 and 88% of estimated species (Fig. 2). Species richness was greater in high tree cover than low tree cover landscapes but was similar in the three restoration treatments, though controls were under-sampled which may lead to inaccurate estimates of species richness. One outlying plantation plot was identified and removed from subsequent analyses.

We captured 68% more fruit bat individuals in plantation plots ($\bar{x} \pm 1$ SD: 7.9 ± 4.5) as in controls (4.7 ± 4.6; $z = -2.31$, $p = 0.02$), and this trend was observed at 8 of 10 sites and for 10 of 11 taxa. Tree island plots had intermediate captures (6.3 ± 4.8) but were not significantly different from other treatments. The most common species, *Sturnira lilium*, was equally abundant across all treatments, but was more dominant in controls and islands than plantations. Three *Carollia* species were more abundant in plantations.

Landscape tree cover had the greatest influence on total fruit bat captures at a scale of 200 m (Fig. 3). *Sturnira lilium* and three *Carollia* species were best-predicted by tree cover within

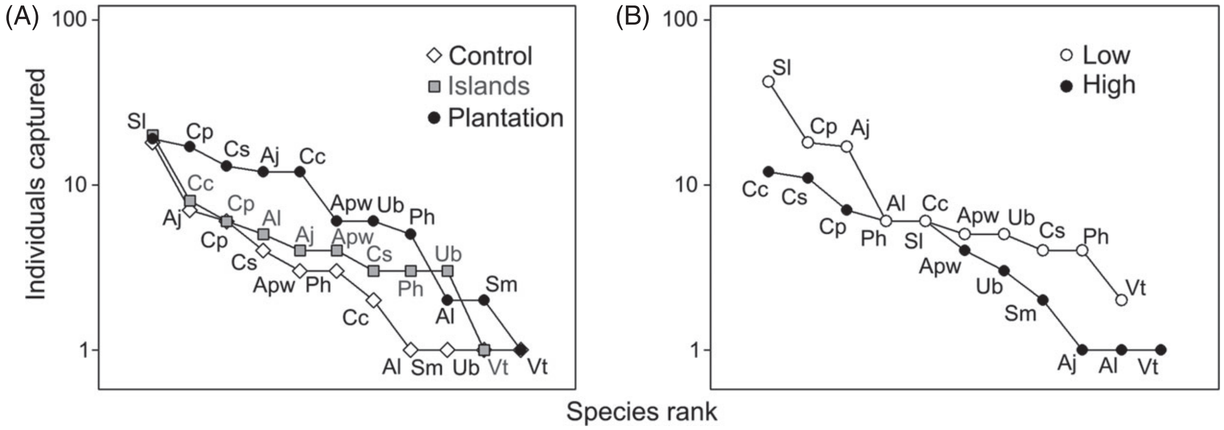

Figure 1. Rank abundance distributions for (A) three restoration treatments replicated at 10 sites and (B) restoration sites with low and high landscape tree cover within 200 m. Species codes: Aj, *Artibeus jamaicensis*; Al, *A. lituratus*; Apw, *A. phaeotis*/*A. watsoni*; Cc, *Carollia castanea*; Cp, *C. perspicillata*; Cs, *C. sowelli*; Ph, *Platyrrhinus helleri*; Sl, *Sturnira lilium*; Sm, *S. mordax*; Ub, *Uroderma bilobatum*; Vt, *Vampyressa thyone*. Sl and Vt were the most abundant and scarce species, respectively, in each restoration treatment (A).

