

# Cavity-nesting birds are limited by nesting habitat in Neotropical agricultural landscapes

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## Abstract

Most studies comparing biodiversity between natural and human-modified landscapes focus on patterns in species occurrence or abundance, but do not consider how different habitat types meet species' breeding requirements. Organisms that use or nest in tree cavities may be especially threatened by habitat conversion due to the loss of their nesting sites. Although cavity-nesting bird diversity is highest in the tropics, little is known about how tropical birds use cavities, how agriculture affects their reproductive biology, and how effective nest boxes could be as a conservation strategy in tropical agriculture. Here, we explored how habitat conversion from tropical forests to pasture affects the abundance, nesting habitat availability, and nest success of cavity-nesting birds in Northwest Ecuador. We conducted bird surveys and measured natural cavity availability and use in forest and agriculture. We also added artificial nest boxes to forest and agriculture to see whether cavity limitation in agriculture would elicit higher use of artificial nest boxes. We found evidence of cavity limitation in agriculture—there were many more natural cavities in forest than in agriculture, as well as more avian use of nest boxes placed in agriculture as compared to forest. Our results suggest that it is important to retain remnant trees in tropical agriculture to provide critical nesting habitat for birds. In addition, adding nest boxes to tropical agricultural systems could be a good conservation strategy for certain species, including insectivores that could provide pest-control services to farmers.

Abstract in Spanish is available with online material.

## KEYWORDS

conservation, Ecuador, nest boxes, nest success, tropical agriculture, tropical forest

## 1 | INTRODUCTION

Habitat conversion is the primary driver of modern terrestrial biodiversity loss (Newbold et al., 2015), causing local extinctions by decreasing population sizes, increasing population isolation, and, in turn, increasing the influence of stochastic events (Brooks

et al., 2002; Wiens, 1992). Understanding how to conserve biodiversity in human-modified landscapes is therefore critical to mitigating the ongoing biodiversity crisis (Kremen & Merenlender, 2018). To date, most studies comparing biodiversity between natural and human-modified landscapes focus on patterns in species occurrence or abundance (e.g., Newbold et al., 2013; Sekercioglu et al., 2007).

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However, even if species are present, agricultural habitats may still not support sufficient reproductive rates to allow populations to persist. For example, observing the presence of species in agriculture may not be sufficient to classify its importance if highly mobile organisms regularly move through agricultural systems but still rely on nearby natural habitats to complete their lifecycles and/or reproduce (Frishkoff et al., 2019). In addition, species in agricultural landscapes may be subject to source-sink dynamics (Pulliam, 1988) and/or ecological traps (Gates & Gysel, 1978), in which animals are regularly found in suboptimal habitats and then suffer lower population-level fitness. One component of fitness that is important for maintaining populations is reproductive success. Failing to understand species' breeding requirements, and the degree to which these requirements can be met in different habitat types, may thus draw focus away from optimal habitats and cause conservation practitioners to protect areas that cannot support populations over the long term.

Organisms that use or nest in tree cavities may be especially threatened by deforestation due to the loss of their nesting sites. These organisms include many mammal species (e.g., bats, squirrels, and mice; Czeszczewik et al., 2008), as well as cavity-nesting birds, which depend on tree cavities to breed and roost (Martin & Eadie, 1999). Worldwide, at least 18% of land bird species nest in cavities (van der Hoek et al., 2017). Many of these species are known to decline in areas where humans remove cavities, for example, in forests that are selectively logged (Cockle et al., 2010; Engblom et al., 2002). Human disturbances may also increase nest predator abundances, facilitating increased predation pressure and lowering nesting success (Robinson et al., 1995).

Most of our knowledge concerning how habitat conversion affects cavity-nesting birds comes from studies in temperate landscapes (Newton, 1998). However, cavity-nesting bird diversity peaks in the Neotropics, where 678 cavity-nesting bird species occur (van der Hoek et al., 2017). Though tropical species are generally thought to be more sensitive than temperate species to habitat conversion (Newbold et al., 2020), a general lack of knowledge surrounding their ecology, nesting preferences, and reactions to human disturbances impedes efforts to conserve tropical cavity-nesting birds (Cornelius et al., 2008).

