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RESEARCH ARTICLE

Remnant forest in Costa Rican working landscapes fosters bird communities that are indistinguishable from protected areas

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Abstract

- The outcome of the ongoing biodiversity crisis depends on the capacity of the Earth's wildlife to persist in working landscapes. Yet, the species that occupy working landscapes are often distinct from those in protected areas, with a large group of "sensitive species" thought to rarely venture into human-dominated landscapes. As governments have committed to restoring degraded lands world-wide, determining whether and how working landscapes can be restored to benefit sensitive species remains a major challenge.
- 2. We surveyed Neotropical birds across Northwestern Costa Rica in protected areas, farms and forests embedded within working landscapes. We analysed community composition to understand how gradients of forest cover, fragmentation and regional precipitation determine how conserving (or restoring) tropical forests in working landscapes could safeguard entire communities, especially sensitive species with limited ranges.
- 3. We found agricultural sites maintained relatively high bird diversity but hosted very distinct communities from those found in protected areas. The average range size of species found in agricultural communities was double the size of species in protected areas. However, high forest cover sites in working landscapes housed bird communities with small range sizes that were equivalent to those in nearby protected areas, despite being twice as fragmented and significantly more disturbed.
- 4. The effect of local forest cover on bird composition was contingent on both landscape context and regional climate. When local forest cover increased in wetter regions and more forested landscapes, bird communities in working landscapes exhibited a stronger shift towards the assemblages found in protected areas. Specifically, we found that reforesting the wettest sites would increase similarity to protected areas fourfold compared to only a twofold increase in the driest sites.
- 5. Synthesis and applications. Despite experiencing much more fragmentation and degradation than protected areas, forests in Costa Rican working landscapes can maintain bird communities that strongly resemble those found in protected areas. This suggests that conserving or restoring forests in working landscapes,

particularly within wetter regions and already forested landscapes, may safeguard bird communities when creating protected areas is infeasible.

KEYWORDS

avian, deforestation, fragmentation, habitat loss, landscape context, reserve, restoration, working landscapes

1 | INTRODUCTION

Conservation biologists and practitioners are increasingly recognizing the value of working landscapes for safeguarding biodiversity (Chazdon et al., 2009; Kremen & Merenlender, 2018). Indeed, "working landscapes," or human-dominated lands composed of pastures, multiple crop species and patches of forests, grasslands and other natural habitats, have been repeatedly shown to sustain diverse communities (Melo, Arroyo-Rodriguez, Fahrig, Martinez-Ramos, & Tabarelli, 2013). Yet, the species that occupy working landscapes are often distinct from those in protected areas, with the most vulnerable species failing to persist (Karp et al., 2015; Newbold et al., 2016; Pfeifer et al., 2017). Even minor disturbances in otherwise intact forests sometimes exact declines in vulnerable forest species, necessitating the creation of protected areas (Barlow et al., 2016; Betts et al., 2017). Thus, despite encouraging findings related to the maintenance of local diversity, human modification of intact landscapes is still restructuring biological communities (Newbold et al., 2016).

Nonetheless, ongoing and projected trends in land-use are impeding efforts to sufficiently expand the global reserve network to slow the ongoing biodiversity crisis (Pouzols et al., 2014). Therefore, while reserve creation must remain a cornerstone of conservation policy, the fate of Earth's wildlife will at least partially depend on the hospitability of working landscapes (Chazdon et al., 2009). Ecologists and practitioners are increasingly calling for conservation initiatives that target working landscapes (Kremen & Merenlender, 2018), including landscape-scale restoration projects. For example, the world's governments have been challenged to restore 150 M ha of degraded land world-wide—an area the size of Mongolia (Menz, Dixon, & Hobbs, 2013).

A key question facing such initiatives is where to target efforts to maximize the benefits for both people and nature (Menz et al., 2013). At regional scales, the relative reliance of different species on intact forest may shift across climate gradients, which could influence restoration placement strategies (Karp et al., 2018). At landscape scales, a variety of factors are known to mediate the speed and capacity for restoration projects to recruit viable populations of native species (Reid, Mendenhall, Rosales, Zahawi, & Holl, 2014). For example, the "intermediate landscape-complexity hypothesis" posits that conservation interventions should be targeted in human-modified landscapes with intermediate amounts of remaining natural habitat (Tscharntke et al., 2012). The thinking is that in completely cleared landscapes, source populations may not exist to send colonists to restored sites, and, in very intact landscapes, so much habitat exists that colonists may "spill over" into cleared areas, with or without any conservation interventions.

