Active restoration accelerates recovery of tropical forest bird assemblages over two decades

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ARTICLE INFO

ABSTRACT

Choosing effective methods to restore habitat for the diverse faunal assemblages of tropical forests is hampered by lack of long-term data comparing multiple restoration treatments. We conducted area counts of bird assemblages over 12 years (~5–17 years since restoration) in a blocked experiment with two active planted treatments (tree plantations and applied nucleation) and a passive restoration treatment (natural regeneration) replicated at 11 sites in Costa Rica. We also surveyed six pastures and five remnant forest sites to assess recovery of avian species richness, composition, forest specialists, and range-restricted species in restoration plots relative to degraded and reference systems. Restoration treatments showed increased resemblance of avian assemblages to remnant forest over time. Applied nucleation proved equally effective as plantation, despite a reduced planted area, whereas natural regeneration recovered more slowly. Assemblage-level trends in avian species richness and compositional similarity to reference forest are underpinned by reductions in use by pasture birds and by gradual increases in richness of forest-affiliated species. Because forest-affiliated species tend to have narrower distributions than the open-country species they replace, forest restoration can reduce biotic homogenization at the local scale. Restoration practitioners should consider applied nucleation as an alternative to standard plantations if seeking rapid recovery of bird assemblages. However, the ecological return on investment from natural regeneration increases over a couple of decades. Managers should monitor trends in forest-affiliated and range-restricted species to track the recovery of the full avian assemblages, since coarse metrics like species richness and overall compositional similarity may plateau relatively quickly.

1. Introduction

Understanding how different restoration approaches influence faunal recovery is essential to guide tropical forest restoration efforts and achieve desired outcomes for biodiversity conservation. Birds are a key group in tropical forest restoration because they both benefit from restoration and promote forest regeneration through pollination and seed dispersal interactions (Catterall, 2018). The choice of restoration approach can strongly affect vegetational trajectories and in turn local habitat characteristics that influence avian habitat use (Reid et al., 2012). Two common approaches are native tree plantations, which are

resource-intensive but develop canopy cover faster, and passive restoration, in which sites are protected from disturbance but otherwise left to regenerate naturally. As passive restoration generally involves lower costs, it has been promoted for forest restoration at large scales (Chazdon and Uriarte, 2016). However, trajectories of natural regeneration are highly variable and depend on land use history and proximity to source populations (Holl and Aide, 2011). In the absence of intervention, areas under passive restoration can remain in a state of arrested succession (Sarmiento, 1997). Meanwhile, there is growing evidence that intermediate strategies along an intervention continuum (Chazdon et al., 2021), such as applied nucleation (i.e., when plants are planted or

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seeded in clusters within a larger area), can accelerate vegetation recovery at lower cost while creating more structural complexity (Holl et al., 2020).

The long-term efficacy of differing restoration methods for creating forest habitats for birds depends both on initial differences among restoration treatments and how they change over time. Comparing active and passive restoration is difficult because they have typically been assessed using different study designs and in different locations (Shoo and Catterall, 2013). Past studies have often relied on chronosequences (Acevedo-Charry and Aide, 2019; Sayer et al., 2017), which sometimes confound temporal variability and past land use (Johnson and Miyanishi, 2008), or comparisons of passively and actively restored sites selected years after restoration, which are subject to positive selection bias for passively restored sites (i.e., sites that showed successful recovery, Reid et al., 2018). Meta-analyses comparing bird assemblages in paired secondary and primary forest sites throughout the tropics show that forest specialist species increase with secondary forest age (Acevedo-Charry and Aide, 2019; Sayer et al., 2017), but observational data of naturally regenerated forests from disparate locations may not represent realistic recovery trajectories, especially for sites that were severely degraded, and provide limited insight into recovery at actively-restored sites. Few studies directly compare passive recovery with active restoration strategies in the same system (Jones et al., 2018) and those that do typically have just a few years of data (de Carvalho Barros et al., 2022; Vogel et al., 2015), which may not reflect longer-term trajectories. Most studies assessing nucleation have used seedling richness or density as metrics of restoration outcomes (de Oliveira Bahia et al., 2023), rather than fauna. Accordingly, how bird assemblages in restoration treatments of varying intensity recover over time at the same sites remains an open question.

Evidence from multiple continents demonstrates that native tree plantations can benefit bird recovery by providing a closed canopy and vertical stratification (e.g., Catterall et al., 2012; Hariharan and Raman, 2021; Latja et al., 2016). However, forest-dependent birds may require specific microclimates, food items, or nest sites, that can take decades to develop (Vesk et al., 2008). Understory insectivores in particular are sensitive to disturbance and show limited dispersal across anthropogenic matrices (Powell et al., 2015; Şekercioğlu et al., 2002). Forest-affiliated species also tend to have more specialized habitat requirements and are more likely to be range-restricted. In contrast, species found in agricultural lands tend to be disturbance-adapted and have large range sizes. As such, land conversion can result in biotic homogenization of avifauna by extirpating specialist species and favoring disturbance-tolerant species over wide areas (Karp et al., 2012), but the degree to which restored forests regain forest specialists and range restricted species over observable time frames is poorly understood.

Disentangling the effects of restoration treatment on avian habitat use from those of site age and context requires long-term, multi-site, and multi-treatment studies that also include reference and degraded sites surveyed multiple times to account for regional trends which may be occurring independently of local restoration efforts, for example population declines (e.g., Blake and Loiselle, 2016; Sigel et al., 2006) or range expansions. Here, we report on avian assemblage recovery over 12 years in restoration plots that were subjected to three different restoration interventions replicated widely across an agricultural landscape in southern Costa Rica (Holl et al., 2020). Specifically, we compared the effects of two active restoration treatments (plantation and applied nucleation) and a passive natural regeneration restoration treatment on bird species richness and compositional similarity to reference forests, relative to degraded pastures and reference forests. We asked: (1) How do bird species richness, community composition, and similarity to reference forest differ among restoration treatments and how do they change over time? (2) How do pasture-affiliated and forest-affiliated bird species vary among restoration treatments over time? (3) Are restored sites gaining range-restricted species?

