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Title

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

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

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Abstract:	<p>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.</p>
Suggested Reviewers:	<p>Priyanka Hariharan, M.S. University of Florida priyanka.h615@gmail.com Relevant expertise in restoration ecology of tropical rain forest birds.</p> <p>Shankar Ralman, PhD Nature Conservation Foundation trsr@ncf-india.org Relevant expertise in restoration ecology of tropical rain forest birds.</p> <p>Marie Laure Rurangwa Wildlife Trust Rwanda rurangwaura8@gmail.com Expertise in avian community ecology and restoration ecology.</p>

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SANTA BARBARA • SANTA CRUZ

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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,

A handwritten signature in cursive script that reads "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 and 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 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 is 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.

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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~~

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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; Şekereioğlu 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

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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). Understorey insectivores in particular are sensitive to disturbance and show limited dispersal across anthropogenic matrices (Powell et al., 2015; Sekercioglu 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

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11 135 ~~than in natural regeneration. We also anticipated that differing responses by pasture- and forest-~~
12 136 ~~affiliated birds would underlie community-level changes in richness and composition over time~~
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14 138 ~~metrics of geographic range size (Dunn and Romdal, 2005; Karp et al., 2019).~~

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16 140 **2. Materials and methods**

17 141 2.1 Study area
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22 146 ~~regeneration, given that the planted species would increase physical structure and provide the~~
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31 155 native ecosystem is transitional between tropical premontane wet forest and premontane rain
32 156 forest (~~Holdridge and Grenke, 1971~~)(Holdridge et al., 1971). Site elevation ranges from 1080-
33 157 1430 m.a.s.l. Mean annual temperature is ~21°C at the Las Cruces Biological Station, which is
34 158 within the study landscape. Median annual rainfall for 2005-2022 was 3.7 m (range 2.8-4.9 m),
35 159 with a dry season from December to March. The landscape was largely deforested between
36 160 1947-1980 and is now a fragmented mosaic of cattle pastures and agricultural fields interspersed
37 161 with patches of remnant and secondary forest, with overall regional forest cover ~28% as of
38 162 2014 (Zahawi et al., 2015). In recent decades ongoing deforestation has been partially offset by
39 163 second growth, and for the 2005-2014 period the study landscape experienced a small net
40 164 increase in forest cover (Amar, 2020).

41 165
42 166 2.2 Restoration experimental design
43 167 The three forest restoration treatments (Holl et al., 2020) were established at 11 sites (Fig.
44 168 1, Table S1) over three years (2004-2006). All sites are separated by >700 m. At each site three
45 169 0.25 ha (50 × 50 m) plots were established and assigned to one of three treatments: plantation
46 170 (PL), applied nucleation (AN), or natural regeneration (NR). Plots were separated by ≥5 m.
47 171 Plantation plots were planted uniformly with tree seedlings, whereas ~~in the~~ applied nucleation
48 172 ~~treatment we~~plots were planted with six tree nuclei of three sizes: two each of 4 × 4, 8 × 8 and 12
49 173 × 12 m. Tree spacing was ~2.8 m, with 313 trees planted in plantation and 86 in applied
50 174 nucleation. In both active restoration treatments, we planted two native tree species, *Terminalia*
51 175 *amazonia* (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two naturalized fast-
52 176 growing N-fixing species, *Erythrina poeppigiana* and *Inga edulis* (both Fabaceae) that are used
53 177 in agricultural intercropping systems. Naturally established vegetation was cleared prior to

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11 178 planting and at ~3-mo intervals for 2.5 years in all plots to allow planted seedlings to grow above
12 179 other vegetation.

13 180 ~~By 2019 (13-15 years after plot set up), most plantation plots had a tall (~15 m),
14 181 homogeneous canopy cover and fairly sparse mid-story shrub and small tree cover (Holl et al.,
15 182 2020). The two fast-growing planted Fabaceae species experienced substantial mortality, with
16 183 ~36% of *Erythrina* and ~34% of *Inga* surviving to 2020 (14-16 y after planting; Holl & Zahawi
17 184 unpublished data). This mortality, combined with falling branches, has led to greater
18 185 accumulation of coarse woody debris and standing dead wood in planted treatments compared to
19 186 natural regeneration (Fernandez Barrancos et al., 2022). Applied nucleation plots are
20 187 characterized by high overall canopy cover of variable height. By 2019, most natural
21 188 regeneration plots had patchy, relatively short canopy cover surrounded by dense exotic pasture
22 189 grass cover, although some had greater tree and shrub cover.~~

23 190 By 2019 (13-15 years after plot set up, toward the end of the study period), most
24 191 plantation plots had a tall (~15 m), homogeneous canopy cover and fairly sparse mid-story shrub
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28 195 combined with falling branches, has led to greater accumulation of coarse woody debris and
29 196 standing dead wood in planted treatments compared to natural regeneration (Fernandez
30 197 Barrancos et al., 2022). Applied nucleation plots were characterized by greater canopy roughness
31 198 than plantation plots and intermediate canopy cover ($60 \pm 7.1\%$) and height (11.5 ± 0.9 m). By
32 199 2019, most natural regeneration plots had patchy ($20.6 \pm 4.6\%$ cover) and short (7.0 ± 0.5 m)
33 200 canopies surrounded by dense exotic pasture grass cover, although some had greater tree and
34 201 shrub cover. At least 155 tree species had naturally recruited in each restoration treatment by
35 202 2022, despite the low number of planted species (or total absence of planting in natural
36 203 regeneration); some of these recruits had reached the tree (> 10 cm DBH) size class (Schubert et
37 204 al., submitted).

37 206 *2.3 Bird data collection*

38 207 From 2010-2021 (12 years), we surveyed birds in all restoration plots (n = 33 plots).
39 208 Between 2013-2021 (9 years), we also surveyed birds in 0.25 ha (50 × 50 m) survey areas within
40 209 five reference forests (RF) and six active cattle pastures (PA) for a total of 44 total survey plots
41 210 (Fig. 1, Table S1). Reference forests and active pastures were located within the same study
42 211 region and elevational range but not precisely paired with restoration blocks (distance to nearest
43 212 restoration plot: ~20-1000 m for reference forests; ~300-1000 m for active pastures). Reference
44 213 forests were subject to variable fragmentation and disturbance but represent “best available”
45 214 examples of local remnant forest habitat. Three times per year (Apr-May, Jul-Aug, Nov-Dec), a
46 215 single skilled observer ~~{(REDACTED)}~~ (JA Rosales) actively searched each sampling area for
47 216 20 min, walking along existing trails, and recorded all birds seen or heard within the plot area.
48 217 Each plot had a trail of similar length that provided access to the plot interior, although trail
49 218 configuration varied. The observer used his extensive experience in our research plots to
50 219 conservatively judge whether heard-only birds were calling from within the plot. Observations of
51 220 flyover birds not perching or foraging were excluded from analyses. Surveys were conducted
52 221 between 05:50-09:00 h in mild weather, including light fog or mist but not high wind or rain.
53 222 The Plots within the same site were surveyed on the same day, and the order in which ~~restoration~~
54 223 treatments were surveyed within a site was varied to avoid systematic bias in survey start time.

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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 *redlist* 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~~*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.

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.

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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.

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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 $\alpha = 0.05$ 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 $\leq 50,000$ km²), 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. 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 treatments 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

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11361 nucleation plots were significantly more similar to reference forest than were natural
12362 regeneration assemblages (Fig. [S44C](#), Table S6, Table S7). However, natural regeneration was
13363 the only treatment showing a significant increase in similarity to forest over the last nine years of
14364 surveys (Fig. 4B, Table S8).

15365 In contrast, assemblages in pasture and reference forest plots varied from year to year but
16366 not in a consistent directional manner (Fig. 4). As anticipated, pasture communities were the
17367 least similar to reference forest (Fig. [44A](#), Fig. [S44C](#)) and did not show a significant time effect
18368 (Fig. 4B, Table [S8S9](#)). Reference forest communities were also heterogeneous among sites.
19369 Within-year similarity among reference forests (i.e., the similarity of each forest community to
20370 the other four) ranged from 0.33-0.60 (estimated marginal mean = 0.41). Although planted
21371 restoration treatments reached comparable levels of pair-wise similarity to reference forests, their
22372 between-group dissimilarity was driven by distinct composition (Fig. 4A, Fig. [S3S2](#)).

23374 3.3 Habitat association

24375 Indicator species analysis ~~with all treatments~~ identified ~~104120~~ species (~~3742~~%) that
25376 were significantly associated with ~~a particular habitat type (either pasture (39) or reference~~
26377 ~~forest: 63; pasture: 39; plantation: 1; natural regeneration: 1; p < 0.05).~~ ([89](#)) ([Appendix 2](#)). The
27378 species most strongly associated with reference forest were *Henicorhina leucosticta*, *Corapipo*
28379 *altera*, *Lophotriccus pileatus*, *Catharus aurantiirostris*, *Pachysylvia decurtata*, Arremon
29380 *aurantiirostris*, and *Dysithamnus mentalis*. *Myioborus miniatus*. Widespread open-country birds
30381 such as *Troglodytes aedon*, *Tiaris olivaceus*, *Sporophila corvina*, *Zonotrichia capensis*, *Thraupis*
31382 *episcopus*, and *Tyrannus melancholicus* were associated with pasture sites. ~~The indicator species~~
32383 ~~for plantation was *Pachyramphys polychopterus*, a species typically found in wooded areas but~~
33384 ~~generally not mature forest. The natural regeneration indicator species was *Laterallus*~~
34385 ~~*albigularis*, a rail typically found in areas with dense grass. When we only considered reference~~
35386 ~~forest and pasture surveys, we identified similar sets of reference forest (81) and pasture (39)~~
36387 ~~indicator species ([Appendix 2](#)). These included some species that had a clear habitat preference~~
37388 ~~when only considering pasture and reference forest but were also commonly found in restoration~~
38389 ~~treatments and thus were not identified as indicators in the previous analysis. For example,~~
39390 ~~*Thraupis episcopus* was a generalist pasture indicator, whereas *Catharus aurantiirostris* was a~~
40391 ~~generalist forest indicator.~~

41392 Only half of the pasture-affiliated species were found in restoration plots, and only one-
42393 sixth were found in reference forests. There were no temporal trends in pasture indicator richness
43394 for any treatment (Fig. [5A-B](#), Table [S9S10](#)). In contrast, forest indicator species richness
44395 gradually increased over time in all three restoration treatments, with higher intercepts in planted
45396 treatments but a slightly higher slope in natural regeneration (Fig. [5B5C-D](#), Tables [S10-S12](#), [S11-](#)
46397 [S13](#)). Some forest indicator species used restoration plots with increasing frequency (e.g.,
47398 *Tangara icterocephala* and *Henicorhina leucosticta*). A few forest species (e.g., *Zentrygon*
48399 *chiriquensis*) were never recorded in restoration plots.

48401 3.4 Range restriction

49402 Patterns for community weighted mean range size and richness of range-restricted
50403 species mirrored those of pasture and reference forest indicator species richness. The average
51404 individual in pasture had a geographic range size approximately twice that of other habitats (Fig.
52405 [6A-B](#)). Range-restricted species richness in restoration treatments was intermediate between
53406 pasture and forest and increased over time (Fig. [6B6C-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

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11 452 configuration in this study system influence use of restored habitats by large frugivores and other
12 453 forest dependent birds (Reid et al., 2021; San José et al., 2022). Thus, in the absence of
13 454 landscape scale efforts to increase connectivity, some forest restricted species are not expected
14 455 to use restored plots with minimal nearby forest.
15 456 Long term monitoring of reference systems at multiple sites was a key feature of this
16 457 study. Importantly, the natural variability of tropical wet forest bird communities is high, such
17 458 that for a pairwise community similarity index, a value of 0.4 may be a realistic restoration
18 459 target. The fact that we did not observe directional shifts in pasture or reference forest
19 460 community metrics suggests that directional changes observed in restoration plots were due to
20 461 local scale change rather than regional dynamics. This is important because both tree and bird
21 462 communities in remnant forests within agricultural landscapes are likely to experience ongoing
22 463 and time lagged effects of regional scale forest loss, degradation, and fragmentation (Hendershot
23 464 et al., 2020; Newmark et al., 2017; Rutt et al., 2019; Şekercioğlu et al., 2019). Even at relatively
24 465 undisturbed sites, bird communities have experienced long term shifts, possibly due to climate
25 466 change (Freeman et al., 2018; Pollock et al., 2022; Stouffer et al., 2021).
26 467 Given the layout and size of treatment plots, we interpret our results with some caveats
27 468 regarding spatial proximity and habitat use. First, while spillover effects were possible given that
28 469 our three treatments were adjacent to each other, we still observed differences despite close
29 470 spatial proximity; this suggests that our results represent lower bound estimates of differences
30 471 between treatments. Second Bird assemblages in all restoration treatments have recovered at least
31 472 partially over time for all metrics examined, indicating that restoration approaches across a
32 473 gradient of effort facilitate recovery. Whereas species richness and a multivariate similarity
33 474 index provide a broad picture of recovery in different treatments, trends in habitat-associations of
34 475 constituent species are informative for understanding the processes of and constraints on
35 476 recovery, as emphasized by previous studies on the recovery of habitat specialists in other faunal
36 477 groups (e.g. Acevedo- Charry and Aide, 2019; Audino et al., 2014; Díaz-García et al., 2020;
37 478 Thompson and Donnelly, 2018). Within this study, recovery in restoration plots is characterized
38 479 by (a) rapid loss of some pasture species after agricultural abandonment, and (b) gradual increase
39 480 in the presence of forest species, with initial net gains in overall species richness due to the return
40 481 of generalists. Nonetheless, all restoration treatments contained some range-restricted species,
41 482 which suggests their potential to support regional biodiversity conservation and at least partially
42 483 offset biotic homogenization driven by land use change. This is consistent with evidence that
43 484 relatively small revegetated areas can offset the loss of woodland birds at landscape scales
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46 487 planted treatments for many metrics, but that disparity is narrowing. Although natural
47 488 regeneration started with the fewest species and least similar composition to reference forest,
48 489 forest indicators increased at a higher rate over the 12 years assessed here, and it was the only
49 490 restoration treatment with increasing similarity to reference forest over the full study period. This
50 491 suggests that natural regeneration may be a cost-effective approach for restoration practitioners
51 492 working on longer (i.e., multidecadal) time horizons, and the tradeoff between cost and habitat
52 493 quality during the first decade of succession is an important consideration in choosing a
53 494 restoration approach. Although natural regeneration harbored fewer forest indicators, generalist
54 495 insectivore species that also consume fruit can be important for dispersing seeds and driving
55 496 forward vegetation succession (Carlo and Morales, 2016).

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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

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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; Sekercioğlu 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).