In temperate landscapes, artificial nest boxes are used extensively as a conservation tool to increase cavity availability for a wide range of species (e.g., birds, bats, and non-volant mammals; Ardia et al., 2006; Czeszczewik et al., 2008; Rueegger, 2016). Such efforts have enjoyed varying degrees of nest box use depending on the study region and attributes of the nest boxes. For example, Lindenmayer et al. (2009) found that nest boxes that were higher and on steeper slopes had higher occupancy by arboreal marsupials in southeastern Australia, north-facing boxes were adopted the fastest, but there was no effect of nest box dimensions on occupancy. On the contrary, Goldingay et al. (2015) found that native birds very rarely used nest boxes in eastern Australia. While there are some studies evaluating whether nest boxes could be used for particular species in tropical regions (e.g., Scarlet Macaw,

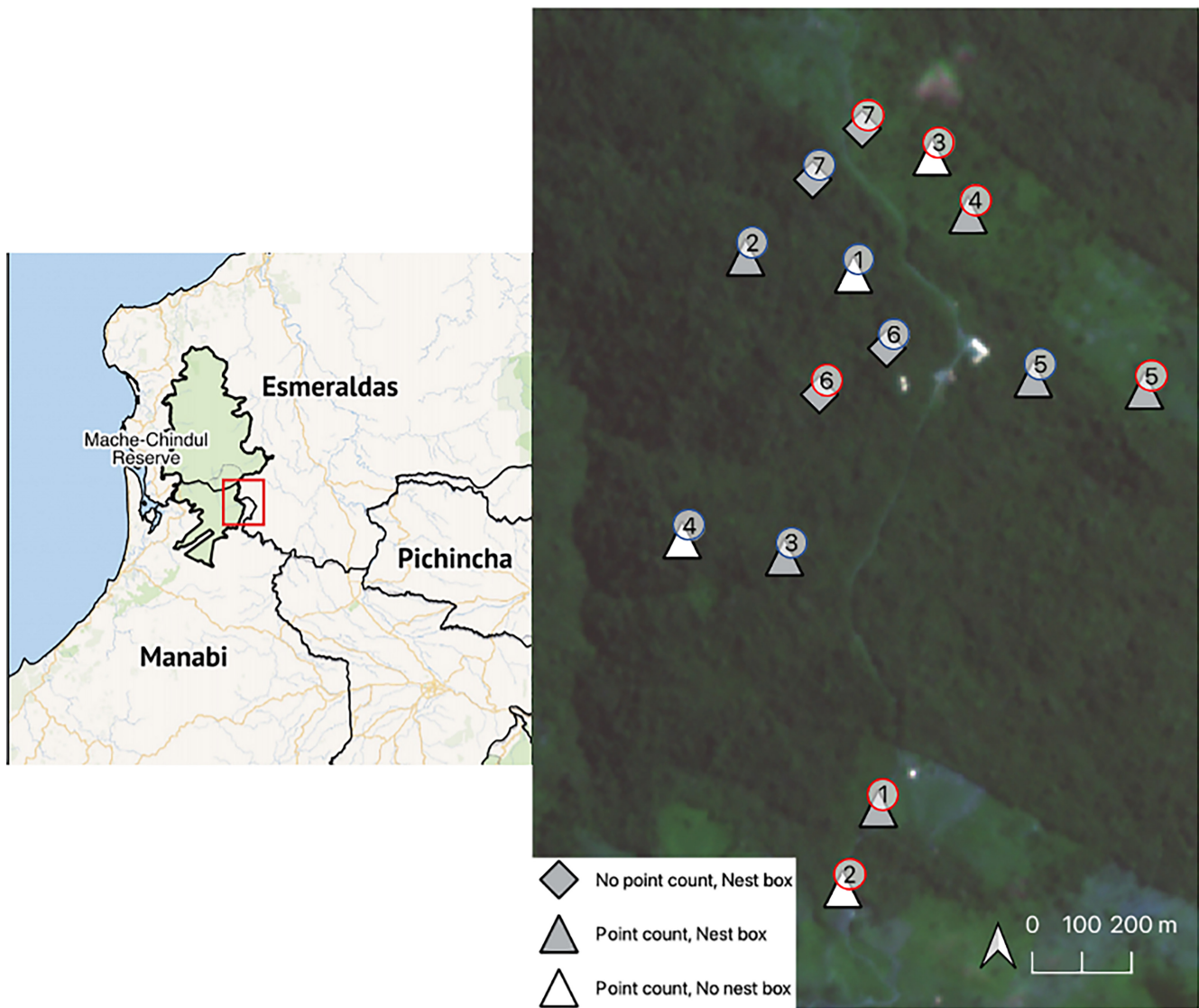
*Ara macao*; Olah et al., 2014), very few have evaluated whether the reproduction of cavity nesters is limited by nesting habitat in agricultural landscapes (Fimbel et al., 2001), let alone whether nest boxes could be used to bolster their abundances. In particular, very few nest box experiments have occurred in tropical pastures, which make up a large percentage of Earth's land surface and are a leading cause of tropical habitat loss worldwide (Curtis et al., 2018; Pendrill et al., 2022).