Based on an early comparisons in this study system (Reid et al., 2014)

and studies in other systems, we expected that recovery of richness (Edwards et al., 2009) and composition (Hariharan and Raman, 2021) would be greater in planted restoration treatments than in natural regeneration, given that the planted species would increase physical structure and provide the same resources to both treatments. We also anticipated that differing responses by pasture- and forest-affiliated birds would underlie community-level changes in richness and composition over time (Catterall et al., 2012), and that shifts in forest specialists would be reflected in community metrics of geographic range size (Dunn and Romdal, 2005; Karp et al., 2019).

2. Materials and methods

2.1. Study area

This study took place in southern Costa Rica (8°44′ – 8°47′ N, 82°56′ – 82°57′ W). The native ecosystem is transitional between tropical premontane wet forest and premontane rain forest (Holdridge et al., 1971). Site elevation ranges from 1080 to 1430 m.a.s.l. Mean annual temperature is ~21 °C at the Las Cruces Biological Station, which is within the study landscape. Median annual rainfall for 2005–2022 was 3.7 m (range 2.8–4.9 m), with a dry season from December to March. The landscape was largely deforested between 1947 and 1980 and is now a fragmented mosaic of cattle pastures and agricultural fields interspersed with patches of remnant and secondary forest, with overall regional forest cover ~28 % as of 2014 (Zahawi et al., 2015). In recent decades ongoing deforestation has been partially offset by second growth, and for the 2005–2014 period the study landscape experienced a small net increase in forest cover (Amar, 2020).

2.2. Restoration experimental design

The three forest restoration treatments (Holl et al., 2020) were established at 11 sites (Fig. 1, Table S1) over three years (2004–2006). All sites are separated by >700 m. At each site three 0.25 ha (50 × 50 m) plots were established and assigned to one of three treatments: plantation (PL), applied nucleation (AN), or natural regeneration (NR). Plots were separated by ≥5 m. Plantation plots were planted uniformly with tree seedlings, whereas applied nucleation plots were planted with six tree nuclei of three sizes: two each of 4 × 4, 8 × 8 and 12 × 12 m. Tree spacing was ~2.8 m, with 313 trees planted in plantation and 86 in applied nucleation. In both active restoration treatments, we planted two native tree species, *Terminalia amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two naturalized fast-growing N-fixing species, *Erythrina poeppigiana* and *Inga edulis* (both Fabaceae) that are used in agricultural intercropping systems. Naturally established vegetation was cleared prior to planting and at ~3-mo intervals for 2.5 years in all plots to allow planted seedlings to grow above other vegetation.

By 2019 (13–15 years after plot set up, toward the end of the study period), most plantation plots had a tall (~ 15 m), homogeneous canopy cover and fairly sparse mid-story shrub and small tree cover (Holl et al., 2020; Zahawi, unpublished data). The two fast-growing planted Fabaceae species experienced substantial mortality, with ~36 % of *Erythrina* and ~ 34 % of *Inga* surviving to 2020 (14–16 y after planting; Holl & Zahawi, unpublished data). This mortality, combined with falling branches, has led to greater accumulation of coarse woody debris and standing dead wood in planted treatments compared to natural regeneration (Fernandez Barrancos et al., 2022). Applied nucleation plots were characterized by greater canopy roughness than plantation plots and intermediate canopy cover (60 ± 7.1 %) and height (11.5 ± 0.9 m). By 2019, most natural regeneration plots had patchy (20.6 ± 4.6 % cover) and short (7.0 ± 0.5 m) canopies surrounded by dense exotic pasture grass cover, although some had greater tree and shrub cover. At least 155 tree species had naturally recruited in each restoration treatment by 2022, despite the low number of planted species (or total
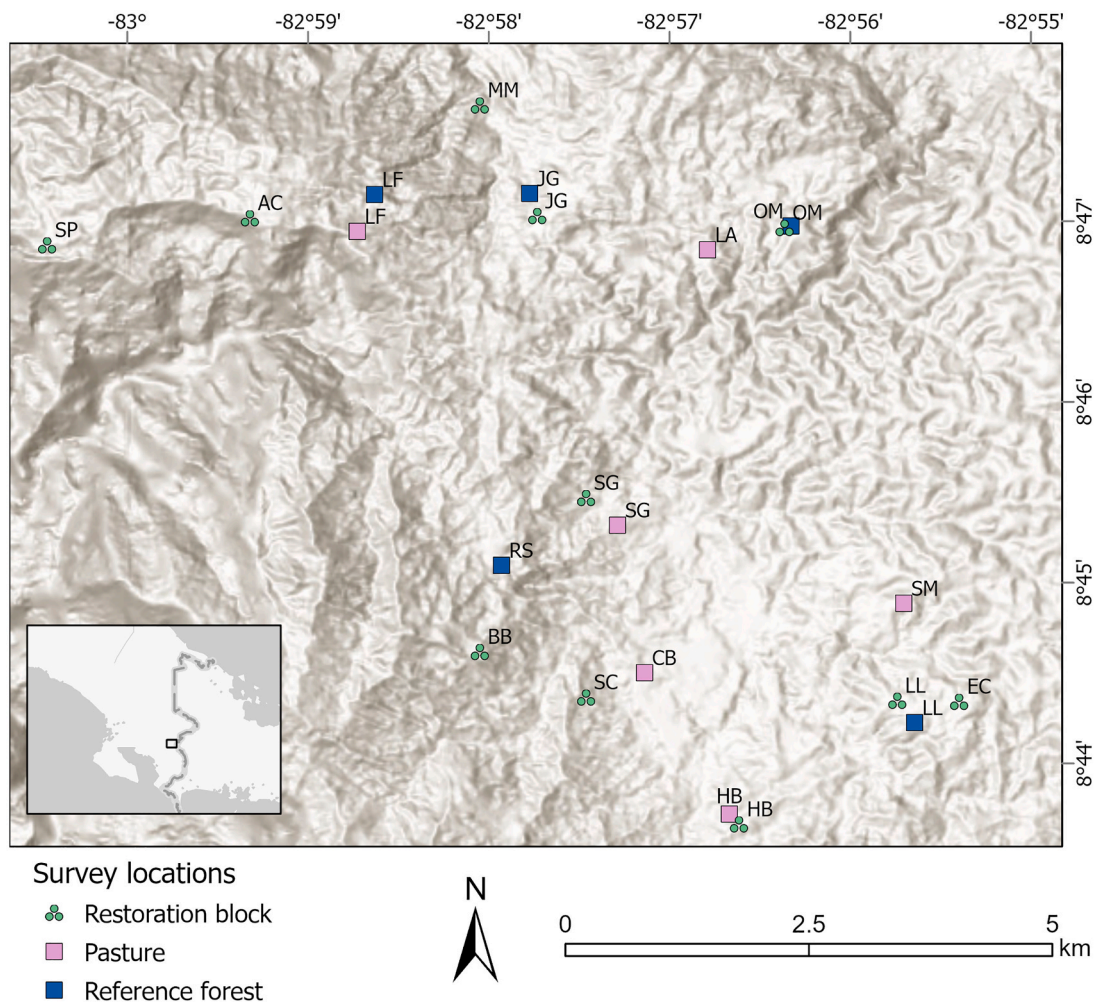
Fig. 1. Bird survey locations in Coto Brus, southern Costa Rica. Each restoration block contains one plot of each restoration treatment (plantation, applied nucleation, and natural regeneration). Locations <450 m apart were assigned to the same site grouping (2-letter code) for analysis in mixed-effect models. Terrain basemap attribution: Esri, NASA, NGA, USGS, Esri, TomTom, Garmin, FAO, NOAA, USGS.

