Title

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

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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. Over longer time horizons, however, the ecological return on investment from natural regeneration increases. Managers should monitor trends in forest-affiliated species 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.
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24 January 2024

Dear Dr. Xingfeng Si,

On behalf of myself and my co-authors, I am resubmitting Biological Conservation manuscript BIOCON-D-23-01226, which we have revised to address the thorough and constructive comments from reviewers. We feel that the manuscript is greatly improved.

We appreciate your considering the revised version of this manuscript and look forward to hearing from you soon.

Sincerely,

Francis H. Joyce

Francis H. Joyce (on behalf of all co-authors)

Dear Dr. Xingfeng Si,

We are resubmitting Biological Conservation manuscript BIOCON-D-23-01226, which we have revised to address the thorough and constructive comments from reviewers. Please see our individual responses below in italics. Note that for the purposes of double-blind review, the revised manuscript remains anonymized.

We appreciate your considering the revised version of this manuscript and look forward to hearing from you soon.

Sincerely,

Corresponding author

REVIEWER COMMENTS:

Reviewer #1

The article is well written, the questions, hypotheses and predictions are clear. The methods are adequate to answer the questions. My main concern is that there seems to be a lack of evidence (references) on the application, costs and ecological results the three restoration treatments assessed in the introduction and discussion, mainly for nucleation (plantation islands) since I believe it is a central strategy in their results and discussion. It seems to me that the authors take many assertions for granted. My suggestion is to add the necessary references.

For example, there are different meta-analyses that review the outcomes of nucleation (Boanares & de Azevedo, 2014 https://doi.org/10.1016/j.ncon.2014.09.002; De Oliveira-Bahia et al. 2023 https://doi.org/10.1111/rec.13932), studies that compare different indicators (some including birds) among plantations, nucleation an natural regeneration treatments (Corbin et al. 2016 https://doi.org/10.1890/15-0075; Bechara et al. 2015. https://doi.org/10.1007/s10531-016-1186-7; de Carvalho Barros et al. 2022 https://doi.org/10.1016/j.ecoleng.2022.106721; Vogel et al. 2015 https://doi.org/10.1177/194008291500800404), and costs among restoration treatments in different socio-economic contexts (Campanha Bechara et al. 2021 https://doi.org/10.1016/j.foreco.2021.119088; Ramírez-Soto et al. 2018).

In addition, I consider that more ecological information can be added in the discussion about the differences that were found in the metrics measured for bird communities among the restoration treatments, and and how your results behave with respect to other similar studies (https://doi.org/10.1177/194008291500800404, https://doi.org/10.1016/j.ecoleng.2022.106721).

We have added more references to the manuscript. Please see below for specifics.

I think also it is relevant to mention that this is one of the first studies where fauna is used as an indicator of success in plantation islands according the bibliographic review done by De Oliveira-Bahia et al. (2023; https://onlinelibrary.wiley.com/doi/abs/10.1111/rec.13932). And highlight the need to increase the use of this type of indicators of animal communities to have a broader overview of the ecological results of nucleation, in comparison with knowledge of the indicators that have been most used in the literature (i.e. richness, density and abundance of seedlings).

The scope of the systematic review by De Oliveira-Bahía was explicitly restricted to response variables related to plant establishment, and thus did not include studies where fauna were used as indicators of success in planted islands. Nonetheless, we agree that seedling richness and abundance are much more common metrics of restoration success compared to faunal metrics. We added the following text in the introduction:

"Most studies assessing nucleation have used seedling richness or density as metrics of restoration outcomes (de Oliveira Bahia et al., 2023), rather than fauna."

We also now cite de Carvalho Barros et al. 2022 and Vogel et al. 2015 as examples of multi-treatment experiments undertaken over shorter time scales (one to eight-years post-intervention).

Below are some specific observations:

Line 43 Please define nucleation as you did for traditional plantations and natural regeneration

We revised the text to include a definition of applied nucleation: "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 seeded in clusters within a larger area*) *can accelerate vegetation recovery at lower cost while creating more structural complexity (Holl et al., 2020)."*

Line 80 – 87 In the introduction they propose that restoration techniques can be approached from a continuum of intervention, where plantations and nucleation can have different ecological benefits in habitat recovery. Why do you mention in your research questions and predictions that you expect similarities between plantations and nucleation?

We consider that the three research questions as phrased did not actually pre-suppose similarity between plantations and nucleation. Likewise, our predictions did not explicitly expect similarity between plantations and nucleation, but rather that "recovery of richness and composition would be greater in planted treatments than in natural regeneration." As described, this expectation is based on earlier bird research within this study system (Reid et al. 2014), which lacked a temporal component, as well as broader research indicating that the increased structure resulting from planting native trees facilitates recovery. Some degree of similarity between planted treatments is expected given that they were planted with the same small number of tree species. We have added some text to further explain this expectation:

"Based on an early comparison 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 similar resources to both treatments."

Line 114 – 117 Plantations and nucleation were carried out with only four plant species. I consider that this species richness is very low to represent the reference ecosystem. Was the purpose of these restoration strategies to recover only the structure of the vegetation, but not the species composition? What effect might this have on the birds' response? It would be interesting to add information to the discussion on the response of birds in restoration projects where more diverse plant assemblages were considered.

The reviewer is correct that four plant species do not represent the reference ecosystem. The initial goal of the restoration experiment was largely to test how different planting designs of a small number of species would facilitate the natural recruitment of trees and in turn forest recovery in this system (Zahawi et al., 2013). Within this experiment, any recovery of vegetation composition was expected to result from natural recruitment over time, rather than be achieved directly by the initial intervention (tree planting). Studies of natural recruitment within the restoration treatments documented at least 155 species naturally recruiting within each restoration treatment, which is lower than the richness in reference forests but still considerable. Some of the non-planted, naturally-recruiting species have reached the tree size class (> 10 cm dbh).

We added a sentence at the end of Section 2.2 (Restoration experimental design) emphasizing that although few species were planted, many tree species have naturally recruited:

"At least 155 tree species had naturally recruited in each restoration treatment by 2022, despite the low number of planted species (or total absence of planting in natural regeneration); some of these recruits had reached the tree (> 10 cm DBH) size class (Schubert et al., submitted)."

We also added the following sentence to the paragraph on recovery gaps in the discussion:

"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."

We agree that it would be very interesting to know how planting design and species composition or richness interact but given the scale of our experiment and replication at multiple sites, it simply was not feasible to manipulate both spatial and composition patterns simultaneously in planted treatments. Since we did not manipulate species composition, we feel that any further discussion of the effect of planted tree composition or richness on bird communities would go beyond the scope of the study.

Lines 139 – 141 Please mention if the number and length of the traits was similar between all treatments. The detectability of birds may vary in open spaces (grasslands), and in spaces in succession processes where there is a dense undergrowth (such as in plots in natural regeneration). How did you check that the accessibility provided by trails and the detectability of birds will not affect your results?

Trails within restoration plots existed to provide access to permanent vegetation sampling plots distributed throughout each restoration plot. In reference forest and pasture plots the trail configuration as approximately linear and 50 m long. Thus, the total trail length within each survey plot was similar, although the configuration of trails varied. The fact that the person surveying birds could detect unseen birds singing/calling in close proximity lessened the potential effects of dense undergrowth. We added the following sentence: "Each plot had a trail of similar length that provided access to the plot interior, although trail configuration varied."

Line 142 The auditory records were treated in the same way as the visual ones, that is, how could you know that the song of a species corresponded to an individual that was perching or foraging inside the plots?

We recognize that there is some uncertainty associated with the auditory records. Nonetheless, we consider that the exclusion of this information would weaken our characterization of bird assemblages. It is worth noting that some unseen, heard-only records were considered flyovers and excluded when the birds (e.g. parrots or parakeets) were vocalizing in flight above or within the plot. Juan Abel Rosales, who conducted all bird observations, was involved in the initial plot establishment and has collected various types of data year-round in these plots for nearly 20 years and knows exactly where the plot boundaries are. We added the following sentence to the methods:

"The observer used his extensive field experience in our research plots to conservatively judge whether heard-only birds were calling from within the plot."

Line 249. It is not very clear to what sample coverage you made the comparisons of expected richness. My concern that sample coverage was greater in the pastures is correct. It is necessary to add information to the discussion about the effect this could have on your results.

We did not compare estimated richness at a standardized sample coverage value. We used the asymptotic estimate (in other words, the AsyEst$Estimator value from the iNEXT() output. This will also be transparent to readers because the analysis code will be archived with the data.

Sample coverage was higher in pastures but not statistically different among the other four habitat types. Since pastures were generally already distinct from the other habitat types, this is unlikely to confound our main conclusions about assemblage recovery. The greater sample coverage in pastures may have increased apparent similarity of pasture species richness to the restoration treatments (Figure 3), but would not have confounded comparisons among restoration treatments.

We added the following sentence to the paragraph in the discussion regarding study caveats:

"Second, greater bird detectability in pastures could have reduced the observed differences in species richness compared to restoration plots."

Line 257 Your results suggest that the bird species composition of the three restoration treatments is more similar to each other than to the reference ecosystems. I assume that due to the low number of species used, the species composition of the areas under restoration is also different with respect to the forest. Could this situation be related to the fact that the restoration strategies also presented a different species composition than the forest? I think it would be good to add information in the discussion on whether birds are responding only to the recovery of habitat structure due to the lack of resources that a diverse forest can provide.

We added the following sentence about the potential role of vegetation composition on bird assemblage responses, following an existing sentence about resources limiting recovery in the discussion:

"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."

Our existing data do not allow us to conclude further about the relative influence of vegetation physical structure vs. the resources provided.

Line 309 The recovery of bird assemblages was partially, did not reach the references forests. Furthermore, this sentence suggests that recovery was the same in all treatments.

We have revised this sentence with more nuance, to emphasize that the recovery of bird assemblages using restoration plots was partial: "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."

In addition, existing text in the fourth paragraph of the discussion was clear that recovery was partial "a recovery gap remains after almost two decades."

We disagree that we implied that recovery was the same in all treatments, and the differences between treatments are clearly discussed in the subsequent paragraphs.