The intermediate landscape-complexity hypothesis, however, was primarily conceived with the goal of bolstering generalist, ecosystem-service providers that rely on forests but readily move into agriculture. Consequently, restoring or conserving habitat in intermediate landscapes may fail to conserve vulnerable species that rarely utilize agriculture (Tscharntke et al., 2012). Moreover, many forest-restricted birds refuse crossing any deforested gaps to colonize new fragments (Ibarra-Macias, Robinson, & Gaines, 2011). Thus, restoration may be most successful at bolstering forest-associated species when sites are located in landscapes with large blocks of contiguous forest (Reid et al., 2014).

We surveyed bird communities in Costa Rica to evaluate the potential for working-landscape conservation to bolster forest-restricted birds. Specifically, we censused birds at 150 sites over 2 years in 5 reserves and 20 working landscapes, arrayed across an independent precipitation gradient encompassing wet and dry forests (~1.5-2.8 m, annual rainfall). Reserves varied in size (range: 9.1-183 km², mean: 59 km²) and time since establishment (range: 1974–1994, mean: 1984). Agricultural sites encompassed pastures, rice, sugarcane, and Taiwan grass (a forage crop). Forests in working landscapes varied in the amount of forest cover within 50 m (i.e. local scale; range: 44%-100%, mean: 85%) and within 610 m (i.e. landscape scale; range: 16%–96%, mean: 63%; see methods for scale definitions). Our work was organized around three questions. First, to what extent can forests and farms in working landscapes maintain local bird richness relative to protected areas? Second, given that forests in working landscapes are often fragmented and degraded, how distinct are bird communities in working landscapes versus protected areas? In particular, can species of conservation concern persist? Third, where should forest conservation and restoration be targeted to facilitate reserve-like bird communities?

2 | MATERIALS AND METHODS

2.1 | Bird surveys

We selected 25 focal landscapes in Northwest Costa Rica: 20 in working landscapes and 5 in protected areas (Reserva Biológica Lomas Barbudal, Reserva Natural Monte Alto, and Parques Nacionales Palo Verde, Barra Honda, and Diriá). Protected areas encompassed most of the precipitation gradient (1.6–2.4 m vs. 1.5–2.8 m at other sites). Other protected areas in the region would not have served as fair comparisons to our working-landscape sites, as they were either too far away or encompassed habitat types that we did not survey.

In each landscape, we identified six bird survey sites (N = 150 total). In working landscapes, three sites were located in agriculture and three in adjacent, privately owned forests. Sites within the same landscape were separated by 500 m on average and were chosen so that local forest cover varied independently from landscape-level forest cover and configuration. That is, we systemically varied site locations within each landscape, placing sites in forest interiors and forest edges, in areas surrounded by substantial forest cover and in small fragments surrounded by agriculture (Figure S1 and Table S1 in Methods S1). In protected areas, four sites were located in forest interiors and two at the reserves' edges.

One expert observer (J. Zook) conducted 20 min, 50 m fixed radius point counts at each site. Because our focus was on the resident avifauna, survey effort was concentrated on the Boreal summer (May-August). Dry season surveys would have resulted in few resident detections, as many species leave dry forests during the dry season and vocalize less frequently. Sites in working landscapes were surveyed in 2016 and 2017; protected areas were surveyed only in 2017. Approximately half of the sites were sampled three times each year (for binomial mixture modelling, see below) and the others were only surveyed once. Zook surveyed one farm or protected area per day (six sites). Surveys began at sunrise and continued for ~5 hr. All birds seen or heard during counts were recorded, in addition to the time of day, the presence of loud noise (e.g. cicadas, streams and farm machinery), number of people nearby, wind speed (using an anemometer) and distance to nearest river.