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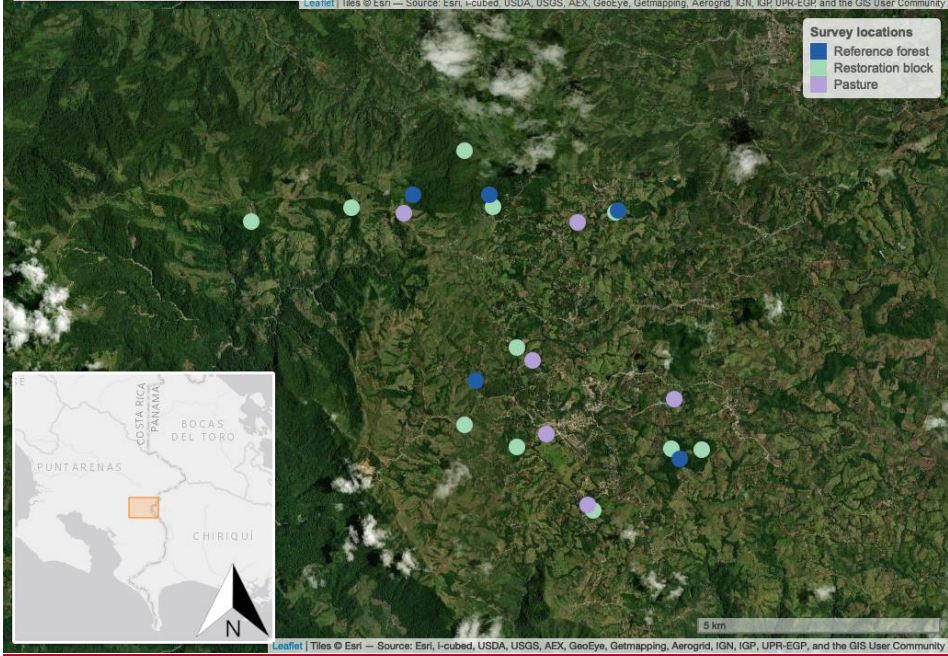
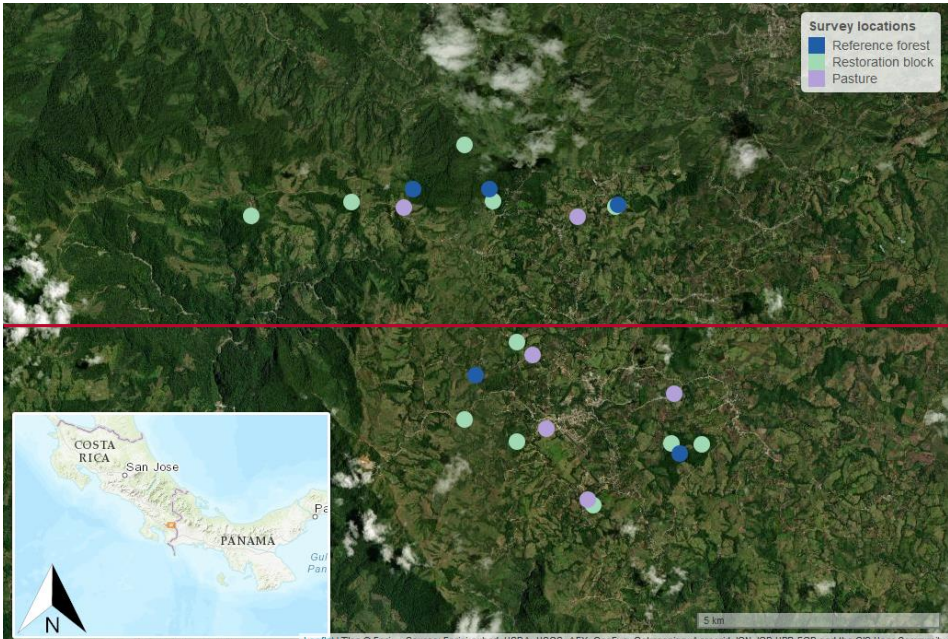
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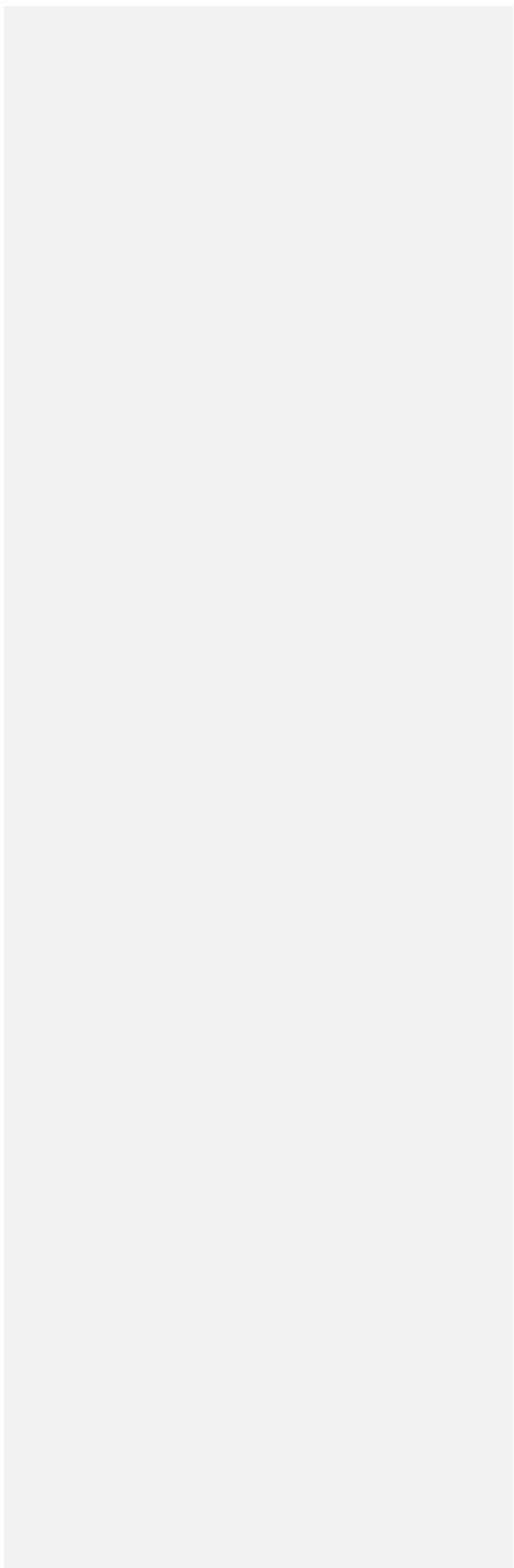
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Figure 1. Bird survey locations in Coto Brus, southern Costa Rica. Each restoration block contains one plot of each restoration treatment (plantation, applied nucleation, and natural regeneration).



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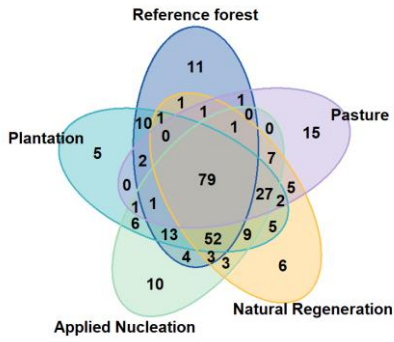


Figure 2. Venn diagram of bird species detected in each habitat type over the study period (9 years for pastures and reference forests, 12 years for restoration plots; n = 281 species total).

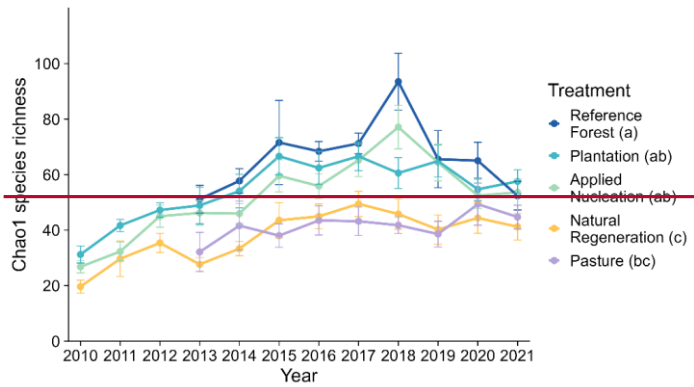


Figure 3. Plot level species richness (Chao1 estimator) grouped by treatment (mean \pm SE).

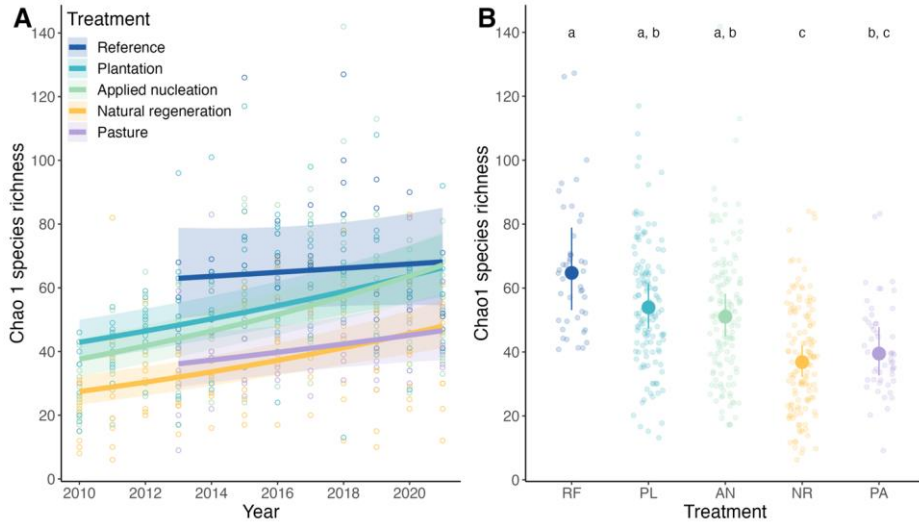


Figure 3. Species richness (Chao1 estimator) varied over time and among habitat types. **(A)** Model predictions (lines with 95% confidence interval bands) show positive slopes for applied nucleation and natural regeneration and marginally significant positive slopes for plantation. Time since restoration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

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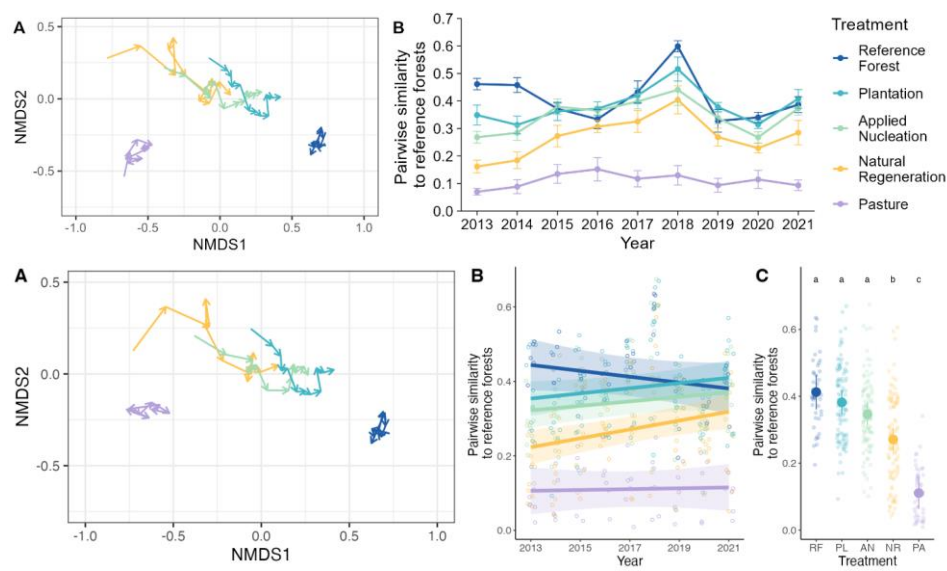


Figure 4. Community trajectories and similarity to reference forests. **(A)** Community trajectories in NMDS ordination space, based on a Morisita-Horn dissimilarity matrix of annual communities. Points represent the annual average (centroid) for each treatment. Arrows represent compositional change 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 (2013-2021) for each habitat type (2013-2021). Points, Lines and ribbons represent the treatment means (\pm 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).

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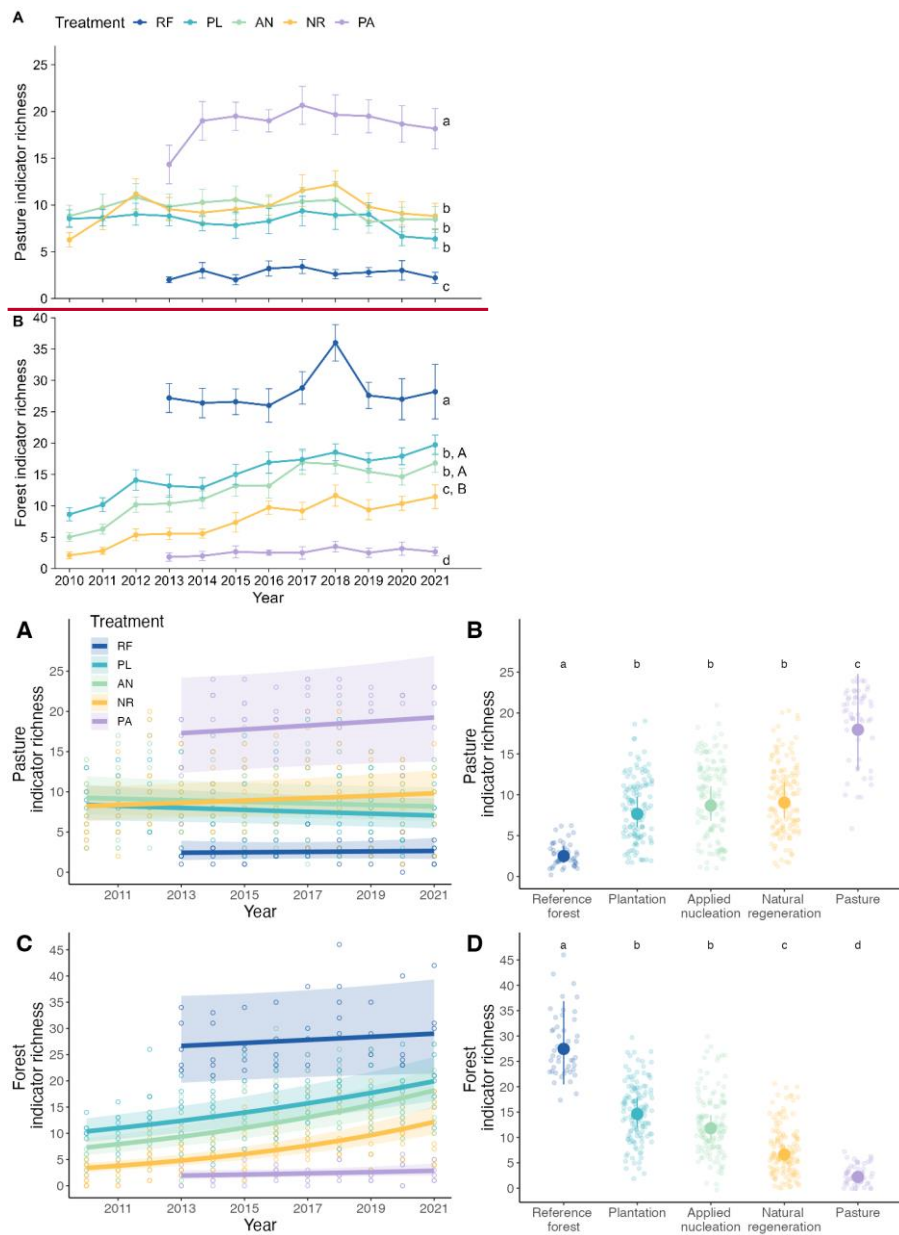