Line 311 At least for amphibians, ants, and dung beetles there is evidence (https://doi.org/10.1111/oik.06252 https://doi.org/10.1016/j.biocon.2013.11.023 https://doi.org/10.1643/CH-17-654 https://doi.org/10.1371/journal.pone.0242020) on the different responses that species of the same biological group can present to forest restoration depending on their degree of specificity to the habitat. I consider it important to strengthen this sentence with some references.

Thank you for this suggestion. We have added references to this point about recovery of habitat specialists:

"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)."

Line 332 – 336 I think that the discussion between these two strategies is scarce. Especially for the ecological and economics results of nucleation, since you later recommend it in the conclusions.

We have added discussion of the ecological outcomes of this study compared to previous studies:

"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."

We agree that further comparison to similar studies would be desirable. To date, however, few studies have compared bird community responses in applied nucleation and other restoration approaches and those studies have all been short-term.

We also contextualized the potential for cost-savings from applied nucleation: "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). In contrast, conservation practitioners in Mexico have argued that the increased planning complexity of applied nucleation projects makes them more expensive (Ramírez-Soto et al., 2018)."

Reviewer 2

– the 'longer time horizons' point is unclear – needs more context if including in the abstract

We revised this sentence to be more specific and have a simpler structure:

"However, the ecological return on investment from natural regeneration increases over decadal time horizons."

Note that the abstract is currently at the word limit (250 words).

Intro

L49 – can you briefly report the findings of the studies that are based on chronosequence, or those that have showed successful recovery, to set the scene for what you might expect from this (more robust) study?

We added the following sentence: "Meta-analyses comparing bird assemblages in paired secondary and primary forest sites throughout the tropics show that forest specialist species *increase over time (Acevedo‐ Charry and Aide, 2019; Sayer et al., 2017), but disparate data points are unlikely to represent realistic trajectories, and this pattern bears further testing in multi-treatment experiments."*

L63 – 'forest-affiliated species also tend to include' is an odd phrasing for this sentence. Do you mean that "forest-affiliated species tend to have more specialized habitat requirements, and are more likely to be range restricted" ? Talking about the species, rather than 'forest-affiliated species' as a unit/group.

Thank you for this suggestion. We have adopted the suggested phrasing: "Forest-affiliated species also tend to have more specialized habitat requirements and are more likely to be range-restricted."

L67 – missing word 'species' after 'disturbance-tolerant'

Done.

L80 and L72 – can you briefly state here the timespan over which your study collected data given the statement that this is necessary?

We revised the text from "Here, we report on decadal avian assemblage recovery" to be more explicit about the timespan: "Here, we report on avian assemblage recovery over 12 years…"

L111 – use either passive voice or active, not both!

We revised the text to passive voice: "whereas applied nucleation plots were planted with six nuclei of three sizes."

L126 – applied nucleation plots were, rather than are? Other text is past tense.

Revised as suggested.

L127 – was canopy height more variable in applied nucleation plots than in plantation plots? ~15m vs variable height vs relatively short (for natural regen) is difficult to compare. Can you clarify?

We revised the text to provide quantitative descriptions of canopy height for each treatment:

"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."

Methods

L147 – it's not clear what aspect of the data were missing these cases, and it's not completely clear whether all plots (e.g. all restoration treatments, and their pasture and forest reference plots) were surveyed on the same days. Does this mean no surveys were done at all on some days (which doesn't make much sense), or that on some days, one or more of the survey plots was not completed? 'relatively evenly' is a qualitative statement – can you be more specific, or represent patterns of missing data somehow?

We have clarified these important points. First, we added text to explain that plots within the same site were surveyed on the same day. Then, we clarify that data were entirely missing for nineteen plot surveys and describe the pattern of missing surveys in more detail. We do not know for each one if they were not conducted or more likely that the data sheets were misplaced given the timespan of the study. In checking these numbers, we also corrected the total number of completed surveys (1466) and missing surveys (19).

"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 hours 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."

L193-196 – this isn't clear: so community composition of restoration communities was not just compared to the nearest forest community, but to each of the five forest communities separately? And for some reason also compared each forest community to the other forest communities? This latter clause works better alongside the following sentence about beta diversity.

This interpretation is correct: the community composition of assemblages in restored plots (and pastures) was compared to each of the five forest communities separately and then averaged. Each forest community was compared to the other forest communities (and then averaged), as well. We have revised the text to clarify and better explain this approach:

"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 to 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)."

L162 – so all models were fitted as mixed effects models, but with different error distributions? If so, please standardise reporting your model structure and error structure throughout this section e.g. at L199 you report fitted a linear mixed model but don't state which error structure you used, aside from saying you didn't use a beta distribution. Are we to assume this had a Gaussian error structure? Please be clear. A table of model structures in the SOM would probably clarify this rapidly.

We have added a table of model structures to the supplementary materials (Table S2). We renumbered the other supplementary tables and their in-text references accordingly. We also revised this section of text for clarity:

"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)."

Yes, our linear mixed model assumed a Gaussian error structure and we have revised the text to be explicit: "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."

L179 – similarly, was this species richness model also fitted as a mixed model?

Correct. We revised the text to explicitly indicate this: "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."

Figure 1 - please make the survey location in the inset map clearer. Showing the survey sites instead of/also in relation to a DEM of elevation may be more useful than the satellite imagery, as the plot points obscure imagery at the sampling points in any case. Can the 'site' IDs also be shown on this map i.e. a 'site number' used to link reference forests/pastures with restoration blocks, to clearly show which reference forests/pastures were used in each case?

We have reduced the extent of the inset map in order to make the study area rectangle more clear. We chose to keep the satellite imagery as the base map, because the elevation for most sites is similar, and elevation values are already listed in the supplementary materials (Table S1). Although the points obscure the imagery immediately below, we feel that showing forest cover surrounding each restoration sites is valuable context. We felt that including 'site numbers' would clutter the map excessively. Table S1 contains site codes linking reference forests/pastures with restoration blocks (described below), and individual plot locations will be available in the archived data on Dryad.

L202 – is assessing habitat association and indicator species for the restoration treatments a little circular – aren't you mainly aiming to assess the degree of return to the forest reference state – what is the meaning of an indicator species for a restoration plot that's in the process of regrowth/regeneration towards a reference forest baseline? This may need further explanation. In the results you don't seem to report this analysis – Figure 2 is just based on presence/absence – so I'm not clear why the indicator analysis for the restoration plots was done?

The original rationale for checking for indicator species in restoration treatments was that restoration treatments can represent novel habitats that could host species that specialize on successional or other types of habitats, and potentially benefit those species neither associated with remnant forest nor pasture. They could also potentially indicate "alternative trajectories" for bird assemblages toward a novel state. Given that there were only two restoration treatment indicator species (one in plantation and one in natural regeneration), we had briefly mentioned them in the habitat association section of the results, but not included them in any figures or as response variables in models. We agree that the analysis of indicator species is not a central result and therefore we have removed it from both the methods and the results.

L214 – again, a table of module structures (word equations) would help greatly to understand the various models fitted to answer these different questions.

As noted previously, we added Table S2 listing model structures. We also edited this sentence to clarify that we fit two separate GLMMs for indicator richness (one for pasture indicators and one for forest indicators).

Table S1 – it's not clear which reference forests and pastures were linked with which site in the analyses – this could be shown here with a 'site number' column, or similar

The existing "Site code" column indicates which survey plots were considered to be in the same site/block (i.e. for inclusion as a random effect in GLMMs). For example, reference forests OM, LL, and JG were paired with the restoration plots in the corresponding site code, and pastures HB and SG were considered paired with restoration plots at those sites. The remaining pasture and reference forest survey plots were distant enough (>450 m) from restoration plots that they were not considered linked to any particular restoration block.

Results

Excellent to see Appendix 1 with full species list included, and that data and code will be made available on Dryad/GitHub (this would be very valuable for future studies of faunal recovery and restoration trajectories elsewhere).

Throughout the results, I strongly suggest reporting the results of the statistical models in the main text – not referring the reader to 12 different supplementary tables. This could be inline, or you could include a single table showing all model results, with word equations for the models, and then the estimates (effect size) and significance for each predictor, in each case. Currently, it is hard to follow. Alternatively, you could show fitted (predicted) estimates for each treatment effect across all years in a second panel to the figures, which would ease interpretation e.g. bring in the results presented in Fig S1 to the main text and link to the time series figure using the same colours.

*We added a table (S2) listing the model structure for all models, as previously suggested. We chose to show model results graphically (i.e. fitted/predicted estimates) for ease of interpretation, because the number of coefficients (time + 5 habitat types + 5 habitat type*time interaction terms) would make a table unwieldy. This involved extensive revision to Figures 3, 4, 5, and 6. Accordingly, we also removed supplementary figures S1 (richness marginal means) and S4 (marginal means of similarity to reference forest).*

For completeness we still present full model results in supplementary tables.

Figure 3 – I'm not completely clear whether the differences between treatments signified by the letters are the result of a model fitted for the entire dataset for all time, and/or whether differences were assessed within each year? This should be clarified in the figure legend. The year 2018 stands out as an example where differences between reference forest and the restoration treatments were stronger – why was this, and is it worth assessing these differences year by year? As above – suggest adding a second panel showing estimates from the model for the overall effect across all years and/or the interaction, with significance highlighted.

We extensively revised Figure 3 to illustrate model estimates. Panel A shows model predictions over time. Panel B shows estimated marginal means with a compact letter display (previously in the legend) to show significant differences among treatment means.

Given that the goal was to assess the effect of time on species richness, year was included as a continuous predictor, not as a categorical predictor that would yield year by year comparisons for each of the 12 years. We are unsure of the ecological explanation for the larger differences in reference forest richness in 2018, but note that in addition to having higher mean species richness, reference forests also had higher variance. This is also apparent in the revised version of the figure, which shows assemblages as individual points.

Figure 4 – Fig 4a is very powerful and an excellent and interesting figure. Please add some further explanation of the forest-forest comparison in similar to the caption, otherwise this is rather confusing.

We interpreted this comment as "please add some further explanation of the forest-forest comparison [similar to that in the main text] to the caption."

We extensively revised Figure 4 and now include model predictions for similarity to reference forest (panel B: time series, panel C: treatment-level estimated marginal means). In the caption we include text on the interpretation of the forest-forest comparison as representing spatial beta diversity.

