Avian Habitat Preference in Tropical Forest Restoration in Southern Costa Rica

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ABSTRACT

An important question for tropical forest restoration is whether degraded lands can be actively managed to attract birds. We censused birds and measured vegetation structure at 27 stations in young (6–9-yr old) actively and passively restored pasture and old growth forest at Las Cruces Biological Station in southern Costa Rica. During 481 10-min point counts, we detected a high diversity—186 species—of birds using the restoration area. Surprisingly, species richness and detection frequency did not differ among habitats, and proportional similarity of bird assemblages to old growth forest did not differ between restoration treatments. Bird detection frequency was instead explained by exotic grass cover and understory stem density—vegetation structures that were not strongly impacted by active restoration. The similarity of bird assemblages in actively and passively restored forest may be attributed to differential habitat preferences within and among feeding guilds, low structural contrast between treatments, or the effect of nucleation from actively restored plots into passively restored areas. Rapid recovery of vegetation in this recently restored site is likely due to its proximity to old growth forest and the lack of barriers to effective seed dispersal. Previous restoration studies in highly binary environments (*i.e.*, open pasture vs. tree plantation) have found strong differences in bird abundance and richness. Our data contradict this trend, and suggest that tropical restoration ecologists should carefully consider: (1) when the benefits of active restoration outweigh the cost of implementation; and (2) which avian guilds should be used to measure restoration success given differential responses to habitat structure.

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

AN IMPORTANT QUESTION FOR ECOLOGICAL RESTORATION IN THE TROPICS is whether degraded lands can be actively managed to attract birds, both for their own conservation and for the ecological services they provide. Of about 10,000 species of birds worldwide, 1223 (12 percent) are threatened with extinction, and 70 percent of these live in lowland and montane tropical forests (IUCN 2010). Most are primarily endangered by habitat loss and degradation (Sodhi & Smith 2007), which are problems that restoration ecologists strive to address (Young 2000). Potential species loss is particularly troubling when viewed in light of the ecosystem services that birds provide (*e.g.*, Sekercioglu *et al.* 2004). In addition to pollination and insect control, tropical birds play a dominant role in forest restoration by dispersing tree seeds into degraded lands where a lack of seed dispersal is a principle barrier to forest recovery (Holl 1999, Wijdeven & Kuzee 2000, Sekercioglu 2006).

The composition and relative abundance of birds attracted into degraded habitats are particularly useful measurements for restoration ecologists. Whereas composition denotes what ecosystem functions may be provisioned, relative abundance may be a good predictor of the magnitude of those functions (*e.g.*, total number of seeds dispersed; Pejchar *et al.* 2008). Several studies have documented the effects of tropical forest restoration on bird visitation (Holl 1998, Zahawi & Augspurger 2006, Fink *et al.*

2009) and foraging behavior (Morrison *et al.* 2010, Morrison & Lindell 2011), but few tropical studies have assessed bird habitat preference at a community level across different restoration treatments (reviewed by Ruiz-Jaen & Aide 2005, Aerts *et al.* 2008, Lindell 2008, Reid *et al.* 2008).

Restoration practice can be broadly categorized into passive or active restoration (Rey Benayas 2000). Funding for active forest restoration is limited, so passive restoration, or natural regeneration without intervention, is frequently the process by which secondary tropical forests are created (Aide *et al.* 2000, Guerrero & da Rocha 2010). Conservation biologists must therefore weigh carefully the added benefits of active intervention in degraded sites (Rey Benayas 2000, Holl & Aide 2011, Morrison & Lindell 2011).

Tree planting is a predominate method of active forest restoration and alters degraded tropical habitats through changes in vegetation structure and composition, both of which affect bird community composition (MacArthur & MacArthur 1961, James 1971, Rotenberry 1985). Within a few years, successful tree plantings will typically increase canopy height and cover, which augment foraging surface area for bark-gleaning insectivores and foliage-gleaning insectivores (Holmes *et al.* 1979, Arriaga-Weiss *et al.* 2008) and potentially cover from predators for frugivores and others (Fink *et al.* 2009). After many decades, the spacing of tree plantings may even determine the rate of formation of old growth structures, such as tree hollows and large boughs that are

important to many forest-dwelling birds (Vesk *et al.* 2008). While plant composition tends to have a stronger influence on bird communities within homogeneous forest, structure is more important between or among habitats (Jayapal *et al.* 2009), such as tree plantations and abandoned pastures. Because simple vegetation structure measurements are taken for the majority of restoration projects (Ruiz-Jaen & Aide 2005), relationships between these structures and bird habitat preferences could be useful for informing models that predict the effectiveness of restoration treatments for attracting birds.

To compare the ability of active and passive forest restoration to attract a diverse Neotropical bird community, we censused birds and measured vegetation structure in a six to nine year old recovering pasture and adjacent old growth forest in southern Costa Rica. The goals of this research were to determine whether active restoration (tree planting) increased the species richness, abundance, and compositional similarity to old growth forest of birds using the site and how these effects, if present, were mediated by vegetation structure. We hypothesized that (1) bird species richness, abundance, and compositional similarity to old growth would be greater in actively restored than passively restored areas; and (2) vegetation structure would largely predict the richness, abundance, and composition of birds using the restoration site and adjacent old growth forest.