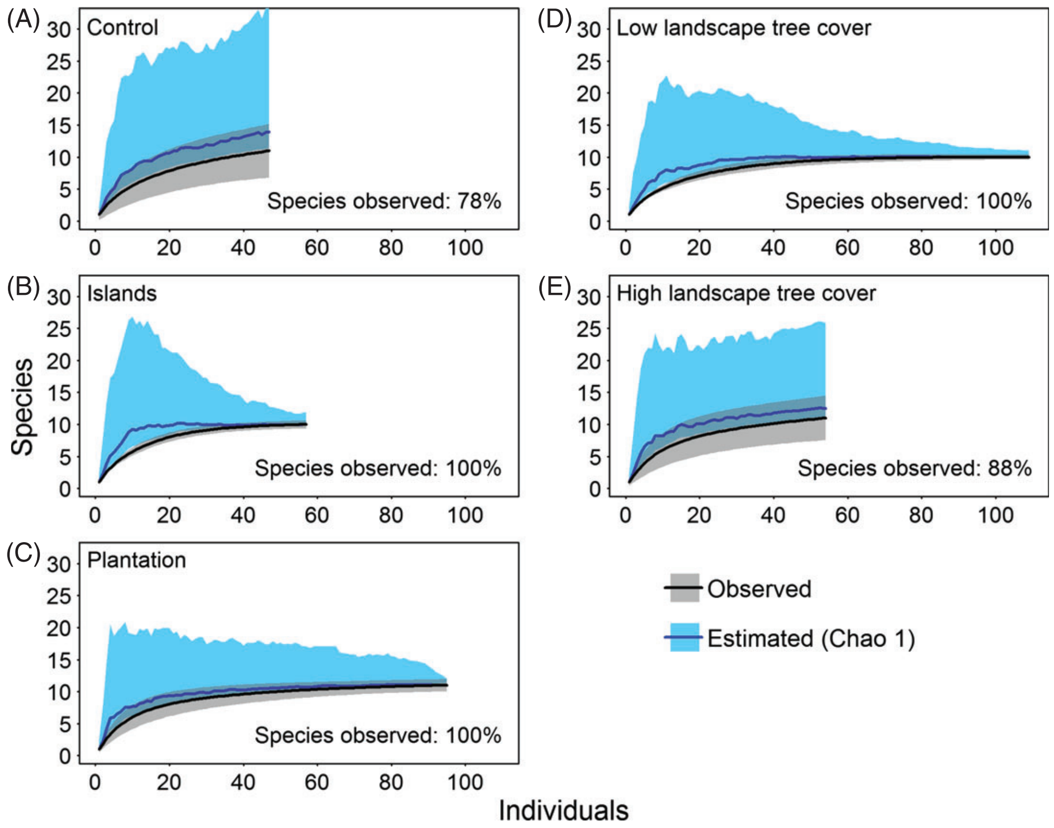

Figure 2. Species accumulation curves with observed and estimated species richness for restoration treatments (A–C) and landscape tree cover categories (D, E; 200-m buffer). Low landscape tree cover sites (D, $n = 3$) had 14–25% tree cover; high landscape tree cover sites (E, $n = 3$) had 58–77% tree cover.

smaller buffer sizes (50 m) and *Artibeus jamaicensis* by tree cover at a larger scale (400 m; Table S2). Species abundances in high tree cover sites appeared more even than in low tree cover sites. Landscape tree cover explained more capture variance than edge density for four species; only *C. sowelii* was more influenced by edge density (scale: 650 m).

Total fruit bat captures in controls and islands were greatest in low tree cover landscapes, but captures in plantations were consistent, or slightly greater in high tree cover landscapes (Fig. 4). Individual species showed strikingly different responses to landscape-scale tree cover and restoration treatments (Fig. 5). *Sturnira lilium* and, to a lesser degree, *A.*

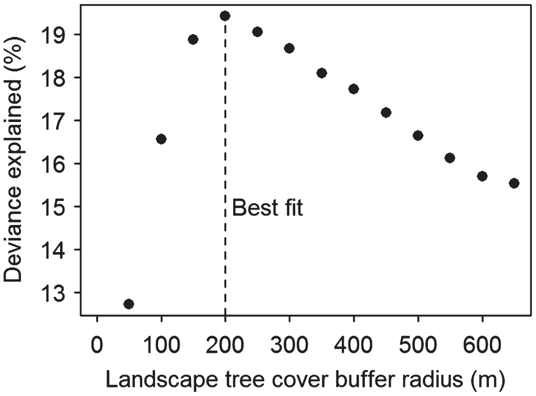

Figure 3. Model selection for the number of fruit bat individuals captured. The best fit spatial scale for landscape tree cover effect was identified by comparing models using landscape tree cover calculated within different-sized buffers.