Here, we conducted an observational study and nest box addition experiment to explore how habitat conversion from tropical forests to pasture affects the abundance, nesting habitat availability, and nest success of cavity-nesting birds in Northwest Ecuador. First, we conducted observational surveys to understand how cavities, cavity use, and abundances of cavity-nesting birds compare between forest and pastures. We hypothesized that, due to a lack of large trees, there would be lower abundances of cavity-nesting birds, lower cavity availability, and higher cavity occupancy rates in agriculture than in forest. Then, we conducted an experiment, constructing artificial nest boxes to understand how nest box use and nest success compare between forest and pastures. We hypothesized that cavity limitation in pastures would elicit higher use of artificial nest boxes compared to forests (Cockle et al., 2010) but that the nest boxes in pastures would experience lower success due to higher predation levels in more open areas (Andren & Angelstam, 1988). We also predicted that nest boxes in pastures would not be used by species of conservation concern in the Neotropics, as rarer, range-restricted species are often disproportionately sensitive to land-use change (Cockle et al., 2010; Sykes et al., 2020).

## 2 | METHODS

### 2.1 | Study sites

We studied cavity-nesting bird communities in Northwest Ecuador, around the Mache-Chindul Ecological Reserve (0.3900, -79.6840; elevation 390–510m near our study site) in the Esmeraldas Province (Figure 1). The area has been delineated as a BirdLife International "Important Bird Area" ("BirdLife Data Zone", 2019) within the Chocó biogeographic zone, characterized by high biodiversity and severe rates of deforestation (Orme et al., 2005; Sierra, 1999). The Mache-Chindul Ecological Reserve was created in 1996 and consists of pristine forest, secondary forest fragments, and agricultural lands. The area has experienced rapid agricultural expansion in the last 50 years. About 6500 people live in the Reserve, typically on farms of 20–50ha with agriculture including cacao, pasture for cattle, corn, beans, rice, plantain, and oil palm (Carrasco et al., 2013). Dominant forest types are humid evergreen and sub-humid evergreen forests, with canopy heights in primary forest spanning 30–40m. Average monthly temperatures range from 26 to 28°C, and total annual precipitation ranges from 2 to 3.5m, with the majority of the rainfall occurring between January and May. To study cavity limitation, we established fourteen 0.5-ha rectangular plots (100m×50m), half



**FIGURE 1** Map of study region (left) and map of study sites (right). In map of study sites, labels outlined in red represent agriculture and labels outlined in blue represent forest. Shapes and colors indicate if sites were surveyed for bird communities (“point count”) and/or had nest boxes. Natural cavity surveys and monitoring occurred at points 1–4 in agriculture and forest.

within forest and half in agriculture, the latter consisting mostly of pasture but also with occasional cacao or plantain plants. Minimum distance between plots was 137 m, maximum distance was 1532 m, and mean distance was 650 m.