L245 – what i*s an "Active pasture plot" ? typo?*

“Active pasture plot” referred to the fact that the pasture survey plots were in actively grazed cattle pastures (i.e. not abandoned pastures, which is an important distinction). However, for clarity and brevity we deleted “active” here, since the pastures were described in the methods section.

Figure 6/L301 – can you represent model results over all years on this figure?

We revised Figure 6 to show model results. Since we had previously not presented model results (i.e. significance) in the text of the results, we do so now. We also now include the model details in Table S2 and in section 2.8.

Table S2 – missing word in caption “There were significant (alpha = 0.05)” – significant what?

Note that this is now in Table S3. We revised this sentence: “The main effect of habitat type was significant (alpha = 0.05).”

In all supplementary results, I would strongly suggest using a word to describe the treatments in all supplementary tables and figures, rather than an acronym. Acronyms really obscure understanding in all the supplementary material.

Throughout the supplementary results we now refer to habitat types (treatments) using words rather than acronyms.

Figure S3 – the yellow points were almost invisible on my screen – suggest increasing the opacity, or switching the symbols so the small crosses are used for one of the treatments with a darker colour.

We increased the symbol opacity in Figure S3 to improve visibility.

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

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. ~~Over longer time horizons, however~~However, the ecological return on investment from natural regeneration increases~~.~~ over a couple of decades. Managers should monitor trends in forest-affiliated~~ species~~ 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.

Keywords

Applied nucleation, avian communities, Costa Rica, habitat recovery, natural regeneration, tree plantation

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, can accelerate vegetation recovery at lower cost while creating more structural complexity (Holl et al., 2020)~~(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 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). 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, which may not reflect longer-term trajectories. 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 include more specialized habitat requirements and include range-restricted species. 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 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)~~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), 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 over time (Acevedo- Charry and Aide, 2019; Sayer et al., 2017), but disparate data points are unlikely to represent realistic trajectories, and this pattern bears further testing in multi-treatment experiments. 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; Şekercioḡlu 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 ~~decadal~~ 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 early ’snapshot’ 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. 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).~~

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 and Grenke, 1971)~~(Holdridge et al., 1971). Site elevation ranges from 1080-1430 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 1947-1980 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 ~~in the~~ applied nucleation ~~treatment we~~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), 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). 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 are characterized by high overall canopy cover of variable height. By 2019, most natural regeneration plots had patchy, relatively short canopy cover surrounded by dense exotic pasture grass cover, although some had greater tree and shrub cover.~~

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

2.3 Bird data collection

From 2010-2021 (12 years), we surveyed birds in all restoration plots (n = 33 plots). Between 2013-2021 (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 ~~[(**REDACTED**)]~~(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 05:50-09:00 h in mild weather, including light fog or mist but not high wind or rain. ~~The~~Plots within the same site were surveyed on the same day, and the order in which ~~restoration~~ treatments were surveyed within a site was varied to avoid systematic bias in survey start time.

The resulting data set includes ~~1467~~1466 surveys representing 489 hours of sampling effort. ~~Data for twenty~~Nineteen plot surveys (1.3%) were missing; pasture and ~~spread relatively evenly across treatments~~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)~~(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 ~~separate~~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) or linear mixed effect models using *lme4* v1.1.30 (Bates et al., 2015) for each response variable.~~(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.

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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 negative binomial error distribution with a log link function because a Poisson model had overdispersed residuals. We modeled sample coverage (bounded 0-1) using beta-distributed residuals with~~(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)~~(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)~~(De Cáceres et al., 2019). To ~~assess whether~~quantify the degree to which bird assemblages ~~using~~in restoration plots ~~were approaching~~and pastures approached those of reference forest~~ while taking into account the spatial and temporal variability of reference forests, we also~~, we calculated the mean similarity (1- dissimilarity) of each annual ~~community~~assemblage to each of the reference forest ~~communities for~~assemblages within each of the last nine years of the data set, when reference forests were surveyed (2013-2021; n = 5 reference forest ~~communities for comparison to each restoration and pasture~~assemblages). We compared each plot~~; n = 4 communities for forest-to-forest comparisons).~~ 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)~~(Anderson et al., 2011), and this natural variability constrains the average similarity to reference forest attainable by restoration treatments ~~(Gerwing and Hawkes, 2021)~~(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)~~("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)~~(following Hariharan and Raman, 2021). ~~To first explore associations between bird species and the five habitat types, we identified indicator species based on the full data set. Second, to~~To assess temporal trends in the richness of pasture and forest affiliated birds in restoration treatments, 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)~~(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

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assemblage “commonness” and as a metric of biotic homogenization ~~(Godet et al., 2015)~~(Godet et al., 2015). We also used the observed richness of range-restricted species (range size ≤50,000 km^2), which is commonly used as a metric of endemism ~~(Ocampo-Peñuela et al., 2016).~~(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. ~~3~~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. ~~Active pasture~~Pasture plots were not statistically different from natural regeneration (~~Table S2~~Fig 3B, Table S3, ~~Fig. S1~~Table S4). Predicted species richness increased over time only in restoration plots (Fig. 3A, Table ~~S2~~S3), with ~~the steepest increase in applied nucleation, intermediate increase in natural regeneration, and only a marginal increase in the plantation treatment~~similar slopes among treatments (Table ~~S4~~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 ~~higher~~greater in pasture plots (Fig. ~~S2~~S1, Table ~~S5~~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.

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. ~~S3~~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. ~~S4~~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. ~~4~~4A, Fig. ~~S4~~4C) and did not show a significant time effect (Fig. 4B, Table ~~S8~~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 0.33-0.60 (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. ~~S3~~S2).

3.3 Habitat association

Indicator species analysis ~~with all treatments~~ identified ~~104~~120 species (~~37~~42%) that were significantly associated with ~~a particular habitat type (~~either pasture (39) or reference forest~~: 63; pasture: 39; plantation: 1; natural regeneration: 1; p <0.05).~~ (89) (Appendix 2). The species most strongly associated with reference forest were *Henicorhina leucosticta*, ~~*Corapipo altera*~~*Lophotriccus pileatus, Catharus aurantiirostris, Pachysylvia decurtata*, *Arremon aurantiirostris*, and ~~*Dysithamnus mentalis*.~~*Myioborus miniatus*. Widespread open-country birds such as *Troglodytes aedon*, *Tiaris olivaceus*, *Sporophila corvina*, ~~*Zonotrichia capensis*~~*Thraupis episcopus*, and *Tyrannus melancholicus* were associated with pasture sites. ~~The indicator species for plantation was *Pachyramphys polychopterus*, a species typically found in wooded areas but generally not mature forest. The natural regeneration indicator species was *Laterallus albigularis*, a rail typically found in areas with dense grass. When we only considered reference forest and pasture surveys, we identified similar sets of reference forest (81) and pasture (39) indicator species (Appendix 2). These included some species that had a clear habitat preference when only considering pasture and reference forest but were also commonly found in restoration treatments and thus were not identified as indicators in the previous analysis. For example, *Thraupis episcopus* was a generalist pasture indicator, whereas *Catharus aurantiirostris* was a generalist forest indicator.~~

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 ~~S9~~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. ~~5B~~5C-D, Tables ~~S10-S12~~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. ~~6B~~6C-D).

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4. Discussion

~~Bird assemblages in all restoration treatments have recovered 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. 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 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. 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). Results are consistent with patterns of natural seedling recruitment in these plots 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).~~

~~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). 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 mediated by forest connectivity, and faunal selection of available habitat (Freeman et al., 2015; Mayhew et al., 2019; Reid et al., 2021, 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~~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 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 mediated by forest connectivity, and faunal selection of available habitat (Freeman et al., 2015; Mayhew et al., 2019; Reid et al., 2021, 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)~~(Newmark et al., 2017).

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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 ~~an ~80% reduction in~~~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)~~(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.

Data availability statement

Data and code are available in a GitHub repository and will be archived on Dryad prior to publication.

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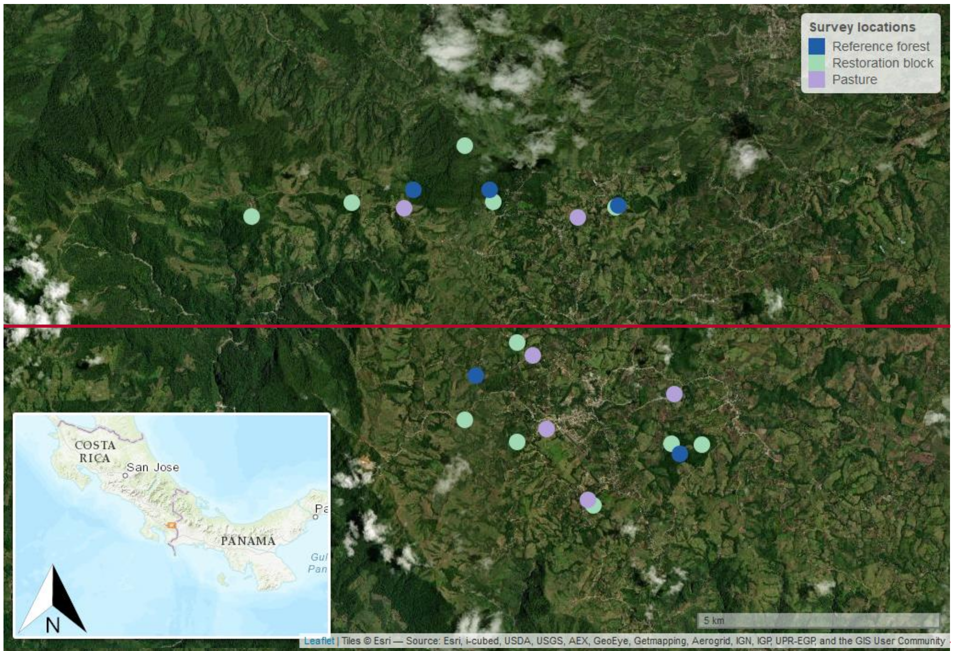

