Received: 11 March 2021 | Accepted: 25 August 2021

DOI: 10.1111/1365-2664.14052

Journal of Applied Ecology BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Active restoration fosters better recovery of tropical rainforest birds than natural regeneration in degraded forest fragments

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Funding information
Science and Engineering Board, India, Grant/Award Number: EMR/2016/007968; Nature Conservation Foundation; AMM Murugappa Chettiar Research Centre; Rohini Nilekani Philanthropies; Arvind Datar

Handling Editor: Gavin Siriwardena

Abstract

1. Ecological restoration has emerged as a key strategy for conserving tropical forests and habitat specialists, and monitoring faunal recovery using indicator taxa like birds can help assess restoration success. Few studies have examined, however, whether active restoration (AR) achieves better recovery of bird communities than natural regeneration, or how bird recovery relates to habitat affiliations of species in the community.
2. In rainforests restored over the past two decades in a fragmented landscape (Western Ghats, India), we examined whether bird species richness and community composition recovery in 23 actively restored (AR) sites were significantly better than recovery in paired naturally regenerating (NR) sites, relative to 23 undisturbed benchmark (BM) rainforests. We measured eight habitat variables and tested whether bird recovery tracked habitat recovery, whether rainforest and open-country birds showed contrasting patterns, and assessed species-level responses to restoration.
3. We recorded 92 bird species in 460 point-count surveys. Rainforest bird species richness was highest in BM, intermediate in AR and lowest in NR. Contrastingly, open-country bird species richness was least in BM, intermediate in AR and highest in NR.
4. Bird community composition varied significantly across treatment types with composition in AR in transition from NR to BM. Bird community dissimilarity between sites was positively related to dissimilarity in habitat structure and floristics, and geographical distance between sites. Variance partitioning indicated that structural and floristic dissimilarity explained 90% of the variation in community composition.
5. Indicator species analysis revealed significant associations of 34 species with one or more treatment types. Species associated with BM and AR treatment types were all rainforest species, while only 38% of species associated with AR and NR treatment types were rainforest species.
6. *Synthesis and applications*. We show that active restoration (AR) of degraded fragments benefits rainforest birds and reduces the infiltration of open-country birds, and highlight the importance of considering rainforest and open-country species separately. In human-modified tropical rainforest landscapes, AR of degraded

fragments fosters partial recovery and complements protection of mature forests for bird conservation.

KEYWORDS
bird community, bird conservation, ecological restoration, faunal recovery, forest structure, habitat fragmentation, rainforest birds, Western Ghats

1 | INTRODUCTION

Methods of ecological restoration, such as natural regeneration (NR, passive restoration) and active restoration (AR, involving activities such as weed removal and native tree planting), are complementary strategies for the recovery of degraded tropical forests (Bullock et al., 2011; Crouzeilles et al., 2017; Dobson et al., 1997; Holl, 2017). Naturally regenerating degraded tropical forests may, however, remain floristically species-poor (Tabarelli et al., 2008) or show poorer recovery, particularly when located in isolated forest fragments (Osuri et al., 2019). This may consequently affect recolonisation by fauna, an indicator of restoration success (Cross et al., 2020; Wortley et al., 2013), which can further affect vegetation recovery, such as through changes in seed dispersal by faunal vectors (Fraser et al., 2015).

Birds have often been used as a faunal indicator of restoration (Catterall et al., 2012; Paxton et al., 2018) because of their mobility and ability to colonise recovering sites, and their relatively high abundance and detectability (Gould & Mackey, 2015). Past research, using meta-analysis, has suggested that NR may be a better strategy than AR for recovery of biodiversity, including vertebrates like birds, when the richness and abundance of all species are considered (Crouzeilles et al., 2017). However, the responses of birds to restoration can vary depending on the habitat affiliations of species in the regional species pool from which the local species pool is derived. The local pool of species in disturbed or fragmented tropical forest landscapes comprises both birds affiliated to open-country habitats and forest-specialist birds, with the former tending to be widespread species that colonise disturbed areas, and the latter including more forest-specialist and range-restricted species (Raman, 2001; Rutt et al., 2019). In contrast to open-country species, rainforest birds tend to be more affected by habitat alteration (Muthuramkumar et al., 2006; Perera et al., 2017; Raman & Sukumar, 2002), mining (Deikumah et al., 2014), farming (Otieno et al., 2011) or conversion to monoculture plantations (Mandal & Raman, 2016). While considerable research exists on recovery of tropical bird communities following NR and secondary forest succession (Acevedo-Charry & Aide, 2019), studies have not examined differences in bird recovery with AR of tropical forest and how responses of forest and open-country species vary (but see Ansell et al., 2011).

Bird communities also respond to changes in habitat structure and the plant community following restoration. Catterall et al. (2012) found that bird species composition in restored pastures was intermediate between that of reference forest and deforested pasture land. Comparisons of restoration success in actively restored sites and reference ecosystems indicate that bird community composition changes along a gradient of habitat structure with time (Batisteli et al., 2018; Latja et al., 2016). In tropical forests and restoration sites, rainforest-specialist species may track changes in vegetation structure in degraded areas and preferentially use more structurally complex habitats (Moura, 2015; Müller et al., 2010; Munro et al., 2011; Raman & Sukumar, 2002; Stouffer, 2020). Many rainforest birds rely on the canopy layer and trees to forage, nest and breed, and the planting of native trees can result in the rapid recovery of bird species richness in degraded sites (Roels et al., 2019). Tropical rainforest bird communities tend to show vertical stratification with different sets of species foraging in different vertical layers (terrestrial to canopy) of the forest (Robin & Davidar, 2002). Secondary and degraded forests usually have dense understorey, open canopy and less vertical stratification of foliage (Chazdon, 2003; Wright, 2005). As the canopy and mid-storey develops through early stages of forest recovery after restoration, the number of bird species of these vertical layers may be expected to increase. Tropical forest bird community composition may respond to both forest structural recovery and floristic recovery of tree species composition as the occurrence of birds such as nectar-, fruit- and seed-eaters may depend on the occurrence of plant species of mature forests (Jayapal et al., 2009; Raman et al., 1998). As spatial proximity between sites is also likely to influence bird community composition, the influence of forest structure and floristics needs to be examined while controlling for geographical distance (Lichstein, 2007).

