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Research Paper

Recovery of bird activity and species richness in an early-stage tropical forest restoration

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ABSTRACT. Bird habitat creation is often a goal of tropical forest restoration because bird-driven ecosystem services can accelerate forest recovery. However, resident tropical bird responses are not well characterized in the earliest years following restoration action. During a five-year study of the bird community in an experimental tropical forest restoration, we examined temporal trends in bird activity and diversity and the effects of habitat variables on the distribution of bird species within the site. Our site consisted of 16 replicate plots with 1, 2, 4, or 8 native tree species planted into former heavily-grazed pasture. Four years after tree planting, we observed a 3-fold increase in bird activity and 11-fold increase in species richness compared to preplanting. We also found changes in proportions of habitat guilds, with marked declines in open country birds and increases in birds associated with brushy, early secondary growth, and forest edge habitats. Number of bird species observed differed strongly between plots four years postplanting. Using a multispecies occurrence model under a Bayesian framework, we considered possible reasons for these differences related to plot content and context. Content features within plots (“content”), including number of tree species planted, canopy cover, tree species identity, and presence of legacy trees, did not explain differences in number of bird species observed, potentially because of small plot size relative to bird mobility. Neighborhood features (“context”) of each plot did explain differences; more bird species were detected in plots with more adjacent woodland and farther from actively grazed pasture. Our results demonstrate that planting native tree species in highly degraded sites can generate rapid, positive responses from tropical bird communities. These responses are likely mediated by surrounding habitat matrix, which influences rates of bird community recovery. Considering site context can improve predictions of fine-scale distribution of bird activity and diversity within restoration sites.

Rétablissement de l'activité et de la richesse aviaire au cours des premiers stades de régénération d'une forêt tropicale

RÉSUMÉ. La création d'habitat pour les oiseaux est souvent envisagée dans le cas de restauration de forêts tropicales parce que les services écosystémiques découlant de la présence des oiseaux peuvent accélérer le rétablissement forestier. Toutefois, le comportement des oiseaux tropicaux résidents n'est pas bien connu au cours des premières années suivant les activités de restauration. Pendant cinq années, nous avons examiné les tendances temporelles de l'activité et de la diversité des oiseaux et l'effet des variables d'habitat sur la répartition des espèces d'oiseaux dans un site d'étude au cœur d'une forêt tropicale faisant l'objet d'une restauration expérimentale. Notre site d'étude était composé de 16 parcelles répétées comportant 1, 2, 4 ou 8 espèces d'arbres indigènes plantés dans d'anciens pâturages extrêmement broutés. Quatre ans après la plantation d'arbres, nous avons observé que l'activité aviaire avait triplé et que le nombre d'espèces s'était multiplié par 11. Nous avons aussi constaté des changements dans la proportion des guildes d'habitat, les oiseaux de milieux ouverts ayant beaucoup diminué au contraire des oiseaux de milieux arbustifs, de forêt de seconde venue et de lisières forestières qui ont augmenté. Quatre ans après la plantation d'arbres, le nombre d'espèces d'oiseaux observés était très différent dans les parcelles. Au moyen d'un modèle de présence multiespèces bayésien, nous avons examiné les raisons pouvant expliquer ces différences relatives au contenu et au contexte des parcelles. Les attributs de contenu dans les parcelles (« contenu »), dont le nombre d'espèces d'arbres plantés, le couvert forestier, les espèces d'arbres et la présence d'arbres conservés pour leur valeur, n'ont pas expliqué les différences dans le nombre d'espèces d'oiseaux observés, peut-être en raison de la petite taille des parcelles relativement à la mobilité des oiseaux. Les attributs voisinant les parcelles (« contexte ») ont expliqué ces différences; davantage d'espèces d'oiseaux ont été détectées dans les parcelles situées plus près de boisés et éloignées de pâturages activement broutés. Nos résultats montrent que la plantation d'espèces d'arbres indigènes dans des sites très dégradés peut entraîner une réaction rapide et positive des communautés d'oiseaux tropicaux. Ces réactions sont vraisemblablement modulées par la matrice de milieux environnants, qui influe sur le rétablissement des communautés d'oiseaux. La prise en considération du contexte du site peut améliorer les prédictions de la répartition à petite échelle de l'activité et de la diversité aviaire dans les sites en régénération.

Key Words: *faunal recovery; occupancy; Panama; species richness estimation; tree plantation; wildlife habitat*

INTRODUCTION

Interest in forest restoration is increasing in tropical regions because forests provide significant ecosystem services such as carbon sequestration, timber production, recreational opportunities, and wildlife habitat (Lamb et al. 2005, Chazdon 2008, Rodrigues et al. 2011, Suding et al. 2015). Although disturbed tropical forests can recover via natural regeneration (Aide et al. 2000), native tree planting may accelerate forest and ecosystem service recovery (Parrotta et al. 1997, Carnevale and Montagnini 2002, Fink et al. 2009, Holl et al. 2016). Recovery of wildlife habitat is often a rationale for forest restoration (Miller and Hobbs 2007) but how wildlife populations respond to different restoration techniques is often uncertain. Furthermore, wildlife-plant interactions can influence long-term restoration outcomes via mutualisms, herbivory, and trophic cascades so an improved understanding of wildlife activity during the early stages of forest restoration is important for restoration planning (Fraser et al. 2015, McAlpine et al. 2016).

Among wildlife taxa, birds are conspicuous early responders to forest restoration (Dunn 2004, MacGregor-Fors et al. 2010, Lindell et al. 2012, Rolo et al. 2017). Because of their diverse life history strategies including wide variation in diet, specialized foraging strategies, and microniche preferences, birds can act as an indicator taxon for recovering ecological complexity during forest restoration (Da Silva and Vickery 2002). In addition, birds provide ecosystem functions that facilitate forest recovery including seed dispersal, pollination, and herbivorous insect reduction (Sekercioglu 2006, Morrison and Lindell 2012, Lindell et al. 2013, Frick et al. 2014, Carlo and Morales 2016). Bird-driven ecosystem functions are tied to activity levels and composition of the local-scale bird community and should be closely related to habitat affiliations of species using restoration sites. For example, bird species that regularly use trees are more likely to carry seeds of woody species than open-country species (Lindell et al. 2013). Forest restoration sites experience rapid changes in the bird community during the early stages of forest recovery, potentially affecting bird ecosystem function (Gould and Mackey 2015, Lindenmayer et al. 2016).

The return of forest-associated birds to forest restorations is a metric of restoration progress (Twedt et al. 2002, Nichols and Nichols 2003, Rolo et al. 2017). Increasing compositional overlap with forest bird communities at less disturbed reference sites indicates progress toward biodiversity conservation goals (Catterall et al. 2012, Rolo et al. 2017). In restorations intended as wildlife corridors between forest fragments, forest-associated birds demonstrate restorations are functioning as planned (Jansen 2005). Finally, forest-associated species can carry seeds and pollen from forest plant species into restorations, encouraging the re-establishment of a diverse native plant community (Wunderle 1997, Frick et al. 2014, Carlo and Morales 2016). Prior studies of regenerating tropical forests have found bird activity and species richness rapidly increase in the first decade or two, although a return to compositional similarity with primary forest bird communities may take over a century (Dunn 2004, Catterall et al. 2012, Paxton et al. 2018).