METHODS

STUDY SITE.—This study was conducted from 26 August to 2 October 2007 in a restoration site at Las Cruces Biological Station in Coto Brus County in southern Costa Rica (8°47′7 N, 82°57′32 W; rainfall $\approx$4000 mm/yr; LCBS 2011). Melissa's Meadow (1100 m asl) is a 31-ha regenerating pasture, which was actively grazed by cattle until 1998 (Fig. 1). At the time of abandonment, Melissa's Meadow was a pasture dominated by exotic African grasses including *Pennisetum purpureum* and *Urochloa brizantha*. Some remnant trees were present at that time, especially in the steeper areas. The abundance of remnant trees, however, did not differ among treatments in 2007 (ANOVA $F = 1.5$, df $= 2,16$, $P = 0.24$). Adjacent remnant forest had characteristics of old growth forest including an open understory, multilayered canopy, and large windfall gaps. To our knowledge there had been no disturbance, such as logging, for at least 50 yr, though the forest may have been affected previously by shifting agriculture (Young 1971).

During 2000-2001, eight 1 ha plots were cleared and actively restored as plantations with seedlings of native tree species (R. Quiros, pers. comm.). At least five hectares were left as untreated, abandoned pasture (*i.e.*, passive restoration). Two hectares were also burned with a single prescribed fire; these plots were surveyed but were excluded from some analyses due to lack of replication.

By 2007 a young secondary forest dominated by *Cecropia* spp. and *Heliocarpus appendiculatus* had developed across much of Melissa's Meadow in both actively and passively restored areas (Fig. 2). Exotic pasture grasses persisted in dense patches throughout.

BIRD SURVEYS.—We conducted 481 10-min point counts distributed among 27 stations in the restoration site (active × 8; passive
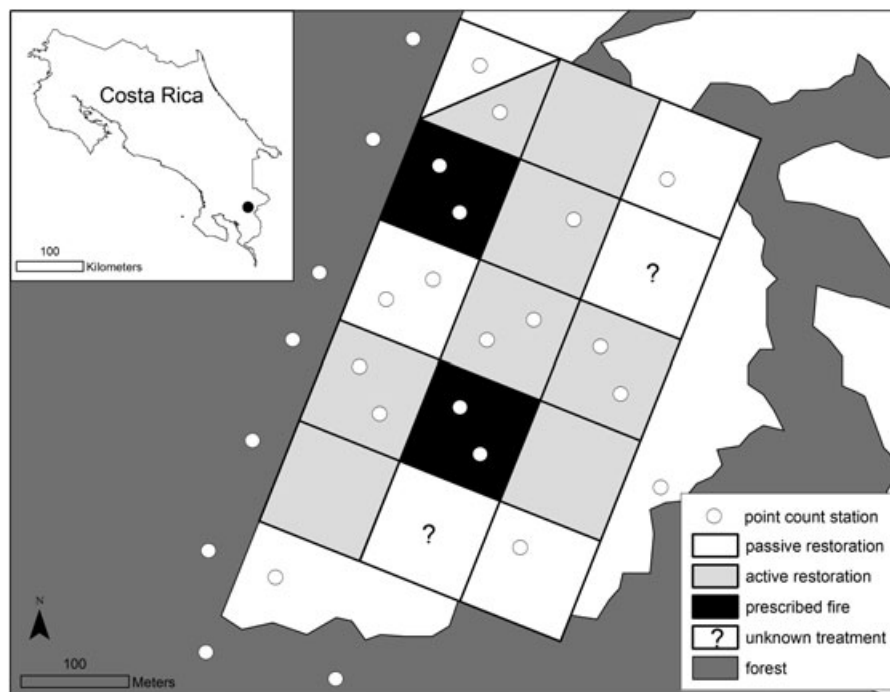

FIGURE 1. Location of point count stations in the Melissa's Meadow study area and surrounding forest at Las Cruces Biological Station, Coto Brus, Costa Rica. Forest cover based on digitization of a 1992 aerial photograph.

FIGURE 2. Passive and active forest restoration in Melissa's Meadow, Las Cruces Biological Station: (A) passively restored pasture with succession arrested by exotic grasses; (B) passively restored pasture with rapid recovery of woody vegetation structure; (C) actively restored pasture planted with native tree seedlings in 2000–2001.

× 7; prescribed fire × 4) and adjacent old growth forest (× 8) (Fig. 1). Counts were conducted in fair weather during the first 5 hr after dawn, and point count order was randomized. The mean number of counts conducted at each point was 18.2 (SD = 0.6); eight sites received 19 counts (maximum) and three sites received 17 counts (minimum).