absence of planting in natural regeneration); some of these recruits had reached the tree (> 10 cm DBH) size class (Schubert et al., 2024, submitted).

2.3. Bird data collection

From 2010 to 2021 (12 years), we surveyed birds in all restoration plots (n = 33 plots). Between 2013 and 2021 (9 years), we also surveyed birds in 0.25 ha (50 × 50 m) survey areas within five reference forests (RF) and six active cattle pastures (PA) for a total of 44 total survey plots (Fig. 1, Table S1). Reference forests and active pastures were located within the same study region and elevational range but not precisely paired with restoration blocks (distance to nearest restoration plot: ~20–1000 m for reference forests; ~300–1000 m for active pastures). Reference forests were subject to variable fragmentation and disturbance but represent "best available" examples of local remnant forest habitat. Three times per year (Apr-May, Jul-Aug, Nov-Dec), a single skilled observer (JA Rosales) actively searched each sampling area for 20 min, walking along existing trails, and recorded all birds seen or heard within the plot area. Each plot had a trail of similar length that provided access to the plot interior, although trail configuration varied. The observer used his extensive experience in our research plots to conservatively judge whether heard-only birds were calling from within the plot. Observations of flyover birds not perching or foraging were excluded from analyses. Surveys were conducted between 05:50 and

09:00 h in mild weather, including light fog or mist but not high wind or rain. Plots within the same site were surveyed on the same day, and the order in which treatments were surveyed within a site was varied to avoid systematic bias in survey start time.

The resulting data set includes 1466 surveys representing 489 h of sampling effort. Nineteen plot surveys (1.3 %) were missing; pasture and reference forest were missing eight and six surveys, respectively, whereas each restoration treatment was missing just one or two surveys. Species names were standardized to the 7th Checklist of the American Ornithological Society (Chesser et al., 2022). We obtained the IUCN Red List extinction risk assessment category for each species using the *rredlist* package v0.7.0 (IUCN, 2022).

2.4. Data analysis

We aggregated survey-level bird abundance data by plot and year to obtain annual assemblages (n = 495) and used these as sampling units for analyses. Rather than summing individuals detected for each species across the three survey seasons, we aggregated by the maximum count (sensu Julliard et al., 2006), to (a) minimize counting highly resident individuals multiple times and (b) avoid interpolating abundances in missing surveys. We performed all analyses with R version 4.1.2 (R Core Team, 2022).

To assess the effects of habitat type (hereafter synonymous with 'treatment') and treatment-specific effects of time on community

recovery we calculated multiple metrics and fitted a separate model for each response variable using an appropriate error structure (Table S2). We fitted linear mixed effect models using *lme4* v1.1.30 (Bates et al., 2015) and generalized linear mixed models (GLMMs) using *glmmTMB* v1.1.4 (Brooks et al., 2017). We used survey year (calendar year - first year of monitoring) as the time covariate rather than years since restoration because the latter is not a meaningful variable for pastures and reference forests. In all models we included a random intercept term for plot nested within site to account for non-independence of bird assemblages sampled within the same plots and clustered within sites. Forest and pasture plots within 450 m of a restoration block were assigned to that site. Because forest and pasture survey locations were not always paired with restoration blocks, the fixed effects of reference forest and pasture habitat types were partly confounded with site effects. Therefore, there was lower power for testing the effects of reference forest and pasture habitats. For all fitted models, we examined residual diagnostics, including temporal autocorrelation functions, in package *DHARMa* v0.4.6 (Hartig, 2020). To compare the predicted main effects of treatments and their interactions with time we used package *emmeans* v1.8.1.

2.5. Species richness

To compare species richness while accounting for undetected species, we calculated the abundance-based Chao1 species richness estimator for each annual assemblage using package *iNEXT* v3.0.0 (Chao et al., 2014b; Hsieh et al., 2016). To evaluate sample completeness for each annual community we calculated sample coverage (Chao et al., 2014a). We modeled species richness using a GLMM with a negative binomial error distribution and a log link function because a Poisson model had overdispersed residuals. We modeled sample coverage (bounded 0–1) using beta-distributed residuals and a logit link function.