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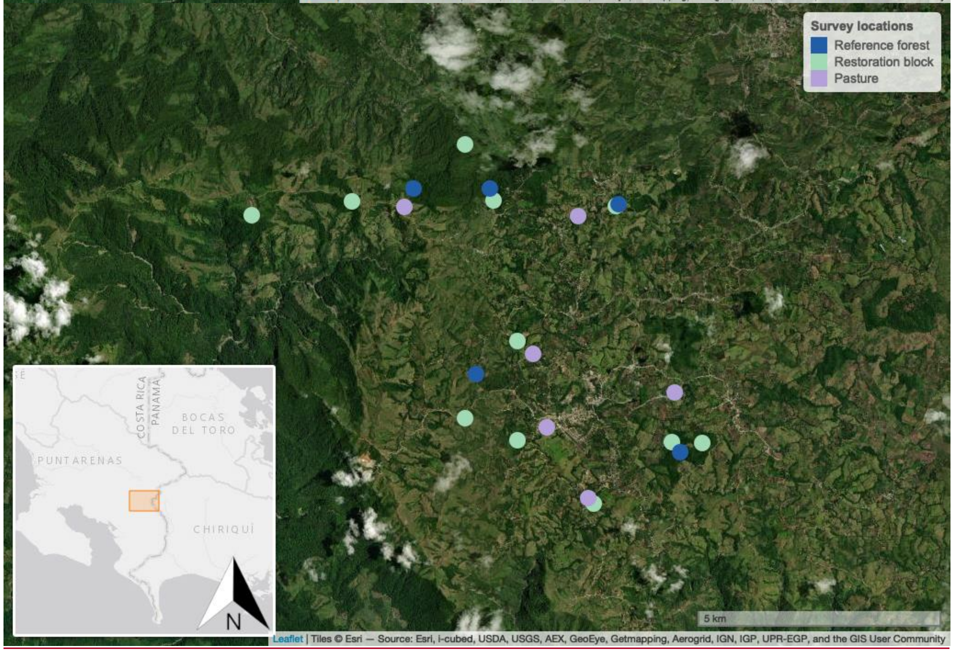

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Figure 1. Bird survey locations in Coto Brus, southern Costa Rica. Each restoration block contains one plot of each restoration treatment (plantation, applied nucleation, and natural regeneration).

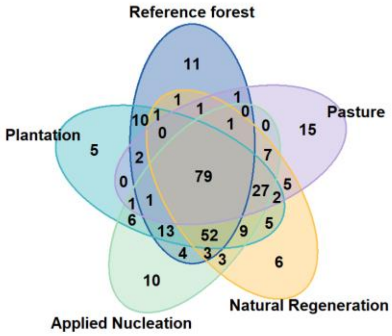
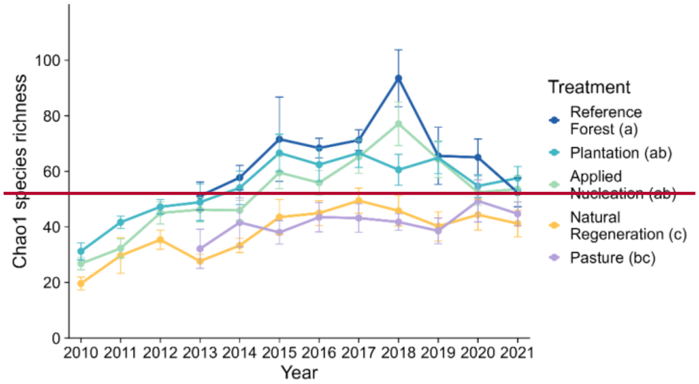


Figure 2. Venn diagram of bird species detected in each habitat type over the study period (9 years for pastures and reference forests, 12 years for restoration plots; n = 281 species total).



~~**Figure 3.** Plot-level species richness (Chao1 estimator) grouped by treatment (mean ± SE).~~

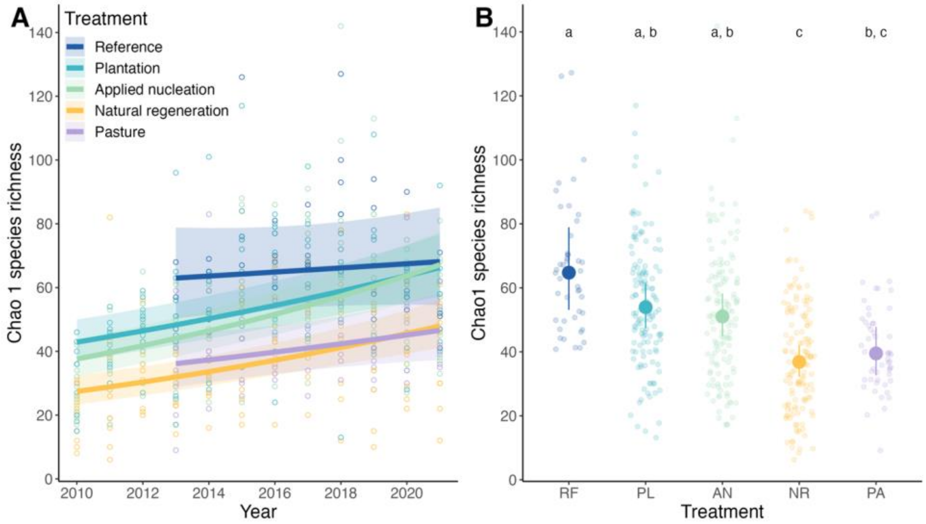
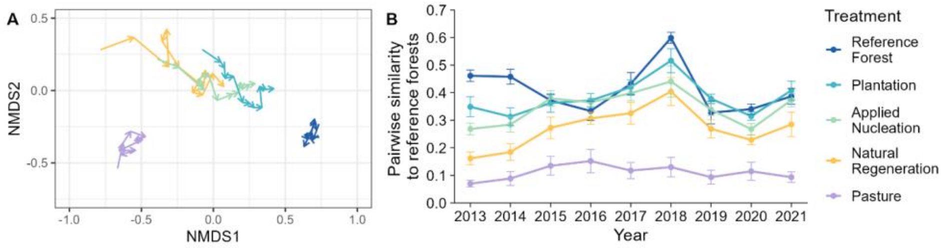


Figure 3. Species richness (Chao1 estimator) varied over time and among habitat types. **(A)** Model predictions (lines with 95% confidence interval bands) show positive slopes for applied nucleation and natural regeneration and marginally significant positive slopes for plantation. Time since restoration ranges from 4-6 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 ~~legend label letters in parentheses~~letter labels indicate significantly different (p < 0.05) estimated marginal ~~mean richness~~means (over all years). In both panels, small circles represent individual annual assemblages.



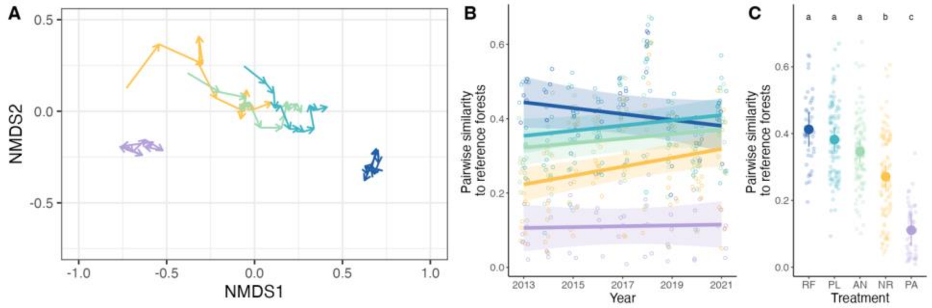
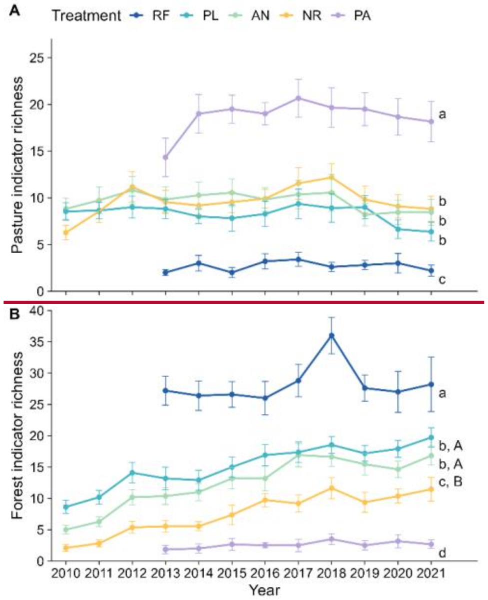


Figure 4. Community trajectories and similarity to reference forests. **(A)** Community trajectories in NMDS ordination space, based on a Morisita-Horn dissimilarity matrix of annual communities. Points represent the annual average (centroid) for each treatment. Arrows represent compositional change between consecutive years (reference forest and pasture: 8 segments, 2013-2021; restoration treatments: 11 segments, 2010-2021). **(B)** ~~Mean pairwise~~Pairwise community similarity to all reference forest communities within the same ~~year~~years (2013-2021) for each habitat type~~ (2013-2021). Points~~. Lines and ribbons represent ~~the treatment means (± SE) of plot-level mean pairwise~~model predictions and 95% CI. For forest-forest comparisons~~ to each reference forest~~, 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 90% 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).