In the Anamalai Hills of the southern Western Ghats of India, tropical rainforest fragments surrounded by tea and coffee plantations have been actively restored over the past two decades (Mudappa et al., 2014; Raman et al., 2009). These fragments continue to support populations of around 130 rainforest bird species, including 21 of 27 range-restricted species of the Western Ghats biodiversity hotspot and other conservation priority species (Kumar et al., 2004; Muthuramkumar et al., 2006; Sridhar & Sankar, 2008). A previous study in degraded rainforests in this landscape revealed that AR led to significantly better recovery in forest structure and carbon storage than through NR (Osuri et al., 2019). Correspondingly, we assess here whether rainforest birds respond better to AR than to NR (or passive restoration) when compared to bird communities in relatively undisturbed benchmark (BM) rainforests. (a) We tested the hypothesis that the responses of birds to restoration would vary with habitat affiliation. Specifically, we expected rainforest bird species richness and abundance in AR sites to increase (and open-country bird species richness to decrease) relative to NR sites, and towards levels in BM sites. (b) We also hypothesised that bird community composition in AR sites would be in transition from NR sites to BM sites and that similarity in bird community composition would be directly related to the recovery in forest (vegetation) structure and floristic composition. (c) We tested the hypothesis that the recovery in bird species richness and the number of bird species of different vertical layers of the forest, particularly the canopy and mid-storey layers, increased with vegetation recovery. (d) Finally, we explored responses at the level of individual species to corroborate the broader patterns and establish whether AR is associated with significant recovery of rainforest birds.

2 | MATERIALS AND METHODS

2.1 | Study area

Fieldwork was carried out in the Anamalai Hills of the southern Western Ghats, within the 220 km² Valparai Plateau (10°15′–10°22′N, 76°52′–76°59′E) and adjoining rainforest tracts of the 958 km² Anamalai Tiger Reserve (10°12′–10°35′N, 76°49′–77°24′E). The study area receives about 2,600 mm of rainfall annually, a majority of which falls from June to September, during the southwest monsoon. Altitudinally, it ranges from 700 to 1,500 m a.s.l., classified the natural vegetation as mid-elevation tropical wet evergreen rainforests of the *Cullenia exarillata-Mesua ferrea-Palaquium ellipticum* type (Pascal et al., 2004).

The Valparai Plateau predominantly supports monoculture plantations of tea (51% by area) and shade coffee (11% by area), and some areas are under cardamom and *Eucalyptus* plantations (Mudappa & Raman, 2007). The Plateau also retains over 40 rainforest fragments, remnants from large-scale land-use change from the 1890s to the 1940s. These forest fragments range in size from 1 to 300 ha, and support a significant diversity of wildlife (Harikrishnan et al., 2018; Muthuramkumar et al., 2006; Sidhu et al., 2010; Sridhar et al., 2008; Sridhar & Sankar, 2008; Wordley et al., 2017). The rainforest fragments had become degraded due to prior land use in the forest patches including selective felling, fuelwood removal and past cultivation of shade crops such as coffee and cardamom in parts of the fragments followed by abandonment and weed invasion (Mudappa & Raman, 2007; Mudappa et al., 2014). Since 2002, a number of rainforest fragments have been ecologically restored using an AR protocol that involves weed (i.e. non-native invasive plant species; Neve et al., 2018) removal followed by high diversity mixed native species plantings with the cooperation of three plantation companies (Mudappa et al., 2014; Osuri et al., 2019; Raman et al., 2009). Weeding, particularly targeting *Lantana camara*, *Mikania micrantha* and *Chromolaena odorata*, was carried out 1–4 months before planting, with care taken during weeding to retain any pre-existing rainforest plants. At the onset of the southwest monsoon, a high diversity (27–82 species) of nursery-raised, 2–4 years old, native species saplings were planted at an average density of 1,099 saplings/ha (1 *SE* = 154 saplings/ha) per site. To date, the companies also extended protection to over 1,075 ha of forest biodiversity plots across 35 rainforest remnants, taking steps to prevent tree felling, hunting and fuelwood extraction, allowing NR (passive restoration) to occur in these areas (Mudappa & Raman, 2007). The restoration project has actively restored about 100 ha of degraded forests within these protected remnants since 2000 (Osuri et al., 2019).

We surveyed for birds and sampled vegetation in 69 sites: 23 actively restored (AR) sites, each paired with 23 naturally regenerating (NR) or passively restored sites, and 23 BM sites within relatively undisturbed tropical rainforest (Supporting Information, Table S1). The AR sites, restored between 2002 and 2010 (9–17 years since restoration, average area: 1 ha), and NR sites were located within 10 rainforest fragments on the Valparai Plateau. The AR-NR site pairs were located <0.5 km apart and chosen to be comparable in terms of degradation, edge-distance, topography, flora and physiognomy, as in an earlier study in the same landscape that looked at the effect of restoration on carbon storage and tree communities (Osuri et al., 2019). Paired sites were situated within the same forest fragment, with some fragments having up to four pairs. The 23 BM sites were within the Anamalai Tiger Reserve, and represented relatively undisturbed, contiguous rainforest habitat similar to the restored sites in terms of climate, altitude and natural vegetation type (Muthuramkumar et al., 2006; Osuri et al., 2019). BM sites were located 1–4 km from AR-NR pairs.