Birds were detected by sight or vocalization using 30-m fixed radius point counts. The size of the fixed radius represented a compromise between a larger radius for relatively open points and a smaller radius that would have been more appropriate for dense secondary growth (Hutto et al. 1986, Ralph et al. 1995). Stations were located about 60 m from one another, so individuals recorded at one station were likely to have been recorded at other stations as well. This distance reflects the spatial limitations imposed by the restoration area, and it is appropriate for this study because we looked for differences among treatments in bird behavior (i.e., extent of use of a particular treatment when other treatments were also available), not in the ability of a treatment to restore the bird assemblage. Undoubtedly the birds in this study require more habitat than is provisioned by a single 1-ha restoration area (Hill & Hamer 2004), but the variation in their usage of one treatment over another will be proportional to the provisioning of ecosystem services (e.g., seed dispersal, arthropod control).

Point counts were conducted by JLR, JBCH, and Jeisson Figueroa, who are experienced in the identification of Costa Rican birds by sight and sound. Observers conducted point counts together for the first two days of the study, and each observer conducted point counts with another observer for at least two-thirds of the study period to reduce observer bias (Ralph et al. 1995). Birds flying over the habitat were excluded. Nocturnal groups were poorly sampled by our methodology. Unknown vocalizations were recorded using a Sennheiser ME 66 shotgun microphone and an M-audio Microtrack digital recorder. Most of these recordings were later identified to species with help from James Zook, an authority on the identification of Costa Rican birds. High quality, positively identified recordings (134 species) were deposited at the Macaulay Library (http://macaulaylibrary.org).

VEGETATION SURVEYS.—We characterized vegetation structure at each point-count station by measuring four characteristics: (1) canopy height; (2) canopy cover; (3) understory stem density; and (4) percent cover of exotic grasses. Canopy height was estimated with a 400XL laser rangefinder (Opti-logic Inc., Tullahoma, TN) by taking the mean height of five representative trees, each of which was measured at three points. Canopy cover was estimated with a spherical densiometer. Understory stem density was quantified by counting all trees < 10 m tall within four 5-m^2 circular plots at each point count station—we used the mean value for analysis. Exotic grass cover was estimated visually (0–5 percent, 6–10 percent, 11–25 percent, 26–50 percent, 51–75 percent, 76–95 percent, 96–100 percent) in four 3 m^2 circular plots at each station. We found no significant correlations between these structural variables (Spearman's ρ, $\alpha = 0.05$). While distance to old growth forest has been an important explanatory variable for bird community assemblage in some studies (e.g., Neilan et al. 2006, Reid et al. 2008), it was not included in this analysis because point count stations were always less than 300 m from old growth through closed-canopy secondary forest.

DATA ANALYSIS.—Bird species were classified into nine foraging guilds (Table S1) based on diet and behavioral information presented by Stiles and Skutch (1989). Species were also classified as regionally endemic to Costa Rica and western Panama or not, based on range information in Garrigues and Dean (2007), and given a forest dependence classification; we considered species to be forest-dependent if they received a score less than two (out of three) in Stiles (1985). Seed-predating frugivores (e.g., parrots) were not considered frugivores in our analyses because this study focused on species that disperse seeds into restoration areas (Janzen 1981). Likewise, small raptors (e.g., Barred Forest Falcon [Micrastur ruficollis]) that occasionally consume large insects were not considered insectivores in our analyses.

We used four metrics to describe the bird communities: (1) estimated species richness; (2) detection frequency; (3) proportional similarity to old growth forest; and (4) compositional similarity to old growth forest (ANOSIM). Species richness was estimated using EstimateS (Colwell 2006). We used the Jack1 esti-

mator because it has performed well in similar studies (Arriaga-Weiss *et al.* 2008, Pejchar *et al.* 2008) and its estimates were similar to results from other leading estimators (Fig. S1; Walther & Moore 2005). We estimated species richness for the whole bird community and foraging guilds in each treatment.

Detection frequency (mean number of bird detections per 10-min point count) was used as a measure of relative abundance. Whereas relative abundance refers in a strict sense to a total number of individuals, a high detection frequency could represent multiple detections of a single individual over many point counts or many single observations of different individuals. Importantly, detection frequency in this study represents bird preference for one habitat type over another (*i.e.*, it is proportional to the number of times that birds were found in one habitat when they could have been visiting another), not the degree to which the local bird community was restored by the restoration interventions. Detection frequency is likely more important than species richness for predicting some ecosystem services such as seed dispersal (Pejchar *et al.* 2008).

We used a proportional similarity (PS) index to compare the relative abundance of each species against a reference community—adjacent old growth forest (Brower *et al.* 1989, Provencher *et al.* 2001). A PS = 1 indicates perfect similarity (*i.e.*, plots share the same species in the same proportions) whereas a PS = 0 indicates no similarity. The old growth forest bird community was characterized using mean relative detection frequency across all point-count stations ($N = 8$) because plots in the restoration area were not paired with forest plots.

We also used analysis of similarities (ANOSIM) as a second test of differences in bird community composition among restoration treatments and old growth forest by using the Anosim function in the R vegan package (R Development Core Team 2009, Oksanen *et al.* 2010). Importantly, this method does not require the lumping of all forest points into one community to which all other points are compared. We used a Bray dissimilarity matrix of detection frequencies of 203 species of bird. Ordinations were made using the metaMDS function and included data from old growth forest, active restoration, and passive restoration, but not prescribed fire plots.