2.2 | Environmental gradients

We quantified the local vegetation structure, surrounding forest cover and regional precipitation associated with each site. In four, 5-m-radius subplots at each survey site, we quantified the following vegetation structure variables: canopy cover, proportion of trees with epiphytes or vines, proportion of trees with lianas, understorey density, herbaceous ground cover, shrub cover, tree species richness, number of tree stems, mean tree DBH and mean vegetation height (see Methods S1). To quantify surrounding forest cover, we hand-classified all trees, including plantations, within 1.5 km of each survey site using Google Earth imagery from 2013 to 2017 (Karp et al., 2018). We groundtruthed our final map using the 600 vegetation plots detailed above. We then defined local forest cover as the fraction of tree cover within 50 m of each survey site. Landscape forest cover was calculated at multiple spatial scales and was defined as the proportion of tree cover within "doughnuts," which always had an inner radius of 50 m but the outer radius varied from 60 m to 1.5 km by 10-m increments. To calculate landscape configuration at multiple scales, we first deleted all isolated tree clusters <0.5 ha in size and then calculated the forest edge perimeter within the same "doughnuts." Finally, to calculate regional precipitation, we used data from 29 regional weather stations to model annual precipitation across the region (Karp et al., 2018).

2.3 | Identifying reserve-affiliated bird species

We implemented binomial mixture models to estimate species abundances at each site and factor out variation in detection among different species and sites (Royle & Dorazio, 2008). Species abundances at each site were assumed to result from detection and true abundance processes. True abundances were assumed to vary by species and across the environmental gradients (i.e. *local forest cover, annual precipitation, distance to rivers* and *landscape forest cover* and *landscape edge perimeter*). *Landscape forest cover* and *edge* variables were estimated as the fraction of forest and edge perimeter within 60 to 1,500 m of each sampling the site. The model was allowed to select the most predictive scale (Frishkoff, Mahler, & Fortin, 2017). Here, 610 m was most predictive; thus, we used a 610-m buffer radius in all analyses. For more details about the model and scale selection, see Methods S1.

To identify bird species strongly affiliated with protected areas, we modified our binomial mixture model by adding another variable, "reserve status," which identified whether each site was in a protected area. We extracted the posterior estimates of the effect of "reserve status": "reserve-affiliated" species were defined as species that significantly increased in abundance in reserves (BCI of contrast between protected areas and working landscapes did not overlap 0).

In a second analysis, we modified the binomial mixture model by substituting one categorical land-use predictor for all other local and landscape-level forest cover and edge predictors. This variable defined sites as *reserves* (N = 30), *high-cover forest* (N = 16; sites in working landscapes with >75% forest cover at local and landscape scales), *low-cover forest* (N = 45; forested sites in working landscapes with <75% forest cover) and *agriculture* (N = 59), and allowed us to explicitly compare species abundances between land-use types. We chose 75% forest cover as this threshold roughly corresponded to a substantial turnover in bird community composition (Figure S6 in Methods S1). For each posterior community, we recorded whether each species was predicted to be more or less abundant in protected areas, relative to each of the other land uses. Species were considered to be significantly more abundant in protected areas when they were predicted to decline in the other land uses across >95% of the posteriors.

To compare vegetation structure and landscape attributes between land uses, we implemented Linear Mixed Models (LMMs; Bates, Maechler, Bolker, & Walker, 2015) that included categorical land use as the sole fixed effect and a random effect of *landscape* to account for spatial autocorrelation. We transformed response variables when necessary to satisfy model assumptions (Figure S8 in Methods S1). Variable significance was assessed using likelihood ratio tests, comparing nested models with and without the categorical land-use fixed effect (Zuur, leno, Walker, Saveliev, & Smith, 2009).

2.4 | Modelling species richness, range size, and similarity to reserves

We used the binomial mixture model to estimate species abundances across sites. Specifically, we extracted the modelled abundance of each species at each site in 2017 ($N_{i,i,2017}$)-the year in which all sites were sampled—along each iteration (N = 2,000) of the posterior (Karp et al., 2018). Using each of these 2,000 "posterior communities," we calculated the species richness of each site. We also calculated the average range size across all species present at each site, using estimates from BirdLife International (2019).

Next, we quantified the bird community similarity between each pair of sites using presence-absence (Sørenson similarity) and abundance (Bray-Curtis similarity) metrics. We decomposed these metrics to analyse their turnover components, using "betapart" in R (Baselga, Orme, Villegar, Bortoli, & Leprieur, 2018; R Core Team, 2018). We visualized differences between sites in their species compositions using non-metric multidimensional scaling, and tested whether different land uses hosted significantly different communities via permutational multivariate analysis of variance. We also used the community similarity metrics to calculate the overlap between the bird community found at each site and community found in the nearest protected area. Specifically, for each metric and posterior community, we calculated the multivariate bird community distance from each site to the centroid of the closest protected area (Karp et al., 2018). As we were interested in the most "intact" reserve community, we excluded the two edge sites in each protected area when calculating similarity to reserve communities.