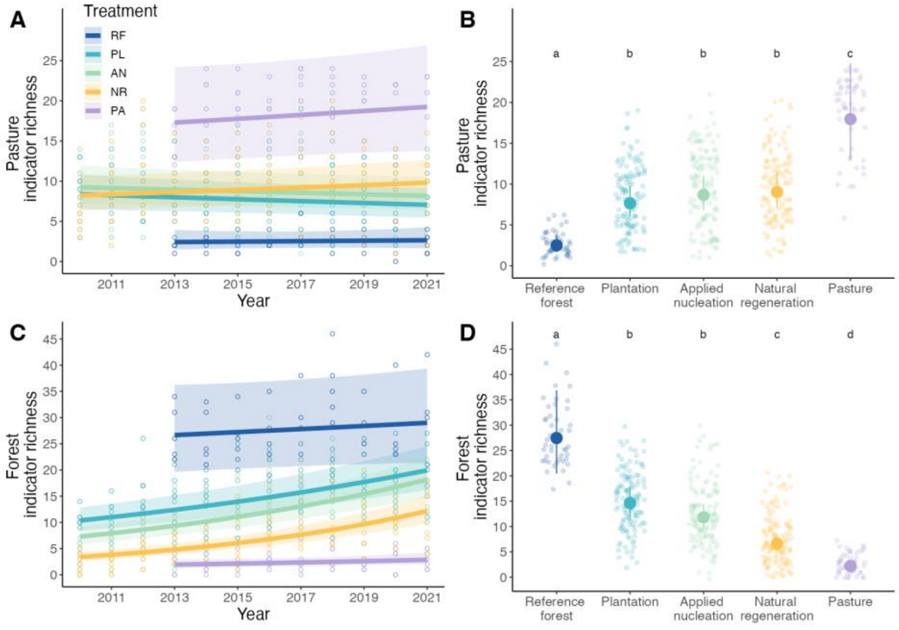


Figure 5. ~~Temporal~~ Indicator species richness trends~~ for~~. **(A)** Observed pasture indicator species richness ~~(mean ± SE) for (A) pasture and~~by treatment and year. Lines with ribbons represent

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 ~~in each habitat type.~~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 ~~lower-case~~lowercase letters within panels (B) and (D) have significantly different estimated marginal means.~~ Treatments labeled in panel B with upper-case letters have non-zero estimated slopes and different upper-case letters denote significantly different slopes.~~

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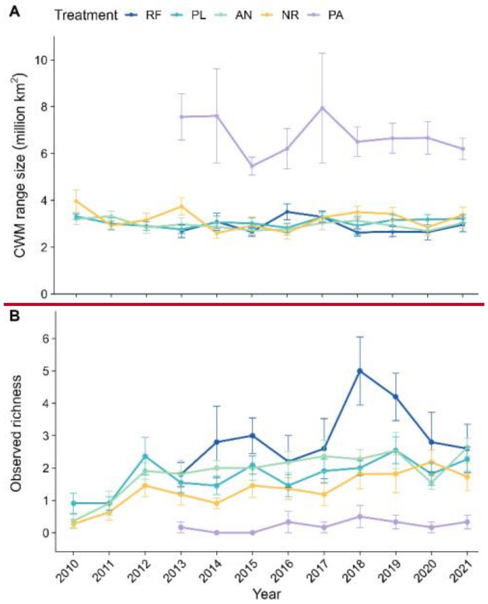
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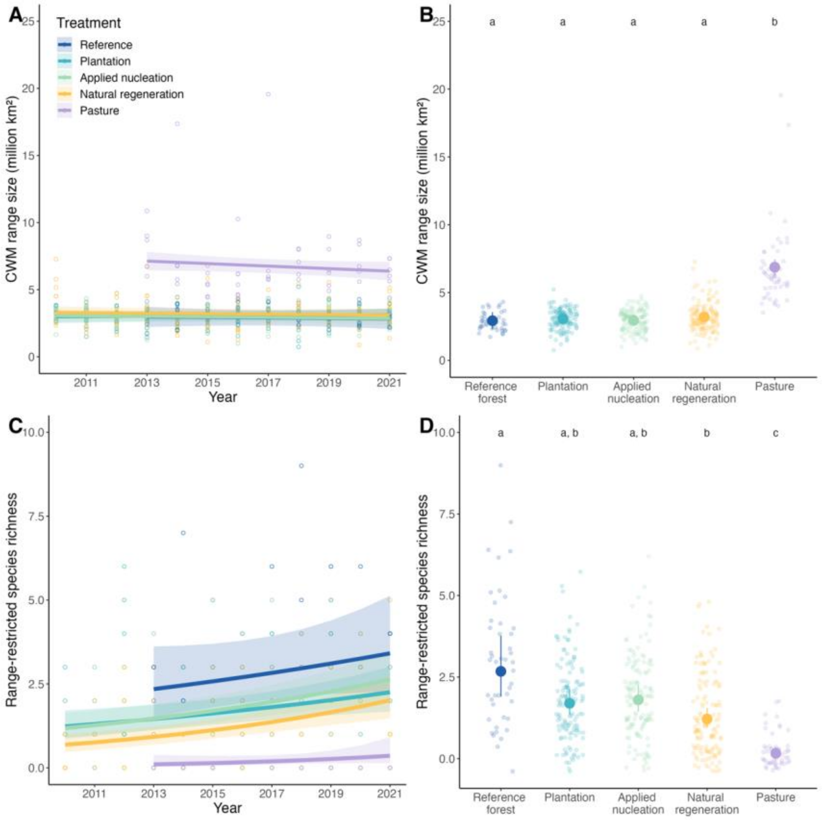

Figure 6. Range size trends. **(A)** Community-weighted mean range size by treatment and year ~~(mean CWM ± SE).~~. Lines with ribbons represent model predictions and 95% CI. **(B)** ~~Observed~~ CWM range size by treatment. Large points represent treatment-level estimated marginal means and vertical lines represent 95% CI. **(C)** Observed richness of range-restricted species ~~richness (mean ± SE).~~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.

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

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.

Keywords

Applied nucleation, avian communities, Costa Rica, habitat recovery, natural regeneration, tree plantation

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 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), 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 over time (Acevedo- Charry and Aide, 2019; Sayer et al., 2017), but disparate data points are unlikely to represent realistic trajectories, and this pattern bears further testing in multi-treatment experiments. 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; Şekercioḡlu 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 1080-1430 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 1947-1980 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 absence of planting in natural regeneration); some of these recruits had reached the tree (> 10 cm DBH) size class (Schubert et al., submitted).

2.3 Bird data collection

From 2010-2021 (12 years), we surveyed birds in all restoration plots (n = 33 plots). Between 2013-2021 (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 05:50-09:00 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 hours 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 $\alpha = 0.05$ 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, 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 km^2), 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.

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 0.33-0.60 (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).

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 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 mediated by forest connectivity, and faunal selection of available habitat (Freeman et al., 2015; Mayhew et al., 2019; Reid et al., 2021, 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.

Data availability statement

Data and code are available in a GitHub repository and will be archived on Dryad prior to publication.

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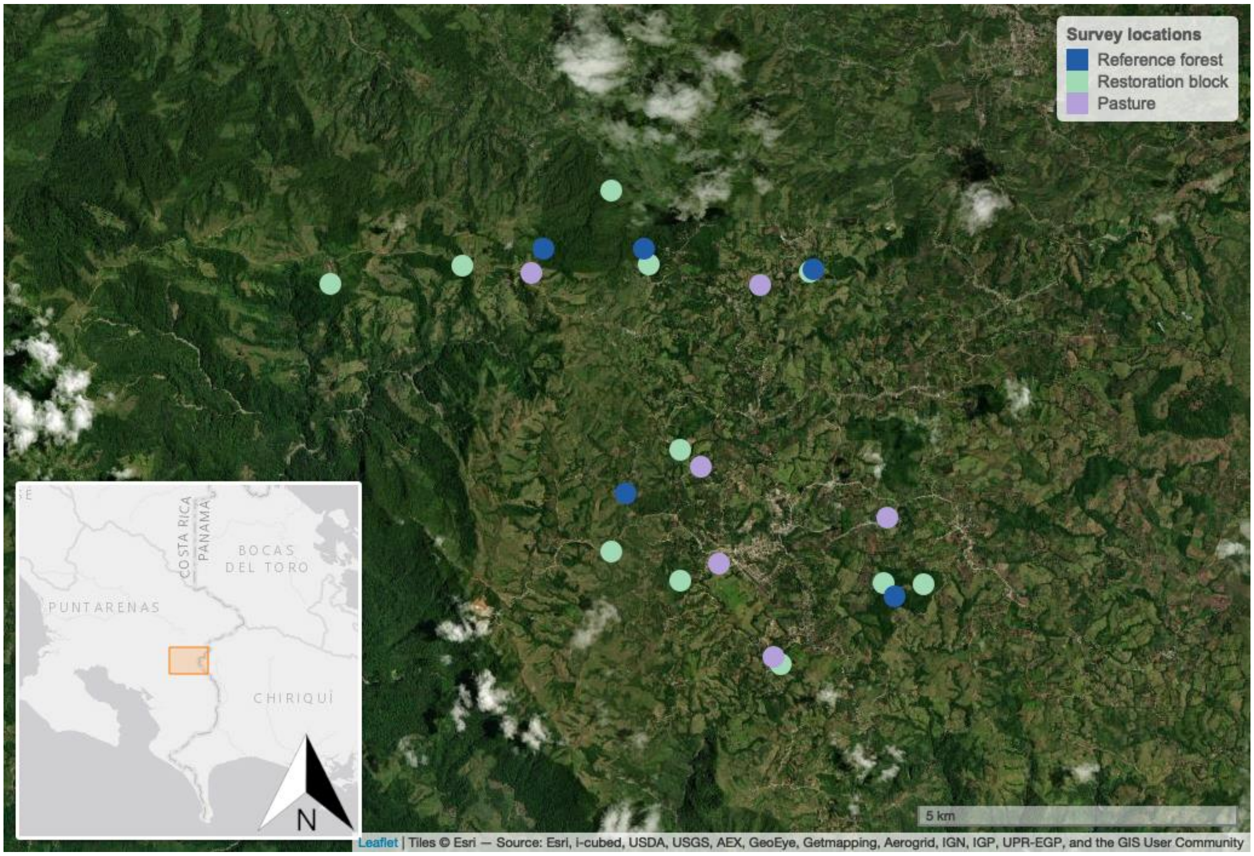

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Figure 1. Bird survey locations in Coto Brus, southern Costa Rica. Each restoration block contains one plot of each restoration treatment (plantation, applied nucleation, and natural regeneration).

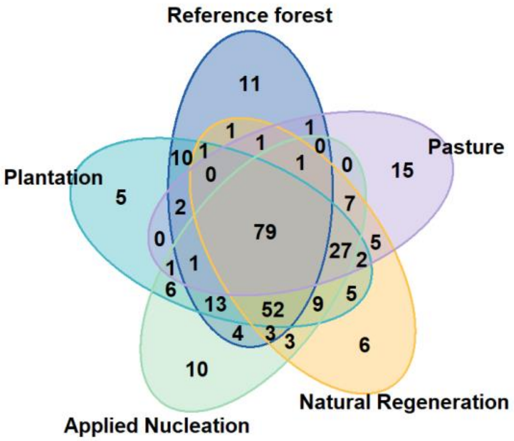

Figure 2. Venn diagram of bird species detected in each habitat type over the study period (9 years for pastures and reference forests, 12 years for restoration plots; n = 281 species total).