2.2 | Bird sampling

In each site, we surveyed birds using variable radius point-count survey method (Raman, 2003). Sites were visited at least once every month from November 2019 to March 2020 (when fieldwork ceased due to the Covid-19 pandemic lockdown), with a gap of at least 3 weeks between each successive visit to reduce temporal autocorrelation. All sites were visited at least six times, and most sites were visited seven times. A total of 460 point-count surveys were carried out.

Point-count surveys of 15 min duration were carried out by a single observer (PH) from the point-count location at the centre of each site. PH had previously conducted bird transects in the Western Ghats and, prior to the start of this study, observed birds for several weeks in the study area with TRSR, who has about two decades experience with the avifauna in the study area. Birds were identified to the species level, both visually and by their vocalisations. Birds in flight were ignored unless they were flying under the canopy or less than 5 m above the canopy. Distances of birds were recorded in the following radial distance bands (in m) from the centre point: 0–5, 6–10, 11–15, 16–20, 21–30 and 31–50. The number of individual birds was always noted down in the case of visual observations, and recorded as the minimum number of birds distinctly heard calling when birds were detected aurally.

2.3 | Vegetation sampling

In all 69 sites, vegetation measurements were taken within 20 × 20 m quadrats located at the centre of each site. As sites were selected to be relatively homogeneous in habitat within each site, measurements from these 20 × 20 m quadrats were considered to be representative of each site and sufficient to capture variation across sites as in an earlier study from the landscape (Osuri et al., 2019). Tree height, basal area, canopy cover, tree species richness and tree density were sampled according to methods detailed in Osuri et al. (2019), with canopy cover estimated using a spherical densiometer rather than visually. Leaf litter depth was measured using a calibrated wooden probe to the nearest 0.5 cm at one point near the centre of the plot. Canopy overlap was scored between 0 (open sky, no branches overhead) and 3 (completely overlapping and obscuring the sky), and vertical stratification was scored on the presence of foliage in eight vertical layers, both estimated at the plot centre, following methods detailed in Raman et al. (1998).

2.4 | Data analysis

Birds were classified as rainforest and open-country species a priori based on Ali and Ripley (1983) and Raman (2006). Rainforest species were birds that were regularly found in undisturbed, mature, closed-canopy wet evergreen forests and open-country species were typically widespread species, and avoided such forests. We also classified species as birds of the terrestrial, shrub, mid-storey or canopy layers based on their primary foraging layer (Ali & Ripley, 1983; personal observations).

All statistical analyses were performed in the R statistical and programming environment (R Core Team, 2020), with community ecology analyses carried out using the VEGAN package in R (version 2.5-7, Oksanen et al., 2013). Bird species richness patterns were examined using rarefaction curves for each of the three treatment types (BM, AR and NR), for all birds, rainforest birds and open-country birds. To estimate bird species richness at each site while accounting for imperfect detectability, we used data from repeated visits to compute the first-order jackknife estimate of the number of all, rainforest and open-country bird species at each of the 69 sites (Brose et al., 2003). Using the LME4 package (version 1.1-23, Bates et al., 2015), we fitted generalised linear mixed models (GLMMs, Bolker et al., 2009) assuming Poisson errors and using natural log as link function to examine the effects of treatment types (AR, NR and BM) on the first-order jackknife estimates of bird species richness and median bird abundance (for all, rainforest and open-country species). Treatment type was considered as categorical fixed effect and the site-pair name (specifying the pairing of AR and NR sites) as random effect in the GLMMs. Multiple comparisons Tukey HSD tests between treatment types were carried out using the glht function in package MULTCOMP in R (version 1.4-17, Hothorn et al., 2008). For fitted GLMMs, we examined dispersion and patterns in residuals using the DHARMA package in R (version 0.4.3, Hartig, 2021). Overall, the models appeared appropriate as we found only mild under-dispersion in a few cases and no distinct pattern in the residuals likely to have affected the interpretation.

Distance sampling density estimation was carried out using the DISTANCE package in R (version 1.0.3, Miller et al., 2019) on variable radius point-count data with detections truncated at 50 m and pooled by treatment type. Candidate detection function models (half-normal, uniform and hazard rate with cosine adjustment terms) were fitted and standard model selection procedures (Buckland et al., 2015; Thomas et al., 2010) indicated that the hazard-rate model best fit our data. Densities were estimated for all birds and the subsets of rainforest species and open-country species for the three treatment types.

Bird abundance data were used to compute the pairwise dissimilarity in community composition across the 69 sites using the Bray–Curtis index. The dissimilarity matrix was used to visualise species compositional change across sites and the three strata, using non-metric multidimensional scaling.

Variation in forest structure was assessed using eight variables: tree height, basal area, canopy cover, tree species richness, tree density, leaf litter depth, canopy overlap and vertical stratification. As some of the variables were correlated, we summarised variation using a principal components analysis (PCA) to extract two orthogonal components (PC1 and PC2) for ordination and modelling.