We modelled species richness, average range size, and reserve similarity using LMMs with landscape as a random effect and the following fixed effects: local forest cover (linear and quadratic terms), landscape forest cover and edge, precipitation, vegetation structure, and interactions between local forest cover and precipitation, landscape forest cover, and forest edge. For the species richness and range size analyses, we included reserve sites and added reserve status (i.e., whether the site was in a reserve or not) as another predictor. For the reserve similarity analysis, we omitted reserve sites but included distance to nearest reserve as another fixed effect to account for community similarity decaying with distance (Karp et al., 2018). We omitted distance to reserves in models that did not focus on community similarity. In all models, vegetation structure was measured as the second and third principal components of a PCA on all vegetation structure variables. The first principal component was highly correlated with local forest cover (Pearson's r = 0.88, df = 148).

All fixed effects were standardized prior to analysis. Models were weighted by the posterior variance of the species richness, reserve size, and reserve similarity estimates (Karp et al., 2018). All models conformed to LMM assumptions (i.e. normality, hetero-scedasticity) and none of the included parameters displayed severe evidence of collinearity (variance inflation factors <2.5; Zuur et al., 2009), although local and landscape forest cover were marginally correlated (Pearson's r = 0.54). To assess the significance of fixed effects, we used forward and backwards model selection, comparing nested models with likelihood ratio tests (Zuur et al., 2009). We repeated analyses of species richness and reserve similarity using raw detections rather than posterior estimates of true abundance to test the robustness of trends. We did not model range sizes from raw detection data as ~25% of the site visits yielded <5 species (too few to calculate reliable community averages for range size). Across

the modelled communities, all sites housed at least 10 species. We report trends in raw communities in the supplement; all figures depict modelled communities.

In separate analyses, we restricted our focus to forest sites to identify which forests hosted the highest levels of local bird diversity, smallest average range sizes, and greatest similarities to forest reserves. Here, models were similar to those previously described except: (a) local forest cover and its interactions were omitted, as our focus was only on the forest sites and (b) all vegetation structure variables were included individually, rather than as composite principal components.

2.5 | Mapping restoration potential

To highlight how our analyses could be used to operationalize conservation prioritization, we used the most predictive model of community similarity to the nearest reserve to map *predicted similarity to reserves* in a 300-m grid encompassing our study region. To drive our model, we estimated precipitation at each grid point (Karp et al., 2018), mapped forest cover across the region (Methods S1) and calculated forest cover within 50 and 610 m of each grid point (Figure S2 in Methods S1). We also used our model to map restoration potential across the Corredor Biológico Hojancha-Nandayure, an area currently being considered for forest restoration. To map restoration potential, we used our reserve-similarity model to predict the expected increase in reserve similarity that would result from reforesting each 50 m agricultural grid cell from 0% to 100% local forest cover.

3 | RESULTS

We detected 150 species and 9,215 individual birds in 2016 and 2017 (Appendix S1). Our binomial mixture model indicated that detection varied across species and between forest and agriculture. Detection also declined in counts conducted later in the morning, in windy conditions and in the presence of loud noises.

3.1 | Can working landscapes house as many species as protected areas?

Local bird richness did not differ between reserves and forests in working landscapes, but exhibited a slight decline in agriculture (Figure S3 in Methods S1). Specifically, richness increased nonlinearly with local forest cover (Table S2 in Methods S1; Figure 1), peaking at 80% forest cover but declining by only 20% (~7 species) at the most deforested sites. Richness did not change with landscape forest cover but did increase with precipitation and with the second principal component of vegetation structure. This PC axis reflected differences between forests with many tree stems (less richness) versus stands with fewer, larger trees (more richness; loadings of number of tree stems and mean tree DBH: -0.30 and 0.93 respectively).