2.6. Community composition

To assess recovery of community composition, we first created a matrix of abundance-based community dissimilarities (package *vegan* version 2.6-2; Oksanen et al., 2013). We used the Morisita-Horn index, since it is robust to variation in sample size and coverage (Chao et al., 2006; Dent and Wright, 2009). We visualized the trajectories of species composition using nonmetric multidimensional scaling, plotting the average (centroid) assemblage for each treatment in each year (De Cáceres et al., 2019). To quantify the degree to which bird assemblages in restoration plots and pastures approached those of reference forest, we calculated the mean similarity (1- dissimilarity) of each annual assemblage to each of the reference forest assemblages within each of the last nine years of the data set, when reference forests were surveyed (2013–2021; n = 5 reference forest assemblages). We compared each plot to multiple reference forests rather than only the nearest reference forest to account for their spatial variability. Similarity among reference forests is interpretable as a metric of reference forest beta diversity (Anderson et al., 2011), and this natural variability constrains the average similarity to reference forest attainable by restoration treatments (Gerwing and Hawkes, 2021). Therefore, we also calculated the mean similarity of each annual reference forest assemblage to the other reference forest assemblages (n = 4 assemblages for forest-to-forest comparisons). We fit a linear mixed effect model (Gaussian error distribution) for mean pairwise similarity to reference forest communities because a beta-distributed model failed to converge.

2.7. Habitat association

To explore how community-scale shifts in species composition reflect responses of birds with different habitat affinities, we first identified species associated with particular habitat types ("indicator species", sensu De Cáceres and Legendre, 2009) using the *indicspecies* v1.7.12

package, based on a priori habitat categorization of survey plots. We used the abundance-based point biserial correlation coefficient as the association function, corrected for unequal numbers of sites per habitat type (func = 'r.g.'), and assessed significance at α = 0.05 based on 999 permutations (following Hariharan and Raman, 2021). To assess temporal trends in the richness of pasture and forest affiliated birds in restoration treatments, we identified indicator species based on the subset of data with just pasture and forest plots. This provided lists of indicator species derived independently of restoration plot surveys. We modeled observed richness of indicator species using a GLMM with a Poisson error distribution and a log link function.

2.8. Geographic range size

We used two metrics to assess patterns of bird geographic range size (from Tobias et al., 2022) across habitats and time. We calculated the community weighted mean (CWM) value of geographic range size using the *FD* v1.0-12.1 package (Laliberté et al., 2014). This is similar to the "community range index," used to characterize one facet of bird assemblage "commonness" and as a metric of biotic homogenization (Godet et al., 2015). We also used the observed richness of range-restricted species (range size ≤50,000 km²), which is commonly used as a metric of endemism (Ocampo-Peñuela et al., 2016). We modeled CWM range size using a linear mixed effects model, and we modeled range-restricted species richness using a GLMM with a zero-inflated Poisson error structure and a log link function.

3. Results

We recorded 34,469 individual bird detections of 281 species in 46 families (Appendix 1). The most abundant families were tanagers (Thraupidae; 23 % of detections), flycatchers (Tyrannidae; 15 %), thrushes (Turdidae, 12 %), warblers (Parulidae; 9 %), and wrens (Troglodytidae; 6 %). The five species with the most individuals detected were *Catharus ustulatus*, *Ramphocelus passerinii*, *Amazilia tzacatl*, *Catharus aurantiirostris*, and *Sporophila corvina*. Seventy-nine species (28 %) were detected in all five habitat types, whereas 47 species (16.7 %) were recorded in a single habitat type (Fig. 2). For 26 species, only a single individual was detected, and for 15 species only two individuals were detected. We recorded five species that have an IUCN extinction risk category of "Near Threatened." Of these, two are residents and both are large frugivores (*Ramphastos ambiguus* and *Penelope purpurascens*). Twenty-one species (7.4 %) were range-restricted, of which the most-detected were *Manacus aurantiacus*, *Arremon costaricensis*, and *Saucerottia edward*.

3.1. Species richness

Over the full study period, species richness was highest in reference forest, followed by plantation, applied nucleation, active pasture, and natural regeneration (Fig. 3B). Reference forest had significantly higher predicted richness than pasture and natural regeneration, whereas plantation and applied nucleation were only statistically more speciose than natural regeneration. Pasture plots were not statistically different from natural regeneration (Fig. 3B, Table S3, Table S4). Predicted species richness increased over time only in restoration plots (Fig. 3A, Table S3), with similar slopes among treatments (Table S5).

Overall mean sample coverage for the 495 annual assemblages was 67 % (range 25–97 %), indicating that on average the three 20-minute surveys per year did not completely sample the assemblages of birds using each plot. Sample coverage was greater in pasture plots (Fig. S1, Table S6), indicating that richness estimates in pastures were more precise than the other habitat types. Natural regeneration was the only habitat type where sample coverage increased slightly with time, which indicates that over time a decreasing proportion of unsampled individuals were undetected species.
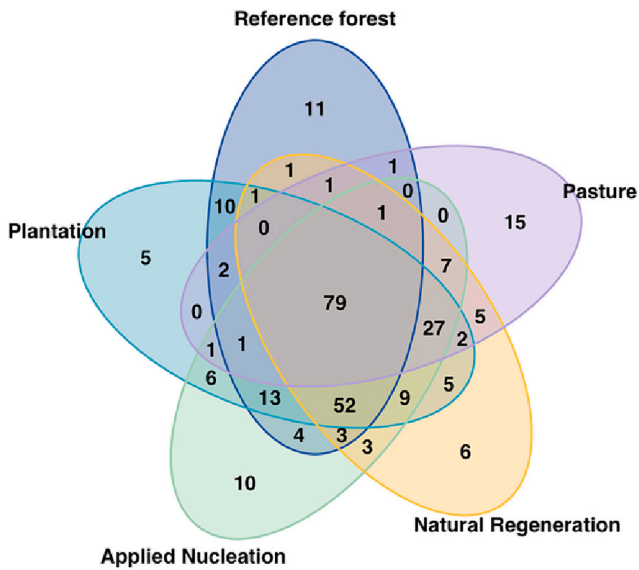
Fig. 2. Venn diagram of bird species detected in each habitat type over the study period (9 years for pastures and reference forests, 12 years for restoration plots; n = 281 species total).