Bird assemblage variables were compared among restoration treatments in R using one-way analysis of variance and Tukey honestly significantly different (HSD) *post-hoc* comparisons. The same variables were regressed against vegetation structures (understory density, canopy cover, canopy height, exotic grass cover) using forward step-wise multiple regressions in SYSTAT 13.0. We used $P < 0.05$ to enter the model. Prescribed fire plots were excluded from analysis of variance tests because of insufficient replication ($N = 4$), however, they were included in step-wise multiple regressions and provided increased ranges of gradation for several vegetation structure variables. All statistics are reported as mean ± standard error. In this study we sought to identify strong differences between restoration treatments, thus $\alpha = 0.05$ represented an appropriate balance between minimizing types I and II errors.

RESULTS

We recorded 4032 bird detections comprising 186 species in the restoration site at Melissa's Meadow (Appendix S1). Of these, 163 (87.6 percent) species were residents, 21 (11.3 percent) were Nearctic-Neotropical migratory songbirds, and one species, Yellow-green Vireo (*Vireo flavoviridis*), was a southern latitudinal migrant. We recorded 123 species in the adjacent old growth forest including 17 species not found in the restoration area. Communities in each treatment were equally well sampled with ratios of observed/expected species richness ranging from 0.812 in active restoration to 0.827 in old growth forest (Fig. S1). The majority (96 percent) of birds detected were identified to species (to genus for *Empidonax* and *Contopus* flycatchers). Many of the unidentified birds were hummingbirds (Trochilidae; 42 percent) and flycatchers (Tyrannidae; 15 percent).

BIRD USE OF RESTORATION TREATMENTS.—Overall detections and species richness of birds were similar among habitats ($F_{2, 20} = 1.1/0.2$, $P = 0.339/0.826$, respectively; Fig. 3), and differences between active and passive forest restoration were subtle. Active restoration had more bark-gleaning insectivore species than passive restoration (5.1 ± 0.5 species in active vs. 3.3 ± 0.5 in passive; $F_{2, 20} = 6.9$, $P = 0.049$; Table S2). Although the difference in foliage-gleaning insectivores between active and passive restoration was not significant ($F_{2, 20} = 3.8$, $P = 0.039$), only passive restoration had significantly fewer detections than old growth forest (17.7 ± 1.8 in passive vs. 22.3 ± 0.9 in old growth). Likewise, both restoration treatments had more frugivore detections than old growth forest ($F_{2, 20} = 4.2$, $P = 0.031$), but this trend was only significant for active restoration treatments (3.21 ± 0.23 det/count in active vs. 3.07 ± 0.31 in passive and 2.29 ± 0.20 in old growth). Regardless of treatment, restoration areas had more nectarivore-insectivore species ($F_{2, 20} = 13.5$, $P < 0.001$) and detections ($F_{2, 20} = 9.3$, $P = 0.001$) than old growth. Proportional similarity of bird communities to old growth forest was slightly greater in active (0.39 ± 0.03) than passive restoration treatments (0.31 ± 0.04), but this difference was not significant ($F_{1, 13} = 2.5$, $P = 0.135$).

Richness and detection frequency of forest-dependent species were significantly greater in old growth forest (16.1 ± 1.2 species; 2.63 ± 0.26 det/count) than either active (5.7 ± 1.0 species; 0.74 ± 0.15 det/count); or passive restoration treatments (5.4 ± 1.8 species; 0.76 ± 0.32 det count; $F_{2, 20} = 21.1/19.5$, $P < 0.001/0.001$). Regional endemics had an opposite trend, with more detections in passive restoration than old growth forest ($F_{2, 20} = 3.9$, $P = 0.036$), but this trend disappeared when Cherrie's Tanager (*Ramphocelus costaricensis*), a common disturbance-tolerant endemic, was removed from the analysis ($F_{2, 20} = 2.0$, $P = 0.156$).