Figure 5. Temporal-Indicator species richness trends for - (A) Observed pasture indicator species richness (mean \pm SE) for (A) pasture and by treatment and year. Lines with ribbons represent

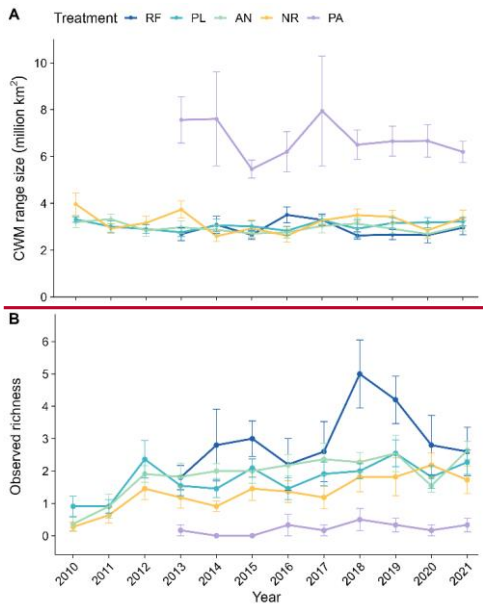
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model predictions and 95% CI. There were no significant trends over time in any of the habitat types. (B) Observed pasture indicator richness by treatment. Large points represent treatment-level estimated marginal means and vertical lines represent 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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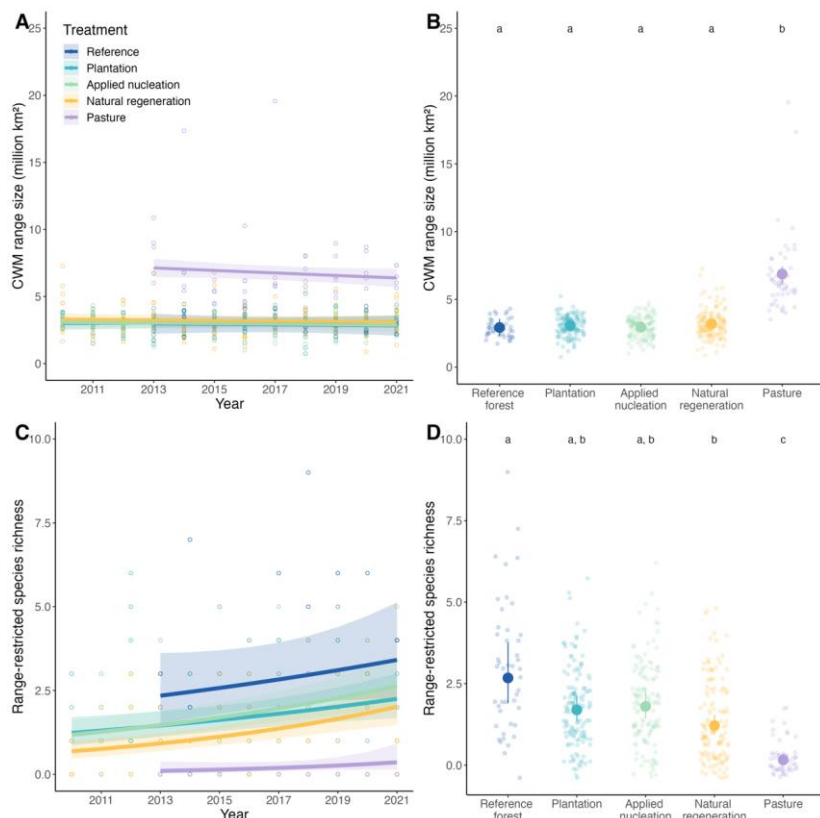


Figure 6. Range size trends. **(A)** Community-weighted mean range size by treatment and year (mean CWM \pm SE). Lines with ribbons represent model predictions and 95% CI. **(B)** Observed CWM range size by treatment. Large points represent treatment-level estimated marginal means and vertical lines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

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1 Active restoration accelerates recovery of tropical forest bird assemblages over two 2 decades

3 Abstract

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

25 Keywords

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

28 1. Introduction

29 Understanding how different restoration approaches influence faunal recovery is essential
30 to guide tropical forest restoration efforts and achieve desired outcomes for biodiversity
31 conservation. Birds are a key group in tropical forest restoration because they both benefit from
32 restoration and promote forest regeneration through pollination and seed dispersal interactions
33 (Catterall, 2018). The choice of restoration approach can strongly affect vegetational trajectories
34 and in turn local habitat characteristics that influence avian habitat use (Reid et al., 2012). Two
35 common approaches are native tree plantations, which are resource-intensive but develop canopy
36 cover faster, and passive restoration, in which sites are protected from disturbance but otherwise
37 left to regenerate naturally. As passive restoration generally involves lower costs, it has been
38 promoted for forest restoration at large scales (Chazdon and Uriarte, 2016). However,
39 trajectories of natural regeneration are highly variable and depend on land use history and
40 proximity to source populations (Holl and Aide, 2011). In the absence of intervention, areas
41 under passive restoration can remain in a state of arrested succession (Sarmiento, 1997).
42 Meanwhile, there is growing evidence that intermediate strategies along an intervention

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4 43 continuum (Chazdon et al., 2021), such as applied nucleation (i.e., when plants are planted or
5 44 seeded in clusters within a larger area), can accelerate vegetation recovery at lower cost while
6 45 creating more structural complexity (Holl et al., 2020).

8 46 The long-term efficacy of differing restoration methods for creating forest habitats for
9 47 birds depends both on initial differences among restoration treatments and how they change over
10 48 time. Comparing active and passive restoration is difficult because they have typically been
11 49 assessed using different study designs and in different locations (Shoo and Catterall, 2013). Past
12 50 studies have often relied on chronosequences (Acevedo- Charry and Aide, 2019; Sayer et al.,
13 51 2017), sometimes confound temporal variability and past land use (Johnson and Miyanishi,
14 52 2008), or comparisons of passively and actively restored sites selected years after restoration,
15 53 which are subject to positive selection bias for passively restored sites (i.e., sites that showed
16 54 successful recovery, Reid et al., 2018). Meta-analyses comparing bird assemblages in paired
17 55 secondary and primary forest sites throughout the tropics show that forest specialist species
18 56 increase over time (Acevedo- Charry and Aide, 2019; Sayer et al., 2017), but disparate data
19 57 points are unlikely to represent realistic trajectories, and this pattern bears further testing in
20 58 multi-treatment experiments. Few studies directly compare passive recovery with active
21 59 restoration strategies in the same system (Jones et al., 2018) and those that do typically have just
22 60 a few years of data (de Carvalho Barros et al., 2022; Vogel et al., 2015), which may not reflect
23 61 longer-term trajectories. Most studies assessing nucleation have used seedling richness or density
24 62 as metrics of restoration outcomes (de Oliveira Bahia et al., 2023), rather than fauna.
25 63 Accordingly, how bird assemblages in restoration treatments of varying intensity recover over
26 64 time at the same sites remains an open question.

31 65 Evidence from multiple continents demonstrates that native tree plantations can benefit
32 66 bird recovery by providing a closed canopy and vertical stratification (e.g., Catterall et al., 2012;
33 67 Hariharan and Raman, 2021; Latja et al., 2016). However, forest-dependent birds may require
34 68 specific microclimates, food items, or nest sites, that can take decades to develop (Vesk et al.,
35 69 2008). Understory insectivores in particular are sensitive to disturbance and show limited
36 70 dispersal across anthropogenic matrices (Powell et al., 2015; Şekercioğlu et al., 2002). Forest-
37 71 affiliated species also tend to have more specialized habitat requirements and are more likely to
38 72 be range-restricted. In contrast, species found in agricultural lands tend to be disturbance-adapted
39 73 and have large range sizes. As such, land conversion can result in biotic homogenization of
40 74 avifauna by extirpating specialist species and favoring disturbance-tolerant species over wide
41 75 areas (Karp et al., 2012), but the degree to which restored forests regain forest specialists and
42 76 range restricted species over observable time frames is poorly understood.

46 77 Disentangling the effects of restoration treatment on avian habitat use from those of site
47 78 age and context requires long-term, multi-site, and multi-treatment studies that also include
48 79 reference and degraded sites surveyed multiple times to account for regional trends which may
49 80 be occurring independently of local restoration efforts, for example population declines (e.g.,
50 81 Blake and Loiselle, 2016; Sigel et al., 2006) or range expansions. Here, we report on avian
51 82 assemblage recovery over 12 years in restoration plots that were subjected to three different
52 83 restoration interventions replicated widely across an agricultural landscape in southern Costa
53 84 Rica (Holl et al., 2020). Specifically, we compared the effects of two active restoration
54 85 treatments (plantation and applied nucleation) and a passive natural regeneration restoration
55 86 treatment on bird species richness and compositional similarity to reference forests, relative to
56 87 degraded pastures and reference forests. We asked: (1) How do bird species richness, community
57 88 composition, and similarity to reference forest differ among restoration treatments and how do

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4 89 they change over time? (2) How do pasture-affiliated and forest-affiliated bird species vary
5 90 among restoration treatments over time? (3) Are restored sites gaining range-restricted species?

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7 91 Based on an early comparisons in this study system (Reid et al., 2014) and studies in
8 92 other systems, we expected that recovery of richness (Edwards et al., 2009) and composition
9 93 (Hariharan and Raman, 2021) would be greater in planted restoration treatments than in natural
10 94 regeneration, given that the planted species would increase physical structure and provide the
11 95 same resources to both treatments. We also anticipated that differing responses by pasture- and
12 96 forest-affiliated birds would underlie community-level changes in richness and composition over
13 97 time (Catterall et al., 2012), and that shifts in forest specialists would be reflected in community
14 98 metrics of geographic range size (Dunn and Romdal, 2005; Karp et al., 2019).

17 99 18 100 **2. Materials and methods**

19 101 *2.1 Study area*

20 102 This study took place in southern Costa Rica (8°44' – 8°47' N, 82°56' – 82°57' W). The
21 103 native ecosystem is transitional between tropical premontane wet forest and premontane rain
22 104 forest (Holdridge et al., 1971). Site elevation ranges from 1080-1430 m.a.s.l. Mean annual
23 105 temperature is ~21°C at the Las Cruces Biological Station, which is within the study landscape.
24 106 Median annual rainfall for 2005-2022 was 3.7 m (range 2.8-4.9 m), with a dry season from
25 107 December to March. The landscape was largely deforested between 1947-1980 and is now a
26 108 fragmented mosaic of cattle pastures and agricultural fields interspersed with patches of remnant
27 109 and secondary forest, with overall regional forest cover ~28% as of 2014 (Zahawi et al., 2015).
28 110 In recent decades ongoing deforestation has been partially offset by second growth, and for the
29 111 2005-2014 period the study landscape experienced a small net increase in forest cover (Amar,
30 112 2020).

31 113 32 114 *2.2 Restoration experimental design*

33 115 The three forest restoration treatments (Holl et al., 2020) were established at 11 sites (Fig.
34 116 1, Table S1) over three years (2004-2006). All sites are separated by >700 m. At each site three
35 117 0.25 ha (50 × 50 m) plots were established and assigned to one of three treatments: plantation
36 118 (PL), applied nucleation (AN), or natural regeneration (NR). Plots were separated by ≥5 m.
37 119 Plantation plots were planted uniformly with tree seedlings, whereas applied nucleation plots
38 120 were planted with six tree nuclei of three sizes: two each of 4 × 4, 8 × 8 and 12 × 12 m. Tree
39 121 spacing was ~2.8 m, with 313 trees planted in plantation and 86 in applied nucleation. In both
40 122 active restoration treatments, we planted two native tree species, *Terminalia amazonia*
41 123 (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two naturalized fast-growing
42 124 N-fixing species, *Erythrina poeppigiana* and *Inga edulis* (both Fabaceae) that are used in
43 125 agricultural intercropping systems. Naturally established vegetation was cleared prior to planting
44 126 and at ~3-mo intervals for 2.5 years in all plots to allow planted seedlings to grow above other
45 127 vegetation.

46 128 By 2019 (13-15 years after plot set up, toward the end of the study period), most
47 129 plantation plots had a tall (~ 15 m), homogeneous canopy cover and fairly sparse mid-story shrub
48 130 and small tree cover (Holl et al., 2020; Zahawi, unpublished data). The two fast-growing planted
49 131 Fabaceae species experienced substantial mortality, with ~36% of *Erythrina* and ~34% of *Inga*
50 132 surviving to 2020 (14-16 y after planting; Holl & Zahawi, unpublished data). This mortality,
51 133 combined with falling branches, has led to greater accumulation of coarse woody debris and

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4 134 standing dead wood in planted treatments compared to natural regeneration (Fernandez
5 135 Barrancos et al., 2022). Applied nucleation plots were characterized by greater canopy roughness
6 136 than plantation plots and intermediate canopy cover (60 ± 7.1 %) and height (11.5 ± 0.9 m). By
7 137 2019, most natural regeneration plots had patchy (20.6 ± 4.6 % cover) and short (7.0 ± 0.5 m)
8 138 canopies surrounded by dense exotic pasture grass cover, although some had greater tree and
9 139 shrub cover. At least 155 tree species had naturally recruited in each restoration treatment by
10 140 2022, despite the low number of planted species (or total absence of planting in natural
11 141 regeneration); some of these recruits had reached the tree (> 10 cm DBH) size class (Schubert et
12 142 al., submitted).