3.2. Community composition

Bird assemblages in restoration plots on average converged toward each other and toward those of reference forest plots over time (NMDS of Morisita-Horn dissimilarity, Fig. 4A, stress = 0.25, see Fig. S2 for NMDS of individual annual communities). Despite this overall convergence, there were differences among restoration treatments in both their similarity to forest and their rate of change in similarity over time. Assemblages in plantation and applied nucleation plots were significantly more similar to reference forest than were natural regeneration assemblages (Fig. 4C, Table S6, Table S7). However, natural regeneration was the only treatment showing a significant increase in similarity to forest over the last nine years of surveys (Fig. 4B, Table S8).

In contrast, assemblages in pasture and reference forest plots varied from year to year but not in a consistent directional manner (Fig. 4). As anticipated, pasture communities were the least similar to reference

forest (Fig. 4A, Fig. 4C) and did not show a significant time effect (Fig. 4B, Table S9). Reference forest communities were also heterogeneous among sites. Within-year similarity among reference forests (i.e., the similarity of each forest community to the other four) ranged from 0.33 to 0.60 (estimated marginal mean = 0.41). Although planted restoration treatments reached comparable levels of pair-wise similarity to reference forests, their between-group dissimilarity was driven by distinct composition (Fig. 4A, Fig. S2).

3.3. Habitat association

Indicator species analysis identified 120 species (42 %) that were significantly associated with either pasture (39) or reference forest (89) (Appendix 2). The species most strongly associated with reference forest were *Henicorhina leucosticta*, *Lophotriccus pileatus*, *Catharus aurantiirostris*, *Pachysylvia decurtata*, *Arremon aurantiirostris*, and *Myioborus miniatus*. Widespread open-country birds such as *Troglodytes aedon*, *Tiaris olivaceus*, *Sporophila corvina*, *Thraupis episcopus*, and *Tyrannus melancholicus* were associated with pasture sites.

Only half of the pasture-affiliated species were found in restoration plots, and only one-sixth were found in reference forests. There were no temporal trends in pasture indicator richness for any treatment (Fig. 5A-B, Table S10). In contrast, forest indicator species richness gradually increased over time in all three restoration treatments, with higher intercepts in planted treatments but a slightly higher slope in natural regeneration (Fig. 5C-D, Tables S11-S13). Some forest indicator species used restoration plots with increasing frequency (e.g., *Tangara icterocephala* and *Henicorhina leucosticta*). A few forest species (e.g., *Zentrygon chiriquensis*) were never recorded in restoration plots.

3.4. Range restriction

Patterns for community weighted mean range size and richness of range-restricted species mirrored those of pasture and reference forest indicator species richness. The average individual in pasture had a geographic range size approximately twice that of other habitats (Fig. 6A-B). Range-restricted species richness in restoration treatments was intermediate between pasture and forest and increased over time (Fig. 6C-D).
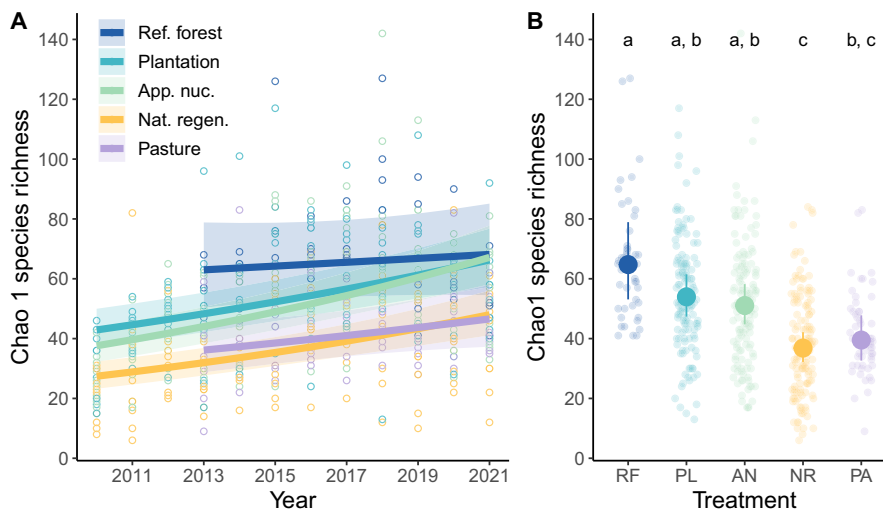