NON-METRIC MULTIDIMENSIONAL SCALING.—A two-dimensional solution was recommended and represented the most parsimonious fit (Fig. S2). Stress for the final ordination was 0.1174, within a range appropriate for interpretation (Clarke 1993).
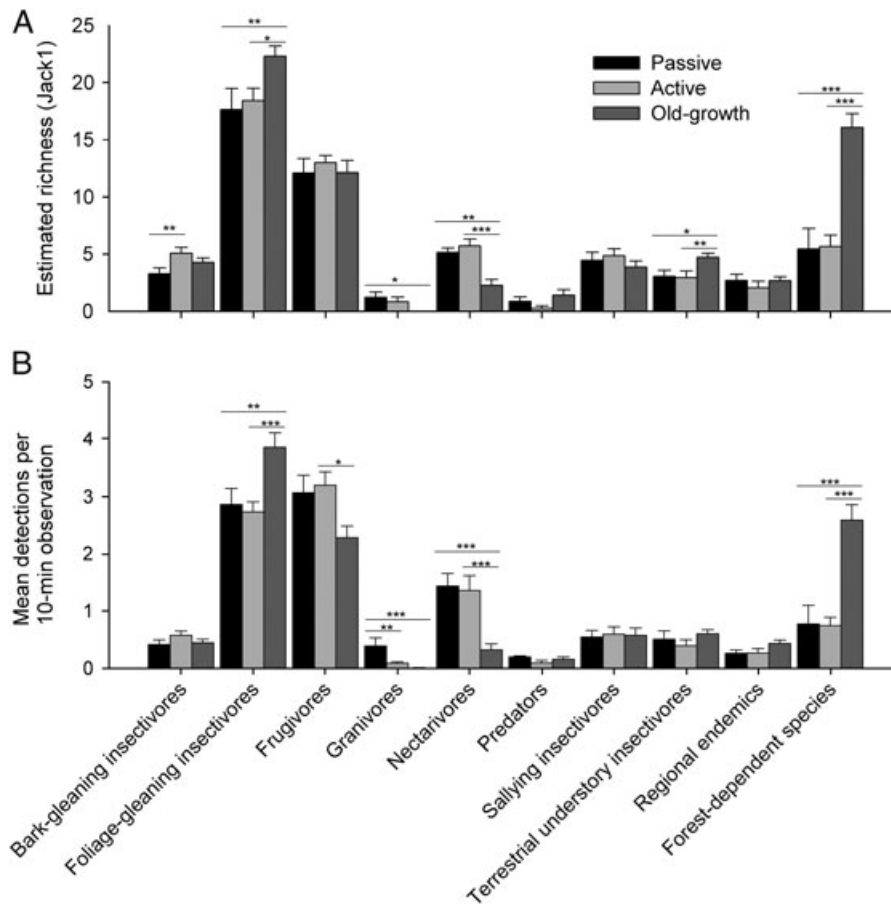
FIGURE 3.   Detection frequency (detections/10-min count) and estimated species richness (Jack1) of bird guilds in actively and passively restored pasture in Melissa's Meadow and adjacent old growth forest.

Most variation among habitats occurred on the horizontal axis, which was defined by a gradient of forest-dependent insectivores (*e.g.*, Rough-legged Tyrannulet [*Phyllomyias burmeisteri*]; Spotted Barbtail [*Premnoplex brunnescens*]) to open-country birds (*e.g.*, Blue-black Grassquit [*Volatinia jacarina*]; Variable Seedeater [*Sporophila americana*]; Bran-colored Flycatcher [*Myiophobus fasciatus*]). The vertical axis was defined by a gradient of moderately forest-dependent residents (*e.g.*, White-vented Euphonia [*Euphonia minuta*]; Green-crowned Brilliant [*Heliodoxa jacula*]; White-shouldered Tanager [*Tachyphonus luctuosus*]) to an assortment of

Neotropical migrants (*e.g.*, Yellow-billed Cuckoo [*Coccyzus americanus*]; Yellow-green Vireo).

Old growth forest was defined on the horizontal axis by a variety of moderately to highly forest-dependent species (*e.g.*, Crested Guan [*Penelope purpurascens*]; Laughing Falcon [*Herpetotheres cachinnans*]; Golden-crowned Spadebill [*Platyrinchus coronatus*]). Bird communities using restoration treatments were fairly distinct but with some overlap between passively and actively restored sites. Passively restored sites were especially diffuse along the horizontal axis with one site interspersed among old growth forest; this

TABLE 1. *Vegetation structure (means ± SE) in Melissa's Meadow restoration area and adjacent old growth forest.*

Structures	Old-growth	Active	Passive	*F/P*
Canopy cover (% cover)	93.1 ± 0.6[A]	91.1 ± 1.8[A]	55.8 ± 15.7[B]	6.12/0.008*
Exotic grass (% cover)	0.0 ± 0.0[A]	7.8 ± 3.1[AB]	30.1 ± 14.3[B]	3.94/0.036*
Canopy height (m)	26.5 ± 0.3[A]	15.9 ± 1.1[AB]	12.8 ± 1.2[B]	56.79/<0.001*
Understory density (stems/ha)	2656 ± 218	1994 ± 153	1858 ± 371	2.89/0.079