15 143 16 144 *2.3 Bird data collection*

17 145 From 2010-2021 (12 years), we surveyed birds in all restoration plots ($n = 33$ plots).
18 146 Between 2013-2021 (9 years), we also surveyed birds in 0.25 ha (50×50 m) survey areas within
19 147 five reference forests (RF) and six active cattle pastures (PA) for a total of 44 total survey plots
20 148 (Fig. 1, Table S1). Reference forests and active pastures were located within the same study
21 149 region and elevational range but not precisely paired with restoration blocks (distance to nearest
22 150 restoration plot: ~ 20 -1000 m for reference forests; ~ 300 -1000 m for active pastures). Reference
23 151 forests were subject to variable fragmentation and disturbance but represent “best available”
24 152 examples of local remnant forest habitat. Three times per year (Apr-May, Jul-Aug, Nov-Dec), a
25 153 single skilled observer (JA Rosales) actively searched each sampling area for 20 min, walking
26 154 along existing trails, and recorded all birds seen or heard within the plot area. Each plot had a
27 155 trail of similar length that provided access to the plot interior, although trail configuration varied.
28 156 The observer used his extensive experience in our research plots to conservatively judge whether
29 157 heard-only birds were calling from within the plot. Observations of flyover birds not perching or
30 158 foraging were excluded from analyses. Surveys were conducted between 05:50-09:00 h in mild
31 159 weather, including light fog or mist but not high wind or rain. Plots within the same site were
32 160 surveyed on the same day, and the order in which treatments were surveyed within a site was
33 161 varied to avoid systematic bias in survey start time.

34 162 The resulting data set includes 1466 surveys representing 489 hours of sampling effort.
35 163 Nineteen plot surveys (1.3%) were missing; pasture and reference forest were missing eight and
36 164 six surveys, respectively, whereas each restoration treatment was missing just one or two
37 165 surveys. Species names were standardized to the 7th Checklist of the American Ornithological
38 166 Society (Chesser et al., 2022). We obtained the IUCN Red List extinction risk assessment
39 167 category for each species using the *rredlist* package v0.7.0 (IUCN, 2022).

40 168 41 169 *2.4 Data analysis*

42 170 We aggregated survey-level bird abundance data by plot and year to obtain annual
43 171 assemblages ($n = 495$) and used these as sampling units for analyses. Rather than summing
44 172 individuals detected for each species across the three survey seasons, we aggregated by the
45 173 maximum count (sensu Julliard et al., 2006), to (a) minimize counting highly resident individuals
46 174 multiple times and (b) avoid interpolating abundances in missing surveys. We performed all
47 175 analyses with R version 4.1.2 (R Core Team, 2022).

48 176 To assess the effects of habitat type (hereafter synonymous with ‘treatment’) and
49 177 treatment-specific effects of time on community recovery we calculated multiple metrics and
50 178 fitted a separate model for each response variable using an appropriate error structure (Table S2).
51 179 We fitted linear mixed effect models using *lme4* v1.1.30 (Bates et al., 2015) and generalized

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4 180 linear mixed models (GLMMs) using *glmmTMB* v1.1.4 (Brooks et al., 2017). We used survey
5 181 year (calendar year - first year of monitoring) as the time covariate rather than years since
6 182 restoration because the latter is not a meaningful variable for pastures and reference forests. In all
7 183 models we included a random intercept term for plot nested within site to account for non-
8 184 independence of bird assemblages sampled within the same plots and clustered within sites.
9 185 Forest and pasture plots within 450 m of a restoration block were assigned to that site. Because
10 186 forest and pasture survey locations were not always paired with restoration blocks, the fixed
11 187 effects of reference forest and pasture habitat types were partly confounded with site effects.
12 188 Therefore, there was lower power for testing the effects of reference forest and pasture habitats.
13 189 For all fitted models, we examined residual diagnostics, including temporal autocorrelation
14 190 functions, in package *DHARMA* v0.4.6 (Hartig, 2020). To compare the predicted main effects of
15 191 treatments and their interactions with time we used package *emmeans* v1.8.1.
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20 193 2.5 Species richness

21 194 To compare species richness while accounting for undetected species, we calculated the
22 195 abundance-based Chao1 species richness estimator for each annual assemblage using package
23 196 *iNEXT* v3.0.0 (Chao et al., 2014b; Hsieh et al., 2016). To evaluate sample completeness for each
24 197 annual community we calculated sample coverage (Chao et al., 2014a). We modeled species
25 198 richness using a GLMM with a negative binomial error distribution and a log link function
26 199 because a Poisson model had overdispersed residuals. We modeled sample coverage (bounded 0-
27 200 1) using beta-distributed residuals and a logit link function.
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31 202 2.6 Community composition

32 203 To assess recovery of community composition, we first created a matrix of abundance-
33 204 based community dissimilarities (package *vegan* version 2.6-2; Oksanen et al., 2013). We used
34 205 the Morisita-Horn index, since it is robust to variation in sample size and coverage (Chao et al.,
35 206 2006; Dent and Wright, 2009). We visualized the trajectories of species composition using
36 207 nonmetric multidimensional scaling, plotting the average (centroid) assemblage for each
37 208 treatment in each year (De Cáceres et al., 2019). To quantify the degree to which bird
38 209 assemblages in restoration plots and pastures approached those of reference forest, we calculated
39 210 the mean similarity (1- dissimilarity) of each annual assemblage to each of the reference forest
40 211 assemblages within each of the last nine years of the data set, when reference forests were
41 212 surveyed (2013-2021; n = 5 reference forest assemblages). We compared each plot to multiple
42 213 reference forests rather than only the nearest reference forest to account for their spatial
43 214 variability. Similarity among reference forests is interpretable as a metric of reference forest beta
44 215 diversity (Anderson et al., 2011), and this natural variability constrains the average similarity to
45 216 reference forest attainable by restoration treatments (Gerwing and Hawkes, 2021). Therefore, we
46 217 also calculated the mean similarity of each annual reference forest assemblage to the other
47 218 reference forest assemblages (n = 4 assemblages for forest-to-forest comparisons). We fit a linear
48 219 mixed effect model (Gaussian error distribution) for mean pairwise similarity to reference forest
49 220 communities because a beta-distributed model failed to converge.
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55 222 2.7 Habitat association

56 223 To explore how community-scale shifts in species composition reflect responses of birds
57 224 with different habitat affinities, we first identified species associated with particular habitat types
58 225 (“indicator species”, sensu De Cáceres and Legendre, 2009) using the *indicspecies* v1.7.12
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4 226 package, based on a priori habitat categorization of survey plots. We used the abundance-based
5 227 point biserial correlation coefficient as the association function, corrected for unequal numbers
6 228 of sites per habitat type (func= 'r.g. '), and assessed significance at $\alpha = 0.05$ based on 999
7 229 permutations (following Hariharan and Raman, 2021). To assess temporal trends in the richness
8 230 of pasture and forest affiliated birds in restoration treatments, indicator species based on the
9 231 subset of data with just pasture and forest plots. This provided lists of indicator species derived
10 232 independently of restoration plot surveys. We modeled observed richness of indicator species
11 233 using a GLMM with a Poisson error distribution and a log link function.
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15 235 2.8 Geographic range size

16 236 We used two metrics to assess patterns of bird geographic range size (from Tobias et al.,
17 237 2022) across habitats and time. We calculated the community weighted mean (CWM) value of
18 238 geographic range size using the *FD* v1.0-12.1 package (Laliberté et al., 2014). This is similar to
19 239 the “community range index,” used to characterize one facet of bird assemblage “commonness”
20 240 and as a metric of biotic homogenization (Godet et al., 2015). We also used the observed
21 241 richness of range-restricted species (range size $\leq 50,000$ km²), which is commonly used as a
22 242 metric of endemism (Ocampo-Peñuela et al., 2016). We modeled CWM range size using a linear
23 243 mixed effects model, and we modeled range-restricted species richness using a GLMM with a
24 244 zero-inflated Poisson error structure and a log link function.
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28 29 246 3. Results

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31 247 We recorded 34,469 individual bird detections of 281 species in 46 families (Appendix
32 248 1). The most abundant families were tanagers (Thraupidae; 23% of detections), flycatchers
33 249 (Tyrannidae; 15%), thrushes (Turdidae, 12%), warblers (Parulidae; 9%), and wrens
34 250 (Troglodytidae; 6%). The five species with the most individuals detected were *Catharus*
35 251 *ustulatus*, *Ramphocelus passerinii*, *Amazilia tzacatl*, *Catharus aurantirostris*, and *Sporophila*
36 252 *corvina*. Seventy-nine species (28%) were detected in all five habitat types, whereas 47 species
37 253 (16.7%) were recorded in a single habitat type (Fig. 2). For 26 species, only a single individual
38 254 was detected, and for 15 species only two individuals were detected. We recorded five species
39 255 that have an IUCN extinction risk category of “Near Threatened.” Of these, two are residents and
40 256 both are large frugivores (*Ramphastos ambiguus* and *Penelope purpurascens*). Twenty-one
41 257 species (7.4%) were range-restricted, of which the most-detected were *Manacus aurantiacus*,
42 258 *Arremon costaricensis*, and *Saucerottia edward*.
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46 260 3.1 Species richness

47 261 Over the full study period, species richness was highest in reference forest, followed by
48 262 plantation, applied nucleation, active pasture, and natural regeneration (Fig. 3B). Reference
49 263 forest had significantly higher predicted richness than pasture and natural regeneration, whereas
50 264 plantation and applied nucleation were only statistically more speciose than natural regeneration.
51 265 Pasture plots were not statistically different from natural regeneration (Fig 3B, Table S3, Table
52 266 S4). Predicted species richness increased over time only in restoration plots (Fig. 3A, Table S3),
53 267 with similar slopes among treatments (Table S5).
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57 269 Overall mean sample coverage for the 495 annual assemblages was 67% (range 25-97%),
58 270 indicating that on average the three 20-minute surveys per year did not completely sample the
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4 271 Table S6), indicating that richness estimates in pastures were more precise than the other habitat
5 272 types. Natural regeneration was the only habitat type where sample coverage increased slightly
6 273 with time, which indicates that over time a decreasing proportion of unsampled individuals were
7 274 undetected species.
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9 276 3.2 Community composition

10 277 Bird assemblages in restoration plots on average converged toward each other and toward
11 278 those of reference forest plots over time (NMDS of Morisita-Horn dissimilarity, Fig. 4A, stress =
12 279 0.25, see Fig. S2 for NMDS of individual annual communities). Despite this overall
13 280 convergence, there were differences among restoration treatments in both their similarity to
14 281 forest and their rate of change in similarity over time. Assemblages in plantation and applied
15 282 nucleation plots were significantly more similar to reference forest than were natural
16 283 regeneration assemblages (Fig. 4C, Table S6, Table S7). However, natural regeneration was the
17 284 only treatment showing a significant increase in similarity to forest over the last nine years of
18 285 surveys (Fig. 4B, Table S8).

19 286 In contrast, assemblages in pasture and reference forest plots varied from year to year but
20 287 not in a consistent directional manner (Fig. 4). As anticipated, pasture communities were the
21 288 least similar to reference forest (Fig. 4A, Fig. 4C) and did not show a significant time effect (Fig.
22 289 4B, Table S9). Reference forest communities were also heterogeneous among sites. Within-year
23 290 similarity among reference forests (i.e., the similarity of each forest community to the other four)
24 291 ranged from 0.33-0.60 (estimated marginal mean = 0.41). Although planted restoration
25 292 treatments reached comparable levels of pair-wise similarity to reference forests, their between-
26 293 group dissimilarity was driven by distinct composition (Fig. 4A, Fig. S2).
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28 295 3.3 Habitat association

29 296 Indicator species analysis identified 120 species (42%) that were significantly associated
30 297 with either pasture (39) or reference forest (89) (Appendix 2). The species most strongly
31 298 associated with reference forest were *Henicorhina leucosticta*, *Lophotriccus pileatus*, *Catharus*
32 299 *aurantiiostris*, *Pachysylvia decurtata*, *Arremon aurantiiostris*, and *Myioborus miniatus*.
33 300 Widespread open-country birds such as *Troglodytes aedon*, *Tiaris olivaceus*, *Sporophila corvina*,
34 301 *Thraupis episcopus*, and *Tyrannus melancholicus* were associated with pasture sites.

35 302 Only half of the pasture-affiliated species were found in restoration plots, and only one-
36 303 sixth were found in reference forests. There were no temporal trends in pasture indicator richness
37 304 for any treatment (Fig. 5A-B, Table S10). In contrast, forest indicator species richness gradually
38 305 increased over time in all three restoration treatments, with higher intercepts in planted
39 306 treatments but a slightly higher slope in natural regeneration (Fig. 5C-D, Tables S11-S13). Some
40 307 forest indicator species used restoration plots with increasing frequency (e.g., *Tangara*
41 308 *icterocephala* and *Henicorhina leucosticta*). A few forest species (e.g., *Zentrygon chiquensis*)
42 309 were never recorded in restoration plots.
43 310

44 311 3.4 Range restriction

45 312 Patterns for community weighted mean range size and richness of range-restricted
46 313 species mirrored those of pasture and reference forest indicator species richness. The average
47 314 individual in pasture had a geographic range size approximately twice that of other habitats (Fig.
48 315 6A-B). Range-restricted species richness in restoration treatments was intermediate between
49 316 pasture and forest and increased over time (Fig. 6C-D).
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318 4. Discussion

319 Bird assemblages in all restoration treatments have recovered at least partially over time
320 for all metrics examined, indicating that restoration approaches across a gradient of effort
321 facilitate recovery. Whereas species richness and a multivariate similarity index provide a broad
322 picture of recovery in different treatments, trends in habitat-associations of constituent species
323 are informative for understanding the processes of and constraints on recovery, as emphasized by
324 previous studies on the recovery of habitat specialists in other faunal groups (e.g. Acevedo-
325 Charry and Aide, 2019; Audino et al., 2014; Díaz-García et al., 2020; Thompson and Donnelly,
326 2018). Within this study, recovery in restoration plots is characterized by (a) rapid loss of some
327 pasture species after agricultural abandonment, and (b) gradual increase in the presence of forest
328 species, with initial net gains in overall species richness due to the return of generalists.
329 Nonetheless, all restoration treatments contained some range-restricted species, which suggests
330 their potential to support regional biodiversity conservation and at least partially offset biotic
331 homogenization driven by land use change. This is consistent with evidence that relatively small
332 revegetated areas can offset the loss of woodland birds at landscape scales (Bennett et al., 2022).

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

344 While applied nucleation is considered an intermediate active restoration intervention,
345 bird assemblages were generally similar to those in plantation plots, despite differences in
346 canopy structure between these treatments (Holl et al., 2020; Zahawi, unpublished data). In
347 contrast, previous short-term studies in Brazil comparing areas restored using nucleation
348 techniques to traditional plantations and natural regeneration observed distinct assemblages
349 associated with nucleation (de Carvalho Barros et al., 2022; Vogel et al., 2015), but this could be
350 explained by the use of brush piles as a nucleation technique, rather than solely nucleation
351 planting. Our results were consistent with patterns of natural seedling recruitment (Holl et al.,
352 2017; Werden et al., 2022) and indicate that applied nucleation performs as well as tree
353 plantations for recovering bird communities over the medium term, and that overall bird
354 recovery may also translate to recovery of specific ecosystem functions like seed dispersal (Reid
355 et al., 2015). The costs of implementing applied nucleation in this study were lower than those of
356 plantations (Holl et al., 2020), as they were in a nucleation experiment in Brazil where nucleation
357 was up to 34% less expensive than high-diversity plantations (Campanhã Bechara et al., 2021).
358 However, conservation practitioners in Mexico have argued that the increased planning
359 complexity of applied nucleation projects makes them more expensive (Ramírez-Soto et al.,
360 2018).