Fig. 3. Species richness (Chao1 estimator) varied over time and among habitat types. (A) Model predictions (lines with 95 % confidence interval bands) show positive slopes for applied nucleation and natural regeneration and marginally significant positive slopes for plantation. Time since restoration ranges from 4 to 6 years in 2010 to 15–17 years in 2021. N = 11 plots per restoration treatment, 5 reference forests, 6 active pastures. (B) Estimated marginal mean richness with 95 % CI (large points with vertical lines). Different letter labels indicate significantly different (p < 0.05) estimated marginal means (over all years). In both panels, small circles represent individual annual assemblages.
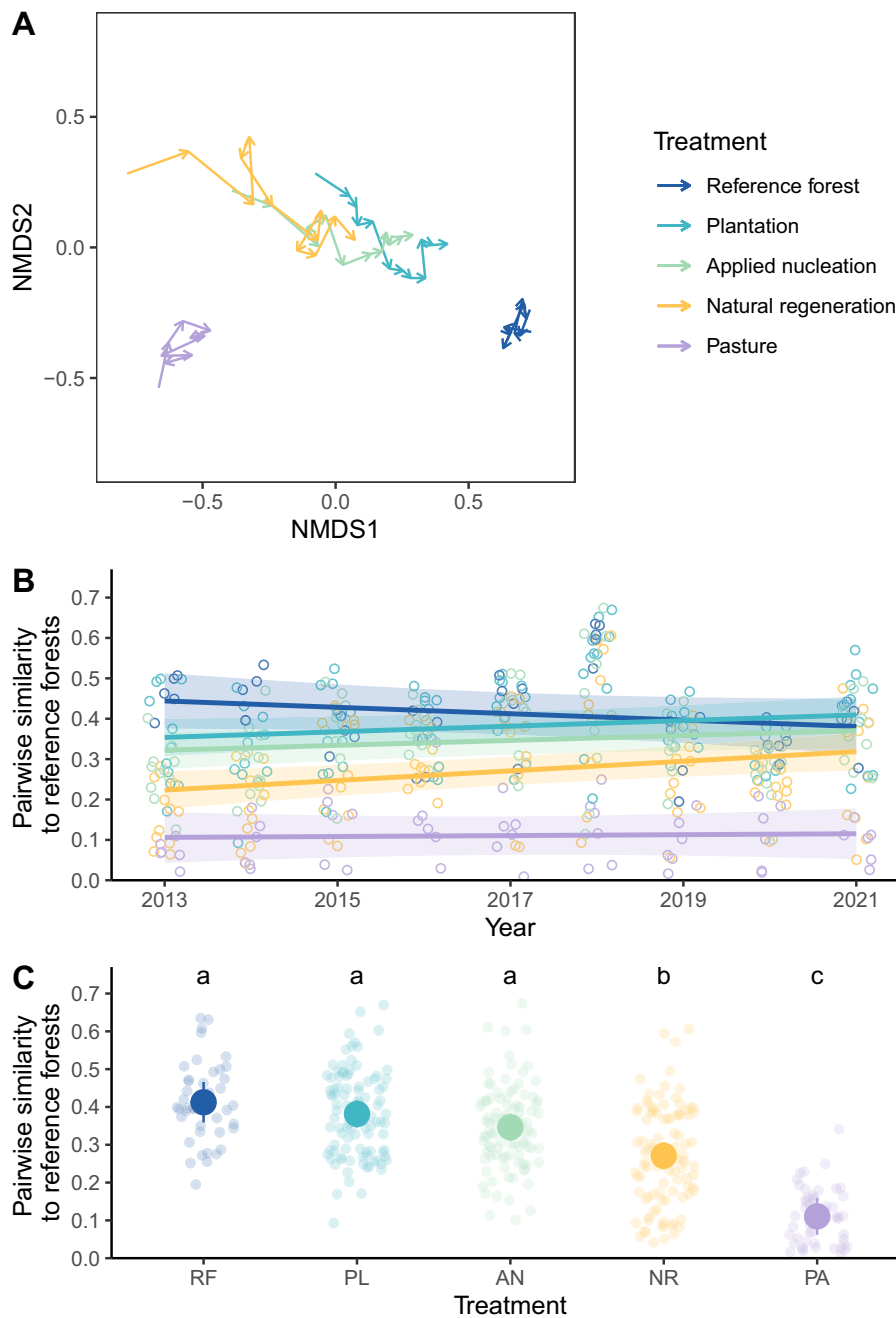
Fig. 4. Community trajectories and similarity to reference forests. (A) Community trajectories in NMDS ordination space, based on a Morisita-Horn dissimilarity matrix of annual communities. Points represent the annual average (centroid) for each treatment. Arrows represent compositional change between consecutive years (reference forest and pasture: 8 segments, 2013–2021; restoration treatments: 11 segments, 2010–2021). (B) Pairwise community similarity to all reference forest communities within the same years (2013−2021) for each habitat type. Lines and ribbons represent model predictions and 95 % CI. For forest-forest comparisons, community similarity represents spatial beta diversity. Time since restoration was 4–6 years in 2010, 7–9 years in 2013, and 15–17 years in 2021. (C) Treatment-level estimated marginal means (large points) and 95 % confidence intervals (vertical lines). In (B) and (C), small circles represent individual plot-level mean pairwise comparisons to each reference forest community. Different letter labels indicate significantly different ($p < 0.05$) estimated marginal means (over all years).

4. Discussion

Bird assemblages in all restoration treatments have recovered at least partially over time for all metrics examined, indicating that restoration approaches across a gradient of effort facilitate recovery. Whereas species richness and a multivariate similarity index provide a broad picture of recovery in different treatments, trends in habitat-associations of constituent species are informative for understanding the processes of and constraints on recovery, as emphasized by previous studies on the recovery of habitat specialists in other faunal groups (e.g. Acevedo-