Understory encompasses trees< 10 m in height. Significant differences are denoted by *(ANOVA, df = 2,20, α = 0.05) and superscript ABC for *post-hoc* comparisons (Tukey HSD, α = 0.05).
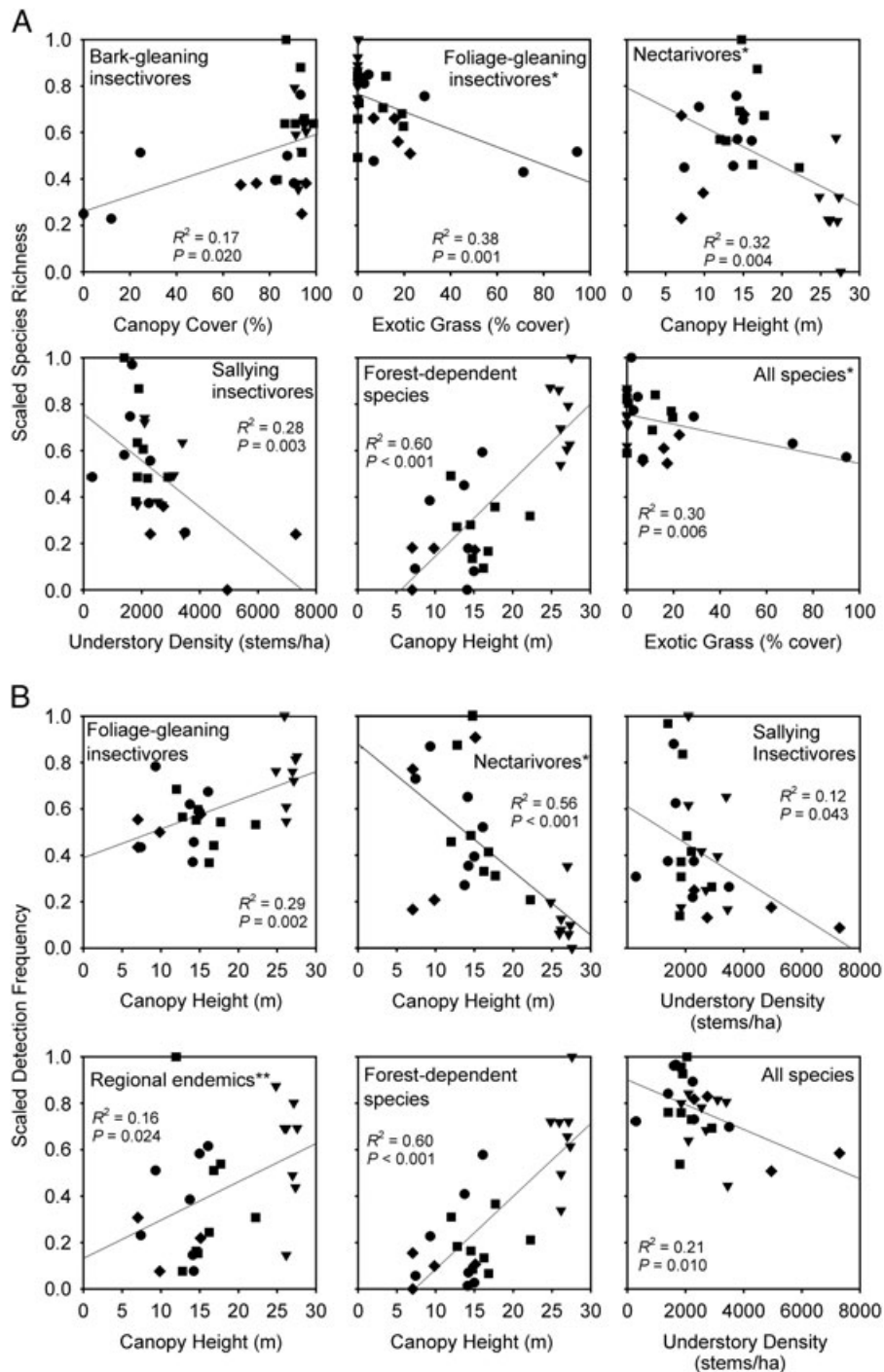
FIGURE 4. Selected regressions of scaled bird species richness (A) and detection frequency (B) against vegetation structures in Melissa's Meadow. Circles = passive restoration; squares = active restoration; triangles = old growth forest; and diamonds = prescribed fire. Y-axes were scaled to the maximum value to facilitate comparison between plots. Regressions with an asterisk (*) had more than one significant independent variable; R^2 and P-values are for the entire model, but only the independent variable with the lowest partial P-value is illustrated (see Table S3). Regional endemics (**) do not include Cherrie's Tanager. Guilds not shown either had no strong correlation with any of the measured variables (i.e., frugivores, predators, terrestrial understory insectivores) or were not as indicative as other groups of environmental service provision (i.e., granivores).

site was unique in being immediately surrounded on two sides by old growth forest, which was expanding into the regenerating area (in Fig. 1 the lower left passive restoration point). Differences among habitats were confirmed by ANOSIM ($R = 0.67$, $\alpha = 0.001$) and were likely driven by the difference between old growth forest and restoration treatments.

VEGETATION STRUCTURE AND BIRD COMMUNITY.—Several vegetation structures including canopy cover, canopy height, and exotic grass cover differed significantly among restoration treatments and old growth forest (Table 1). In all cases mean values for active treatments were intermediate to old growth forest and passive plots. Only canopy cover differed significantly between active and passive restoration. Differences between passive and active plots in exotic grass cover, canopy height, and understory stem density were not significant due to high variability in passive plots (Fig. 2).

Overall bird detections were explained by decreasing understory stem density (Fig. 4). Decreasing understory density and exotic grass cover likewise explained increases in bird species richness and proportional similarity to old growth forest (R^2=0.55, P=0.002; Table S3). Gradients in both exotic grass cover and understory density were primarily driven by a small number of plots.

Individual foraging guilds were correlated with each of the vegetation structures measured (Fig. 4). Among insectivores, bark-gleaner richness increased with canopy cover—the only vegetation structure that was significantly impacted by active restoration. Richness and detection frequency of foliage gleaners both increased with canopy height, whereas sallying insectivores increased with decreasing understory stem density. Nectarivores and granivores were negatively correlated with canopy height, and no aspect of vegetation structure explained variation in frugivore detections or species richness (Table S3).