FIGURE 1 Species richness and average range size changes along gradients. Richness exhibited a slight, nonlinear increase with local forest cover, peaking at ~80% (dotted line; a). Increases in richness with local forest cover were most pronounced at sites with less forest edge in the landscape (b). Richness also increased with precipitation (c) and with the second principal component of a vegetation structure PCA that differentiated sites with many thin trees from sites with fewer, wider trees (d). Unlike richness, average range size across bird communities declined sharply with local forest cover (e). Declines were more rapid in sites with more landscape forest cover (f) and in wetter regions (g). Range size also declined in more fragmented landscapes (h). Lines indicate predicted trends; grey regions delineate 95% confidence intervals. Plus signs are sites in protected areas (PA); grey circles are sites in working landscapes

While habitat fragmentation per se (measured as landscapescale forest edge length) did not affect species richness alone, we did observe an interaction between forest edge and local forest cover amount, such that the strongest richness increases with local forest cover were observed in the least fragmented landscapes (Figure 1b). None of our results changed when implementing forward or backwards model selection. Results were also largely consistent when examining raw detections (rather than modelled abundances). Raw detection models did, however, suggest an interaction between precipitation and local forest cover, such that richness disproportionately increased in wetter, more forested sites. Restricting our focus to forested sites and excluding agriculture, all models supported trends of increasing richness at sites with more landscape forest cover and in wetter regions (Table S3 and Figure S4 in Methods S1). We found less consistent support, however, for richness increasing in stands with fewer, larger trees and at sites with more understorey density and herbaceous ground cover.

3.2 | Are bird communities in working landscapes distinct from those in reserves?

We found strong evidence that community composition shifted across the environmental gradients (Table S4 in Methods S1; Figure 2 and Figure S5 in Methods S1). However, communities were much more responsive to local forest cover and, to a lesser extent, regional precipitation than other variables. We also found that community composition significantly differed between protected areas, high-cover forest (i.e. sites in working landscapes with >75% forest cover at local and landscape scales), low-cover forests and agriculture. One key exception was protected areas and high-cover forests, which could not be differentiated (p > 0.05). Indeed, bird communities rapidly shifted at sites with >75% local and landscape forest cover, with "reserve-affiliated species" increasing in proportional abundance (Figure S6 in Methods S1).

Average range sizes reflected these community shifts. Wideranging birds replaced narrow-ranged birds at sites with less local forest cover, especially in less forested landscapes and in wetter regions (Figure 1). As a result, average range sizes in agricultural communities were more than twice as large as communities in protected areas (Figure S3 in Methods S1). Range size tended to decline in fragmented landscapes (Figure 1), and in forested sites with fewer lianas and more herbaceous vegetation (Figure S7 in Methods S1). Critically, average range size did not differ between protected areas and high-cover forests (Figure S3 in Methods S1).

Indeed, we found that very few bird species uniformly declined in abundance outside protected areas, after controlling for differences in forest cover. Specifically, only 3 of the 150 surveyed species were significantly more abundant in protected areas than working



FIGURE 2 Non-metric multidimensional scaling plots depicting shifts in bird community composition along environmental gradients. The distance between sites (points) corresponds to differences in community composition (Bray–Curtis similarity). Sites that shared similar levels of local forest cover (a; green to orange gradient) or precipitation (b; purple to red gradient) also hosted similar bird communities. (c) Bird communities in reserves (dark green; plus signs), high-cover forests (sites in working landscapes with >75% forest cover at local and landscape scales; olive), low-cover forests (light green) and agriculture (orange) were distinct, except that reserve and high-cover forest communities overlapped. Ovals are ordination ellipses based on the SD of point scores



FIGURE 3 Differences in bird abundance between reserves and other land uses. (a) Bar plots depict comparisons of species abundances between reserves and high-cover forest (sites in working landscapes with >75% forest cover at local and landscape scales; left bar), low-cover forests (<75% forest cover; middle bar) and agriculture (right bar). Green, orange and white shaded regions indicate the number of species that were significantly more, less and equally abundant in reserves relative to sites in working landscapes. Numbers indicate the number of species in each category. Grey lines indicate each species depicted in (b-d). (b) The Rufous-and-white Wren (*Thryophilus rufalbus*) was one of seven species for which abundance was higher in reserves (RS) than in high-cover forests (HCF), low-cover forests (LCF), and agriculture (AG). (c) The Elegant Trogon (*Trogon elegans*) was more abundant in both reserves and high-cover forest than in other forests and agriculture. (d) The Turquoise-browed Motmot (*Eumomota superciliosa*) was more abundant in all forests than in agriculture. Points depict predicted abundances in each land use; lines depict 95% Bayesian Credible Intervals. Different letters indicate statistical significance

landscapes (Figure S8 in Methods S1). Similarly, when our binomial mixture model was modified to compare land-use categories, we found that 7, 32 and 50 species were significantly more abundant in protected areas than high-cover forests, low-cover forests and agriculture respectively (Appendix S2 and Figure 3).