Charry and Aide, 2019; Audino et al., 2014; Díaz-García et al., 2020; Thompson and Donnelly, 2018). Within this study, recovery in restoration plots is characterized by (a) rapid loss of some pasture species after agricultural abandonment, and (b) gradual increase in the presence of forest species, with initial net gains in overall species richness due to the return of generalists. Nonetheless, all restoration treatments contained some range-restricted species, which suggests their potential to support regional biodiversity conservation and at least partially offset biotic homogenization driven by land use change. This is consistent with evidence that relatively small revegetated areas can offset the loss of
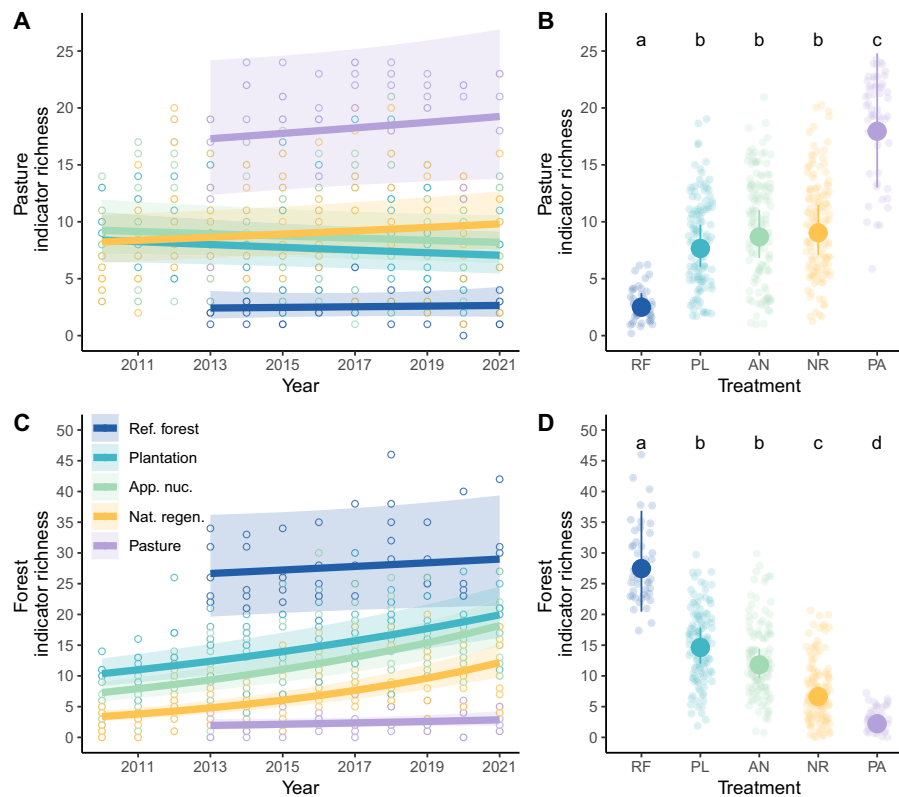
Fig. 5. Indicator species richness trends. (A) Observed pasture indicator species richness by treatment and year. Lines with ribbons represent model predictions and 95 % CI. There were no significant trends over time in any of the habitat types. (B) Observed pasture indicator richness by treatment. Large points represent treatment-level estimated marginal means and vertical lines represent 95 % CI. (C) Observed reference forest indicator species by treatment and year. Lines with ribbons represent model predictions and 95 % CI. Only restoration treatments have non-zero estimated slopes. (D) Observed reference forest indicator richness by treatment. Large points represent treatment-level estimated marginal means and vertical lines represent 95 % CI. In all panels, small points represent individual assemblages. Treatments labeled with different lowercase letters within panels (B) and (D) have significantly different estimated marginal means.

woodland birds at landscape scales (Bennett et al., 2022).

Natural regeneration bird assemblages showed less absolute recovery than those in planted treatments for many metrics, but that disparity is narrowing. Although natural regeneration started with the fewest species and least similar composition to reference forest, forest indicators increased at a higher rate over the 12 years assessed here, and it was the only restoration treatment with increasing similarity to reference forest over the full study period. This suggests that natural regeneration may be a cost-effective approach for restoration practitioners working on longer (i.e., multidecadal) time horizons, and the tradeoff between cost and habitat quality during the first decade of succession is an important consideration in choosing a restoration approach. Although natural regeneration harbored fewer forest indicators, generalist insectivore species that also consume fruit can be important for dispersing seeds and driving forward vegetation succession (Carlo and Morales, 2016).

While applied nucleation is considered an intermediate active restoration intervention, bird assemblages were generally similar to those in plantation plots, despite differences in canopy structure between these treatments (Holl et al., 2020; Zahawi, unpublished data). In contrast, previous short-term studies in Brazil comparing areas restored using nucleation techniques to traditional plantations and natural regeneration observed distinct assemblages associated with nucleation (de Carvalho Barros et al., 2022; Vogel et al., 2015), but this could be explained by the use of brush piles as a nucleation technique, rather than solely nucleation planting. Our results were consistent with patterns of natural seedling recruitment (Holl et al., 2017; Werden et al., 2022) and indicate that applied nucleation performs as well as tree plantations for recovering bird communities over the medium term, and that overall bird recovery may also translate to recovery of specific ecosystem

functions like seed dispersal (Reid et al., 2015). The costs of implementing applied nucleation in this study were lower than those of plantations (Holl et al., 2020), as they were in a nucleation experiment in Brazil where nucleation was up to 34 % less expensive than high-diversity plantations (Campanhã Bechara et al., 2021). However, conservation practitioners in Mexico have argued that the increased planning complexity of applied nucleation projects makes them more expensive (Ramírez-Soto et al., 2018).

Despite increased resemblance of restoration treatments to reference forest, a recovery gap remains after almost two decades, which is not surprising given that forest recovery is a long-term process. Multiple local and landscape-scale factors may limit further recovery. For example, some species require specific resources that can take years to develop, contributing to the slow saturating shape of recovery even in a best-case scenario (Sinclair et al., 2018). The vegetation composition of restoration plots in this study is following a trajectory toward remnant forests but still differs substantially (Werden et al., 2022). Moreover, even with diverse natural recruitment, most of the naturally recruiting trees are not yet reproductive and thus do not provide flower and fruit resources. Even in restoration projects with higher native planted diversity (e.g. >20 species), in which tree composition was more similar to reference forests, actively restored forests host fewer rainforest species than reference forests do (Catterall et al., 2012; Hariharan and Raman, 2021), suggesting that both vegetation composition and structure play a role in bird responses, though it is challenging to tease out the independent effects.