Greater insight into bird responses to fine-scale habitat characteristics in forest restorations will aid restoration

practitioners seeking to create wildlife habitat or harness bird ecosystem services to accelerate the restoration process. Choices made at project initiation, such as the identity and number of tree species planted, affect development of characteristics like vegetation density and canopy cover (Holl et al. 2013, Rolo et al. 2016). Such structural characteristics can, in turn, affect site attractiveness to birds several years after tree planting (Fink et al. 2009, Lindenmayer et al. 2010, Lindell et al. 2012, 2013). Other fine-scale habitat characteristics may be less easy to alter, such as legacy features (e.g., old snags or land use history) or land use on adjacent parcels with different ownerships, but are also potentially relevant to birds and thus restoration planning.

Studies of bird recovery in forest restorations frequently substitute space for time, using chronosequences to assess trajectories in bird abundance and diversity (e.g., Catterall et al. 2012, Rolo et al. 2017). However, chronosequences with limited temporal resolution may not provide insights into the pace of bird recovery during earliest years, when change should be most dynamic (Jansen 2005, Paxton et al. 2018). Setting expectations for the earliest years, such as when the first forest-associated birds will appear, is especially important for restoration projects that plan to use an adaptive management framework with ongoing monitoring (Murray and Marmorek 2003). As such, longitudinal data on bird responses to restoration, starting at project initiation, are useful.

We conducted a five-year study of the bird community in a plantation-style forest restoration in Panama, beginning at the initiation of restoration efforts. Prior research in bird responses to forest restoration strategies has examined effects of planting configuration (Fink et al. 2009, Lindenmayer et al. 2016), understory enrichment plantings (MacGregor-Fors et al. 2010), and fast-growing nurse trees (Hamel 2003). Our study site featured replicate plots to compare bird responses to restoration planting regimes with different numbers and mixes of tree species. Tropical forest restoration efforts are challenged by extremely high diversity of tree species present in natural forests. In central Panama, a single wet lowland forest site can harbor over 300 tree species (Condit et al. 1992). Restoration with a large component of the native tree diversity (e.g., Rodrigues et al. 2009) is ideal but practical considerations, such as seed collection, tree nursery space, and labor costs, mean that plantation-style tropical forest restorations typically occur with far less than a full complement of old-growth forest species. Nevertheless, we hypothesized that planting a few tree species would still be sufficient to quickly induce a strong response from the bird community. A previous restoration study in Central America showed that only two to four years of growth by four planted tree species was enough to attract a diverse bird community to heavily degraded areas (Fink et al. 2009; Lindell et al. 2012).

At the scale of our entire site (all plots aggregated), we predicted bird activity and species richness would increase quickly after restoration initiation because high plant productivity in the tropics supports rapid development of vegetative structure, long known to be a determinant of bird diversity (MacArthur and MacArthur 1961, Karr 1968). We also anticipated vegetative development would result in species turnover as species associated with earlier seral stages abandoned the site (Twedt et al. 2002, Gould and Mackey 2015).

At the scale of individual plots, we hypothesized that a plot planting regime would influence the number of bird species recorded. Specifically, we expected the number of bird species in a plot to be positively associated with greater canopy cover, more planted tree species, and the presence of a particular planted tree genus, *Inga*. Canopy cover and number of tree species have previously been associated with greater bird species diversity in Neotropical coffee plantations (Van Bael et al. 2007, Philpott et al. 2008). Many tropical bird species rely on the canopy layer as foraging, resting, and breeding habitat. Higher tree species diversity could affect bird diversity by providing complementary resources, such as variable foraging substrates, host-specific arthropod prey, open branch structures for foraging, and dense branch structures for nesting and predator protection. However, the original authors who emphasized the importance of vegetative structure to bird also regarded plant species diversity per se as having little effect on bird diversity (MacArthur and MacArthur 1961, Karr 1968). The tree genus, *Inga* (Family: Fabaceae), has a bushy growth form and tends to produce canopy cover more rapidly than other kinds of trees planted at our site. *Inga* trees have previously been shown to be an attractive habitat feature for birds (Fink et al. 2009). In addition to aspects of our planting regimes, we expected a positive response of bird diversity to the presence of legacy trees that remained in the former pasture; such trees can draw a variety of woodland species into otherwise open country (Fischer and Lindenmayer 2002).

During our study, we noticed strong spatial patterns in the distribution of bird activity and number of species observed within plots that appeared unrelated to planting regime or legacy trees. We collected data on the distance to nearest pasture and amount of woodland adjacent to our plots to examine the hypothesis that habitat features external to plots influenced number of species observed. Understanding the relative importance of restoration “content,” i.e., habitat features within restoration sites, and restoration “context,” i.e., features of the surrounding neighborhood, is key to effective restoration planning for faunal recovery (Lindenmayer et al. 2010, Reid et al. 2014, Gould and Mackey 2015).

METHODS

Field site

We conducted our study at a forest restoration site in the Mamoni Valley, Panama (09°18.6' N, 79°07.8' W, 185 m a.s.l.). The valley was historically forested but is now a mosaic of pasture, small agricultural plots, secondary growth of various ages, tree plantations, and primary forest fragments. In July 2010, sixteen 50 m x 50 m forest restoration plots were established on 4 ha of recently abandoned, heavily grazed pasture featuring only a few scattered trees. Plots were arranged in a loose grid with 12-m minimum buffers between plots, avoiding steep slopes and excessively wet soils that could negatively affect the survival and performance of planted trees.

Each plot was manually cleared of herbaceous vegetation and planted with seedlings of native trees grown from locally collected seed. Seedlings were planted in a grid with 3 m between rows, resulting in 256 seedlings per plot. Plots were planted with 1, 2, 4, or 8 species with equal shares in multispecies plots (see Table A1.1 for planting mixes). Tree species were selected based on a

variety of characters including ease of seed germination, ability to act as a wildlife resource, e.g., nectar producing flowers or edible fruits, potential for eventual timber harvest, and performance in plantation contexts. Planting mixes were chosen based on seedling availability and also to include at least one nitrogen-fixing legume (Family Fabaceae). One tree type, *Inga*, was discovered postplanting to be a mix of several *Inga* species. The majority were *I. thibaudiana*, but *I. stenophylla*, *I. ruiziana*, and *I. sapindoides* were also planted (Rolando Perez, *personal communication*). Because these *Inga* species have similar growth forms, we grouped them as “*Inga* spp.” for our analyses. The seedlings of one species (*Minquartia guianensis*) in the plots planted with eight species died and were replaced in 2011, primarily with a new species (*Hieronyma alchorneoides*) and secondarily with other species already present in those plots. To reduce competition for the young trees, nonplanted vegetation in plots and buffers was manually cleared multiple times in the first two years and again in the fifth year. Although we did not measure tree growth, we observed that canopy height four years after planting was typically 3–5 m, with some tall trees exceeding 6 m.

Bird surveys

We define bird “Activity” as the cumulative number of birds recorded during surveys. Thus, Activity can increase because of (1) more individuals using a survey location; (2) more time by the same individuals at a survey location; or (3) a combination of 1 and 2. We did not attempt to distinguish between these possibilities because our objectives were to characterize general habitat suitability for birds and potential changes in bird ecological function. To distinguish between numbers of species in individual plots (“plot-scale”) and the site as a whole (“site-scale”) within a year, we call the number of species in a single plot across all replicate counts “Species Use” and the number of unique species across all counts for all plots “Species Richness.” We attempted to correct for detection bias when measuring Species Use and Species Richness four years postplanting (see Analyses) but did not do so for Activity because of data limitations.