When analysis was limited to species of conservation concern, canopy height explained significant variation in detections and richness of forest-dependent species as well as detections of regional endemics (Fig. 4). Initially, regional endemics declined with canopy height (R^2=0.27, P=0.003), but when Cherrie's Tanager was removed from the analysis this trend reversed (Fig. 4).

DISCUSSION

Contrary to our expectations, we found no relationships between the type of restoration treatment in Melissa's Meadow and bird species richness, detection frequency, or proportional similarity to old growth forest. Rather, detection frequency and proportional similarity to old growth forest, were best explained by exotic grass cover and understory stem density—vegetation structures that were not strongly affected by active tree planting. The apparent inefficacy of active intervention for attracting birds in Melissa's Meadow contrasts with previous studies, which concluded that restoration was successful based on increased bird visitation to tree islands in Honduras (Zahawi & Augspurger 2006) and greater forest species richness in grazer-exclosured regenerating Afromontane forest in Ethiopia (Aerts et al. 2008). Why was Melissa's Meadow different?

The inconsistency may be best explained by (1) a weak contrast between actively and passively restored pastures; (2) differential habitat selection among avian foraging guilds; and (3) an ideal local context for passive restoration. O'Dea and Whittaker (2007) noted that species richness in Andean bird communities does not always decline monotonically with habitat degradation. They con-

cluded that this was due to relatively minor structural differences between advanced second-growth forests and old growth forest. If restoration studies are similar (and inverse) to degradation studies, we should not be surprised to find a similar trend in Melissa's Meadow, where many of the control plots had formed closed canopy, secondary forest in the six to nine years since abandonment. Unlike open pastures, which have consistently been shown to be depauperate in bird diversity (MacArthur & MacArthur 1961, reviewed by Bowen et al. 2007), closed canopy secondary forests provide foraging and nesting resources and cover from predators that increase bird abundance and species richness (Blake & Loiselle 2001, Selwood et al. 2009).

A second factor that reduced the observed impact of restoration was differential habitat selection among and within avian foraging guilds (Fig. 3). Foliage-gleaning insectivores, for example, preferred tall, closed canopy forest, while nectarivores and granivores preferred open plots with slower regeneration. Within guilds, interspecific differences likely accounted for nonsignificant trends. Among frugivores, for instance, large species like Grey-headed Chachalaca (Ortalis cinereiceps) and Chestnut-mandibled Toucan (Ramphastos swainsonii) were detected more frequently in closed canopy forest while smaller generalists like Buff-throated Saltator (Saltator maximus) and Cherrie's Tanager were more common in shorter, second-growth (Appendix S1). Such differences in habitat affinities among explicit foraging guilds are well known in temperate North American forests (Holmes et al. 1979, De-Graaf et al. 1998) but can be missed in tropical restoration studies, which sometimes lump all birds together (Fink et al. 2009).

Melissa's Meadow may have also had particularly small difference in bird usage between treatments because of the ideal context for passive recovery in which the site is situated. As a recently abandoned pasture on a steep, Central American hillside, Melissa's Meadow is representative of a growing proportion of secondary tropical forests (Asner et al. 2009). It may also be considered a best-case scenario due to its proximity to a medium-sized old growth forest fragment, a low ratio of secondary to mature forest in the surrounding area, and protection from anthropogenic disturbances (e.g., hunting, cattle grazing; Chazdon et al. 2009, Holl & Aide 2011). Restoration studies with greater landscape-scale replication will likely observe stronger contrast in vegetation structure between actively and passively restored pastures, and we predict that such differences will affect the attraction of some avian foraging guilds.

Alternatively, the lack of observed differences between active and passive restoration plots may have been driven by a nucleation effect, where active intervention in some areas increased bird visitation and forest recovery in passive areas. Natural forest regeneration often develops spatially in patches that expand or nucleate outward over time (Yarranton & Morrison 1974). This effect is exemplified by increased rates of forest recovery near isolated, remnant trees (Schlawin & Zahawi 2008), and several restoration ecologists have suggested using applied nucleation (i.e., planting small patches of trees with the expectation that they will coalesce) as a cost effective and ecologically sound alternative to extensive tree plantations (Zahawi & Augspurger 2006, Cole et al.

TABLE 2. *Implications of avian habitat preference for tropical forest restoration design.*