Forest structural dissimilarity between sites was estimated as the Euclidean distance between sites in the PCA ordination space. Geographical distance between sites in kilometres was estimated using the site locations (latitude and longitude) recorded on a hand-held GPS unit (Garmin e-trex). We carried out multiple regression of distance matrices (MRM) using package ECODIST in R (version 2.0.7, Goslee & Urban, 2007) with 999 permutations to assess statistical significance of the regression coefficients (Lichstein, 2007). To identify the relative importance of each predictor variable (floristics, habitat structure and geographical distance), we used the hierarchical partitioning package HIER.PART (version 1.0-6, Walsh & Mac Nally, 2020).

For modelling relationships between birds and habitat, we used bird species density (number of species per point) considering all species or subsets of rainforest birds, open-country birds and number of species of different vertical layers. Furthermore, we used GLMMs to relate bird community variables to forest structural scores (PC1 and PC2), assuming Poisson errors and log link functions. The GLMMs incorporated PC1 and PC2 scores as fixed effects, and repeat visits and site-pair name (specifying the pairing of AR and NR sites) as random effects.

Finally, we used the INDICSPECIES package in R (version 1.7.9, Cáceres & Legendre, 2009; Cáceres et al., 2020), to explore significant bird species associations with the three treatment types based on abundance data. We estimated the point biserial correlation coefficient (abundance-based counterpart of the Pearson's phi coefficient, setting func=‘r.g’ to correct for unequal group sizes), with 999 permutations to assess statistical significance.

3 | RESULTS

We recorded a total of 92 bird species in 7,148 detections (7,916 individuals) across all 69 sites in the point-count surveys (Supporting

Information Appendix). This included 62 (67%) rainforest species, and 30 (33%) open-country species overall. The Nilgiri Flowerpecker *Dicaeum concolor*, Greenish Warbler *Phylloscopus trochiloides*, White-cheeked Barbet *Megalaima viridis*, Yellow-browed Bulbul *Acritillas indica* and Vernal-Hanging Parrot *Loriculus vernalis* were the most frequently observed species overall, with over 300 detections each. In all, 12 species were recorded only once.

3.1 | Bird species richness and abundance

Overall bird species richness as revealed by the rarefaction curves was slightly higher in NR sites, compared to AR and BM sites (Figure 1). While rainforest bird species richness was similar across the three treatment types, open-country bird species richness was highest in NR sites, followed by AR sites, and least in BM sites (Figure 1).

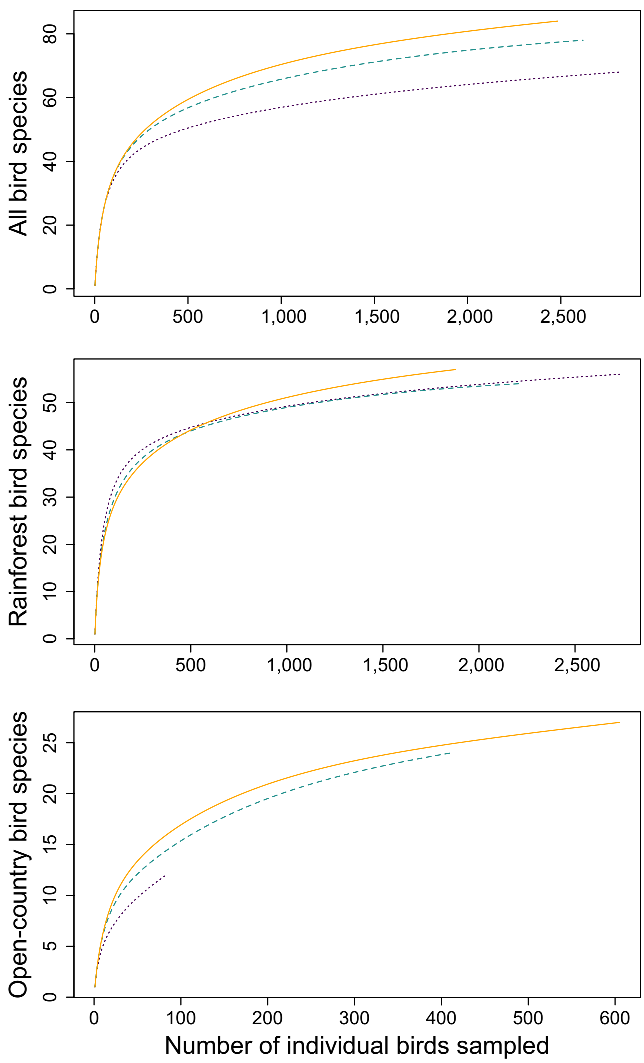

FIGURE 1 Rarefaction curves of bird species richness for all, rainforest and open-country birds in benchmark (BM = purple dotted curve) rainforest, actively restored (AR = green dashed curve) and naturally regenerating (NR = orange solid curve) sites

There were no significant differences across the three treatment types in the first-order jackknife estimate of bird species richness when all bird species were considered (Supporting Information, Table S2). The jackknife estimate of rainforest bird species richness varied significantly across treatment types, being highest in BM sites (mean ± *SD*: 37 ± 5.0), intermediate in AR (34 ± 6.0) and lowest in NR (29 ± 7.5), and between AR-NR, AR-BM and NR-BM pairs (Figure 2, Tukey HSD test, $p < 0.05$). The jackknife estimate of open-country species richness also varied significantly across treatment types but showed a contrasting pattern being lowest in BM sites (mean ± *SD*: 3 ± 2.0), intermediate in AR (9 ± 4.0) and highest in NR (12 ± 4.0), with significant difference between AR-NR, AR-BM and NR-BM pairs (Tukey HSD test, $p < 0.05$, Figure 2).