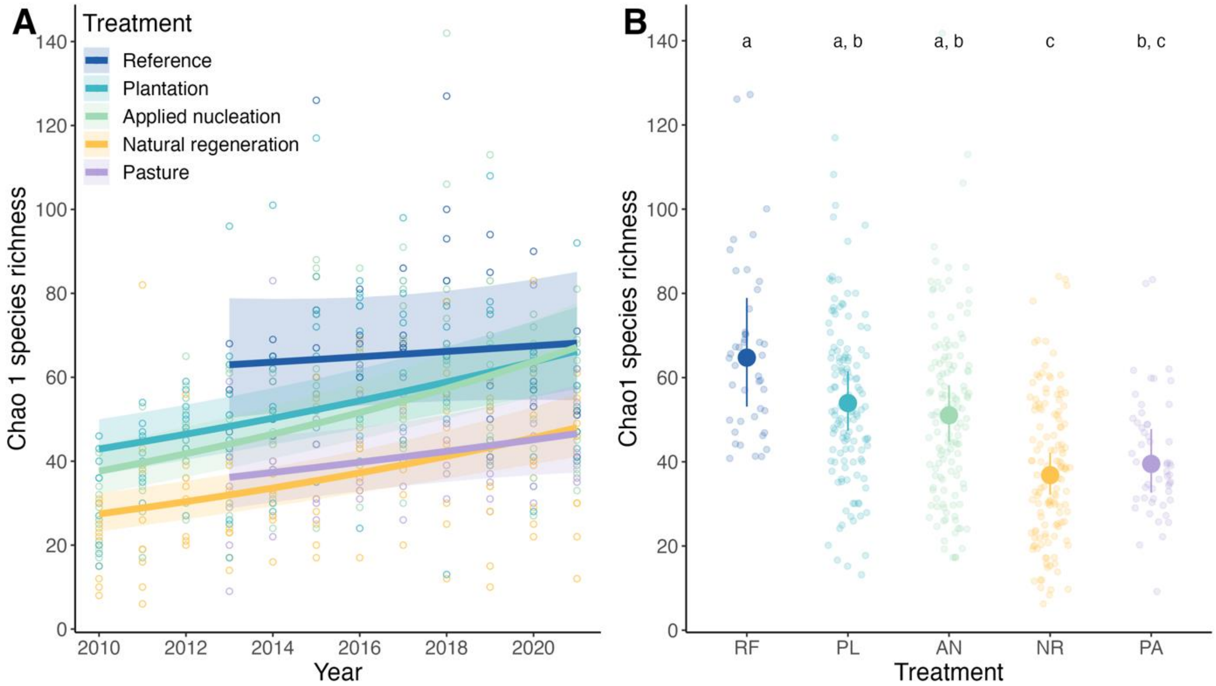

Figure 3. Species richness (Chao1 estimator) varied over time and among habitat types. **(A)** Model predictions (lines with 95% confidence interval bands) show positive slopes for applied nucleation and natural regeneration and marginally significant positive slopes for plantation. Time since restoration ranges from 4-6 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.

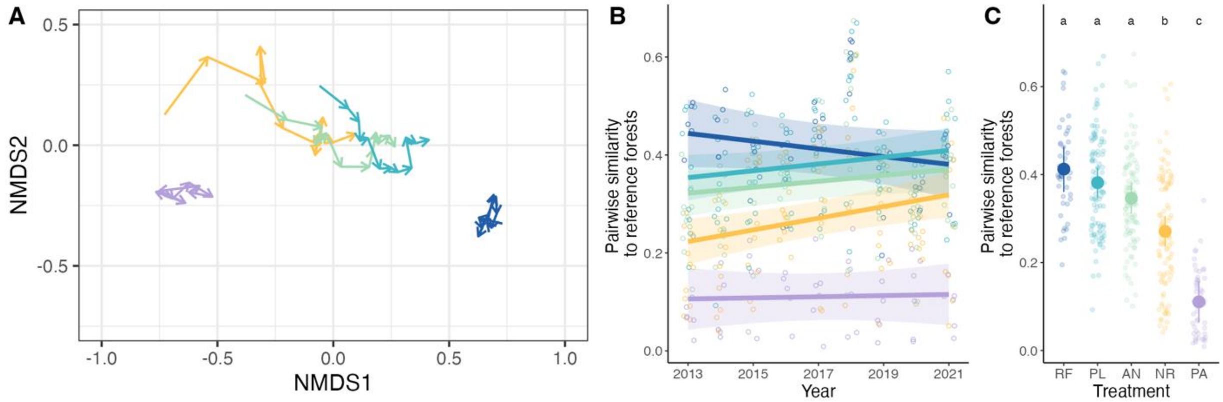

Figure 4. Community trajectories and similarity to reference forests. **(A)** Community trajectories in NMDS ordination space, based on a Morisita-Horn dissimilarity matrix of annual communities. Points represent the annual average (centroid) for each treatment. Arrows represent compositional change 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 90% 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).

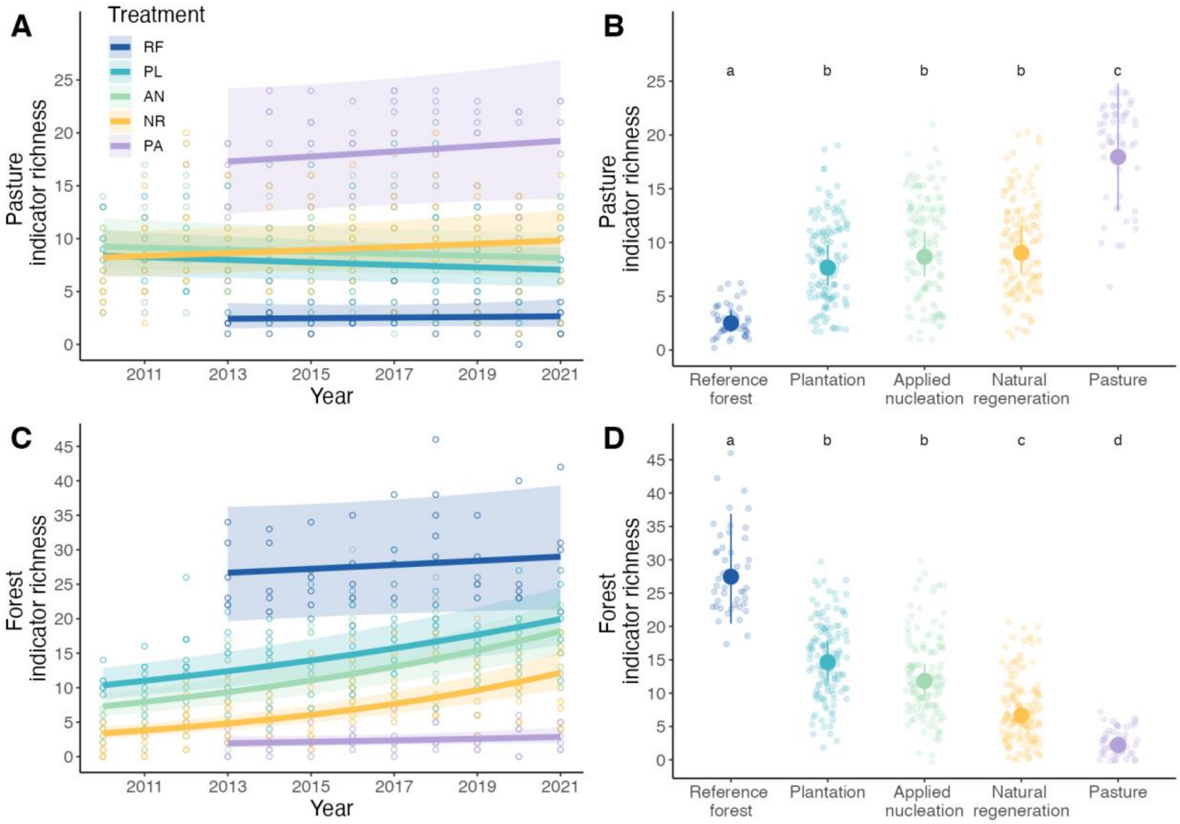

Figure 5. Indicator species richness trends. **(A)** Observed pasture indicator species richness by treatment and year. Lines with ribbons represent model predictions and 95% CI. There were no significant trends over time in any of the habitat types. **(B)** Observed pasture indicator richness by treatment. 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.