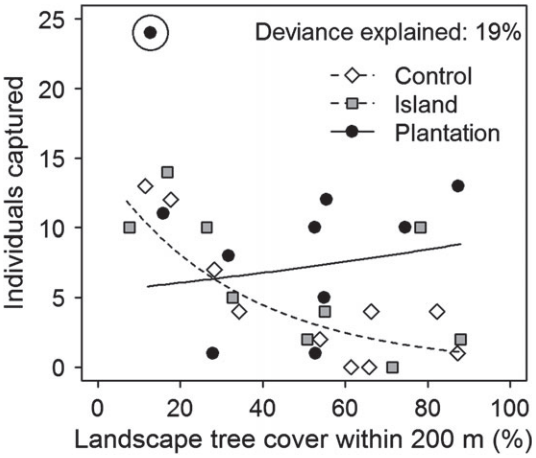

Figure 4. Number of fruit bat individuals captured predicted by landscape tree cover (% within 200 m) and restoration treatment. Line type denotes interaction between restoration treatment and landscape tree cover; solid, plantation; dashed line, control and islands. An outlier excluded from the analysis is circled.

jamaicensis were most common in low tree cover landscapes regardless of restoration treatment (Table S3). In contrast, *Carollia castanea* and *C. sowelii* were captured in plantations more often than controls regardless of landscape tree cover, and *Carollia perspicillata* captures reflected the pattern observed for all species combined.

Discussion

We found that Neotropical fruit bat responses to ecological restoration were contingent on tree cover at multiple spatial scales. Fruit bats were captured more frequently in mixed-species tree plantations than in unplanted controls, and tree islands were intermediate. This pattern was strongest, and species richness was greatest, at sites with high tree cover in the surrounding landscape.

Tree Planting Effects

Our results are consistent with a study from southeastern Brazil that found greater fruit bat abundance in two tree plantations compared with a naturally regenerating coffee farm (Mendes et al. 2014). That study attributed tree planting effects to the creation of transit habitat for bats commuting between roosts and food resources. Our tree plantations may have contributed to transit habitat, but we also expect that the greater fruit bat captures we observed in plantations could have stemmed from augmented roosting habitat. Several fruit bat species in our study area roost in concealed branches and in foliage (Kunz & Lumsden 2003; Mendenhall et al. 2014), and these resources would be more abundant in plantations than island or control plots. Although restoration plantings in this experiment did not include trees that produce fruits consumed by bats, plantations may have also contributed indirectly to food resources for *Carollia* species, which are omnivorous (York & Billings 2009) and could have been attracted by arthropods feeding on leaves or extrafloral nectaries of *Inga edulis* (Koptur 1994; Morrison et al. 2010).

Planting tree islands (also referred to as woodland islets or applied nucleation) has been suggested as a forest restoration strategy that better simulates natural forest recovery and is less resource intensive (Rey Benayas et al. 2008; Corbin & Holl 2012); the expectation is that these patches will expand and coalesce over time by attracting frugivores and facilitating seedling regeneration. Accordingly, we expected to capture more fruit bat individuals in tree island plots compared with natural regeneration, but we found no significant difference between tree islands and either controls or plantations for fruit bat abundance or species richness. Our results indicate that the efficacy of the tree island planting strategy for enhancing seed rain (Reid et al. 2015) and accelerating native tree seedling establishment (Zahawi et al. 2013; Piiroinen et al. 2015) is not primarily attributable to fruit bats. Further study is needed to differentiate among potential reasons why some fruit bats may have preferred larger tree plantations over smaller tree islands. Possibilities include greater roosting opportunities in plantations, relative difficulty of navigating through dense, second-growth vegetation in tree island plots, or differences in predation risk (Heithaus & Fleming 1978).

Previous studies in this experimental framework have evaluated frugivorous birds' responses to restoration treatments, and it is useful to compare results because birds and bats are the two most important groups of seed dispersers in many regenerating forests (e.g. Whittaker & Jones 1994; Galindo-González et al. 2000; Ingle 2003). Both groups were detected more commonly in tree plantations than controls, but the magnitude of these effects differed. Reid et al. (2014) reported a higher magnitude difference between plantations and controls for frugivorous bird detections (+133%) than we found for fruit bat captures (+68%). Similarly, Lindell et al. (2013) found a greater difference between plantations and controls for frugivorous birds captured in mist nets in three wet season samples (+200–600%), though not during a dry season sample. These comparisons suggest that fruit bats might be less attracted to tree plantations than are frugivorous birds, a conclusion that is further supported