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4 361 Despite increased resemblance of restoration treatments to reference forest, a recovery
5 362 gap remains after almost two decades, which is not surprising given that forest recovery is a
6 363 long-term process. Multiple local and landscape-scale factors may limit further recovery. For
7 364 example, some species require specific resources that can take years to develop, contributing to
8 365 the slow saturating shape of recovery even in a best-case scenario (Sinclair et al., 2018). The
9 366 vegetation composition of restoration plots in this study is following a trajectory toward remnant
10 367 forests but still differs substantially (Werden et al., 2022). Moreover, even with diverse natural
11 368 recruitment, most of the naturally recruiting trees are not yet reproductive and thus do not
12 369 provide flower and fruit resources. Even in restoration projects with higher native planted
13 370 diversity (e.g. >20 species), in which tree composition was more similar to reference forests,
14 371 actively restored forests host fewer rainforest species than reference forests do (Catterall et al.,
15 372 2012; Hariharan and Raman, 2021), suggesting that both vegetation composition and structure
16 373 play a role in bird responses, though it is challenging to tease out the independent effects.

17 374 Whereas restoration practitioners have most direct control over local habitat
18 375 characteristics, bird community recovery is constrained at multiple larger landscape-level spatial
19 376 scales through the composition of regional species pools, colonization and extinction
20 377 probabilities mediated by forest connectivity, and faunal selection of available habitat (Freeman
21 378 et al., 2015; Mayhew et al., 2019; Reid et al., 2021, 2014). In the absence of adjacent forest,
22 379 these restoration plots represent small habitat patches with intrinsic edge effects, two factors that
23 380 limit understory insectivores (Lindell et al., 2007; Martensen et al., 2012). Edge effects also
24 381 likely contribute to the persistence of some pasture species in restoration plots. Indeed, landscape
25 382 tree cover and configuration in this study system influence use of restored habitats by large
26 383 frugivores and other forest-dependent birds (Reid et al., 2021; San-José et al., 2022). Thus, in the
27 384 absence of landscape-scale efforts to increase connectivity, some forest-restricted species are not
28 385 expected to use restored plots with minimal nearby forest.

29 386 Long-term monitoring of reference systems at multiple sites was a key feature of this
30 387 study. Importantly, the natural variability of tropical wet forest bird communities is high, such
31 388 that for a pairwise community similarity index, a value of ~0.4 may be a realistic restoration
32 389 target. The fact that we did not observe directional shifts in pasture or reference forest
33 390 community metrics suggests that directional changes observed in restoration plots were due to
34 391 local-scale change rather than regional dynamics. This is important because both tree and bird
35 392 communities in remnant forests within agricultural landscapes are likely to experience ongoing
36 393 and time-lagged effects of regional-scale forest loss, degradation, and fragmentation (Hendershot
37 394 et al., 2020; Newmark et al., 2017; Rutt et al., 2019; Şekercioglu et al., 2019). Even at relatively
38 395 undisturbed sites, bird communities have experienced long-term shifts, possibly due to climate
39 396 change (Freeman et al., 2018; Pollock et al., 2022; Stouffer et al., 2021).

40 397 Given the layout and size of treatment plots, we interpret our results with some caveats
41 398 regarding spatial proximity and habitat use. First, while spillover effects were possible given that
42 399 our three treatments were adjacent to each other, we still observed differences despite close
43 400 spatial proximity; this suggests that our results represent lower-bound estimates of differences
44 401 between treatments. Second, greater bird detectability in pastures could have reduced the
45 402 observed differences in species richness compared to restoration plots. Third, the size of
46 403 restoration plots means that our observations reflect recovery patterns of habitat use by bird
47 404 species, not recovery dynamics of populations, which is a common issue with assessing effects
48 405 of restoration plots on vertebrates (Robinson, 2010). Even if some species only transited through
49 406 the small restoration plots rather than using them as core habitat for foraging or reproduction,
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4 407 their presence shows promise for improving functional connectivity, which is key to preventing
5 408 extirpations at larger scales (Newmark et al., 2017).
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8 410 **5. Conclusions**

10 411 Passive and active restoration approaches can both be viable options for facilitating bird
11 412 community recovery on degraded agricultural land in initial decades and may help counteract
12 413 biotic homogenization. Although planting trees accelerated recovery relative to natural
13 414 regeneration, a planting design with ~25% of the planting intensity performed comparably to
14 415 traditional uniformly-planted plots. Therefore, we strongly encourage restoration practitioners to
15 416 (a) consider interventions that are intermediate between natural regeneration and intensive
16 417 planting, (b) match their approach to specific desired outcomes and timeframes, and (c) evaluate
17 418 progress using interim targets (Watts et al., 2020). Insights from outcomes of long-term,
18 419 replicated, multi-treatment restoration experiments compared to the background variability in
19 420 reference systems represent an invaluable guide for large-scale tree planting initiatives and for
20 421 gauging faunal recovery trajectories in species-rich tropical ecosystems.
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25 423 **Data availability statement**

26 424 Data and code are available in a GitHub repository and will be archived on Dryad prior to
27 425 publication.
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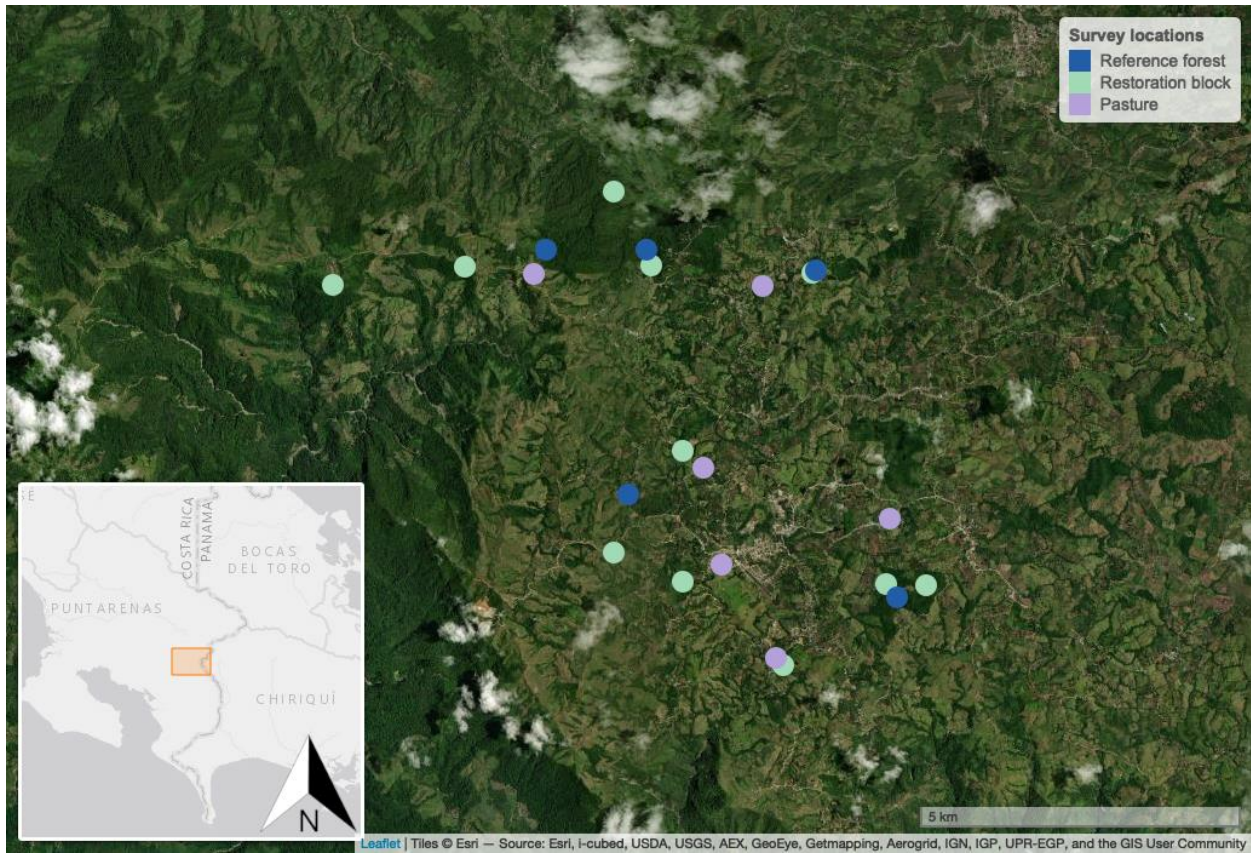
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678 Figure 1. Bird survey locations in Coto Brus, southern Costa Rica. Each restoration block
679 contains one plot of each restoration treatment (plantation, applied nucleation, and natural
680 regeneration).

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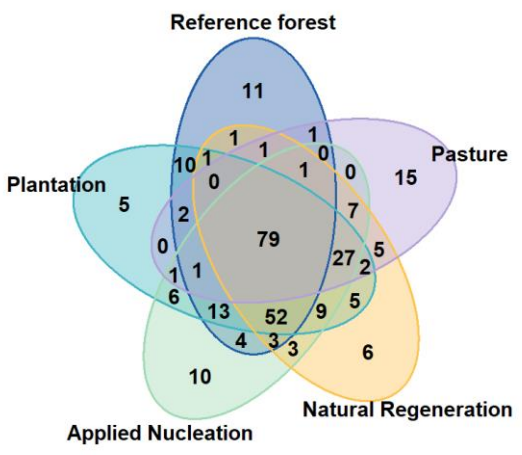


Figure 2. Venn diagram of bird species detected in each habitat type over the study period (9 years for pastures and reference forests, 12 years for restoration plots; n = 281 species total).

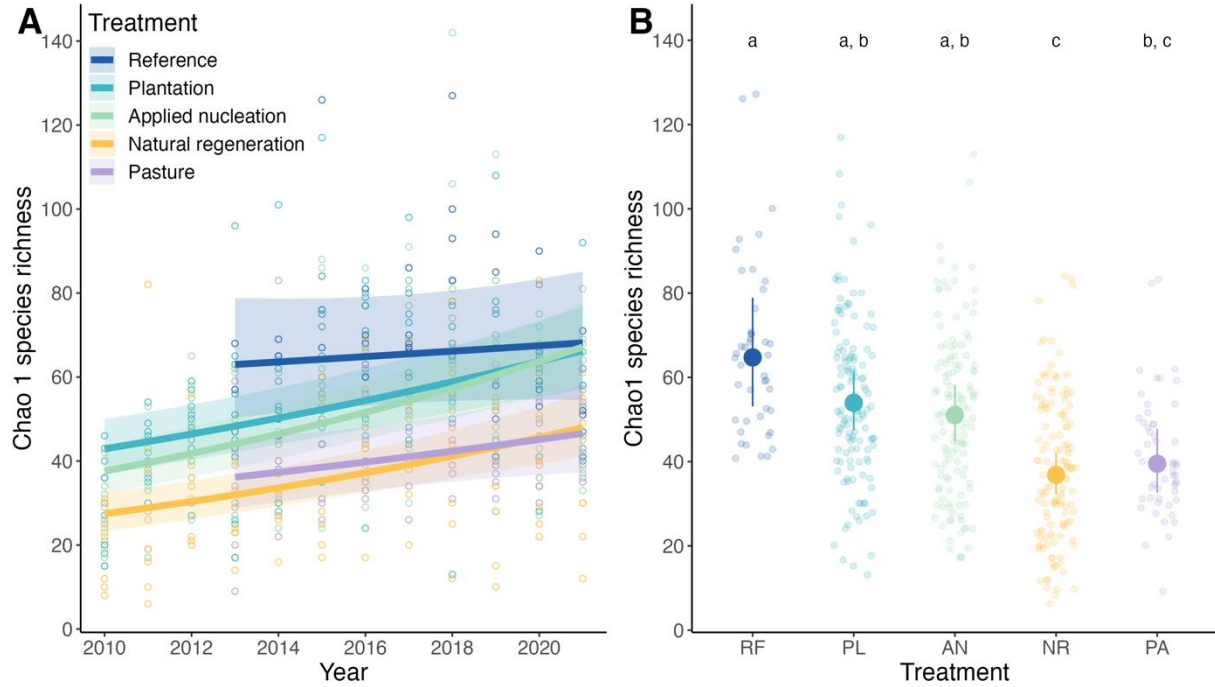


Figure 3. Species richness (Chao1 estimator) varied over time and among habitat types. **(A)** Model predictions (lines with 95% confidence interval bands) show positive slopes for applied nucleation and natural regeneration and marginally significant positive slopes for plantation. Time since restoration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

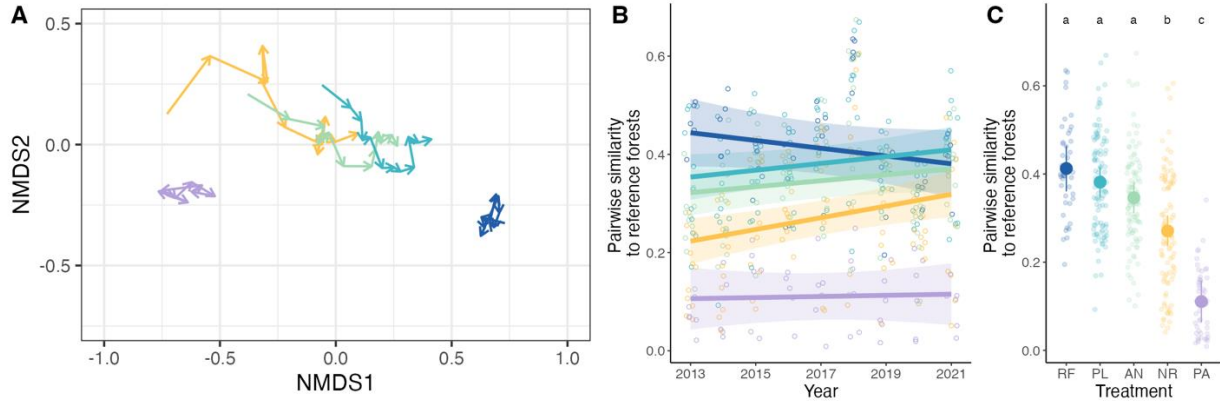


Figure 4. Community trajectories and similarity to reference forests. **(A)** Community trajectories in NMDS ordination space, based on a Morisita-Horn dissimilarity matrix of annual communities. Points represent the annual average (centroid) for each treatment. Arrows represent compositional change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