Multiyear survey protocol

To measure changes in Activity and Species Richness through time, we conducted annual bird surveys midrainy season (July–August) for five years (“Multiyear survey”), beginning with a baseline survey prior to tree planting in 2010. In each plot, we conducted 12-min area counts, recording all birds present by sight and sound while taking care to avoid double-counting of individuals within counts. We used two to four vantage points in each plot to limit the effect of obstructive vegetation and terrain on bird detection. Counts were conducted four times in each plot within a single day each year, with a minimum of 15 min between counts. All counts were conducted between 0630–1100 hr. Daily temperatures were fairly consistent (low: ~23°C, high: ~32°C) but morning fog, cloud cover, and scattered rain showers were highly variable. To reduce detection bias, counts were not conducted during rain, fog, or high winds. However, other weather variables such as cloud cover may have affected detection. Birds flying overhead or flying through plots without landing or foraging were not included in the final data set.

2014 Single-year survey protocol and mist netting

In July–August 2014, a single observer (S. Roels) conducted replicated surveys (“Single-year survey”) to evaluate hypotheses regarding plot content and context effects on Species Use. Repeated 10-min area counts were made in each plot except Plot 16, which was excluded due to difficult access. The change from 12-min (multiyear survey protocol) to 10-min counts was due to the need to accommodate travel time between plots while still completing surveys in the morning hours. All plots were surveyed once each day and visited in a set sequence with a randomized starting plot. Count protocol was otherwise similar to the annual protocol. Ten surveys were conducted over a 20-day period, resulting in a Single-year data set containing 10 replicates for each plot. As a supplement to our surveys in 2014, we operated mist nets at 10 locations across the site for total of 180 net hours from May–July 2014. Mist net sampling is a complementary approach to point counts that can effectively detect taxa often undersampled by point counts in tropical forests (e.g., Blake and Loiselle 2001). Net operations were conducted under fair weather conditions between 0600–1130 hr and nets were checked every half hour. Captures were identified to species and were banded or had a tail feather trimmed to identify recaptures.

2014 Plot content and context measurements

In 2014, we collected data for six variables that described the plot (content variables) or surrounding neighborhood (context variables). Content variables were (1) Percent canopy: amount of canopy cover in a plot; (2) Tree species: the number of tree species planted in a plot; (3) Inga: whether *Inga* spp. were planted in a plot; and (4) Residual trees: whether legacy trees greater than 5 m tall were present in a plot prior to planting. Context variables were (5) Adjacent woodland: percentage of land adjacent to plot that was forest restoration or forest fragment; and (6) Pasture distance: distance from plot center to nearest actively grazed pasture.

To quantify canopy cover, we divided each plot into quadrants and took canopy measurements with a spherical densiometer at three random points per quadrant (12 points per plot). Measurement points were between rows of planted trees to avoid inflating canopy cover values by standing directly next to tree trunks. Densiometer readings were taken in the four cardinal directions and then averaged to create the percent canopy estimate for an individual point. The mean of all points within a plot is our estimate of percent canopy cover for a plot. Variables “Tree species” and “Inga” were known aspects of the original plot design and were confirmed with tree survivorship surveys in 2014. Residual trees, either alive or dead, were noted as “present” or “absent” in each plot.

We calculated “Adjacent woodland” by visually estimating percentage of wooded land cover at a set distance of 25 m from each of the four plot edges. We defined woodland as any area of forest restoration or secondary forest. Forest restoration included an adjacent restoration planting with a similar tree species mix initiated one year prior to our study. Nonwoodland vegetation included active pasture, weedy fields, marsh, and brushy areas. To create a single value for each plot, we averaged the percentage of wooded land cover from the four plot edges. The variable “Pasture distance” was calculated in QGIS 2.18 (QGIS Development Team

2017) using the straight-line distance between plot center points and the nearest pasture.

Bird guild assignment

We assigned all recorded bird species to habitat guilds based on published natural history descriptions (Ridgely 1981, Stiles and Skutch 1989, Angehr and Dean 2010, Cornell Lab of Ornithology 2018) and personal experience (Table A1.2). We placed species into one of four guilds: Open Country, Brushy, Early Secondary, and Forest Edge. Open Country habitats are characterized by a lack of woody vegetation, although perches such as isolated tall trees may be present. Brushy habitats are weedy and have woody growth less than 2 m tall. Early Secondary habitats feature dense, woody growth greater than 2 m tall. Forest Edge habitats are established woodland/forest adjacent to other, less heavily wooded areas. Individual birds not identified to species level were assigned to guilds based on partial identifications if possible, e.g., all members of the genus were in the same guild.

Analyses

Changes in Activity and Species Richness through time

All analyses were conducted in R (version 3.4.3; R Development Core Team, 2017). Activity and Species Use were low in individual plots during the first three years of the study (many plots with 1 or 0 species recorded) so we investigated trends in the Multiyear data for the restoration site as a whole, rather than conduct plot-scale analyses. To facilitate analyses of Multiyear data, we pooled all plot-scale surveys within a year into a single site-scale data set. Thus, annual site-scale Activity was the total number of birds recorded each year. Annual site-scale observed Species Richness was the total of unique species recorded each year. To estimate actual Species Richness, including hypothetical species present but unobserved, for a given year, we used the first-order jackknife estimator (Walther and Moore 2005; function “specpool” in package “vegan,” Oksanen et al. 2018). The first-order jackknife is a resampling technique that estimates undersampling bias using the number of “singletons,” that is, observations that were recorded only once in the data set. As applied to species richness estimation, the first-order jackknife is calculated as $S_{\text{actual}} = S_{\text{observed}} + (n-1)f_1/n$, where S is the number of species, n is the sample size, and f_1 is the number of singletons. To compare survey methods (Multiyear vs. Single-year) and richness estimation techniques, we also produced Species Richness estimates for 2014 from the Single-year data set using the first-order jackknife and our occurrence model.

Species use responses to plot content and context variables

To examine effects of content and context variables on use of plots by birds, we analyzed the Single-year (2014) data set collected by SR in a multispecies hierarchical occurrence model (Dorazio et al. 2006, Zipkin et al. 2010). This class of models uses aggregate occurrence data for all species and replicate surveys to improve parameter estimates for rare and unobserved species and also accounts for imperfect detection of individuals inherent in avian surveys. In our context, with plot sizes smaller than the typical home range of most bird species, we interpret

the model as estimating the effect of variables on probability that a given species will use habitat in a plot rather than site occupancy per se.

Our full model had two components: an occurrence model and a detection model. The occurrence model assesses effects of six plot variables on plot use by birds, which is assumed to be the outcome of a Bernoulli random variable for each species. This distribution is specified as $z_{i,j} \sim \text{Bern}(p_{i,j})$, where z is the actual use, i is the species, and j is the plot. Continuous variables (Percent canopy, Tree species, Adjacent woodland, and Pasture distance) were standardized to have a mean of 0 and standard deviation of 1. Categorical variables (Inga and Residual trees) were treated as binary (0 or 1). To guard against problems with collinearity, we confirmed all pairwise correlations of variables had $r < |0.7|$ (Dormann et al. 2013). The occurrence model for species i at plot j is represented as:

$$\text{logit}(\psi_{i,j}) = \alpha_0 + \alpha_1 \text{PercentCanopy}_j + \alpha_2 \text{TreeSpecies}_j + \alpha_3 \text{Inga}_j + \alpha_4 \text{ResidualTrees}_j + \alpha_5 \text{AdjacentWoodland}_j + \alpha_6 \text{PastureDistance}_j$$

The term α_0 represents the probability of plot use (on a logit scale) by species i given mean values for continuous variables and zero values for binary variables, i.e., *Inga* and Residual trees absent. Coefficients α_1 - α_6 represent the effects of predictor variables on plot use by species i . Effects are either linear (continuous variables) or the effect of changing states (binary variables).