There were no significant differences in the median number of individual birds per site of all bird species across treatment types (Supporting Information, Table S2; Figure 2D–F). BM sites (mean ± *SD*: 18 ± 3.0) had the highest abundance of rainforest species, and was significantly different from the both AR (14 ± 3) and NR (12 ± 3) treatment types (Tukey HSD test, $p < 0.05$). In the case of open-country birds, this trend was reversed: abundance was highest in NR sites (mean ± *SD*: 4 ± 2), intermediate in AR (3 ± 1) and lowest in BM (1 ± 1), the latter being significantly different from the other treatment types (Tukey HSD test, $p < 0.05$).

Density estimation using distance sampling revealed that density of all bird species was highest in AR sites (density ± SE: 108 ± 5.0 individuals/ha), followed by NR sites (97 ± 5.2) and BM sites (90 ± 3.9). The density of rainforest species in AR sites was 25% higher than the density in NR sites, while BM sites showed an intermediate value. In the case of open-country birds, NR sites showed 61% higher average bird density than AR sites, and BM sites showed the lowest densities (Supporting Information, Table S3).

3.2 | Forest recovery and bird community composition

Principal components analysis (PCA) indicated that the first two components (PC1 and PC2) together accounted for 60% of the variation in vegetation structure (Supporting Information, Table S4). PC1 was negatively correlated to canopy cover, tree species richness, tree density, basal area, vertical stratification and leaf litter depth. PC2 was negatively correlated with tree height and positively correlated with tree density and canopy overlap (Figure 3). Ordination of sites indicated that BM sites were characterised by higher tree density, tree species richness, basal area and other PC1 variables than NR sites, while AR sites occupied an intermediate position. This indicated that most AR sites had recovered in forest structural variables (on the PC1 axis) in the direction of BM sites.

The pattern of recovery in vegetation was reflected in the changes in bird community composition as revealed in the NMDS ordination (stress = 0.08, Figure 4). As in the PCA analysis, BM sites and NR sites formed relatively loose but distinct clusters, with AR sites occupying intermediate locations. This indicated the direction of change in bird community composition from NR to AR brought the latter

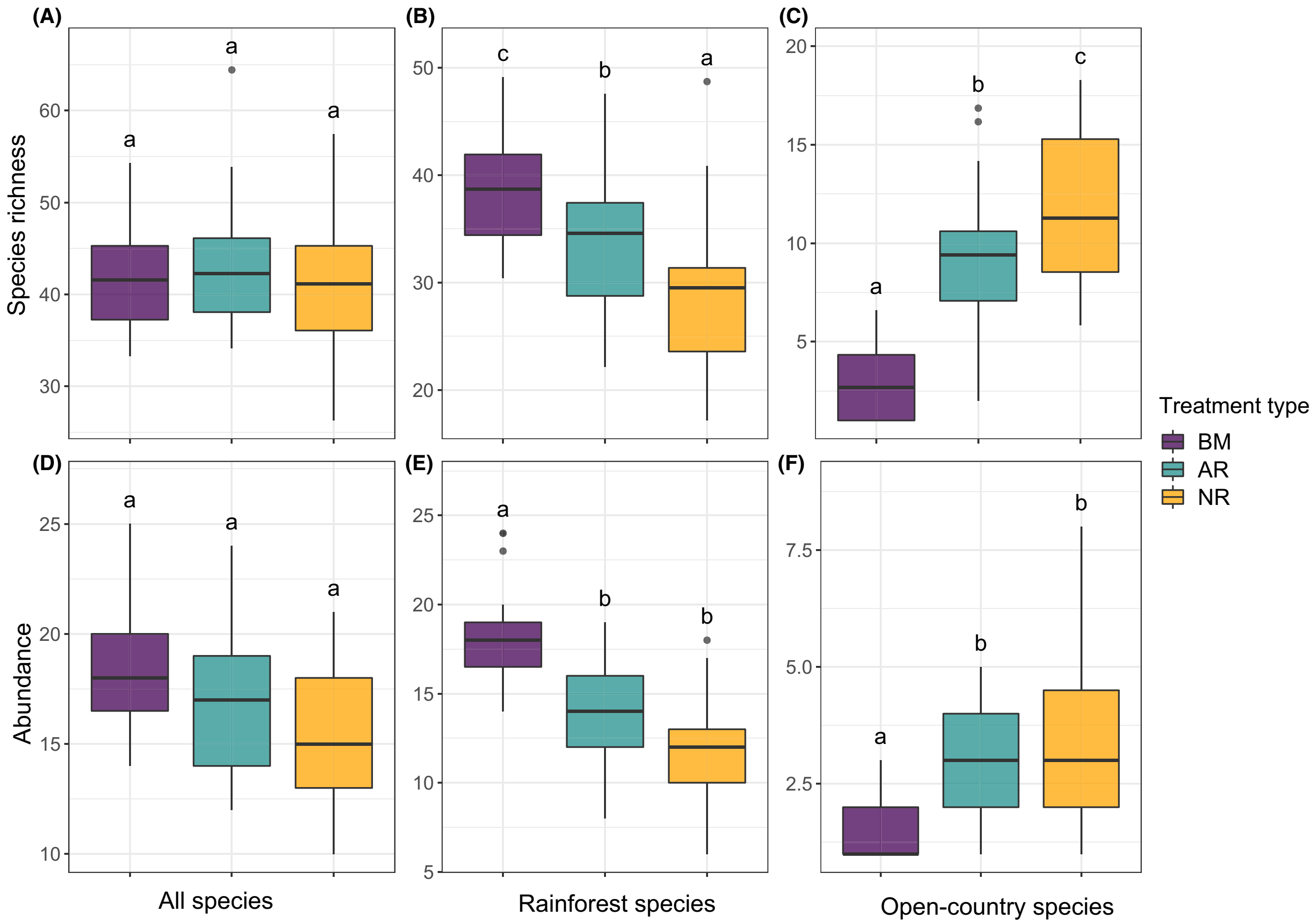

FIGURE 2 Jackknife estimates of bird species richness (A–C), and bird abundance (D–F), for all, rainforest and open-country birds in benchmark (BM) rainforest, actively restored (AR) and naturally regenerating (NR) sites. Boxplots indicate median, interquartile range and minimum–maximum values. Treatment types marked with different lowercase alphabets above the bars are statistically significantly different from each other based on Tukey HSD tests ($p < 0.05$)