This near equivalency in bird community composition between protected areas and high-cover forests existed despite structural differences (Figure S9 in Methods S1). High-cover forests were embedded in landscapes that were more than twice as fragmented as protected areas. Logging and other disturbances also contributed to distinct vegetation structures. Specifically, compared to protected areas, highcover forests exhibited 13% lower canopy cover, 30% shorter tree heights, 20% lower tree richness and 35% less dense understories.

3.3 | How could working landscapes be managed to promote reserve-like bird communities?

Communities in working landscapes with more forest cover at local and landscape scales exhibited a high degree of overlap with communities in nearby reserves (Figure 4; Table S7 in Methods S1). The



FIGURE 4 Effects of forest at local and landscape scales on a reserve similarity. Bird community similarity to the nearest reserve (Bray-Curtis similarity) increased in sites with more local (a) and landscape forest cover (b). Local forest effects interacted with landscape forest cover (d) and regional precipitation (e), such that reserve similarity increased most rapidly with local forest cover in forested landscapes and wetter regions. As a visual reference on the same scale, identical (c) and (f) depict the similarity of each reserve site to other sites in the closest reserve (black dots) and to other sites in the same reserve (grey dots). Non-reserve sites generally do not attain similarity levels of within-reserve comparisons, but many attain similarity levels of among-reserve comparisons. Lines depict predicted trends from linear models; shaded regions depict confidence intervals; points depict individual sites

effect of local forest cover was nonlinear, with sites accelerating in reserve similarity as forest cover increased. This was mostly the result of accelerating abundance increases of "reserve-affiliated species" at high levels of forest cover; "agriculture-affiliated species" exhibited a more linear decline with forest cover (Figure S10 in Methods S1). Thus, the most forested sites in working landscapes exhibited roughly the same degree of reserve similarity as actual reserve sites did with sites in different reserves (Figure 4c,f). We also found that increasing local forest cover in wetter regions and/ or in more forested landscapes increased reserve similarity more so than an equivalent amount of forest increase in dry regions or deforested landscapes. Fragmentation had no detectable effect on community similarity with reserves. These results were qualitatively similar when analysing raw detections and the turnover component of dissimilarity (Tables S7 and S8 in Methods S1). Our findings were also generally consistent when reserve similarity was calculated with metrics that only considered species presences and ignored abundances (Figure S11 and Table S7 in Methods S1).

Within forest sites, findings were less consistent across similarity metrics, model selection procedures and analysis targets (i.e. modelled communities vs. raw detections; Tables S9 and S10 and Figure S12 in Methods S1). In every case, we found that reserve similarity increased at sites with more landscape forest cover. We found less consistent support for increased similarity with greater tree heights, canopy cover, understorey density, proportion of lianas,

tree richness and shrub cover. Finally, we found very inconsistent support that reserve similarity declined with precipitation, forest edge, number of tree stems and DBH.

Our model of abundance-based reserve similarity adequately fit the observed data (conditional $R^2 = 0.90$) and could thus be used to predict spatial variation in the projected overlap between bird communities found in working landscapes and nearby reserves across Northwest Costa Rica. Both across Northwest Costa Rica and within the Corredor Biológico Hojancha-Nandayure (Figure 5), resulting maps highlighted the value of maintaining or restoring forests in wetter regions and in regions with more landscape forest cover. Specifically, models predicted that restoring agricultural pixels in the wettest areas resulted in twice the gains in reserve similarity as restoring in the driest areas. Similarly, restoring agriculture in 100% forested landscapes was 2.65 times more effective in terms of increasing reserve similarity than in deforested landscapes.