The detection model assesses the effect of survey Date and Time on the detection of birds. Like species occurrence, species detection is assumed to be the outcome of a Bernoulli random variable for each species. This distribution is specified as: $y_{i,j,k} \sim \text{Bern}(p_{i,j,k} * z_{i,j})$, where y is the observed use, p is the probability of detection, i is the species, j is the plot, and k is the replicate survey. Thus, our observed use is the product of the probability of detection (p) and true use state (z). Both predictor variables were standardized to have a mean of 0 and standard deviation of 1. The detection model for species i at plot j in replicate survey k is represented as:

$$\text{logit}(p_{i,j,k}) = \beta_0 + \beta_1 \text{Date}_j + \beta_2 \text{Time}_j$$

The term β_0 represents the probability of detection (on a logit scale) for species i given mean values for variables. Coefficients β_1 and β_2 represent the linear effects of each survey variable on detection of species i .

We analyzed our model in a Bayesian framework in R (R Development Core Team 2017) and JAGS (Plummer 2017) using the package “jagsUI” (Kellner 2017). To represent unobserved species, we augmented our species occurrence data with 40 additional “species,” all having encounter histories of zero (Royle et al. 2007). We assessed effects of model variables on plot use by the bird community as a whole by examining posterior estimates for mean parameters at the community level of the hierarchical model. We used uninformed priors for these mean “hyper-parameters,” each having normal distributions with mean = 0 and variance = 2.70, as proposed by Lunn et al. (2012). The shape and scale parameters of the gamma priors for the variance parameters were set to 0.1. The hyper-parameters govern estimation of species-level occurrence and detection parameters, which we assume are drawn from the corresponding community-level

distributions (Zipkin et al. 2010). We ran three Markov chain Monte Carlo (MCMC) chains for 275,000 iterations with a burn-in of 225,000 (10,000 in the adaptive phase). Posterior chains were thinned by 5, yielding a total of 30,000 estimates for each model parameter. We used the R-hat statistic, and evaluated chains, to confirm model convergence (Gelman and Hill 2007).

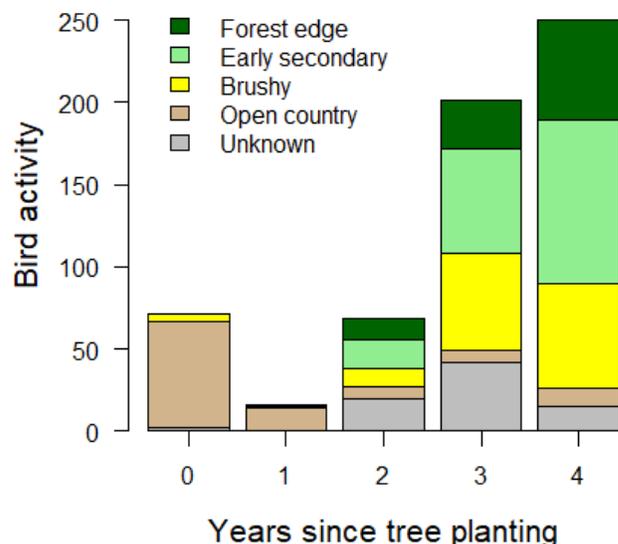
RESULTS

Over the Multiyear survey (five years), we recorded 40 bird species with 607 occurrence records (Table A1.2). In the Single-year survey of 2014, four years postplanting, we recorded 525 birds representing 41 species (Table A1.2). That same year, our mist nets captured 252 birds representing 47 species (Table A1.2).

Multiyear trends in site-scale Activity and Species Richness

Site-scale Activity and observed Species Richness were strongly correlated postplanting (Multiyear data: 2011–2014, $r = 0.988$). Activity prior to tree planting was moderate and initially declined after planting before a sustained three-year increase (Fig. 1). Four years after tree planting, our Multiyear survey protocol recorded over three times as much Activity as before planting (Fig. 1). Open Country Activity decreased rapidly following tree planting and remained at low levels throughout the study. One Open Country species, Eastern Meadowlark (*Sturnella magna*), represented 89.9% of Activity (62 of 69 birds identified) preplanting and was not recorded after one year postplanting. All other habitat guilds showed year-to-year gains in Activity.

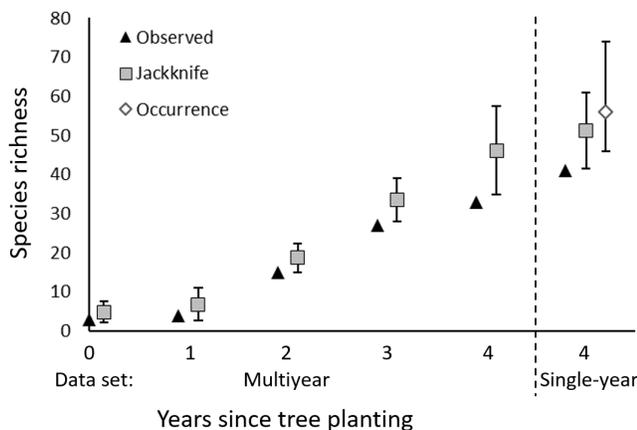
Fig. 1. Multiyear trends in site-scale Activity for four habitat guilds following tree planting in a forest restoration in the Mamoni Valley, Panama. Some birds could not be assigned to a guild because of insufficient taxonomic identification during field surveys.



Site-scale Species Richness was low prior to tree planting and did not significantly change until two years postplanting (Fig. 2). Four years after tree planting, we observed 11 times as many

species as before planting (Fig. 2). The actual difference in richness may be even greater than directly observed; estimates of true richness (total observed and unobserved species) increased at a faster rate than observed species. First-order jackknife estimates of Species Richness four years after planting were similar between Multiyear (46.1 species, 95% confidence interval: 34.9–57.4) and Single-year data sets (51.3 species, 95% confidence interval: 41.6–61.0; Fig. 2). The Single-year occurrence model estimate (56.1 species, 95% credible interval: 46.0–74.0) was also similar to the Single-year jackknife estimate (Fig. 2). All habitat guilds except Open Country demonstrated a general pattern of increasing Species Richness from two years after planting onward (Table A1.2).

Fig. 2. Estimates of site-scale bird Species Richness following tree planting. For the Multiyear survey data set, we present observed species and the first-order jackknife estimate. For the Single-year data set (2014), we present observed species, the first-order jackknife estimate, and the occurrence model estimate. Error bars are 95% confidence or credible intervals for the jackknife and occurrence estimates, respectively.