closer to bird community composition in BM sites. Permutational multivariate analysis of variance using distance matrices indicated that bird community composition differed significantly among the three treatment types (adonis $F_{2,66} = 9.3$, $p = 0.001$, $R^2 = 0.22$) and AR and BM had not yet converged in bird community composition.

MRM analyses indicated that bird community compositional dissimilarity was significantly positively related to dissimilarity in habitat structure, floristic dissimilarity and geographical distance ($R^2 = 0.14$, $p < 0.001$). Hierarchical partitioning of the contribution of each of the predictors to bird community compositional variation between sites showed that geographical distance contributed to <10% of the explained variation, while forest structure and floristics equally contributed to 90% of explained variation in bird community composition.

3.3 | Modelling bird–habitat relationships

The GLMM results on bird–habitat relationships (Supporting Information, Table S5) indicated that overall bird species richness was negatively related to PC1 and therefore increased with increasing canopy cover and tree species richness. Rainforest birds were negatively related to PC1 and positively with PC2, indicating that rainforest species richness decreased with tree height, but increased with canopy overlap, canopy cover, leaf litter depth and tree density. Positive association of open-country species with PC1 indicated more open-country bird species occurred in sites with lower tree species richness, tree density, vertical stratification, basal area and canopy cover. Negative association with PC1 indicated that more canopy and mid-storey bird species richness occurred in sites with higher tree species richness, canopy cover, vertical stratification and tree density (Supporting Information, Table S5). Species richness of birds of the shrub layer also showed a similar negative association with PC1 ($p = 0.023$), while that of terrestrial birds did not show any significant association with either PC axis.

3.4 | Responses of individual species

The indicator species analysis showed that 34 species were significantly associated with either a single treatment type or a

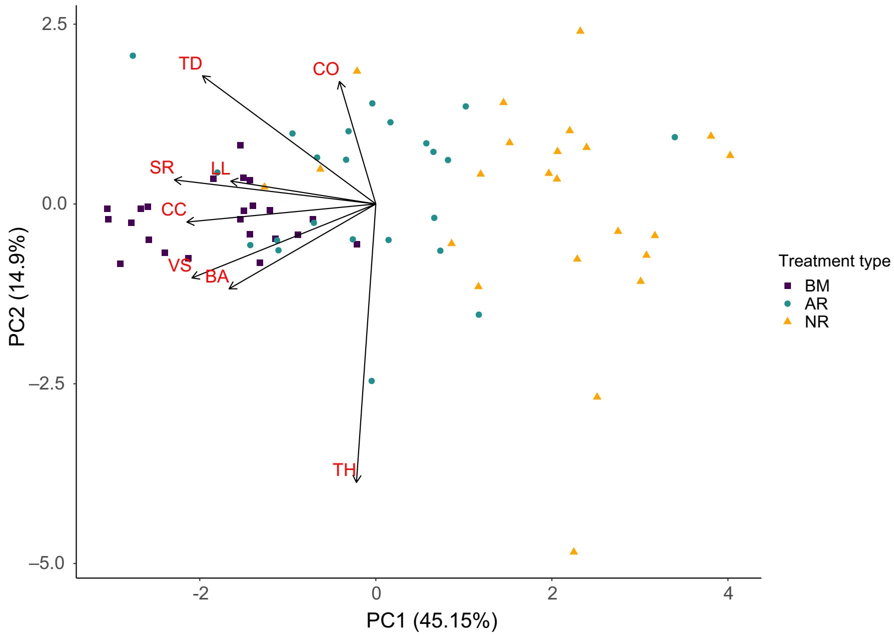

FIGURE 3 Principal component analysis (PCA) of habitat variables. TD = tree density, SR = tree species richness, TH = tree height, BA = basal area, VS = vertical stratification score, CC = canopy cover, CO = canopy overlap and LL = leaf litter depth in benchmark (BM) rainforest, actively restored (AR) and naturally regenerating (NR) sites