## 2.2 | Bird surveys

To survey bird communities, FC and LC conducted 10-min point counts in four periods (February 2020, July 2020, May 2021, and July 2021) at the center of five agriculture plots and five forest plots (Figure 1). There are two peaks of avian breeding activity in the region, from February to May and October to November (Carrasco et al., 2013). During surveys, we recorded all birds seen or heard within 50 m from the stationary observer. We used circular plots for

point count surveys so that the probability of detecting individuals was consistent in all directions. Within each of the four survey periods, each site was sampled three times within a week. Point counts took place between 6:00 and 11:30 a.m. (97% took place between 6:00 and 10:00 a.m.). We recorded the survey time, wind conditions (qualitative 0–3 scale, where 0=no movement of branches, 1=light breeze that moves leaves and small branches, 2=moderate wind that moves shrubs and medium branches, and 3=strong wind that moves large branches in the canopy), and fog conditions (qualitative 0–3 scale where 0=no fog, 1=fog present, visibility up to 100 m, 2=visibility up to 50 m due to fog, and 3=visibility up to 30 m due to fog) to help account for variation in detection between species, weather conditions, and habitats. No surveys were conducted in the rain. Finally, we used an existing database to identify cavity-nesting species (del Hoyo, 2015).

## 2.3 | Modeling bird communities

To estimate the abundance of each bird species at each site while accounting for imperfect detection, we implemented a N-mixture model, where the number of individuals is counted during spatially and temporally replicated surveys (Kéry, 2018; Royle, 2004). We implemented the N-mixture model within a community modeling framework such that species-specific parameters were estimated using community-wide hyperparameters, allowing us to share information among species in the community and estimate parameters of rarer species (Dorazio & Royle, 2005; Kéry & Royle, 2015).

The number of individuals of species ( $i$ ) at site ( $j$ ) was modeled using a Poisson distribution; specifically, the expected abundance  $\lambda_{i,j}$  was modeled as:

$$\log(\lambda_{i,j}) = \alpha 0_i + \alpha 1_i * LU_j + \alpha 2 * cavity_i + \alpha 3 * cavity_i * LU_j + \delta 0_j + \delta 1_{year[survey(j)]}$$

where “LU” is a binary variable representing either forest (1) or agriculture (0), and “cavity” is a binary variable where 1 indicates that the species nests in cavities.  $\alpha 0$  and  $\alpha 1$  were estimated for each species, and  $\alpha 2$  was a fixed effect representing the interaction between cavity-nesting species and land-use type. The  $\delta$  terms represent random effects that were included to account for spatial and temporal autocorrelation in bird abundances, explaining variation among point-count locations ( $\delta 0$ ) and years ( $\delta 1$ ). Site and year random effects were applied equally across the community: allowing them to vary by species caused issues with model convergence.

We modeled the detection probability of an individual of species ( $i$ ) at site ( $j$ ), visit ( $k$ ), and point count survey ( $l$ ), where point count survey represents surveys in February 2020, July 2020, May 2021, or July 2021, ( $P_{i,j,k,l}$ ) as

$$\text{logit}(P_{i,j,k,l}) = \gamma 0_{LU[j]} + \gamma 1_i + \gamma 2 * \text{time}_{j,k,l} + \gamma 3 * \text{wind}_{j,k,l} + \gamma 4 * \text{fog}_{j,k,l} + \gamma 5_i * \text{date}_{j,k,l} + \gamma 6_i * \text{date\_sq}_{j,k,l}$$

Here, “time” represents time of day, “wind” is the level of wind from 0 to 3, “fog” is the level of fog from 0 to 3, and “date” is the Julian day of the year. All variables, including the 0–3 scales, were scaled and centered prior to analysis.  $\gamma 0$  is a land-use specific intercept (for forest versus agriculture),  $\gamma 1$  is a species intercept, and  $\gamma 3$  and  $\gamma 4$  are fixed effects for wind and fog, respectively. Wind and fog were treated as fixed effects because we believed that each would have a consistent negative effect on the detectability of all species.  $\gamma 5$  and  $\gamma 6$  are species-specific slopes for date and date squared, as each species' activity (and thus detectability) could peak at different times of the year.

We implemented the model in R Version 4.0.0 using the package *R2jags*, which runs Markov chain Monte Carlo (MCMC) algorithms (R Core Team, 2013; Su & Yajima, 2012). We ran three chains starting at random initial values and 50,000 burn-in iterations. We included 50,000 post burn-in iterations, thinned at a rate of 50. We considered the chains to converge if the Gelman-Rubin statistics of the chains of every parameter were  $\leq 1.1$  (Gelman et al., 2004).