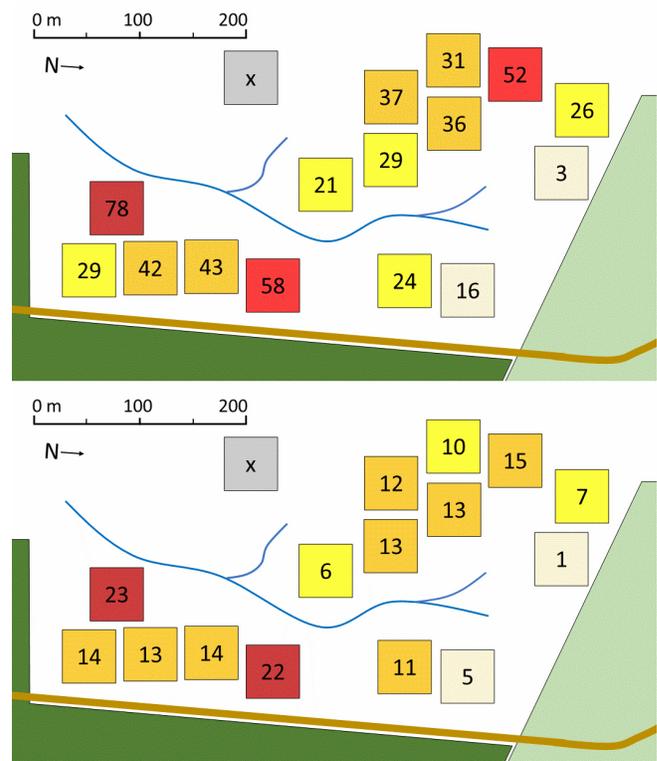


Plot-scale Activity and Species Use four years after planting

In the Single-year survey of 2014, plot-scale Activity and Species Use were strongly correlated ($r = 0.935$), with a tendency toward higher values in southeastern plots and lower values in northern plots (Fig. 3). At the community level, i.e., hyper-parameters, of our occurrence model, the context variables Adjacent woodland and Pasture distance were significant (95% credible intervals did not overlap 0) while all content variables were not (Fig. 4). Accounting for unobserved species in our model made the univariate relationships between context variables and plot-scale Species Use more evident (Fig. 5). The regression slope for the relationship between estimated Species Use and Adjacent woodland predicts one additional species for every ~2.8% increase in Adjacent woodland (Species = $16.67 + 0.359 \cdot \text{Adjacent woodland}$, $r^2 = 0.431$). For the relationship between the estimated Species Use and Pasture distance, the model predicts one additional species for each additional ~10.8 m from the nearest pasture (Species = $15.72 + 0.0929 \cdot \text{Pasture distance}$, $r^2 = 0.745$). In the detection component of our model, Date was a significant

variable, with higher detection on later dates (mean: 0.35, 95% credible interval: 0.14–0.56), while Time was not significant (mean: -0.04, 95% credible interval: -0.19–0.11).

Fig. 3. Plot-scale bird Activity (upper panel) and observed Species Use (lower) by plot in 2014 Single-year survey. Numbers in plot are total individual birds (upper) and species (lower) observed in 10 surveys. One plot (“x”) was not surveyed.



Number of Species	Number of Birds	Feature
21-25	65-80	Pasture
16-20	49-64	Planting
11-15	33-48	Road
6-10	17-32	Stream
0-5	0-16	

At the species level, our occurrence model produced posterior distributions with wide credible intervals and point estimates that rarely deviated significantly from those of community-level hyper-parameters (Fig. A1.1). Low detection of Species Use, likely due to single plots being smaller than typical home range sizes, limited our ability to recover evidence of species-specific responses to plot variables. For example, several species demonstrated use of a plot, i.e., at least one record, but were only

recorded once out of 10 replicate surveys making it difficult to infer those species' willingness to use plots where they were not recorded. We were also unable to discern any patterns in responses to plot variables when species were grouped by guild (Fig. A1.1).

Fig. 4. Effect of plot variables on Species Use. Ninety-five percent credible intervals are presented for the posterior distributions of six plot variables. Variables are (1) Percent canopy: amount of canopy cover in plot; (2) Tree species: the number of tree species planted in plot; (3) Inga: *Inga* spp. were planted in plot; (4) Residual trees: legacy trees (alive or dead) were present in plot; (5) Adjacent woodland: percentage of land adjacent to plot that was forest restoration or forest fragment (see text for explanation); and (6) Pasture distance: distance from plot center to nearest actively grazed pasture. Credible intervals not overlapping zero are deemed significant variables and are denoted with an *.

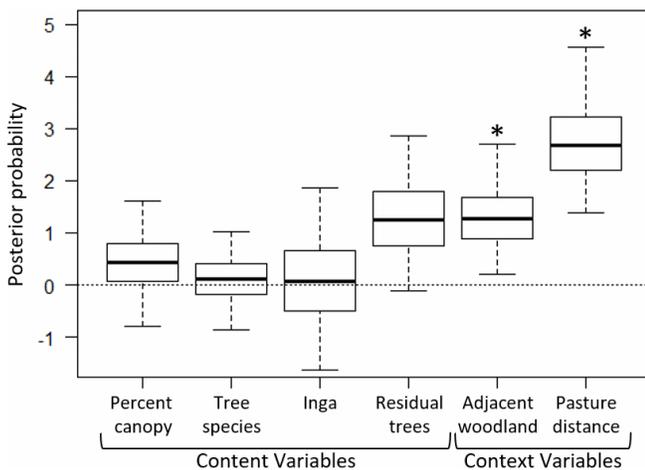
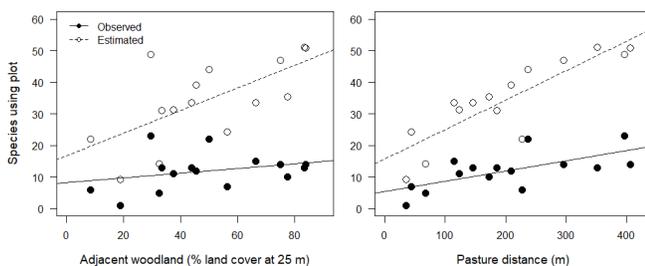


Fig. 5. Relationships between plot context variables, Adjacent woodland and Pasture distance, and plot use by bird species. The bird community at the restoration site contained many species that irregularly used plots, leading to low estimates of detection. Accounting for detection with a multispecies occurrence model yields estimates for the true number of species using each plot higher than was actually observed. Estimating true use may more effectively recover relationships between plot variables and use by birds.



DISCUSSION

Trends and turnover

Over four years, we documented an increase in Activity and Species Richness at the restoration site, supporting our hypothesis that planting even a limited number of tree species can elicit a strong, rapid response from a tropical bird community. However, there was also an unexpected two-year time lag postplanting before increases in Activity and Species Richness were realized, which included a temporary drop in Activity one year postplanting. The few studies that have conducted annual monitoring starting with restoration initiation show varying results for the speed of avian response, possibly due to landscape context. Paxton et al. (2018) reported low bird densities in a Hawaiian montane forest region during the first five years postplanting, with more substantial gains occurring in the following 20 years. Jansen (2005) observed a strong response by birds in the first three years, including forest-associated species, to tree planting in an Australian rainforest region. Such differences are likely in part due to variable distance to large blocks of existing forest, with Paxton et al.'s (2018) surveys up to approximately 800 m from forest and Jansen's (2005) surveys no more than approximately 200 m. Our site was approximately 500 m from extensive forest but with smaller fragments at shorter distances. Different survey methodologies and community sizes make comparisons between studies difficult, but we regard the speed of bird response in our study to be intermediate to rates observed by Paxton et al. (2018) and Jansen (2005).

A meta-analysis of tropical forest bird community recovery found that species richness, standardized to that of mature forest, typically recovers after 20 years of forest regeneration (Dunn 2004). Exhaustive sampling of wet lowland forest in central Panama by Robinson et al. (2000) yielded average species densities of 111 resident species per 2 ha plot. Although our study site was slightly larger (4 ha), this suggests that species richness at our site had returned to approximately half of what would be expected in mature forest only four years after native tree planting.

The decline in Open Country guild dominance presents a case of rapid faunal turnover during the transition from pasture to young restored forest. This shift was essentially due to disappearance of Eastern Meadowlark, the most abundant species prior to restoration. Unlike continued substantial increases in Activity by Early Secondary and Forest Edge guilds, Brushy guild Activity leveled off from three to four years postplanting (Fig. 1). This may indicate a peak for this guild, which we expect will eventually decline as the site matures. In an Australian tropical forest, turnover of nonwoodland species occurred in the first 10–15 years while woodland-associated species demonstrated a steady accumulation of species richness for at least the first 20 years after revegetation (Gould and Mackey 2015). If our site follows similar patterns, and eventually reaches a species density similar to mature forest as predicted by the model of Dunn (2004), then species accumulation rather than species turnover will be the primary driver of community changes at the site in the coming decade or two.