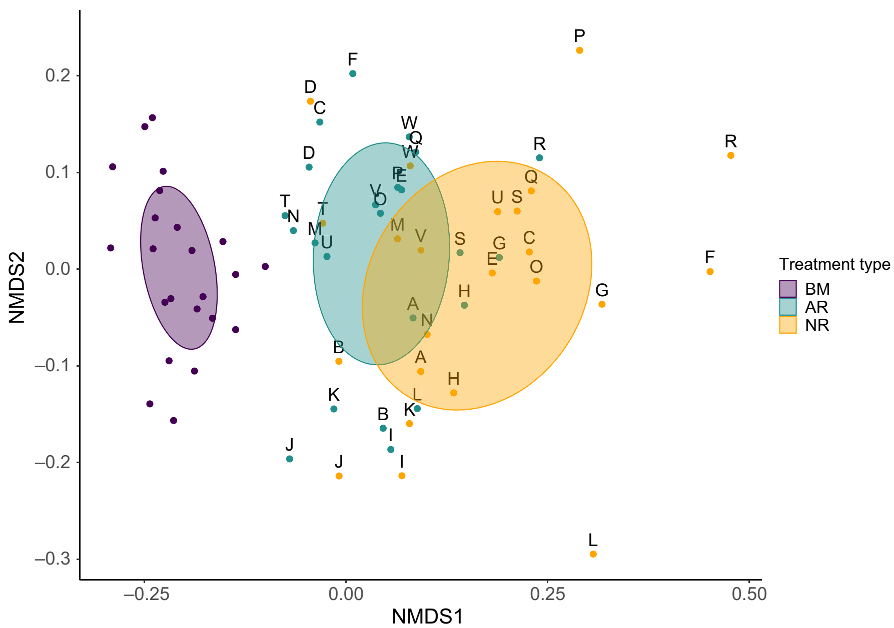

FIGURE 4 Ordination of sites belonging to benchmark (BM) rainforest, actively restored (AR) and naturally regenerating (NR) sites treatment types superimposed on principal component factor axes based on habitat variables. See Supporting Information (Table S1) for paired NR-AR sites corresponding to alphabets

combination of two types (BM: 17, NR: 5, BM+AR: 4, AR+NR: 8; Supporting Information, Table S6, $p < 0.05$).

Species associated with BM sites included the endemic White-bellied Blue Flycatcher *Cyornis pallidipes* and forest specialists such as the Black-naped Monarch *Hypothymis azurea* and Yellow-browed Bulbul *A. indica*. Migrants such as the Brown-breasted Flycatcher *Muscicapa muttui* and Green Warbler *Phylloscopus nitidus* were associated with both BM and AR sites, along with the endemic Crimson-backed Sunbird *Leptocoma minima*. Species with wide ranges throughout the subcontinent such as the Red-whiskered Bulbul *Pycnonotus jocosus* and Common Tailorbird *Orthotomus sutorius* were associated with both AR and NR sites, while open-country species such as the Blyth's Reed Warbler *Acrocephalus dumetorum* and Purple Sunbird *Cinnyris asiaticus* were associated with NR sites.

4 | DISCUSSION

This study from the Western Ghats rainforests in India provides support for the hypothesis that AR increases rainforest bird species richness and decreases open-country bird species richness relative to the passive approach of allowing sites to regenerate naturally (NR). While overall bird abundance showed little difference between AR and NR sites, rainforest species were more abundant in AR sites, while open-country species were more abundant in NR sites. The bird community composition also changed with AR sites clearly in transition from NR to BM rainforest sites. The bird community composition and birds of canopy, mid-storey and shrub layers appeared to track corresponding recovery in habitat structure and floristic composition of the sites. All species associated with BM and AR treatment types were rainforest birds, while only 38% of species associated with AR and NR treatment types were rainforest species.

Our study adds to the growing body of literature that indicates that restoration activities can directly enhance species richness of rainforest birds and bird community recovery, and help reverse biodiversity declines (Latja et al., 2016; MacGregor-Fors et al., 2010). We find AR supports an increase in rainforest birds and reduction in open-country species, suggesting that research on the relative value of active over passive approaches to restoration should consider the responses of subsets of forest specialists and not merely rely on aggregate indices of richness and abundance (Crouzeilles et al., 2017).

The responses of rainforest birds may be related to the significant recovery of forest structure in AR sites as compared to NR sites in this fragmented rainforest landscape (Osuri et al., 2019). While open-country birds are known to avoid even newly restored sites (Roels et al., 2019), increased diversity of forest birds parallels recovery of more complex habitat structure and heterogeneity with AR (Osuri et al., 2019; Vogel et al., 2015). Similar patterns have been observed in mine sites that have been rehabilitated (Gould & Mackey, 2015), in African tropical forests (Latja et al., 2016) and Australian forests (Munro et al., 2011). Poorer recovery of rainforest birds in NR sites can be attributed to poorer recovery of mature forest attributes such as tree density and canopy cover, suppression of regeneration by weeds and persistence of more open vegetation (Osuri et al., 2019; Tabarelli et al., 2008). A caveat of our study is that the restoration plots are relatively small compared to the area that birds may be using in the landscape. The AR-NR paired sites were <0.5 km apart and most fragments where the sites were located were 1–4 km from BM sites. However, the significant differences we observe in the species richness of rainforest and open-country birds across the three treatment sites show that even if there was overlap in habitat use due to proximity of sites, rainforest birds appear to preferentially use structurally complex forests in BM and AR sites more than NR sites, while open-country generalists show the opposite trend. The bird community recovery and species richness patterns we observed in our study area in the Western Ghats may also be expected in similarly fragmented tropical forests where patches are embedded within plantation landscapes and are isolated from continuous forests at moderate (<4 km) distances.

However, the recovery of rainforest birds with AR is only partial and not reflected in significant increase in their overall abundance. Other studies have shown that even in restored sites, bird communities may take several decades to recover in fragmented landscapes, and some sites may never attain communities comparable to that of undisturbed forests (Catterall et al., 2012; Freeman et al., 2015). In surrounding human-modified landscapes, however, even small forest fragments within plantations can benefit significantly from AR practices. Better land-use practices, such as retention of native shade trees in surrounding coffee and tea plantations, may also enhance bird conservation in fragments (Raman, 2006; Raman et al., 2021). As restoration sites in the present study spanned a limited range of 9–17 years since restoration, effects of time since restoration on bird recovery could not be assessed. Future studies that examine temporal trajectory of recovery over a longer timespan (>2 decades) can identify whether recovery with AR plateaus or continues to recover over time.