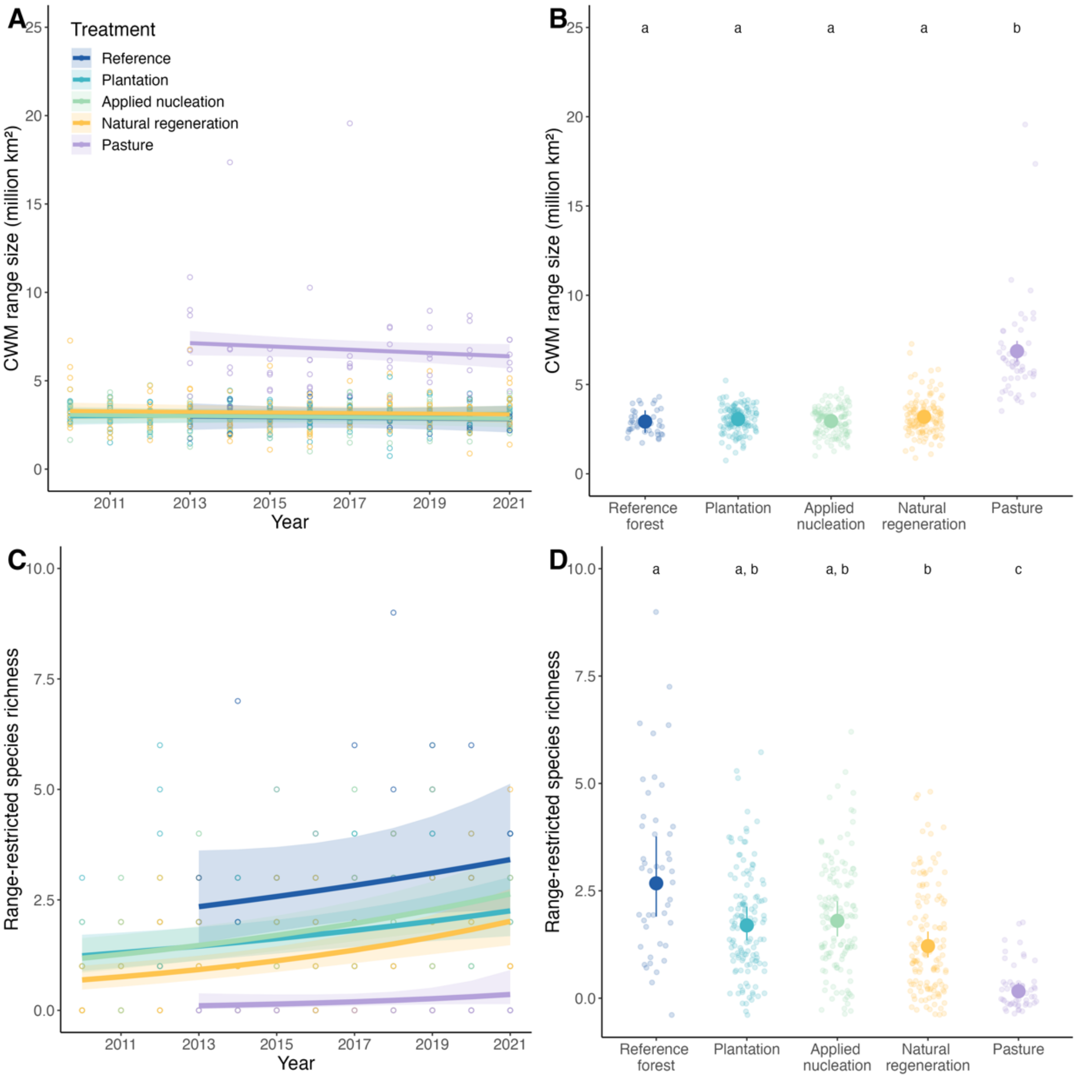

Figure 6. Range size trends. **(A)** Community-weighted mean range size by treatment and year. Lines with ribbons represent model predictions and 95% CI. **(B)** CWM range size by treatment. Large points represent treatment-level estimated marginal means and vertical lines represent 95% CI. **(C)** Observed 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.

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

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Authors’ contributions

K.D.H and R.A.Z. created and implemented the restoration experiment; J.L.R. conceived of the bird monitoring; J.A.R. collected the data; F.H.J. and J.L.R. entered and curated the data; F.H.J and A.B analyzed the data; F.H.J. led the writing of the manuscript. K.D.H, R.A.Z., J.L.R, and A.B. contributed critically to manuscript drafts.

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

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. Over longer time horizons, however, the ecological return on investment from natural regeneration increases. Managers should monitor trends in forest-affiliated species 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.

Keywords

Applied nucleation, avian communities, Costa Rica, habitat recovery, natural regeneration, tree plantation

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, 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). 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, which may not reflect longer-term trajectories. 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; Şekercioǧlu et al., 2002). Forest-affiliated species also tend to include more specialized habitat requirements and include range-restricted species. 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 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 decadal avian assemblage recovery 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 early ’snapshot’ 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. 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 and Grenke, 1971). Site elevation ranges from 1080-1430 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 1947-1980 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 in the applied nucleation treatment we planted 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), 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). 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 are characterized by high overall canopy cover of variable height. By 2019, most natural regeneration plots had patchy, relatively short canopy cover surrounded by dense exotic pasture grass cover, although some had greater tree and shrub cover.

2.3 Bird data collection

From 2010-2021 (12 years), we surveyed birds in all restoration plots (n = 33 plots). Between 2013-2021 (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 [(**REDACTED**)] actively searched each sampling area for 20 min, walking along existing trails, and recorded all birds seen or heard within the plot area. Observations of flyover birds not perching or foraging were excluded from analyses. Surveys were conducted between 05:50-09:00 h in mild weather, including light fog or mist but not high wind or rain. The order in which restoration treatments were surveyed was varied to avoid systematic bias in survey start time.

The resulting data set includes 1467 surveys representing 489 hours of sampling effort. Data for twenty surveys (1.3%) were missing and spread relatively evenly across treatments. 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 separate generalized linear mixed models (GLMMs) using *glmmTMB* v1.1.4 (Brooks et al., 2017) or linear mixed effect models using *lme4* v1.1.30 (Bates et al., 2015) for each response variable. 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 negative binomial error distribution with a log link function because a Poisson model had overdispersed residuals. We modeled sample coverage (bounded 0-1) using beta-distributed residuals with 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 assess whether bird assemblages using restoration plots were approaching those of reference forest while taking into account the spatial and temporal variability of reference forests, we also calculated the mean similarity (1-dissimilarity) of each annual community to each of the reference forest communities for the last nine years of the data set, when reference forests were surveyed (2013-2021; n = 5 reference forest communities for comparison to each restoration and pasture plot; n = 4 communities for forest-to-forest comparisons). 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). We fit a linear mixed effect model 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 $\alpha = 0.05$ based on 999 permutations (following Hariharan and Raman, 2021). To first explore associations between bird species and the five habitat types, we identified indicator species based on the full data set. Second, to assess temporal trends in the richness of pasture and forest affiliated birds in restoration treatments, 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 $\leq$50,000 km^2), which is commonly used as a metric of endemism (Ocampo-Peñuela et al., 2016).

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. 3). 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. Active pasture plots were not statistically different from natural regeneration (Table S2, Table S3, Fig. S1). Predicted species richness increased over time only in restoration plots (Table S2), with the steepest increase in applied nucleation, intermediate increase in natural regeneration, and only a marginal increase in the plantation treatment (Table S4).

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 higher in pasture plots (Fig. S2, Table S5), 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.

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. S3 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. S4, 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. 4, Fig. S4) and did not show a significant time effect (Fig. 4B, Table S8). 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 0.33-0.60 (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. S3).

3.3 Habitat association

Indicator species analysis with all treatments identified 104 species (37%) that were significantly associated with a particular habitat type (reference forest: 63; pasture: 39; plantation: 1; natural regeneration: 1; $p < 0.05$). The species most strongly associated with reference forest were *Henicorhina leucosticta*, *Corapipo altera*, *Arremon aurantiirostris*, and *Dysithamnus mentalis*. Widespread open-country birds such as *Troglodytes aedon*, *Tiaris olivaceus*, *Sporophila corvina*, *Zonotrichia capensis*, and *Tyrannus melancholicus* were associated with pasture sites. The indicator species for plantation was *Pachyramphys polychopterus*, a species typically found in wooded areas but generally not mature forest. The natural regeneration indicator species was *Laterallus albigularis*, a rail typically found in areas with dense grass. When we only considered reference forest and pasture surveys, we identified similar sets of reference forest (81) and pasture (39) indicator species (Appendix 2). These included some species that had a clear habitat preference when only considering pasture and reference forest but were also commonly found in restoration treatments and thus were not identified as indicators in the previous analysis. For example, *Thraupis episcopus* was a generalist pasture indicator, whereas *Catharus aurantiirostris* was a generalist forest indicator.

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, Table S9). 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. 5B, Tables S10-S12). 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). Range-restricted species richness in restoration treatments was intermediate between pasture and forest and increased over time (Fig. 6B).

4. Discussion

Bird assemblages in all restoration treatments have recovered 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. 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 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. 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). Results are consistent with patterns of natural seedling recruitment in these plots 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).

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). 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 mediated by forest connectivity, and faunal selection of available habitat (Freeman et al., 2015; Mayhew et al., 2019; Reid et al., 2021, 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, 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 an ~80% reduction in 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.

Data availability statement

Data and code are available in a GitHub repository and will be archived on Dryad prior to publication.

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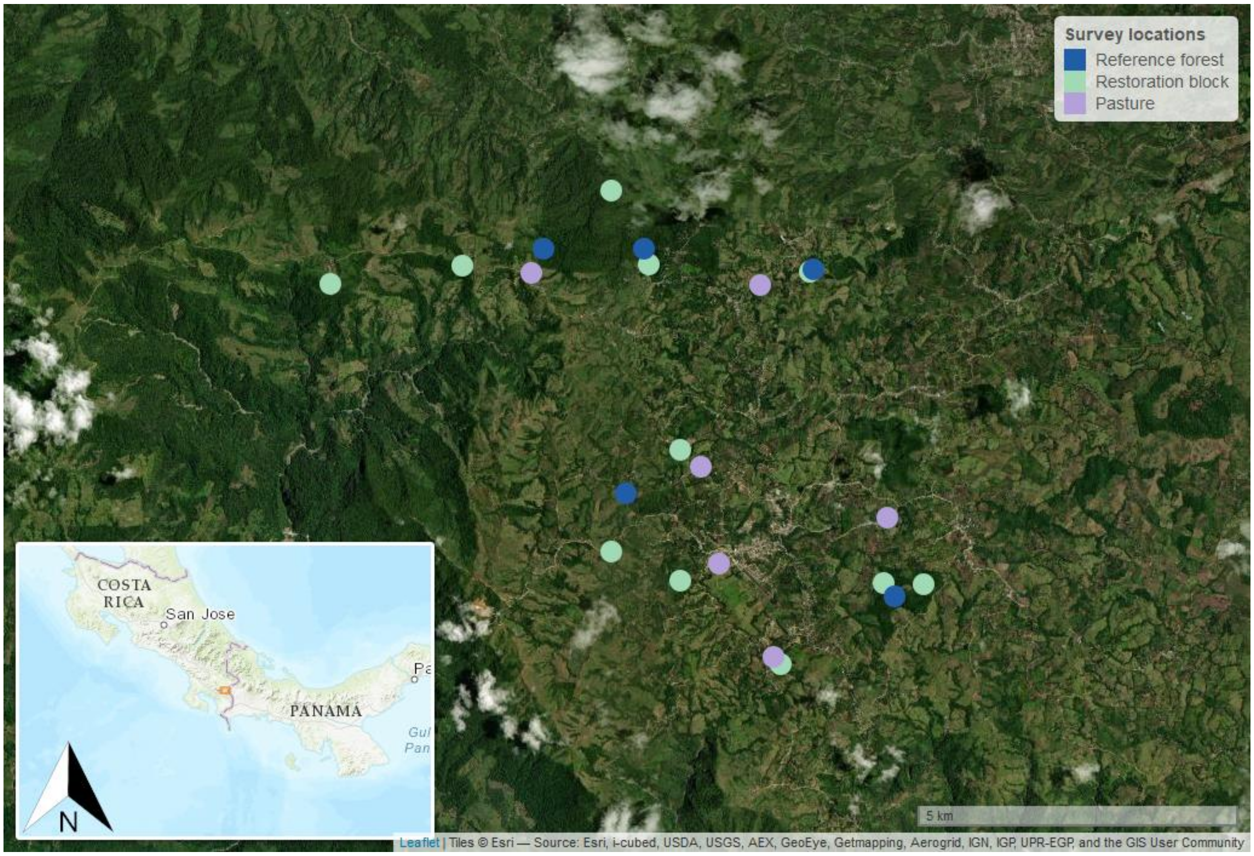

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Figure 1. Bird survey locations in Coto Brus, southern Costa Rica. Each restoration block contains one plot of each restoration treatment (plantation, applied nucleation, and natural regeneration).