Site-scale Species Richness estimates four years postplanting

Regardless of the survey data set or estimation technique, we calculated actual Species Richness considerably higher than

observed (Fig. 2), underscoring the difficulty of exhaustively sampling tropical bird communities and the importance of accounting for undetected species. Combining all observations from formal plot surveys, mist netting, and incidental encounters in 2014 yields a total of 67 species (Table A1.2). This total is beyond the 95% confidence interval limits given by the jackknife estimates but within the 95% credible interval given by the occurrence model. Half of the species not recorded on formal plot surveys were hummingbirds, a group that is difficult to effectively survey with area counts because their behavior and size reduce surveyor ability to make species-level identifications. Forest birds with only mist net records may have been flying through the site but not using it for foraging or other activities. Even so, this would indicate the site is becoming a functional corridor between nearby forest fragments.

Effects of content and context variables on birds

Contrary to our hypothesis that plot planting regime would influence the number of bird species recorded, none of our content variables showed a significant relationship with plot-scale Species Use, suggesting these variables do not strongly differentiate plot attractiveness within a single year. From an avian perspective, differences between plot content may not have been as great as we perceived; most of the species using our site have fairly broad habitat tolerances and may only respond to coarser habitat differences. However, the site-scale multiyear trends of increasing Activity and Species Richness demonstrate vegetation structure, which developed substantially over the study, does matter. The significance of vegetation structure and unimportance of number of tree species planted are consistent with previous research (MacArthur and MacArthur 1961, Karr 1968). Many species using our site have home ranges larger than our plots, or even our entire study area, so within-year content effects may only become apparent at a larger scale. Finally, content effects may have been obscured by the overwhelming influence of context effects on Species Use. We caution our results only indicate content variables did not strongly affect Species Use of plots during our study, in an early stage of restoration. Effects of plot planting design may become more important over time as differences in tree growth habits manifest more strongly and trees become reproductively mature. *Inga*, for example, will not grow as tall as other species but will produce large amounts of flowers and fruit attractive to birds (Johnson 2000).

Like previous studies, we found restoration site context significantly influenced plot-scale Species Use (Lindenmayer et al. 2010, Reid et al. 2014). At our site, there were more species using plots near other woodland habitat and farther from pasture. Increasing Species Use with distance to pasture could be aversion to pasture or because plots nearest pasture represented poorly connected habitat not part of efficient foraging routes. We find the second interpretation more likely because we commonly observed substantial bird activity at forest-pasture interfaces in the Mamoni Valley, provided the forest area was large. Other adjacent land cover types also may have influenced Species Use but could not be included in our model because of small sample size. For example, birds were rarely observed in a dense fern-covered wetland that was within 25 m of some of the northernmost plots. The plot with highest Activity and observed

Species Use was adjacent to a small fragment of riparian woodland. Riparian woodland was pooled inside the Adjacent woodland category but may have unique characteristics that make it especially attractive to birds.

Occurrence model potential and limitations

For tropical communities, where species richness is high and many species are rare, acquiring sufficient sample sizes for individual species is challenging (Gotelli and Colwell 2001, Herzog et al. 2002). In this context, multispecies occurrence modeling, which can assess both community- and species-level responses to environmental variables, may be particularly useful. The results of our model need to be interpreted in light of characteristics of our field site and the plot variables we included in the model. The proximity of our plots to each other means that plot-scale Species Use is likely not independent as birds move about the site. It is unclear why survey date was a significant detection model variable over the brief period when our Single-year survey was conducted (three weeks). Possibilities include acclimation of birds to observer presence, changes in bird space use due to breeding cycle, or changes in local food resources.

Implications for bird conservation, ecological function, and forest restoration

Most species we recorded are typical of disturbed areas and not commonly found in primary or old secondary forest. Of nearly 300 resident species our research group has recorded in the Mamoni Valley, almost 200 occur in intact forest and only a few typical forest species, such as Blue Dacnis (*Dacnis cayana*) and Red-legged Honeycreeper (*Cyanerpes cyaneus*), occurred at our restoration site (S. Roels, unpublished data). This lack of overlap is unsurprising given many studies have found bird species richness recovers more quickly than community composition (Dunn 2004, Catterall et al. 2012, Gould and Mackey 2015). Major groups characteristic of wet lowland forest in central Panama that were absent or nearly absent from our restoration site include antbirds (Thamnophilidae), woodcreepers (Dendrocolaptinae), trogons (Trogonidae), toucans (Ramphastidae), and parrots (Psittacidae). These groups correspond to foraging guilds that are often absent in young restorations and successional areas: understory insectivores (antbirds and woodcreepers) and large frugivores (trogons, toucans, and parrots; Powell et al. 2015, Rolo et al. 2017). Many species within these groups are of conservation concern (Strahl and Grajal 1991, Powell et al. 2015). Presence of large frugivores in forest restorations is especially important for ecological function because they disperse large-seeded trees that are otherwise unlikely to colonize restoration areas (Wunderle 1997). Restoration of habitat for these groups and return of unique ecosystem services associated with them is a long-term prospect, even when native trees are planted in an effort to accelerate forest recovery.

At finer scales, within restoration sites, we should not expect uniform spatial distribution of bird-driven ecological functions. This is true despite early users of restored tropical forest habitat frequently being highly mobile species, e.g., tanager species in our study. Our study suggests that fine-scale patterns of habitat use, and thus ecological functioning, within a restoration site are influenced by neighborhood-scale features like adjacent habitat and connectivity. Relationships between neighborhood-scale

habitat features and fine-scale spatial variation in tropical bird ecological function have been documented for seed dispersal and herbivorous insect control (Wenny and Levey 1998, Karp et al. 2013, Maas et al. 2015, Roels et al. 2018). Our study implies that recovery of bird-driven ecosystem functions may be reduced near pastures, even if vegetative structure is no different than areas farther from pasture that are heavily used by birds. For forest restoration projects that rely on bird-driven ecosystem functions like seed dispersal, areas near pasture and other matrix land covers unfriendly to birds may warrant additional monitoring and investment to ensure restoration goals are met. A complementary strategy would be encouraging silvopastoral techniques in pasture areas adjacent to forest restorations (Murgueitio et al. 2011). Adding native trees and shrubs to active pasture would encourage bird use of habitat at the edges of forest restorations by creating additional foraging habitat and facilitating bird movement along restoration-pasture interfaces.

Responses to this article can be read online at:
<http://www.ace-eco.org/issues/responses.php/1330>

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Appendix 1. Supplemental material for “Recovery of bird activity and species richness in an early-stage tropical forest restoration”

Table A1.1. Tree species planted by experimental plot. Sixteen experimental plots (50 m x 50 m) were planted with 1, 2, 4, or 8 native tree species. Seedlings of *Miconia guianensis* died and were replaced by other species, primarily *Hyeronima alchorneoides*.