Vegetation structure	Effect(s) of active restoration	Correlation(s) with bird use of site	Implications for restoration design
Canopy cover	Strong increase & reduced variability	Increased richness of bark-gleaning insectivores Decreased granivore detections	Active tree planting may increase the number of bark-gleaning insectivore species using a site by promoting rapid canopy closure. Bark-gleaners could benefit planted trees by controlling herbivorous arthropods, but this service has not been explicitly investigated
Exotic grass cover	Potential reduction & reduced variability	Decreased richness of foliage-gleaning insectivores Decreased total species richness Decreased similarity to old growth reference Increased granivore detections	Active tree planting may have the potential to increase bird species richness, especially for foliage-gleaning insectivores, if exotic grass cover can be more strongly reduced over levels found in passively restored areas. Increasing foliage-gleaner richness could help control herbivores. Increasing compositional similarity to reference forests may likewise increase dispersal of forest seeds into restoration sites
Canopy height	Possible increase	Increased richness and detections of forest-dependent species Increased foliage-gleaning insectivore detections Increased detections of regional endemics (when Cherrie's Tanager was removed) Decreased richness and detections of nectarivores	There may be potential for active restoration to increase visitation by foliage-gleaning insectivores and species of conservation concern if canopy height can be increased above 25 m, however, only reference forests had such stature in this study
Understory stem density	Possible increase and reduced variability	Decreased richness and detections of sallying insectivores Decreased overall detection frequency of birds Decreased richness and detections of nectarivores Decreased proportional similarity to old growth forest	Two sites in Melissa's Meadow that received prescribed burns had greatly increased understory stem density, and these sites had considerably fewer birds using them. Practitioners may consider a thinning treatment for sites with over 3000 understory stems/ha to increase overall bird visitation

2010, Sady *et al.* 2010). Because active and passive plots in Melissa's Meadow were adjacent to each other, planted trees in active plots may have impacted bird activity, seed dispersal, and microclimates along the edge of control plots.

The same factors that obfuscated differences between restoration treatments probably contributed to the high species richness observed in Melissa's Meadow. In total, we recorded 186 species in the restoration site. This figure represents more than one-fifth of all Costa Rican birds and nearly half of the 410 species recorded around Las Cruces Biological Station (Obando-Calderón *et al.* 2009, Martínez 2010). To the best of our knowledge, no study has recorded more bird species in any secondary forest of similar age and size (P. Stouffer, pers. comm.). Despite relatively low proportional similarity to old growth forest, the bird community in the restoration site included 11 (of 15) regional endemics and 29 highly forest-dependent species (Appendix S1), including a near-threatened species, Baird's Trogon (*Trogon bairdii*) (IUCN 2010). It therefore seems likely that this secondary forest contributes to the persistence of forest-dependent birds through landscape complementation and neighborhood effects (*sensu*Dunning *et al.* 1992). Baird's Trogon, for example, requires large, decaying tree trunks for nesting, but may use adjacent secondary forests such as Melissa's Meadow to forage for fruits and insects (Stiles & Skutch 1989).

Based on our observations in Melissa's Meadow we have several recommendations for tropical restoration ecologists (Table 2). We advocate the consideration of natural recovery rates prior to actively restoring a site. Our results suggest that passive restoration or applied nucleation (a moderate level of intervention) may have attracted an abundant and diverse bird community to Melissa's Meadow in a short time period. Given that restoration ecologists have limited resources, a wait-and-see approach to restoration may be more efficient than immediate action (Holl & Aide 2011). We also urge restoration ecologists to explicitly state their goals before restoring bird habitat. Our results demonstrate that all bird guilds do not respond to the same aspects of habitat structure, and moreover, that some guilds have conflicting preferences. If pollination services by hummingbirds are desired, for instance, the treatment called for may be considerably different than one to increase visitation by large frugivores. Further studies with greater spatial replication will be needed to separate the effects of restoration treatments on avian habitat use from the effects of restoration on actual bird community restoration.

CONCLUSIONS

Contrary to our expectations, overall avian species richness and detection frequency did not differ between restoration plantations and untreated abandoned pasture, or between restoration treatments and old growth forest. Rather, richness and relative abundance of birds using the site were explained by exotic grass cover and understory stem density, neither of which was strongly affected by active restoration. Other vegetation structures had varying impacts among and within foraging guilds, which obfuscated generalizations. Although proportional similarity to old growth forest was relatively low in both plantations and controls, many forest-dependent species encountered in old growth forest were also found in the restoration site, albeit in lower numbers. We suggest that this highly diverse secondary forest likely contributes to the persistence of forest-dependent birds in an adjacent forest fragment, and that restoration ecologists should (1) assess the natural recovery rate of degraded lands before intervention to strategically deploy limited funds; and (2) carefully consider which avian foraging guilds are most desirable given that no single structural variable sufficiently predicts the detection frequency of all species.

ACKNOWLEDGMENTS

SUPPORTING INFORMATION

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

TABLE S1. *Explicit avian foraging guilds used in this study with summary statistics including number of species and detections per guild.*

TABLE S2. *Analysis of variance results comparing bird detection frequency and estimated species richness between restoration treatments and old growth forest.*

TABLE S3. *Results of stepwise multiple regressions of bird detection frequency and estimated species richness against vegetation structures.*

FIGURE S1. Species accumulation (Mau Tau) of birds in Melissa'ns Meadow and adjacent primary forest with 95 percent confidence intervals and Jack1, Chao2, and Bootstrap estimations of total richness.

FIGURE S2. Non metric multidimensional scaling ordination of birds that used old growth forest and restored habitats (active and passive) in Melissa'ns Meadow, Las Cruces, Costa Rica. Banding codes follow Pyle and DeSante (2010) (http://www.birdpop. org/AlphaCodes.htm).

APPENDIX S1. Bird species recorded in Melissa'ns Meadow and surrounding forest.

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