4 | DISCUSSION

Our study suggests that there is great scope for conserving Neotropical birds in Costa Rican working landscapes. Species richness was no higher in reserves than in working landscapes with substantial forest cover at local and landscape scales, and few species (<5%) were more abundant in reserves than in these high-cover



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FIGURE 5 Maps of study sites and similarity of bird communities in working landscapes to reserve communities. (a) Northwest Costa Rica encompasses a strong precipitation gradient. (b) Map depicts protected areas (dark green), forests in working landscapes (blue) and agriculture (orange) across the region. In (a) and (b), white dots indicate reserve sites and red dots are sites in working landscapes. (c) Wetter sites and sites with more forest cover at local and landscape scales were predicted to host more reserve-like bird communities. Green polygons denote terrestrial reserves (UNEP-WCMC & IUCN, 2018). Yellow polygon denotes the Corredor Biológico Hojancha-Nandayure, a region being prioritized for reforestation. (d) Simulated reforestation of the corridor's agricultural sites from 0% to 100% local forest cover suggests greater increases in bird community similarity to reserves for sites located in wetter regions (i.e. the Southwest) and surrounded by more forest (forest in working landscapes = light green; reserves = dark green; as opposed to other land = grey)

forests. Consequently, high-cover forests and reserves were largely indistinguishable in species composition and both hosted communities of birds with small range sizes. This was surprising as high-cover fragments were embedded in working landscapes that were twice as fragmented as protected areas. Moreover, regular logging, fires, hunting and other disturbances likely altered the vegetation structure of forests in working landscapes compared to protected areas. Indeed, high-cover forests in working landscapes had lower canopy cover, shorter tree heights, fewer tree species, and less dense understories than protected areas. Landowners likely maintain forest for multiple reasons including laws that mandate reforestation near rivers (Ley 7575, 276), Costa Rica's flagship Payment for Ecosystem Services program that incentivizes forest conservation, and because some areas may be marginal areas for cultivation (e.g. steeper slopes; Figure S13 in Methods S1). Regardless, these findings suggest that maintaining forest in Costa Rican working landscapes can promote avian communities that resemble those in protected areas, even when subject to disturbances.

Critically, we found that many species also persisted in totally deforested sites. Specifically, we detected a nonlinear, saturating relationship between species richness and local tree cover, such that richness only declined by 20% (seven species) at the most deforested sites. This finding is not unique to our region: agriculture has been shown to maintain speciose communities in other areas of Costa Rica (Karp et al., 2015) and abroad (e.g. Ranganathan, Daniels, Chandran, Ehrlich, & Daily, 2008; Waltert et al., 2005). Especially because studies of tropical wildlife often focus on forest-restricted species (e.g. Barlow et al., 2016), this diverse community of agricultural species bears further study.

Still, it is important to consider the identity of the species that persisted in farmland. Only two surveyed species are not listed as "least concern" by the IUCN–Great Curassow (*Crax rubra*) and Yellow-naped Parrot (*Amazona auropalliata*)–both which were most regularly detected in forests in working landscapes (but not in agriculture). More importantly, we found that the average range size of species in agricultural sites was more than double that of species in protected areas, indicating that either agriculture facilitates naturally wide-ranging over endemic species or that agriculture favours species that were initially range-restricted but later became wideranging as agriculture expanded.

A divergence in average range size reflects our broader observation that avian community composition strongly differed between agriculture and protected areas. Other studies across the tropics have documented strong shifts in community composition with habitat conversion (Gibson et al., 2011; Newbold et al., 2016). In Cameroon, similar bird richness between forests and farms belied marked differences in community composition (Waltert et al., 2005). Similarly, in Brazil's Atlantic forest, vertebrate communities experienced an abrupt shift from forest specialists to disturbance-adapted species when landscape-level forest cover declined below 30% (Banks-Leite et al., 2014). Here, community similarity to reserves also responded strongly to forest cover, with reserve-affiliated species rapidly increasing in abundance at sites with more than 75% forest cover at local and landscape sites.

In some senses, our finding that the effect of local forest cover amplified in forested landscapes contradicts the intermediate landscape-complexity hypothesis, which predicts stronger effects of local management in landscapes of intermediate forest cover (Tscharntke et al., 22012). However, this hypothesis originally focused on generalist, ecosystem-service providers, rather than more sensitive forest species. Our results suggest that maintaining or restoring larger swaths of tropical forest may be essential if the goal is to preserve more reserve-like biological communities, complete with range-restricted species or others of conservation concern (Betts et al., 2017; Pfeifer et al., 2017; Reid et al., 2014).