Tree Species	Family	Plot Number															
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16
<i>Inga</i> spp.	Fabaceae		X	X	X	X	X				X	X	X	X		X	X
<i>Dipteryx panamensis</i>	Fabaceae	X	X	X	X	X		X	X	X	X	X	X	X	X		X
<i>Manilkara bidentata</i>	Sapotaceae			X		X		X		X		X	X	X			X
<i>Anacardium excelsum</i>	Anacardiaceae			X		X		X		X		X	X	X			X
<i>Miconia guianensis</i>	Olacaceae					*		*		*	*			*	*		
<i>Swietenia macrophylla</i>	Meliaceae					X		X		X	X		X	X			
<i>Calophyllum longifolium</i>	Calophyllaceae					X		X		X	X		X	X			
<i>Terminalia amazonia</i>	Combretaceae					X		X		X	X		X	X			
<i>Hyeronima alchorneoides</i>	Euphorbiaceae					X		X		X	X		X	X			
<i>Tabebuia guayacan</i>	Bignoniaceae							X		X						X	
Total Species		1	2	4	2	8	1	8	1	8	8	2	4	8	8	1	4

Appendix 1. Supplemental material for “Recovery of bird activity and species richness in an early-stage tropical forest restoration”

Table A1.2. Results from five years of bird surveys at a forest restoration in the Mamoni Valley, Panama. Counts should not be directly compared across survey types because of different methodologies (see text) and sampling effort. The Single-year survey was approximately double the effort (total observation time) of the annual effort in the Multi-year survey.

Guild (Common Name)	Latin Name	Multi-year survey					Single-year survey	Mist net
		2010	2011	2012	2013	2014	2014	2014
<i>Open Country</i>								
Ruddy Ground-Dove	<i>Columbina talpacoti</i>	-	-	-	-	-	-	1
Black-throated Mango	<i>Anthracothorax nigricollis</i>	-	1	-	-	-	-	5
American Kestrel	<i>Falco sparverius</i>	-	-	-	-	-	1	-
Tropical Kingbird	<i>Tyrannus melancholicus</i>	-	-	4	6	7	6	-
Fork-tailed Flycatcher*	<i>Tyrannus savana</i>	-	-	-	-	-	-	-
Tropical Mockingbird	<i>Mimus gilvus</i>	3	-	2	1	1	2	1
Eastern Meadowlark	<i>Sturnella magna</i>	62	13	-	-	-	-	-
Shiny Cowbird	<i>Molothrus bonariensis</i>	-	-	-	-	3	3	-
Yellow-faced Grassquit*	<i>Tiaris olivaceus</i>	-	-	1	-	-	-	-
Yellow-bellied Seedeater	<i>Sporophila nigricollis</i>	-	-	-	-	-	-	2
Open Country sub-total		65	14	7	7	11	12	9
<i>Brushy</i>								
Smooth-billed Ani	<i>Crotophaga ani</i>	4	1	-	8	18	23	5
Pale-breasted Spinetail	<i>Synallaxis albescens</i>	-	-	5	13	5	9	4
<i>Cantorchilus</i> sp. 1	<i>Cantorchilus</i> sp.	-	-	2	5	2	8	2
Blue-black Grassquit	<i>Volatinia jacarina</i>	-	-	-	7	-	12	4
Thick-billed Seedfinch	<i>Sporophila funerea</i>	-	-	-	8	13	42	22
Variable Seedeater	<i>Sporophila corvina</i>	-	-	3	18	25	39	10
Seedeater/Seedfinch 2	<i>Sporophila</i> sp.	-	-	1	-	1	16	-
Brushy sub-total		4	1	11	59	64	149	47
<i>Early Secondary</i>								
White-tipped Dove	<i>Leptotila verreauxi</i>	-	-	-	1	1	22	1
Striped Cuckoo	<i>Tapera naevia</i>	-	-	-	2	2	5	1
Common Pauraque	<i>Nyctidromus albicollis</i>	-	-	-	-	-	1	-
Long-billed Starthroat	<i>Heliomaster longirostris</i>	-	-	-	-	-	-	2
Garden Emerald	<i>Chlorostilbon assimilis</i>	-	-	-	3	6	2	17
Scaly-breasted Hummingbird	<i>Phaeochroa cuvierii</i>	-	-	-	-	-	-	7
Snowy-bellied Hummingbird	<i>Amazilia edward</i>	-	1	-	-	-	1	15
Rufous-tailed Hummingbird	<i>Amazilia tzacatl</i>	-	-	-	4	1	13	26
Striped Owl	<i>Asio clamator</i>	-	-	-	-	-	1	-
Barred Antshrike	<i>Thamnophilus doliatus</i>	-	-	-	1	-	2	1
Southern Beardless Tyrannulet	<i>Camptostoma obsoletum</i>	-	-	-	-	-	-	2
Yellow Tyrannulet	<i>Capsiempis flaveola</i>	-	-	-	3	11	33	6
Yellow-bellied Elaenia	<i>Elaenia flavogaster</i>	-	-	3	2	7	20	13
Lesser Elaenia	<i>Elaenia chiriquensis</i>	-	-	3	9	4	5	20
<i>Elaenia</i> sp. 3	<i>Elaenia</i> sp.	-	-	-	-	2	1	-
Bran-colored Flycatcher	<i>Myiophobus fasciatus</i>	-	-	-	-	-	1	-
Black-striped Sparrow	<i>Arremonops conirostris</i>	-	-	4	9	10	12	1
Palm Tanager	<i>Thraupis palmarum</i>	-	-	-	-	-	-	2
White-lined Tanager	<i>Tachyphonus rufus</i>	-	-	-	6	16	22	7
Flame-rumped Tanager	<i>Ramphocelus flammigerus</i>	-	-	2	7	5	6	-
Crimson-backed Tanager	<i>Ramphocelus dimidiatus</i>	-	-	6	17	34	49	10
Early Secondary sub-total		0	1	18	64	99	196	131

Appendix 1. Supplemental material for “Recovery of bird activity and species richness in an early-stage tropical forest restoration”

<i>Guild (Species)</i>	Multi-year survey					Single-year survey	Mist net	
	2010	2011	2012	2013	2014	2014	2014	
<i>Forest Edge</i>								
Scaled Pigeon	<i>Patagioenas speciosa</i>	-	-	-	1	2	5	-
White-necked Jacobin	<i>Florisuga mellivora</i>	-	-	-	-	-	-	2
Rufous-breasted Hermit	<i>Glaucis hirsutus</i>	-	-	-	-	-	-	2
Long-billed Hermit*	<i>Phaethornis longirostris</i>	-	-	-	-	-	-	-
Stripe-throated Hermit	<i>Phaethornis striigularis</i>	-	-	-	-	-	-	2
Violet-headed Hummingbird	<i>Klais guimeti</i>	-	-	-	-	-	-	1
Rufous-crested Coquette	<i>Lophornis delattrei</i>	-	-	-	-	-	-	1
Crowned Woodnymph	<i>Thalurania colombica</i>	-	-	-	-	-	-	1
Olivaceous Piculet	<i>Picumnus olivaceus</i>	-	-	-	-	-	-	2
Red-crowned Woodpecker	<i>Melanerpes rubricapillus</i>	-	-	-	-	-	5	-
Lineated Woodpecker	<i>Dryocopus lineatus</i>	-	-	-	-	1	-	1
Yellow-crowned Tyrannulet	<i>Tyrannulus elatus</i>	-	-	-	-	10	10	9
Ochre-bellied Flycatcher	<i>Mionectes oleagineus</i>	-	-	1	-	-	-	-
Paltry Tyrannulet	<i>Zimmerius vilissimus</i>	-	-	-	-	-	-	1
Common Tody-Flycatcher	<i>Todirostrum cinereum</i>	-	-	-	10	7	32	8
Great Kiskadee	<i>Pitangus sulphuratus</i>	-	-	-	-	1	-	-
Panama Flycatcher	<i>Myiarchus panamensis</i>	-	-	-	-	1	-	1
Rusty-margined Flycatcher	<i>Myiozetetes cayanensis</i>	-	-	-	-	-	2	-
Lesser Greenlet	<i>Pachysylvia decurtata</i>	-	-	-	-	-	-	1
Yellow-green Vireo	<i>Vireo flavoviridis</i>	-	-	-	-	1	3	7
Tropical Gnatcatcher	<i>Polioptila plumbea</i>	-	-	-	-	-	1	-
Clay-colored Thrush	<i>Turdus grayi</i>	-	-	-	1	5	2	7
Thick-billed Euphonia	<i>Euphonia laniirostris</i>	-	-	-	-	1	-	-
Blue-gray Tanager	<i>Thraupis episcopus</i>	-	-	8	9	8	15	9
Golden-hooded Tanager	<i>Tangara larvata</i>	-	-	-	-	21	-	-
Plain-colored Tanager	<i>Tangara inornata</i>	-	-	3	3	1	6	-
Red-legged Honeycreeper	<i>Cyanerpes cyaneus</i>	-	-	-	-	-	2	-
Blue Dacnis	<i>Dacnis cayana</i>	-	-	-	-	-	2	-
Bananaquit	<i>Coereba flaveola</i>	-	-	-	-	-	1	2
Buff-throated Saltator	<i>Saltator maximus</i>	-	-	-	2	1	4	2
Streaked Saltator	<i>Saltator striatipectus</i>	-	-	1	3	1	8	4
Forest Edge sub-total		0	0	13	29	61	98	63
<i>Forest Interior</i>								
Black-crowned Antshrike	<i>Thamnophilus atrinucha</i>	-	-	-	-	-	-	1
Olivaceous Flatbill	<i>Rhynchocyclus olivaceus</i>	-	-	-	-	-	-	1
Forest Interior sub-total		0	0	0	0	0	0	2
<i>No Habitat Guild</i>								
Hummingbird sp.		-	-	4	12	1	20	-
Unidentified bird		2	-	16	30	14	50	-
Total Bird Activity		71	16	69	201	250	525	252