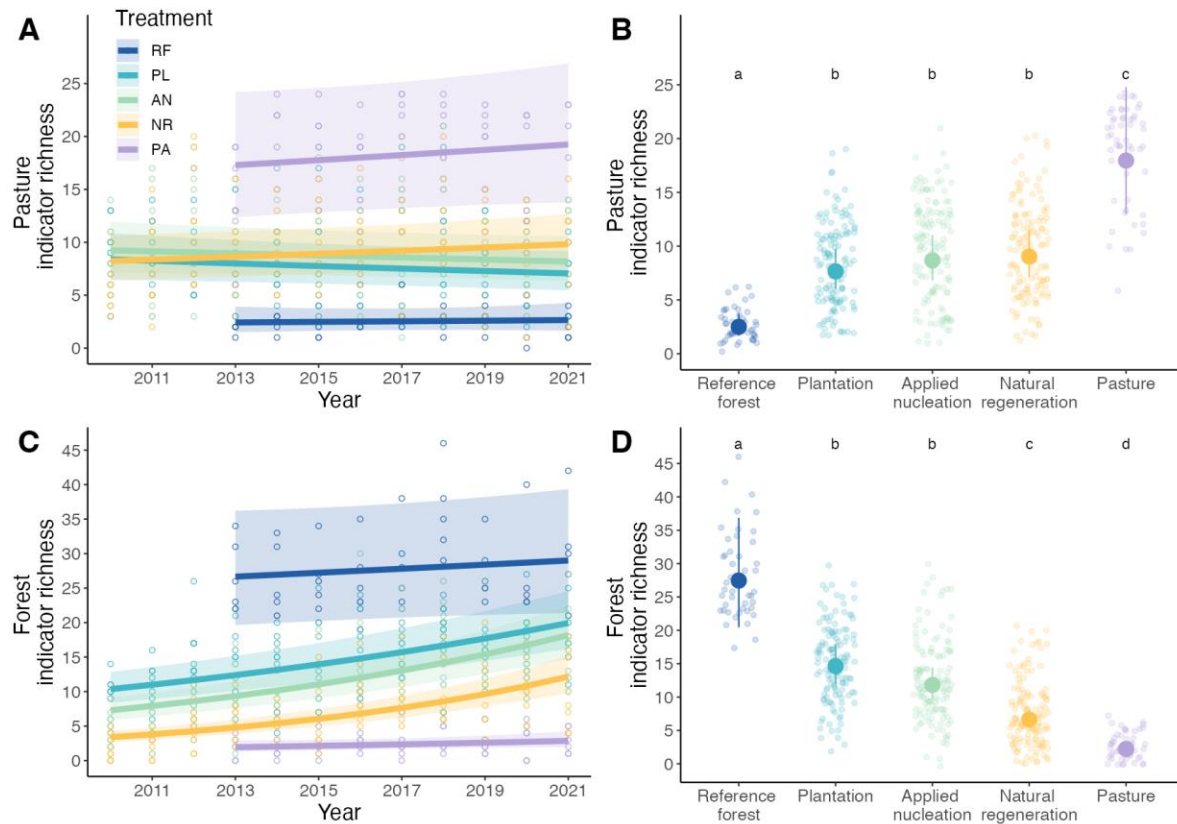


Figure 5. Indicator species richness trends. **(A)** Observed pasture indicator species richness by treatment and year. Lines with ribbons represent model predictions and 95% CI. There were no significant trends over time in any of the habitat types. **(B)** Observed pasture indicator richness by treatment.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

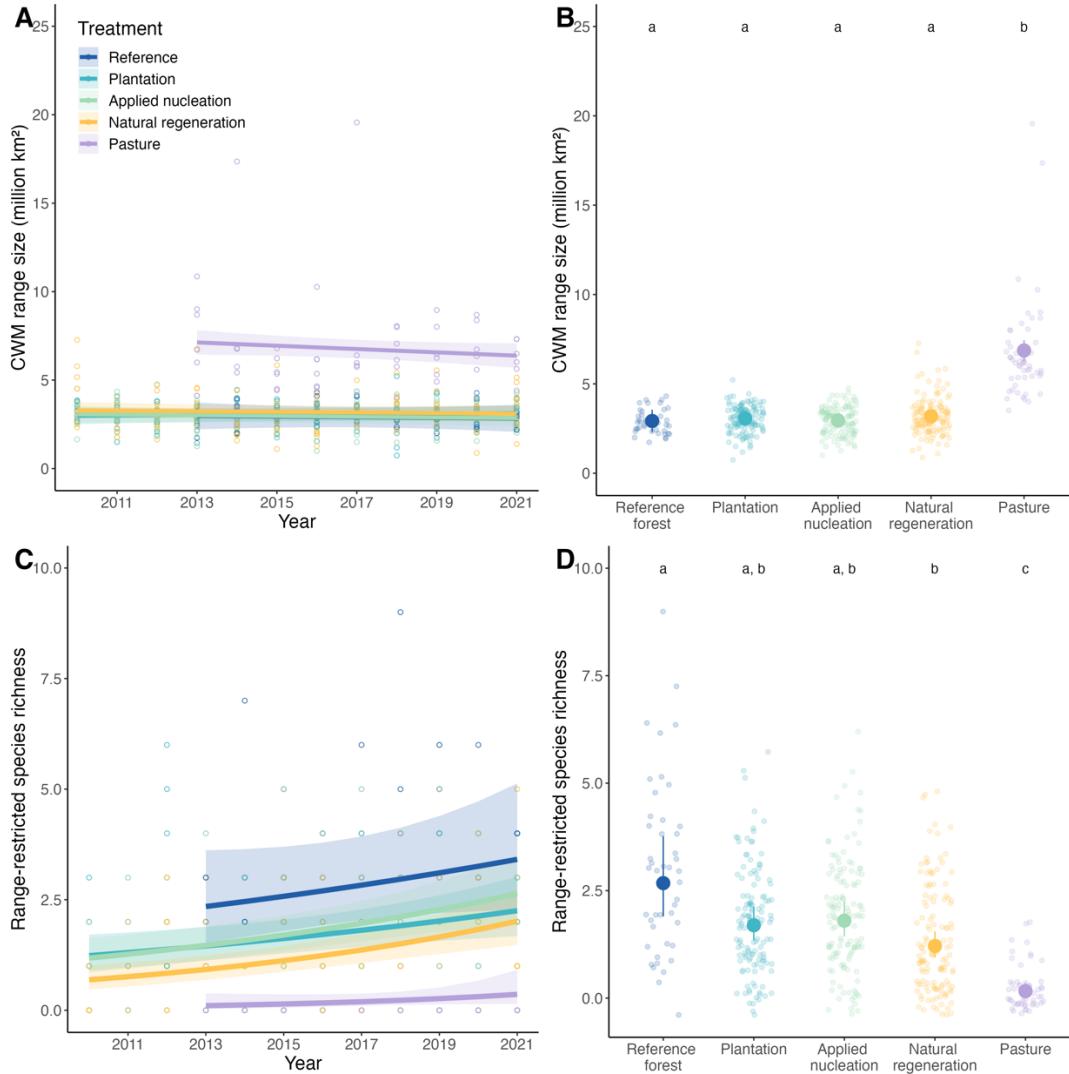


Figure 6. Range size trends. **(A)** Community-weighted mean range size by treatment and year. Lines with ribbons represent model predictions and 95% CI. **(B)** CWM range size by treatment. Large points represent treatment-level estimated marginal means and vertical lines represent 95% CI. **(C)** Observed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

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

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20

21 **Authors' contributions**

22 K.D.H and R.A.Z. created and implemented the restoration experiment; J.L.R. conceived of the bird
23 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
24 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
25 critically to manuscript drafts.

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1 Active restoration accelerates recovery of tropical forest bird assemblages over two 2 decades

3 Abstract

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

25 Keywords

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

28 1. Introduction

29 Understanding how different restoration approaches influence faunal recovery is essential
30 to guide tropical forest restoration efforts and achieve desired outcomes for biodiversity
31 conservation. Birds are a key group in tropical forest restoration because they both benefit from
32 restoration and promote forest regeneration through pollination and seed dispersal interactions
33 (Catterall, 2018). The choice of restoration approach can strongly affect vegetational trajectories
34 and in turn local habitat characteristics that influence avian habitat use (Reid et al., 2012). Two
35 common approaches are native tree plantations, which are resource-intensive but develop canopy
36 cover faster, and passive restoration, in which sites are protected from disturbance but otherwise
37 left to regenerate naturally. As passive restoration generally involves lower costs, it has been
38 promoted for forest restoration at large scales (Chazdon and Uriarte, 2016). However,
39 trajectories of natural regeneration are highly variable and depend on land use history and
40 proximity to source populations (Holl and Aide, 2011). In the absence of intervention, areas
41 under passive restoration can remain in a state of arrested succession (Sarmiento, 1997).
42 Meanwhile, there is growing evidence that intermediate strategies along an intervention

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4 43 continuum (Chazdon et al., 2021), such as applied nucleation, can accelerate vegetation recovery
5 44 at lower cost while creating more structural complexity (Holl et al., 2020).

6 45 The long-term efficacy of differing restoration methods for creating forest habitats for
7 46 birds depends both on initial differences among restoration treatments and how they change over
8 47 time. Comparing active and passive restoration is difficult because they have typically been
9 48 assessed using different study designs and in different locations (Shoo and Catterall, 2013). Past
10 49 studies have often relied on chronosequences (Acevedo- Charry and Aide, 2019; Sayer et al.,
11 50 2017), which sometimes confound temporal variability and past land use (Johnson and
12 51 Miyanishi, 2008), or comparisons of passively and actively restored sites selected years after
13 52 restoration, which are subject to positive selection bias for passively restored sites (i.e., sites that
14 53 showed successful recovery, Reid et al., 2018). Few studies directly compare passive recovery
15 54 with active restoration strategies in the same system (Jones et al., 2018) and those that do
16 55 typically have just a few years of data, which may not reflect longer-term trajectories.
17 56 Accordingly, how bird assemblages in restoration treatments of varying intensity recover over
18 57 time at the same sites remains an open question.

19 58 Evidence from multiple continents demonstrates that native tree plantations can benefit
20 59 bird recovery by providing a closed canopy and vertical stratification (e.g., Catterall et al., 2012;
21 60 Hariharan and Raman, 2021; Latja et al., 2016). However, forest-dependent birds may require
22 61 specific microclimates, food items, or nest sites, that can take decades to develop (Vesk et al.,
23 62 2008). Understory insectivores in particular are sensitive to disturbance and show limited
24 63 dispersal across anthropogenic matrices (Powell et al., 2015; Şekercioğlu et al., 2002). Forest-
25 64 affiliated species also tend to include more specialized habitat requirements and include range-
26 65 restricted species. In contrast, species found in agricultural lands tend to be disturbance-adapted
27 66 and have large range sizes. As such, land conversion can result in biotic homogenization of
28 67 avifauna by extirpating specialist species and favoring disturbance-tolerant over wide areas
29 68 (Karp et al., 2012), but the degree to which restored forests regain forest specialists and range
30 69 restricted species over observable time frames is poorly understood.

31 70 Disentangling the effects of restoration treatment on avian habitat use from those of site
32 71 age and context requires long-term, multi-site, and multi-treatment studies that also include
33 72 reference and degraded sites surveyed multiple times to account for regional trends which may
34 73 be occurring independently of local restoration efforts, for example population declines (e.g.,
35 74 Blake and Loiselle, 2016; Sigel et al., 2006) or range expansions. Here, we report on decadal
36 75 avian assemblage recovery in restoration plots that were subjected to three different restoration
37 76 interventions replicated widely across an agricultural landscape in southern Costa Rica (Holl et
38 77 al., 2020). Specifically, we compared the effects of two active restoration treatments (plantation
39 78 and applied nucleation) and a passive natural regeneration restoration treatment on bird species
40 79 richness and compositional similarity to reference forests, relative to degraded pastures and
41 80 reference forests. We asked: (1) How do bird species richness, community composition, and
42 81 similarity to reference forest differ among restoration treatments and how do they change over
43 82 time? (2) How do pasture-affiliated and forest-affiliated bird species vary among restoration
44 83 treatments over time? (3) Are restored sites gaining range-restricted species?

45 84 Based on early 'snapshot' comparisons in this study system (Reid et al., 2014) and
46 85 studies in other systems, we expected that recovery of richness (Edwards et al., 2009) and
47 86 composition (Hariharan and Raman, 2021) would be greater in planted restoration treatments
48 87 than in natural regeneration. We also anticipated that differing responses by pasture- and forest-
49 88 affiliated birds would underlie community-level changes in richness and composition over time

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4 89 (Catterall et al., 2012), and that shifts in forest specialists would be reflected in community
5 90 metrics of geographic range size (Dunn and Romdal, 2005; Karp et al., 2019).
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8 92 **2. Materials and methods**

9 93 *2.1 Study area*

10 94 This study took place in southern Costa Rica (8°44' – 8°47' N, 82°56' – 82°57' W). The
11 95 native ecosystem is transitional between tropical premontane wet forest and premontane rain
12 96 forest (Holdridge and Grenke, 1971). Site elevation ranges from 1080-1430 m.a.s.l. Mean annual
13 97 temperature is ~21°C at the Las Cruces Biological Station, which is within the study landscape.
14 98 Median annual rainfall for 2005-2022 was 3.7 m (range 2.8-4.9 m), with a dry season from
15 99 December to March. The landscape was largely deforested between 1947-1980 and is now a
16 100 fragmented mosaic of cattle pastures and agricultural fields interspersed with patches of remnant
17 101 and secondary forest, with overall regional forest cover ~28% as of 2014 (Zahawi et al., 2015).
18 102 In recent decades ongoing deforestation has been partially offset by second growth, and for the
19 103 2005-2014 period the study landscape experienced a small net increase in forest cover (Amar,
20 104 2020).
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22 106 *2.2 Restoration experimental design*