Whereas restoration practitioners have most direct control over local habitat characteristics, bird community recovery is constrained at multiple larger landscape-level spatial scales through the composition of regional species pools, colonization and extinction probabilities
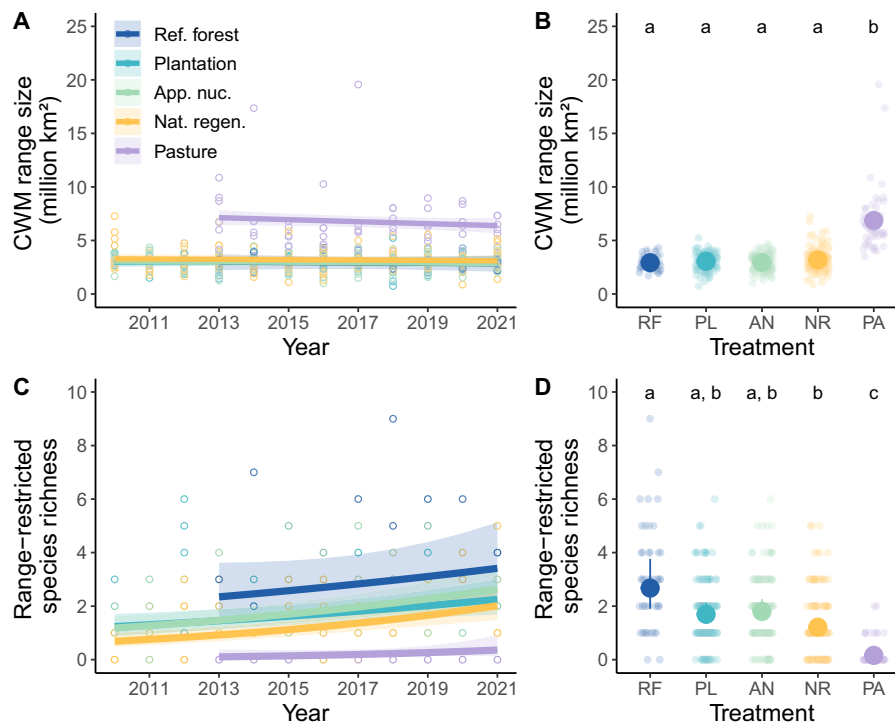
Fig. 6. Range size trends. (A) Community-weighted mean range size by treatment and year. Lines with ribbons represent model predictions and 95 % CI. (B) CWM range size by treatment. Large points represent treatment-level estimated marginal means and vertical lines represent 95 % CI. (C) Observed richness of range-restricted species by treatment and year. Lines with ribbons represent model predictions and 95 % CI. (D) Observed range-restricted species richness by treatment. Large points represent estimated marginal means and vertical lines represent 95 % CI. In all panels, small points represent individual annual assemblages. Different letter labels indicate significantly different ($p < 0.05$) estimated marginal means.

mediated by forest connectivity, and faunal selection of available habitat (Freeman et al., 2015; Mayhew et al., 2019; Reid et al., 2021; Reid et al., 2014). In the absence of adjacent forest, these restoration plots represent small habitat patches with intrinsic edge effects, two factors that limit understory insectivores (Lindell et al., 2007; Martensen et al., 2012). Edge effects also likely contribute to the persistence of some pasture species in restoration plots. Indeed, landscape tree cover and configuration in this study system influence use of restored habitats by large frugivores and other forest-dependent birds (Reid et al., 2021; San-José et al., 2022). Thus, in the absence of landscape-scale efforts to increase connectivity, some forest-restricted species are not expected to use restored plots with minimal nearby forest.

Long-term monitoring of reference systems at multiple sites was a key feature of this study. Importantly, the natural variability of tropical wet forest bird communities is high, such that for a pairwise community similarity index, a value of ~0.4 may be a realistic restoration target. The fact that we did not observe directional shifts in pasture or reference forest community metrics suggests that directional changes observed in restoration plots were due to local-scale change rather than regional dynamics. This is important because both tree and bird communities in remnant forests within agricultural landscapes are likely to experience ongoing and time-lagged effects of regional-scale forest loss, degradation, and fragmentation (Hendershot et al., 2020; Newmark et al., 2017; Rutt et al., 2019; Şekercioğlu et al., 2019). Even at relatively undisturbed sites, bird communities have experienced long-term shifts, possibly due to climate change (Freeman et al., 2018; Pollock et al., 2022; Stouffer et al., 2021).

Given the layout and size of treatment plots, we interpret our results with some caveats regarding spatial proximity and habitat use. First, while spillover effects were possible given that our three treatments were adjacent to each other, we still observed differences despite close spatial proximity; this suggests that our results represent lower-bound estimates of differences between treatments. Second, greater bird

detectability in pastures could have reduced the observed differences in species richness compared to restoration plots. Third, the size of restoration plots means that our observations reflect recovery patterns of habitat use by bird species, not recovery dynamics of populations, which is a common issue with assessing effects of restoration plots on vertebrates (Robinson, 2010). Even if some species only transited through the small restoration plots rather than using them as core habitat for foraging or reproduction, their presence shows promise for improving functional connectivity, which is key to preventing extirpations at larger scales (Newmark et al., 2017).

5. Conclusions

Passive and active restoration approaches can both be viable options for facilitating bird community recovery on degraded agricultural land in initial decades and may help counteract biotic homogenization. Although planting trees accelerated recovery relative to natural regeneration, a planting design with ~25 % of the planting intensity performed comparably to traditional uniformly-planted plots. Therefore, we strongly encourage restoration practitioners to (a) consider interventions that are intermediate between natural regeneration and intensive planting, (b) match their approach to specific desired outcomes and timeframes, and (c) evaluate progress using interim targets (Watts et al., 2020). Insights from outcomes of long-term, replicated, multi-treatment restoration experiments compared to the background variability in reference systems represent an invaluable guide for large-scale tree planting initiatives and for gauging faunal recovery trajectories in species-rich tropical ecosystems.

CRediT authorship contribution statement

Francis H. Joyce: Writing – review & editing, Writing – original draft, Formal analysis, Data curation, Conceptualization. **Juan Abel**

Rosales: Methodology. **Karen D. Holl:** Writing – review & editing, Supervision, Project administration, Funding acquisition. **Rakan A. Zahawi:** Funding acquisition, Supervision, Writing – review & editing. **An Bui:** Formal analysis, Visualization, Writing – review & editing. **J. Leighton Reid:** Writing – review & editing, Supervision, Project administration, Data curation, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data are available from Dryad repository https://doi.org/10.5061/dryad.k6djh9wfd.

Appendices. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2024.110593.

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