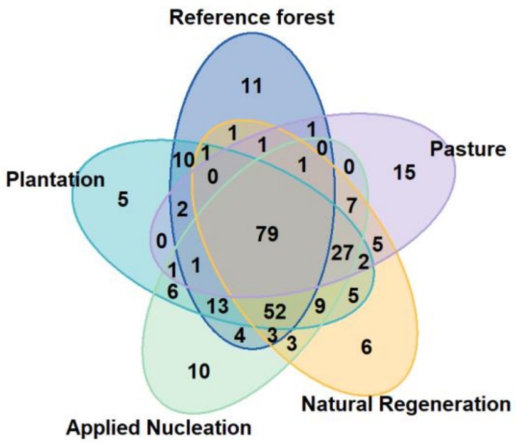

Figure 2. Venn diagram of bird species detected in each habitat type over the study period (9 years for pastures and reference forests, 12 years for restoration plots; n = 281 species total).

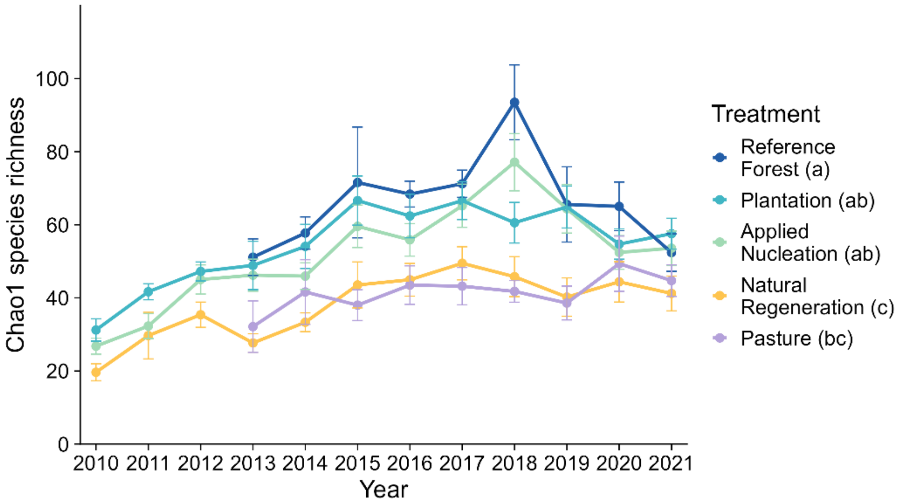

Figure 3. Plot-level species richness (Chao1 estimator) grouped by treatment (mean ± SE). Time since restoration ranges from 4-6 years in 2010 to 15-17 years in 2021. N = 11 plots per restoration treatment, 5 reference forests, 6 active pastures. Different legend label letters in parentheses indicate significantly different ($p < 0.05$) estimated marginal mean richness.

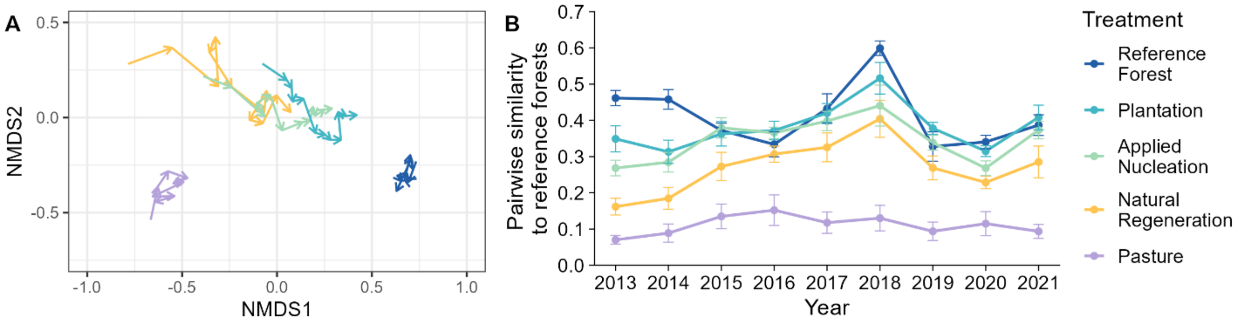

Figure 4. Community trajectories and similarity to reference forests. **(A)** Community trajectories in NMDS ordination space, based on a Morisita-Horn dissimilarity matrix of annual communities. Points represent the annual average (centroid) for each treatment. Arrows represent compositional change between consecutive years (reference forest and pasture: 8 segments, 2013-2021; restoration treatments: 11 segments, 2010-2021). **(B)** Mean pairwise community similarity to all reference forest communities within the same year for each habitat type (2013-2021). Points represent the treatment means (± SE) of plot-level mean pairwise comparisons to each reference forest community. Time since restoration was 4-6 years in 2010, 7-9 years in 2013, and 15-17 years in 2021.

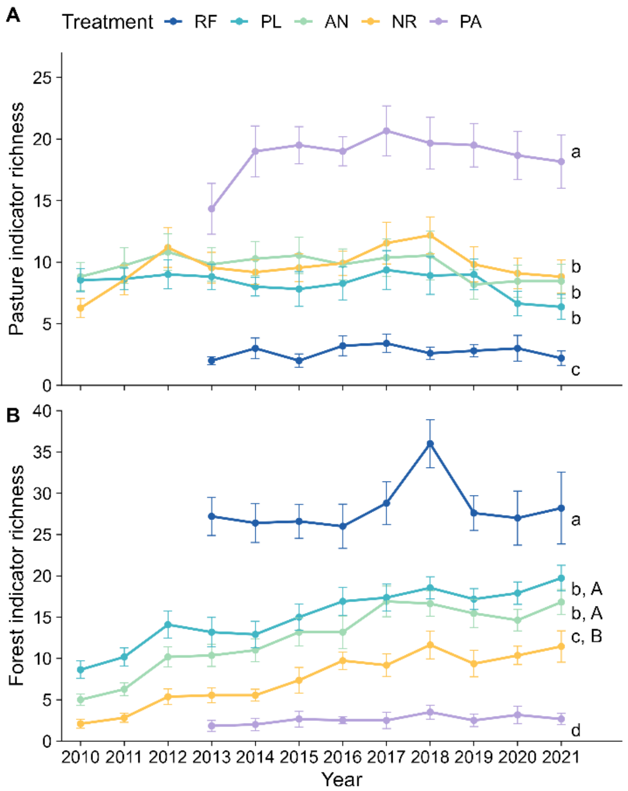

Figure 5. Temporal trends for indicator species richness (mean ± SE) for (A) pasture and (B) reference forest in each habitat type. Treatments labeled with different lower-case letters have significantly different estimated marginal means. Treatments labeled in panel B with upper-case letters have non-zero estimated slopes and different upper-case letters denote significantly different slopes.

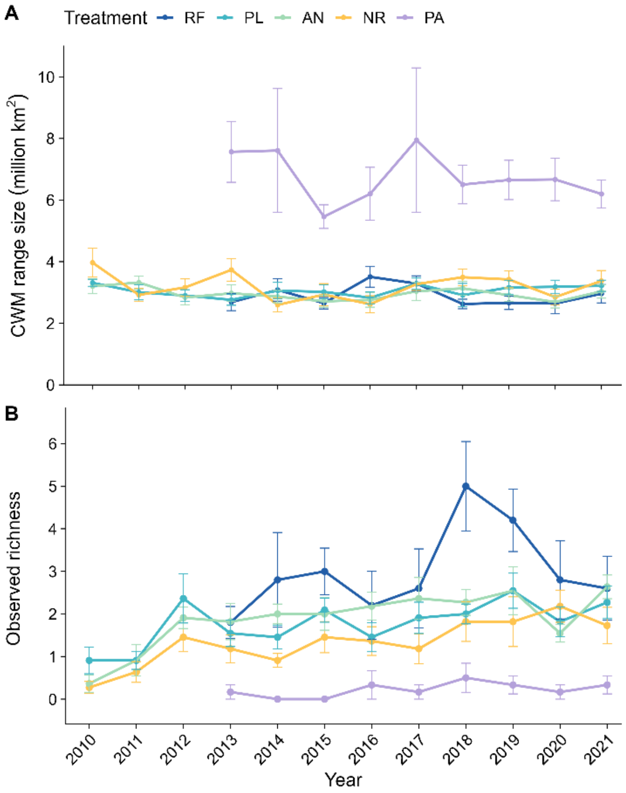

Figure 6. Range size trends. **(A)** Community-weighted mean range size by treatment and year (mean CWM ± SE). **(B)** Observed range-restricted species richness (mean ± SE).

Declaration of interests

☒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.

☐The authors declare the following financial interests/personal relationships which may be considered as potential competing interests:

Authors' contributions

K.D.H and R.A.Z. created and implemented the restoration experiment; J.L.R. conceived of the bird monitoring; J.A.R. collected the data; F.H.J. and J.L.R. entered and curated the data; F.H.J and A.B analyzed and visualized the data; F.H.J. led the writing of the manuscript. K.D.H, R.A.Z., J.L.R, and A.B. contributed critically to manuscript drafts.

Appendix 1- Species list with detection counts by treatment

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Supporting File

Appendix_1_2023-08.docx

Appendix 2- Forest and pasture indicator species

Revised supporting information