Active restoration in our study also resulted in bird communities that begin to resemble those of BM forests, more than is the case with NR, lending support to our second hypothesis. Earlier studies have documented the influence of forest cover and restoration plantings on bird community recovery but have not explicitly contrasted AR with NR. For instance, in tropical forest fragments embedded in an agricultural landscape in Costa Rica, Karp et al. (2019) demonstrated the influence of local and landscape level forest cover on forest bird communities, which led them to suggest that active forest restoration would assist bird recovery. In Uganda, bird community composition in actively restored forests tended towards that of primary forest, reaching approximately 60% similarity with primary forests in 20 years, but sites under NR were not surveyed (Latja et al., 2016). Our present study highlights that AR using weed removal followed by a high diversity mixed native species planting (Raman et al., 2009) led to a bird community that was compositionally intermediate between naturally regenerating and BM forests. This indicates that such a restoration protocol leads to recovery of bird communities in the desired direction and does not just result in a changed composition as noted in earlier studies and tree plantations (Daniels et al., 1990; Farwig et al., 2008; Raman & Sukumar, 2002; Sidhu et al., 2010).

We also found that rainforest species, particularly canopy and mid-storey birds, prefer sites that are structurally complex with high tree density and canopy cover. For many rainforest birds, the canopy layer provides grounds for foraging and breeding, and a high tree species diversity can provide birds with many niches and complementary sources of food (Roels et al., 2019). Terrestrial birds do not show any significant trends in our study, and this could be because only tree species were planted during AR in our sites and the soil and litter layer has not shown similar recovery. Some species may selectively respond to the diversity of the understorey layer of shrubs (Paxton et al., 2018), and bird species richness may be higher in sites where local understorey and shrub species are planted in addition to trees, compared to those in which only native tree species were planted (Munro et al., 2011).

Often, species richness measures are inadequate to assess the response of birds to habitat change (Maas et al., 2009), but our approach of including species identities and their associated habitat affiliations provides us with a well-rounded picture of bird recovery with restoration. In our study site, rainforest specialist species and endemics preferentially occur in BM and AR sites, and no birds that were significantly associated with both these treatment types together are open-country species. Although only four species were significantly associated with BM and AR sites, including the endemic Crimson-backed Sunbird *L. minima*, 39 other rainforest bird species also occurred more frequently in AR sites compared to NR (Supporting Information Appendix). Considering that the habitat structure of AR sites was similar to corresponding NR sites when restoration activities commenced two decades ago, it is significant that these specialist species are now associated with both AR and BM treatment types, within 9–17 years of habitat and floristic recovery. A recent assessment indicates that populations of endemic birds of the Western Ghats, a majority of which are rainforest specialists, are in local and range-wide decline, likely as a result of ongoing habitat alteration and degradation (Pawar et al., 2021; SoIB, 2020). Tropical rainforest specialists and endemic birds are often more susceptible to habitat disturbance (Maas et al., 2009), and their recovery with AR in fragmented forests (Latja et al., 2016; this study) suggests a significant role for AR efforts for bird conservation in tropical forest landscapes.

5 | CONCLUSIONS

An AR protocol involving high diversity mixed native tree species planting can assist in the recovery of rainforest birds and lead to an accompanying decline in open-country species as the habitat structure recovers. While bird community composition in rainforest fragments outside protected areas begins to resemble reference rainforest within two decades, this recovery is only partial. This underscores the importance of protecting and retaining existing tracts of mature rainforests for endemic birds and rainforest specialists. Studies such as ours that focus on monitoring avifauna over the long term in passively and actively restored forests, while separately considering forest specialists and more widespread open-country species, are vital to assess the relative value of active over passive approaches to restoration and determine the trajectory of recovery (Holl et al., 2017).

ACKNOWLEDGEMENTS

This work was carried out as part of the rainforest restoration program of the Nature Conservation Foundation (NCF), supported by AMM Murugappa Chettiar Research Centre, Rohini Nilekani Philanthropies, and Arvind Datar. T.R.S.R. acknowledges funding from the Science and Engineering Board (SERB), India (Research grant: EMR/2016/007968) for the bird research. We thank plantation management of Tata Coffee Ltd, Parry Agro Industries Limited, and Tea Estates India Limited for permissions to work in the estates. We are grateful to Divya Mudappa who helped conceive the idea for this project, and provided support throughout the study period, and to Anand Osuri and Akshay Surendra for discussions related to data analysis. We thank K. Srinivasan, Mrinalini K. Siddhartha, Ganesh Raghunathan, M. Ananda Kumar and Vijay Ramesh for discussions and help, and P. Jeganathan for the Tamil translation of our abstract. We are grateful to T. Vanidas, Manikraj, G. Moorthi and A. Sathish Kumar for assisting with fieldwork. This work would not have been possible without uninterrupted and unfailing access to literature, which SciHub provided.

AUTHORS' CONTRIBUTIONS

T.R.S.R. conceived the ideas and designed the methodology, P.H. collected the data. Both authors were involved in data analysis and writing of the manuscript, contributed critically to the drafts, and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository https://doi.org/10.5061/dryad.rjdfn2zc3 (Raman & Hariharan, 2021).

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SUPPORTING INFORMATION

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How to cite this article: Hariharan, P., & Raman, T. R. S. (2021). Active restoration fosters better recovery of tropical rainforest birds than natural regeneration in degraded forest fragments. *Journal of Applied Ecology*, 00, 1–12. https://doi.org/10.1111/1365-2664.14052