That said, forested landscapes may maintain seed dispersers that could facilitate restoration without active management (Hooper, Legendre, & Condit, 2005), meaning intermediately forested landscapes should still be targeted for active restoration (Tambosi, Martensen, Ribeiro, & Metzger, 2014). Moreover, recent approaches are able to prioritize sites for restoration based on costs and multiple benefits (i.e. not just reserve similarity; Strassburg et al., 2019). For example, if another goal is to enhance ecosystem services, then restoring forest in deforested landscapes would increase farmlandforest interfaces and allow habitat generalists to move from forests to farms (Karp et al., 2015; Ricketts & Lonsdorf, 2013). Similarly, agriculture may be compatible with water bird conservation: in our study system, 80% of detected water bird species (e.g. herons, ducks etc.) were more abundant in agriculture than protected areas.

It is also important to acknowledge the regional context before advocating the benefits of forest conservation in working landscapes elsewhere. First, it is possible that our surveys missed especially rare forest specialists that are restricted to protected areas. However, only 21 additional (non-migratory) species were detected in a 15year bird census effort at 16 sites in our study region (Frishkoff et al., 2014), all of which are listed as "least concern." A possibility that we cannot exclude, however, is that the most sensitive species have already been extirpated from the region. Our study region experienced high rates of deforestation until the 1980s, at which point forest cover began increasing, from 23% in 1986 to 47% in 2005 (Calvo-Alvarado, McLennan, Sanchez-Azofeifa, & Garvin, 2009). This means that sensitive species could have regionally extirpated prior to the 1980s. Second, formal protected areas are often subject to degradation, calling into question their utility as a baseline. Indeed, one-third of protected areas face severe human pressure and Costa Rica is no exception (Jones et al., 2018). Third, our prior work suggests that dry forest-associated species may be preadapted to thrive in working landscapes (Frishkoff et al., 2016; Karp et al., 2018). High similarity between communities in reserves and forested working landscapes

may thus partially reflect the fact that some of our reserves protected dry forests. Indeed, in wetter Amazonian sites, communities turn over between primary forests and the secondary forests that typify working landscapes (Barlow, Mestre, Gardner, & Peres, 2007). Finally, other taxa may respond differently than birds; for example, a recent study found it may take centuries for plant communities in secondary forests to resemble those in primary habitats (Rozendaal et al., 2019). Thus, prioritizing conservation of fragmented, disturbed forests in working landscapes may be still be inadvisable in areas that host more endangered species, are less degraded and/or that are located in wetter regions (Barlow et al., 2016).

5 | CONCLUSIONS

Our work yielded several conservation-relevant insights. First, we report that while biodiverse communities persisted in agriculture, assemblages lacked the range-restricted species of conservation concern found in forests. Second, we found that only 5% of the species surveyed were more abundant in reserves than in high-cover forests, suggesting vulnerable species could greatly benefit from conserving or restoring forest in Costa Rican working landscapes, even if the forest is highly fragmented and disturbed. Third, our mapping exercise illustrates how our method can be used to provide concrete guidance for siting conservation initiatives (e.g. ongoing restoration efforts in the Corredor Biológico Hojancha-Nandayure; Figure 5d). Indeed, Northwest Costa Rica is expected to experience future climate drying (Rauscher, Giorgi, Diffenbaugh, & Seth, 2008) and we have previously shown that birds associated with wetter and more forested sites are the most vulnerable to these changes (Karp et al., 2018). Thus, our work suggests that targeting future restoration and conservation in wetter regions and more forested landscapes could help optimize biodiversity conservation, at least for forest-associated birds in Costa Rica.

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AUTHORS' CONTRIBUTIONS

D.S.K., A.E., K.M.A.C. and L.O.F. designed research; D.S.K., A.E., J.Z., P.J., and A.K. collected data; D.S.K., L.O.F., A.E. and J.K. analysed

data; D. S. K. wrote the manuscript. All authors contributed to drafts and gave final approval for publication.

DATA ACCESSIBILITY

Data available via the Dryad Digital Repository https://doi. org/10.5061/dryad.fg8kq66 (Frishkoff & Karp, 2019).

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