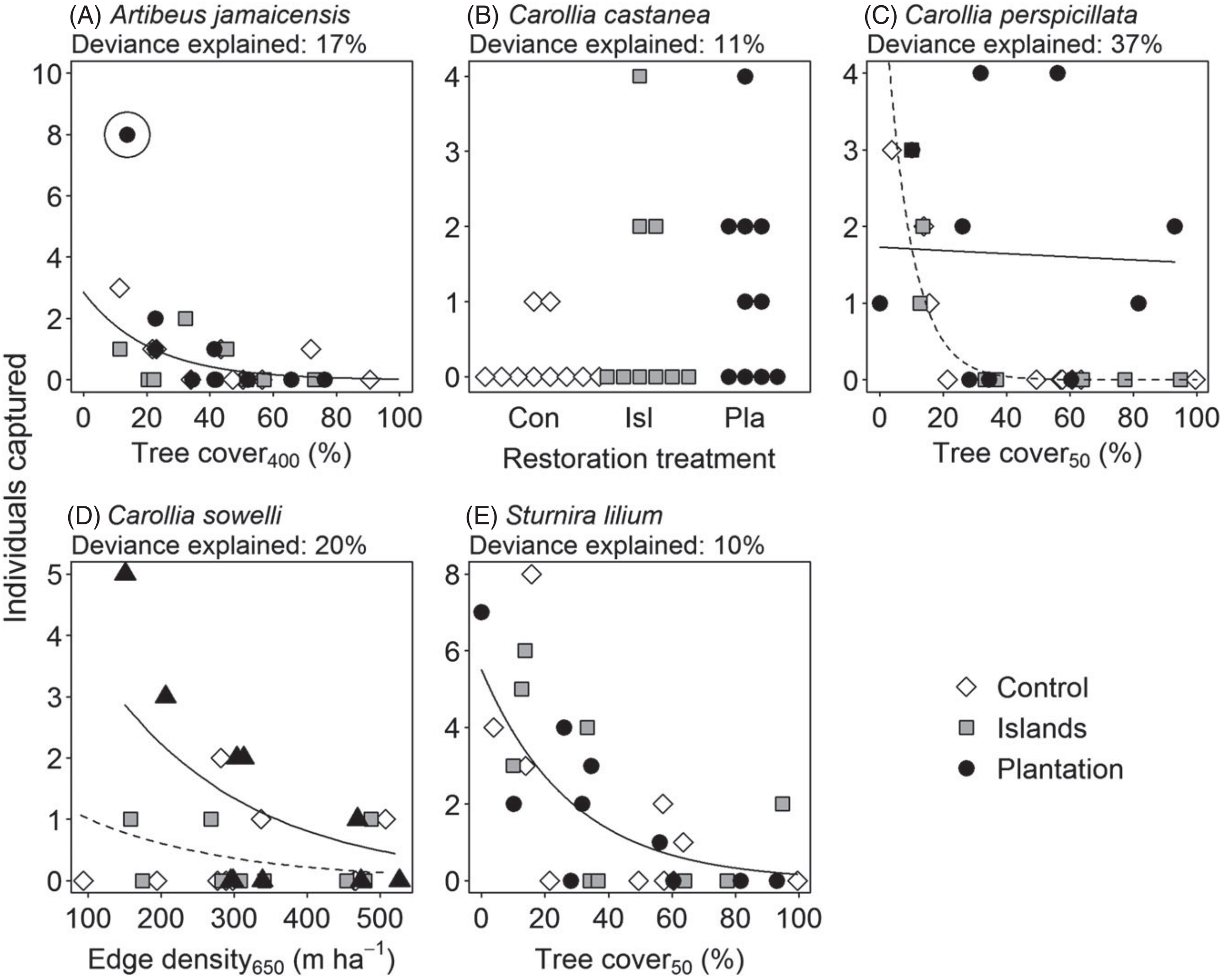

Figure 5. Fruit bat species captures predicted by landscape tree cover, edge density, and/or restoration treatment. Subscript in axis titles denotes buffer size (m). (A) *Artibeus jamaicensis* comprised 12% of captures (23 captures). The circled outlier was removed prior to analysis. (B) *Carollia castanea* (22 captures 11%). (C) *C. perspicillata* (29 captures 15%); solid line, plantation; dashed line, control/islands. (D) *C. sowelli* (20 captures 10%); solid line, plantation; dashed line, control/islands. (E) *Sturnira lilium* (57 captures 29%).

by previous comparisons of bird- versus bat-mediated tree seed dispersal (Cole et al. 2010) and later-successional tree seedling recruitment (de la Peña-Domene et al. 2014). One reason for this trend could be that seeking a shady microhabitat out of view of aerial predators is more motivating for diurnal animals than nocturnal ones (Daily & Ehrlich 1996); however, additional work is needed to determine the generality of and mechanisms for this observed difference.