We expected the bird community on average to be positively associated with forest habitat (i.e.,  $\alpha 1 > 0$ ). We determined if cavity-nesting birds had a stronger positive association with forest than non-cavity-nesting birds by assessing whether  $\alpha 2$  was positive and if its 95% Bayesian Credible Interval (BCI) did not include 0. We also determined if each species had a significant relationship with land-use by assessing whether the 90% BCI for the species slope ( $\alpha 3$ ) crossed zero. We used a 90% BCI for species-level analyses because each parameter was estimated with fewer data than the community means. 90% BCIs are recommended when effective sample sizes are low (Kruschke, 2014; McElreath, 2020).

## 2.4 | Natural cavity availability and use

In 2019, we scanned each tree within four of the agricultural and four of the forest plots with binoculars to identify natural cavities (entrance hole diameter  $> 2$  cm,  $> 2.5$  m high above ground level) (Figure 1; Cockle et al., 2010). We noted the height and orientation (in degrees) of each cavity, as well as the tree's height (using a hypsometer) and diameter at breast height (DBH). We conducted Welch's two-sample  $t$ -tests to determine if cavities in forest versus agriculture differed in height above ground, tree height above ground, and DBH. We conducted Rayleigh tests (Landler et al., 2018) to determine whether cavity entrances tended to face the same direction. Finally, to test whether natural cavity counts differed between land-use types, we conducted a Welch's two-sample  $t$ -test between the number of natural cavities found in agriculture versus forest sites.

We also quantified natural cavity use in each plot. Specifically, we conducted weekly observations of each natural cavity for 15 min from September 2019 to April 2020, noting any the activity of any cavity-nesting bird that we observed. We considered an activity event to be when a bird was observed inside, perching at the entrance, or excavating a cavity. This resulted in 19 observation periods per cavity and 980 observation periods total (multiple cavities were often visible simultaneously so they could be observed in the same 15-min period). To test whether natural cavity activity differed between land-use types, we calculated the total number of bird activity events observed per natural cavity (across all visits to a given plot) and then conducted a Welch's two-sample  $t$ -test to compare the number of activity events in forest versus agriculture.

## 2.5 | Nest box addition experiment

To quantify use and success of artificial nest boxes, we constructed and placed 10 nest boxes in each of the five agricultural and five forest plots (100 nest boxes total; Figure 1). Specifically, we placed nest boxes on trees in six of the plots in September 2019 and the remaining four plots in February 2020. Boxes within a plot were located 10–20 m apart and 5 m off the ground, facing SW to minimize sun exposure. Half of the nest boxes in each plot were small

(12-cm width×12-cm depth×24-cm height, with a 4-cm diameter entrance hole), and the other half were large (18-cm width×18-cm depth×38-cm height, with a 10-cm diameter entrance hole). Because nest box studies are rare in tropical ecosystems, small nest boxes were based on standard dimensions for attracting Western Bluebirds (*Sialia mexicana*) (Jedlicka et al., 2011). Large boxes were ~1.5× the dimensions of small nest box to attract larger species. We put 5 cm of sawdust in each nest box to imitate the conditions of natural cavities. We replaced 31 nest boxes throughout the study period when the boxes decayed or fell.

Nest boxes were monitored on a weekly basis from September 2019 to June 2022 (i.e., 2.5 years), resulting in 10,837 nest box visits. We used a telescoping pole with an endoscope to observe active nests and quantify the proportions of eggs that hatch, chicks that fledge, and nestlings/eggs predated. We noted any new activity from birds or mammals. We defined new activity as evidence of new materials in a nest box after being inactive for several weeks or different materials from what was previously present. Bird nesting materials were often sticks, bark, and leaves. Mammal nesting materials were often leaves (opossum) and dried grasses (squirrel). We considered an activity event to be an avian nesting attempt if any eggs were laid.

To quantify how land-use type and nest-box size affect nest-box activity, we implemented a Poisson mixed-effects model with a log link. The response variable was the total number of bird activity events at each box across the 2.5-year period (including nesting attempts). Explanatory variables included land-use type (binary) and nest-box size (large or small; binary), as well as the interaction between land-use and nest-box size. We included a random effect of “site” to account for spatial autocorrelation (i.e., multiple nest boxes at the same site) and an offset of “months” to account for the fact that some sites had nest boxes active for slightly longer than others (i.e., 28 vs. 33 months). We then repeated this analysis using mammal activity events. We excluded the interaction between land-use type and nest-box size in the mammal model so that the model could be identifiable. Finally, to understand how land-use type affected nest success, we implemented a binomial mixed-effects model with the same explanatory variables and a binary response variable, indicating whether at least one chick fledged during each avian nesting attempt.