23 107 The three forest restoration treatments (Holl et al., 2020) were established at 11 sites (Fig.
24 108 1, Table S1) over three years (2004-2006). All sites are separated by >700 m. At each site three
25 109 0.25 ha (50 × 50 m) plots were established and assigned to one of three treatments: plantation
26 110 (PL), applied nucleation (AN), or natural regeneration (NR). Plots were separated by ≥5 m.
27 111 Plantation plots were planted uniformly with tree seedlings, whereas in the applied nucleation
28 112 treatment we planted six tree nuclei of three sizes: two each of 4 × 4, 8 × 8 and 12 × 12 m. Tree
29 113 spacing was ~2.8 m, with 313 trees planted in plantation and 86 in applied nucleation. In both
30 114 active restoration treatments, we planted two native tree species, *Terminalia amazonia*
31 115 (Combretaceae) and *Vochysia guatemalensis* (Vochysiaceae), and two naturalized fast-growing
32 116 N-fixing species, *Erythrina poeppigiana* and *Inga edulis* (both Fabaceae) that are used in
33 117 agricultural intercropping systems. Naturally established vegetation was cleared prior to planting
34 118 and at ~3-mo intervals for 2.5 years in all plots to allow planted seedlings to grow above other
35 119 vegetation.
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37 121 By 2019 (13-15 years after plot set up), most plantation plots had a tall (~ 15 m),
38 122 homogeneous canopy cover and fairly sparse mid-story shrub and small tree cover (Holl et al.,
39 123 2020). The two fast-growing planted Fabaceae species experienced substantial mortality, with
40 124 ~36% of *Erythrina* and ~34% of *Inga* surviving to 2020 (14-16 y after planting; Holl & Zahawi
41 125 unpublished data). This mortality, combined with falling branches, has led to greater
42 126 accumulation of coarse woody debris and standing dead wood in planted treatments compared to
43 127 natural regeneration (Fernandez Barrancos et al., 2022). Applied nucleation plots are
44 128 characterized by high overall canopy cover of variable height. By 2019, most natural
45 129 regeneration plots had patchy, relatively short canopy cover surrounded by dense exotic pasture
46 130 grass cover, although some had greater tree and shrub cover.
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48 132 *2.3 Bird data collection*

49 133 From 2010-2021 (12 years), we surveyed birds in all restoration plots (n = 33 plots).
50 134 Between 2013-2021 (9 years), we also surveyed birds in 0.25 ha (50 × 50 m) survey areas within
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4 134 five reference forests (RF) and six active cattle pastures (PA) for a total of 44 total survey plots
5 135 (Fig. 1, Table S1). Reference forests and active pastures were located within the same study
6 136 region and elevational range but not precisely paired with restoration blocks (distance to nearest
7 137 restoration plot: ~20-1000 m for reference forests; ~300-1000 m for active pastures). Reference
8 138 forests were subject to variable fragmentation and disturbance but represent “best available”
9 139 examples of local remnant forest habitat. Three times per year (Apr-May, Jul-Aug, Nov-Dec), a
10 140 single skilled observer [(REDACTED)] actively searched each sampling area for 20 min,
11 141 walking along existing trails, and recorded all birds seen or heard within the plot area.
12 142 Observations of flyover birds not perching or foraging were excluded from analyses. Surveys
13 143 were conducted between 05:50-09:00 h in mild weather, including light fog or mist but not high
14 144 wind or rain. The order in which restoration treatments were surveyed was varied to avoid
15 145 systematic bias in survey start time.

16 146 The resulting data set includes 1467 surveys representing 489 hours of sampling effort.
17 147 Data for twenty surveys (1.3%) were missing and spread relatively evenly across treatments.
18 148 Species names were standardized to the 7th Checklist of the American Ornithological Society
19 149 (Chesser et al., 2022). We obtained the IUCN Red List extinction risk assessment category for
20 150 each species using the *rredlist* package v0.7.0 (IUCN, 2022).

21 151 22 152 *2.4 Data analysis*

23 153 We aggregated survey-level bird abundance data by plot and year to obtain annual
24 154 assemblages (n = 495) and used these as sampling units for analyses. Rather than summing
25 155 individuals detected for each species across the three survey seasons, we aggregated by the
26 156 maximum count (sensu Julliard et al., 2006), to (a) minimize counting highly resident individuals
27 157 multiple times and (b) avoid interpolating abundances in missing surveys. We performed all
28 158 analyses with R version 4.1.2 (R Core Team, 2022).

29 159 To assess the effects of habitat type (hereafter synonymous with ‘treatment’) and
30 160 treatment-specific effects of time on community recovery we calculated multiple metrics and
31 161 fitted separate generalized linear mixed models (GLMMs) using *glmmTMB* v1.1.4 (Brooks et al.,
32 162 2017) or linear mixed effect models using *lme4* v1.1.30 (Bates et al., 2015) for each response
33 163 variable. We used survey year (calendar year - first year of monitoring) as the time covariate
34 164 rather than years since restoration because the latter is not a meaningful variable for pastures and
35 165 reference forests. In all models we included a random intercept term for plot nested within site to
36 166 account for non-independence of bird assemblages sampled within the same plots and clustered
37 167 within sites. Forest and pasture plots within 450 m of a restoration block were assigned to that
38 168 site. Because forest and pasture survey locations were not always paired with restoration blocks,
39 169 the fixed effects of reference forest and pasture habitat types were partly confounded with site
40 170 effects. Therefore, there was lower power for testing the effects of reference forest and pasture
41 171 habitats. For all fitted models, we examined residual diagnostics, including temporal
42 172 autocorrelation functions, in package *DHARMA* v0.4.6 (Hartig, 2020). To compare the predicted
43 173 main effects of treatments and their interactions with time we used package *emmeans* v1.8.1.

44 174 45 175 *2.5 Species richness*

46 176 To compare species richness while accounting for undetected species, we calculated the
47 177 abundance-based Chao1 species richness estimator for each annual assemblage using package
48 178 *iNEXT* v3.0.0 (Chao et al., 2014b; Hsieh et al., 2016). To evaluate sample completeness for each
49 179 annual community we calculated sample coverage (Chao et al., 2014a). We modeled species

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4 180 richness using a negative binomial error distribution with a log link function because a Poisson
5 181 model had overdispersed residuals. We modeled sample coverage (bounded 0-1) using beta-
6 182 distributed residuals with a logit link function.
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9 184 *2.6 Community composition*

10 185 To assess recovery of community composition, we first created a matrix of abundance-
11 186 based community dissimilarities (package *vegan* version 2.6-2; Oksanen et al., 2013). We used
12 187 the Morisita-Horn index, since it is robust to variation in sample size and coverage (Chao et al.,
13 188 2006; Dent and Wright, 2009). We visualized the trajectories of species composition using
14 189 nonmetric multidimensional scaling, plotting the average (centroid) assemblage for each
15 190 treatment in each year (De Cáceres et al., 2019). To assess whether bird assemblages using
16 191 restoration plots were approaching those of reference forest while taking into account the spatial
17 192 and temporal variability of reference forests, we also calculated the mean similarity (1-
18 193 dissimilarity) of each annual community to each of the reference forest communities for the last
19 194 nine years of the data set, when reference forests were surveyed (2013-2021; n = 5 reference
20 195 forest communities for comparison to each restoration and pasture plot; n = 4 communities for
21 196 forest-to-forest comparisons). Similarity among reference forests is interpretable as a metric of
22 197 reference forest beta diversity (Anderson et al., 2011), and this natural variability constrains the
23 198 average similarity to reference forest attainable by restoration treatments (Gerwing and Hawkes,
24 199 2021). We fit a linear mixed effect model for mean pairwise similarity to reference forest
25 200 communities because a beta-distributed model failed to converge.
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30 201 *2.7 Habitat association*

31 202 To explore how community-scale shifts in species composition reflect responses of birds
32 203 with different habitat affinities, we first identified species associated with particular habitat types
33 204 (“indicator species”, sensu De Cáceres and Legendre, 2009) using the *indicspecies* v1.7.12
34 205 package, based on a priori habitat categorization of survey plots. We used the abundance-based
35 206 point biserial correlation coefficient as the association function, corrected for unequal numbers
36 207 of sites per habitat type (func= ‘r.g.’), and assessed significance at $\alpha = 0.05$ based on 999
37 208 permutations (following Hariharan and Raman, 2021). To first explore associations between bird
38 209 species and the five habitat types, we identified indicator species based on the full data set.
39 210 Second, to assess temporal trends in the richness of pasture and forest affiliated birds in
40 211 restoration treatments, indicator species based on the subset of data with just pasture and forest
41 212 plots. This provided lists of indicator species derived independently of restoration plot surveys.
42 213 We modeled observed richness of indicator species using a GLMM with a Poisson error
43 214 distribution and a log link function.
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48 216 *2.8 Geographic range size*

49 217 We used two metrics to assess patterns of bird geographic range size (from Tobias et al.,
50 218 2022) across habitats and time. We calculated the community weighted mean (CWM) value of
51 219 geographic range size using the *FD* v1.0-12.1 package (Laliberté et al., 2014). This is similar to
52 220 the “community range index,” used to characterize one facet of bird assemblage “commonness”
53 221 and as a metric of biotic homogenization (Godet et al., 2015). We also used the observed
54 222 richness of range-restricted species (range size $\leq 50,000$ km²), which is commonly used as a
55 223 metric of endemism (Ocampo-Peñuela et al., 2016).
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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 aurantirostris*, 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)

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4 272 ranged from 0.33-0.60 (estimated marginal mean = 0.41). Although planted restoration
5 273 treatments reached comparable levels of pair-wise similarity to reference forests, their between-
6 274 group dissimilarity was driven by distinct composition (Fig. 4A, Fig. S3).
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9 276 3.3 Habitat association

10 277 Indicator species analysis with all treatments identified 104 species (37%) that were
11 278 significantly associated with a particular habitat type (reference forest: 63; pasture: 39;
12 279 plantation: 1; natural regeneration: 1; $p < 0.05$). The species most strongly associated with
13 280 reference forest were *Henicorhina leucosticta*, *Corapipo altera*, *Arremon aurantiirostris*, and
14 281 *Dysithamnus mentalis*. Widespread open-country birds such as *Troglodytes aedon*, *Tiaris*
15 282 *olivaceus*, *Sporophila corvina*, *Zonotrichia capensis*, and *Tyrannus melancholicus* were
16 283 associated with pasture sites. The indicator species for plantation was *Pachyramphys*
17 284 *polychopterus*, a species typically found in wooded areas but generally not mature forest. The
18 285 natural regeneration indicator species was *Laterallus albigularis*, a rail typically found in areas
19 286 with dense grass. When we only considered reference forest and pasture surveys, we identified
20 287 similar sets of reference forest (81) and pasture (39) indicator species (Appendix 2). These
21 288 included some species that had a clear habitat preference when only considering pasture and
22 289 reference forest but were also commonly found in restoration treatments and thus were not
23 290 identified as indicators in the previous analysis. For example, *Thraupis episcopus* was a
24 291 generalist pasture indicator, whereas *Catharus aurantiirostris* was a generalist forest indicator.
25 292

26 293 Only half of the pasture-affiliated species were found in restoration plots, and only one-
27 294 sixth were found in reference forests. There were no temporal trends in pasture indicator richness
28 295 for any treatment (Fig. 5A, Table S9). In contrast, forest indicator species richness gradually
29 296 increased over time in all three restoration treatments with higher intercepts in planted treatments
30 297 but a slightly higher slope in natural regeneration (Fig. 5B, Tables S10-S12). Some forest
31 298 indicator species used restoration plots with increasing frequency (e.g., *Tangara icterocephala*
32 299 and *Henicorhina leucosticta*). A few forest species (e.g., *Zentrygon chiriquensis*) were never
33 300 recorded in restoration plots.
34 301

35 302 3.4 Range restriction

36 303 Patterns for community weighted mean range size and richness of range-restricted
37 304 species mirrored those of pasture and reference forest indicator species richness. The average
38 305 individual in pasture had a geographic range size approximately twice that of other habitats (Fig.
39 306 6A). Range-restricted species richness in restoration treatments was intermediate between
40 307 pasture and forest and increased over time (Fig. 6B).
41 308

42 309 4. Discussion

43 310 Bird assemblages in all restoration treatments have recovered over time for all metrics
44 311 examined, indicating that restoration approaches across a gradient of effort facilitate recovery.
45 312 Whereas species richness and a multivariate similarity index provide a broad picture of recovery
46 313 in different treatments, trends in habitat-associations of constituent species are informative for
47 314 understanding the processes of and constraints on recovery. Recovery in restoration plots is
48 315 characterized by (a) rapid loss of some pasture species after agricultural abandonment, and (b)
49 316 gradual increase in the presence of forest species, with initial net gains in overall species richness
50 317 due to the return of generalists. Nonetheless, all restoration treatments contained some range-

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4 317 restricted species, which suggests their potential to support regional biodiversity conservation
5 318 and at least partially offset biotic homogenization driven by land use change. This is consistent
6 319 with evidence that relatively small revegetated areas can offset the loss of woodland birds at
7 320 landscape scales (Bennett et al., 2022).

9 321 Natural regeneration bird assemblages showed less absolute recovery than those in
10 322 planted treatments for many metrics, but that disparity is narrowing. Although natural
11 323 regeneration started with the fewest species and least similar composition to reference forest,
12 324 forest indicators increased at a higher rate over the 12 years assessed here, and it was the only
13 325 restoration treatment with increasing similarity to reference forest over the full study period. This
14 326 suggests that natural regeneration may be a cost-effective approach for restoration practitioners
15 327 working on longer (i.e., multidecadal) time horizons, and the tradeoff between cost and habitat
16 328 quality during the first decade of succession is an important consideration. Although natural
17 329 regeneration harbored fewer forest indicators, generalist insectivore species that also consume
18 330 fruit can be important for dispersing seeds and driving forward vegetation succession (Carlo and
19 331 Morales, 2016).

22 332 While applied nucleation is considered an intermediate active restoration intervention,
23 333 bird assemblages were generally similar to those in plantation plots, despite differences in
24 334 canopy structure between these treatments (Holl et al., 2020). Results are consistent with patterns
25 335 of natural seedling recruitment in these plots and indicate that applied nucleation performs as
26 336 well as tree plantations for recovering bird communities over the medium term, and that overall
27 337 bird recovery may also translate to recovery of specific ecosystem functions like seed dispersal
28 338 (Reid et al., 2015).

31 339 Despite increased resemblance of restoration treatments to reference forest, a recovery
32 340 gap remains after almost two decades, which is not surprising given that forest recovery is a
33 341 long-term process. Multiple local and landscape-scale factors may limit further recovery. For
34 342 example, some species require specific resources that can take years to develop, contributing to
35 343 the slow saturating shape of recovery even in a best-case scenario (Sinclair et al., 2018). Whereas
36 344 restoration practitioners have most direct control over local habitat characteristics, bird
37 345 community recovery is constrained at multiple larger landscape-level spatial scales through the
38 346 composition of regional species pools, colonization and extinction probabilities mediated by
39 347 forest connectivity, and faunal selection of available habitat (Freeman et al., 2015; Mayhew et
40 348 al., 2019; Reid et al., 2021, 2014). In the absence of adjacent forest, these restoration plots
41 349 represent small habitat patches with intrinsic edge effects, two factors that limit understory
42 350 insectivores (Lindell et al., 2007; Martensen et al., 2012). Edge effects also likely contribute to
43 351 the persistence of some pasture species in restoration plots. Indeed, landscape tree cover and
44 352 configuration in this study system influence use of restored habitats by large frugivores and other
45 353 forest-dependent birds (Reid et al., 2021; San-José et al., 2022). Thus, in the absence of
46 354 landscape-scale efforts to increase connectivity, some forest-restricted species are not expected
47 355 to use restored plots with minimal nearby forest.