* Not recorded during formal surveys or mist netting in 2014 but observed during other field work

1 - Isthmian Wren (*Cantorchilus elutus*)/Buff-breasted Wren (*Cantorchilus leucotis*)

2 - Variable Seedeater/Thick-billed Seedfinch

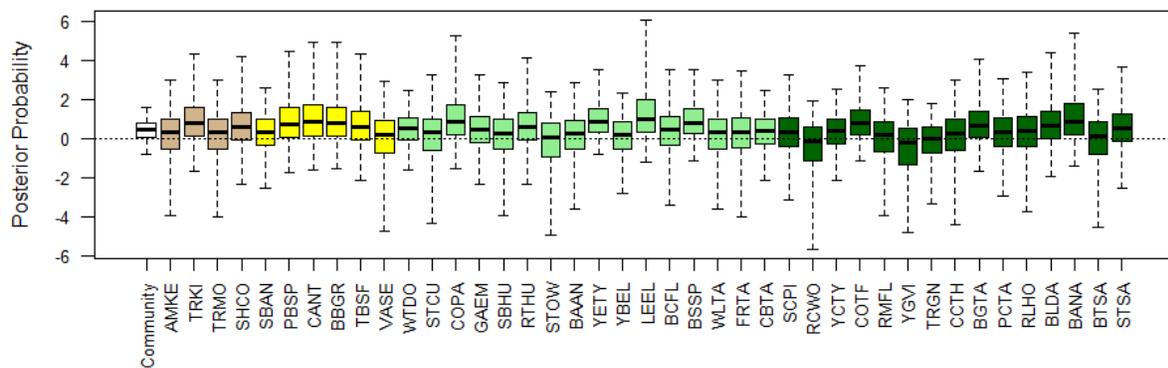
3 - Lesser Elaenia/Yellow-bellied Elaenia

Appendix 1. Supplemental material for “Recovery of bird activity and species richness in an early-stage tropical forest restoration”

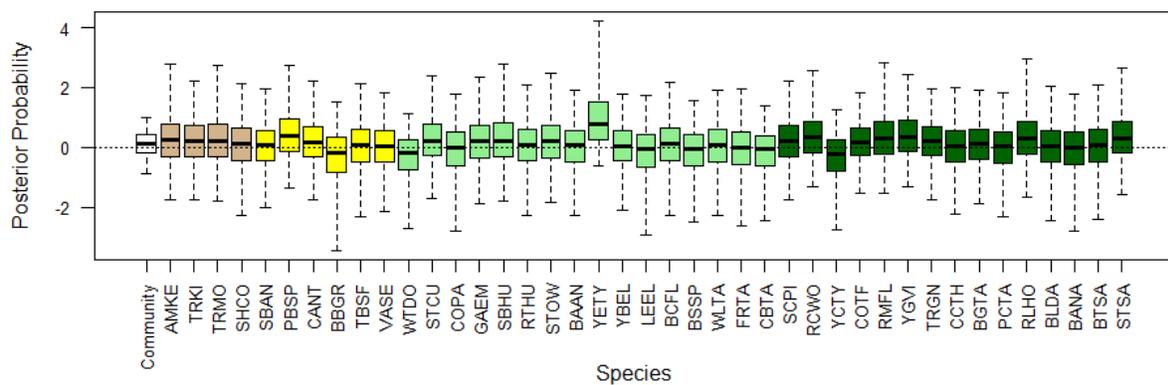
Figure A1.1. Posterior probabilities for effects of plot variables for individual species, sorted by habitat guild. The community-level estimates (hyper-parameters) are in white, Open Country species in tan, Brushy species in yellow, Early Secondary in light green, and Forest Edge in dark green. Species abbreviations in alphabetical order are in the first panel.

Code	Species	Code	Species	Code	Species
AMKE	American Kestrel	FRTA	Flame-rumped Tanager	STOW	Striped Owl
BAAN	Barred Antshrike	GAEM	Garden Emerald	STSA	Striped Saltator
BANA	Bananaquit	LEEL	Lesser Elaenia	TBSF	Thick-billed Seedfinch
BBGR	Blue-black Grassquit	PBSP	Pale-breasted Spinetail	TRGN	Tropical Gnatcatcher
BCFL	Bran-colored Flycatcher	PCTA	Plain-colored Tanager	TRKI	Tropical Kingbird
BGTA	Blue-gray Tanager	RCWO	Red-crowned Woodpecker	TRMO	Tropical Mockingbird
BLDA	Blue Dacnis	RLHO	Red-legged Honeycreeper	VASE	Variable Seedeater
BSSP	Black-striped Sparrow	RMFL	Rusty-margined Flycatcher	WLTA	White-lined Tanager
BTSA	Buff-throated Saltator	RTHU	Rufous-tailed Hummingbird	WTDO	White-tipped Dove
CANT	Cantorchilus wren sp.	SBAN	Smooth-billed Ani	YBEL	Yellow-bellied Elaenia
CBTA	Crimson-backed Tanager	SBHU	Snowy-bellied Hummingbird	YCTY	Yellow-crowned Tyrannulet
CCTH	Clay-colored Thrush	SCPI	Scaled Pigeon	YETY	Yellow Tyrannulet
COPA	Common Parakeet	SHCO	Shiny Cowbird	YGVI	Yellow-green Vireo
COTF	Common Tody-Flycatcher	STCU	Striped Cuckoo		

Effect of Percent Canopy Cover on Bird Species Use of Plots



Effect of Number of Tree Species on Bird Species Use of Plots



Appendix 1. Supplemental material for “Recovery of bird activity and species richness in an early-stage tropical forest restoration”