Landscape Effects

Restoration sites in high tree cover landscapes had greater species richness and magnified treatment effects compared with sites in low tree cover landscapes, but individual species responded differentially. Two stenodermatines, *Sturnira lilium* and *Artibeus jamaicensis*, were captured most often in deforested landscapes regardless of restoration treatment. *Sturnira lilium* commonly uses edges or non-forest habitat (Fenton et al. 2000; Loayza & Loiselle 2008; Klingbeil & Willig 2009) and likely contributes to seed dispersal in the early stages of succession (Mello et al. 2008). It is apparently performing this function in sites with low landscape tree cover regardless of restoration efforts. *Artibeus jamaicensis*, in contrast, does not avoid forest (Vleut et al. 2012), but it does seem robust to fragmentation and habitat change (Meyer & Kalko 2008; McCulloch et al. 2013; Mendenhall et al. 2014). This species flies long distances to exploit fruit resources (Morrison 1978), which could explain the high capture rate we observed near a riparian area with two large, fruiting trees (*Ficus caldasiana* and *Calophyllum brasiliense*).

Three *Carollia* species were captured more often in plantations in most landscape scenarios. *Carollia perspicillata*, the most common species, forages on a variety of shrub and tree fruits, particularly *Piper* spp. [Piperaceae] (Fleming 1988), which grow along fencerows and in overgrown pastures in the study area. It carries fruits in its mouth to a feeding roost, usually located 30–40 m away (Heithaus & Fleming 1978). A likely explanation for the pattern we observed is that *C. perspicillata* individuals tracked *Piper* fruit abundance over relatively small (≤50 m) spatial scales, returning to dense tree plantations to consume them, and likely dispersing *Piper* seeds (Voigt et al. 2012), though probably not enriching seed rain with late-successional species (Vleut et al. 2015).

Greater species richness in sites with high surrounding tree cover suggests that to attract a more complete fruit bat assemblage, restoration sites should be established in more intact forest landscapes (Holl & Aide 2011). We observed only 88% of estimated species in high landscape tree cover sites, but even so species richness was already greater than fully sampled low tree cover sites. As only one of the species we analyzed individually (*C. sowelli*) was more abundant in less edgy sites, we expect that other, less abundant species were responsible for this trend.

Longer term sampling and behavioral data would provide further insights on tree planting, landscape context, and fruit bats. We captured bats during the dry season, but their use of restoration treatments could interact seasonally as bats track shifting resources (Heithaus et al. 1975), especially if trees were planted that produce fruits eaten by bats (Castro-Luna & Galindo-González 2012). Over the longer term, small-scale tree planting may also become more attractive to bats when planted trees are large enough to provide cavities and newly established seedlings mature and fruit (Vesk et al. 2008).

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Supporting Information

The following information may be found in the online version of this article:

Figure S1. Study sites in Coto Brus, Costa Rica, with 200-m buffers. Green denotes tree cover, digitized from aerial imagery. The largest forest fragment on the left is Las Cruces Biological Reserve.

Figure S2. Experimental design. Gray denotes areas initially planted with seedlings (2004–2006). White areas were cleared and allowed to regenerate naturally. Actual tree cover varies in each study plot; in particular, islands are now larger and some have coalesced due to planted trees branching and seedlings recruiting at the margins.

Table S1. Fruit bat species captured in 10 restoration sites in southern Costa Rica.

Table S2. Model comparisons of associations between restoration treatments, landscape variables, and captures of five fruit bat species in the study area. For each model, the number of estimable parameters (K), model fit (% dev.), log-likelihood (Log(L)), sample-size adjusted Akaike information criterion ($\mathrm{AIC_c}$), Akaike differences (Δ_i), and Akaike weights (w_i) are presented. Model fit shows the proportion of deviance in a null model ($\mathrm{dev_{null}}$) that is explained in the fitted model ($\mathrm{dev_{fit}}$): % dev. = $1 - (\mathrm{dev_{fit}}/\mathrm{dev_{null}})$. Supported models ($\Delta_i < 2$) are in bold.

Table S3. Parameter estimates for associations between restoration treatments, landscape factors, and fruit bat captures.

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