52 356 Long-term monitoring of reference systems at multiple sites was a key feature of this
53 357 study. Importantly, the natural variability of tropical wet forest bird communities is high, such
54 358 that for a pairwise community similarity index, a value of ~0.4 may be a realistic restoration
55 359 target. The fact that we did not observe directional shifts in pasture or reference forest
56 360 community metrics suggests that directional changes observed in restoration plots were due to
57 361 local-scale change rather than regional dynamics. This is important because both tree and bird
58 362 communities in remnant forests within agricultural landscapes are likely to experience ongoing

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4 363 and time-lagged effects of regional-scale forest loss, degradation, and fragmentation (Hendershot
5 364 et al., 2020; Newmark et al., 2017; Rutt et al., 2019; Şekercioğlu et al., 2019). Even at relatively
6 365 undisturbed sites, bird communities have experienced long-term shifts, possibly due to climate
7 366 change (Freeman et al., 2018; Pollock et al., 2022; Stouffer et al., 2021).

8 367
9 368 Given the layout and size of treatment plots, we interpret our results with some caveats
10 369 regarding spatial proximity and habitat use. First, while spillover effects were possible given that
11 370 our three treatments were adjacent to each other, we still observed differences despite close
12 371 spatial proximity; this suggests that our results represent lower-bound estimates of differences
13 372 between treatments. Second, the size of restoration plots means that our observations reflect
14 373 recovery patterns of habitat use by bird species, not recovery dynamics of populations, which is a
15 374 common issue with assessing effects of restoration plots on vertebrates (Robinson, 2010). Even
16 375 if some species only transited through the small restoration plots rather than using them as core
17 376 habitat for foraging or reproduction, their presence shows promise for improving functional
18 377 connectivity, which is key to preventing extirpations at larger scales (Newmark et al., 2017).

23 378 **5. Conclusions**

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25 379 Passive and active restoration approaches can both be viable options for facilitating bird
26 380 community recovery on degraded agricultural land in initial decades and may help counteract
27 381 biotic homogenization. Although planting trees accelerated recovery relative to natural
28 382 regeneration, a planting design with an ~80% reduction in planting intensity performed
29 383 comparably to traditional uniformly-planted plots. Therefore, we strongly encourage restoration
30 384 practitioners to (a) consider interventions that are intermediate between natural regeneration and
31 385 intensive planting, (b) match their approach to specific desired outcomes and timeframes, and (c)
32 386 evaluate progress using interim targets (Watts et al., 2020). Insights from outcomes of long-term,
33 387 replicated, multi-treatment restoration experiments compared to the background variability in
34 388 reference systems represent an invaluable guide for large-scale tree planting initiatives and for
35 389 gauging faunal recovery trajectories in species-rich tropical ecosystems.

39 390 **Data availability statement**

40 391 Data and code are available in a GitHub repository and will be archived on Dryad prior to
41 392 publication.
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44 395 **References**

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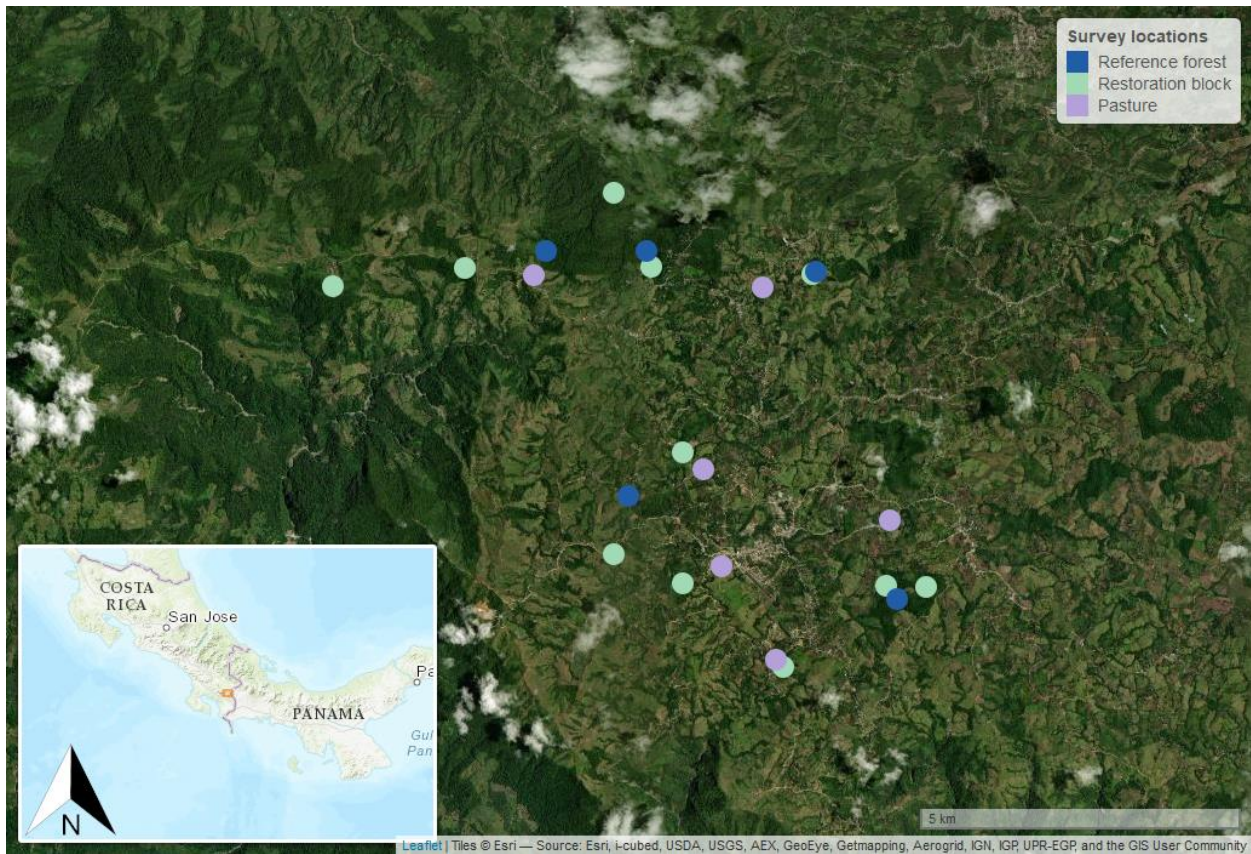
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629 Figure 1. Bird survey locations in Coto Brus, southern Costa Rica. Each restoration block
630 contains one plot of each restoration treatment (plantation, applied nucleation, and natural
631 regeneration).

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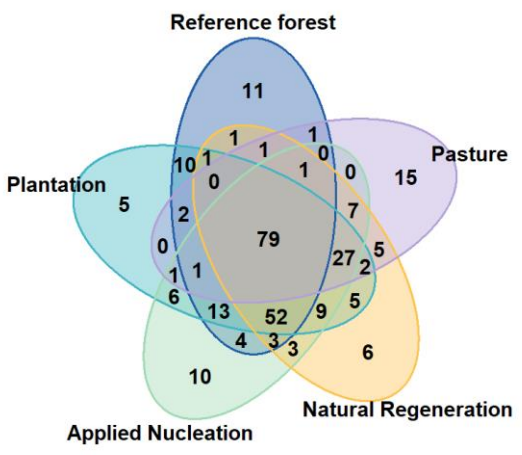


Figure 2. Venn diagram of bird species detected in each habitat type over the study period (9 years for pastures and reference forests, 12 years for restoration plots; n = 281 species total).

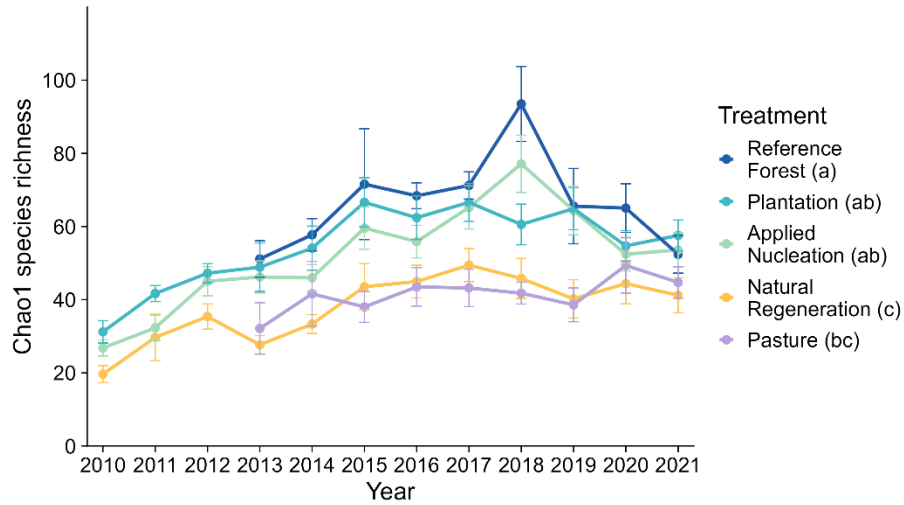


Figure 3. Plot-level species richness (Chao1 estimator) grouped by treatment (mean \pm SE). Time since restoration ranges from 4-6 years in 2010 to 15-17 years in 2021. N = 11 plots per restoration treatment, 5 reference forests, 6 active pastures. Different legend label letters in parentheses indicate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

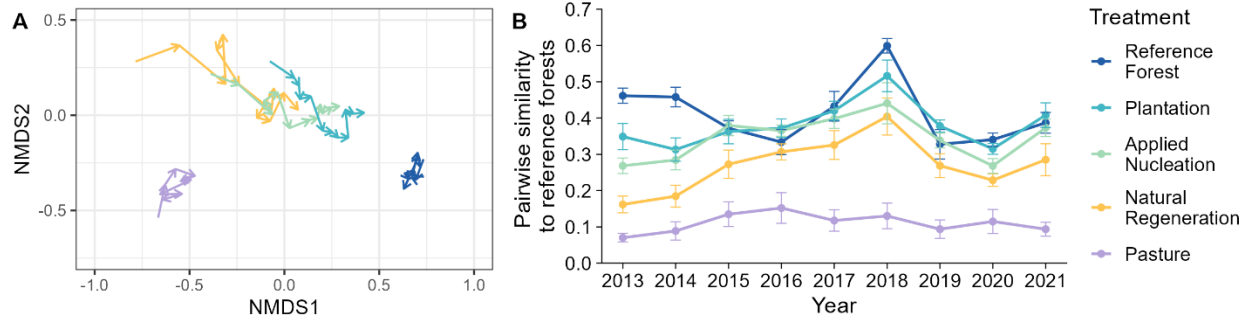


Figure 4. Community trajectories and similarity to reference forests. **(A)** Community trajectories in NMDS ordination space, based on a Morisita-Horn dissimilarity matrix of annual communities. Points represent the annual average (centroid) for each treatment. Arrows represent compositional change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

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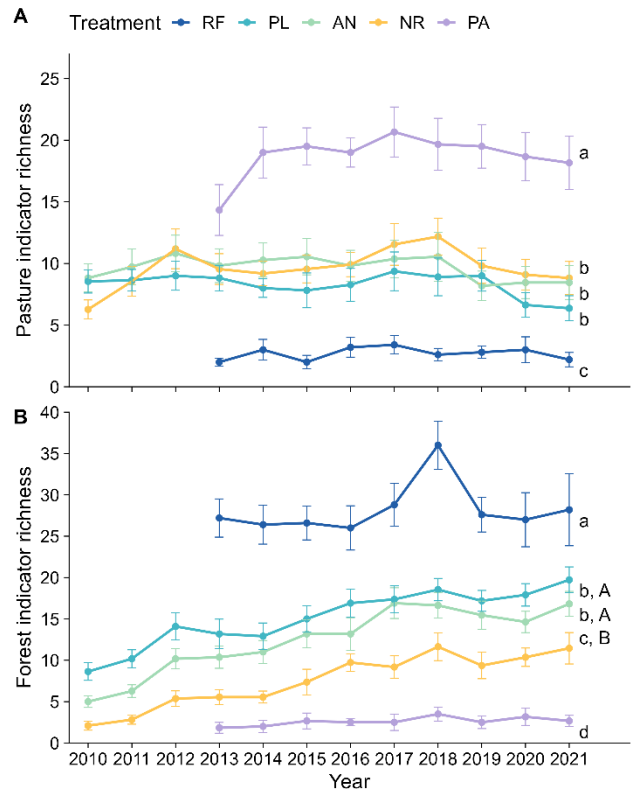


Figure 5. Temporal trends for indicator species richness (mean \pm SE) for (A) pasture and (B) reference forest in each habitat type. Treatments labeled with different lower-case letters have significantly different estimated marginal means. Treatments labeled in panel B with upper-case letters have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

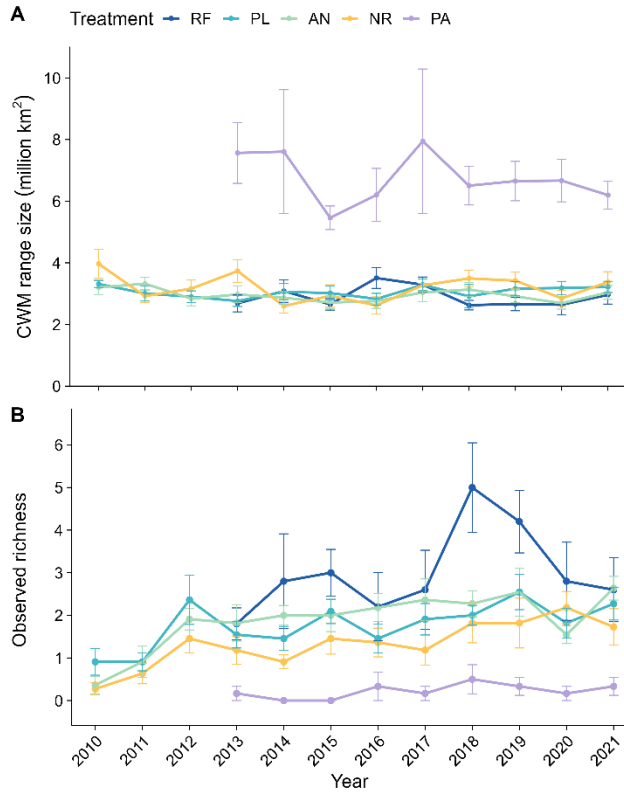


Figure 6. Range size trends. **(A)** Community-weighted mean range size by treatment and year (mean CWM \pm SE). **(B)** Observed range-restricted species richness (mean \pm SE).

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.



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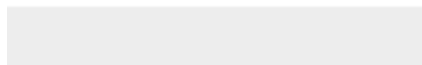




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