### 3 | RESULTS

#### 3.1 | Bird abundances across land-use types

Across 120 point counts, we detected 1093 individuals and 111 species, 26 (23.4%) of which are known to nest in cavities (Table S1). Out of 4440 abundance estimates (N), 38 did not converge (3%; all had  $R\text{-hat} \leq 1.25$ , 88% of which had  $R\text{-hat} < 1.2$ ).  $\gamma_{0_{LU[2]}}$  had an  $R\text{-hat}$  of 1.12, and all other parameters converged, including the core parameters among our log linear predictors. The 95% BCI for the community mean effect of land use on abundance was negative but crossed zero (Figure 2), meaning that, on average, species abundances did

not differ between agriculture and forests. Eight cavity-nesting birds were more abundant in agriculture (House Wren; *Troglodytes aedon*, Dusky-capped Flycatcher; *Myiarchus tuberculifer*, Pacific Parrotlet; *Forpus coelestis*; Social Flycatcher; *Myiozetetes similis*; Red-bellied Macaw; *Orthopsittaca manilatus*, Red-billed Scythebill; *Campylorhamphus trochilirostris*; Masked Tityra, *Tityra semifasciata*; Bronzewing Parrot, *Pionus chalcopterus*). One cavity-nesting bird was more abundant in forest (Collared Aracari; *Pteroglossus torquatus*). There was no significant interaction between being a cavity-nesting species and the effect of land-use on abundance (effect size  $-0.10$ , 95% BCI  $[-1.39, 1.21]$ ). This suggests that cavity-nesting species did not differ from non-cavity nesting species in their responses to land use.

#### 3.2 | Natural cavity availability and use

As expected, there were significantly more natural cavities in forest than agriculture (mean 34 cavities/ha vs. 7.25/ha;  $t = -5.85$ ,  $p\text{-value} = .0014$ ; Figure 3). The mean cavity height above ground level in forest and agriculture were similar (13.8 [range 3–43 m] and 13.9 m [range 4–34 m], respectively;  $t = -0.04$ ,  $p\text{-value} = .97$ ) and natural cavities did not tend to be oriented in any cardinal direction (Figure S1; Rayleigh test statistic in forest = 0.11,  $p\text{-value} = .21$ ; Rayleigh test statistic in agriculture = 0.06,  $p\text{-value} = .89$ ). Mean DBH of trees with cavities was larger in agriculture than in forest (agriculture: 42.9 cm, range 7–200 cm; forest: 33.7 cm, range 10–63 cm;  $t = 1.96$ ,  $p\text{-value} = .05$ ). However, mean height above ground level of trees with cavities in forest and agriculture did not differ (agriculture: 22.0 m, range 3–46 m; forest: 21.6 m, range 6–35 m;  $t = 0.26$ ,  $p\text{-value} = .80$ ).

Across the nearly 1000 observation periods, we observed surprisingly low bird activity around natural cavities, with only seven instances of birds inside cavities in agriculture and two in forest (Table 1). Five of the seven observations of a bird inside a cavity in agriculture were of the Collared Aracari using the same cavity. In contrast, there was one observation of a Collared Aracari inside a cavity in forest. Other species observed inside natural cavities included Golden-olive Woodpecker (*Colaptes rubiginosus*; in forest and agriculture), Blue-and-white Swallow (*Notiochelidon cyanoleuca*; in agriculture), Black-cheeked Woodpecker (*Melanerpes pucherani*; in forest and agriculture), and Olivaceous Woodcreeper (*Sittasomus griseicapillus*; in forest). This low rate of observation precluded a statistical comparison of cavity activity events between forest versus agriculture.

#### 3.3 | Nest box addition experiment

Avian activity and nesting attempts (i.e., where an egg was laid) were much more common in experimentally placed nest boxes within agriculture compared to forest (Tables 2 and 3). There were 109 total avian activity events in agriculture and 5 in forest. Of those activity

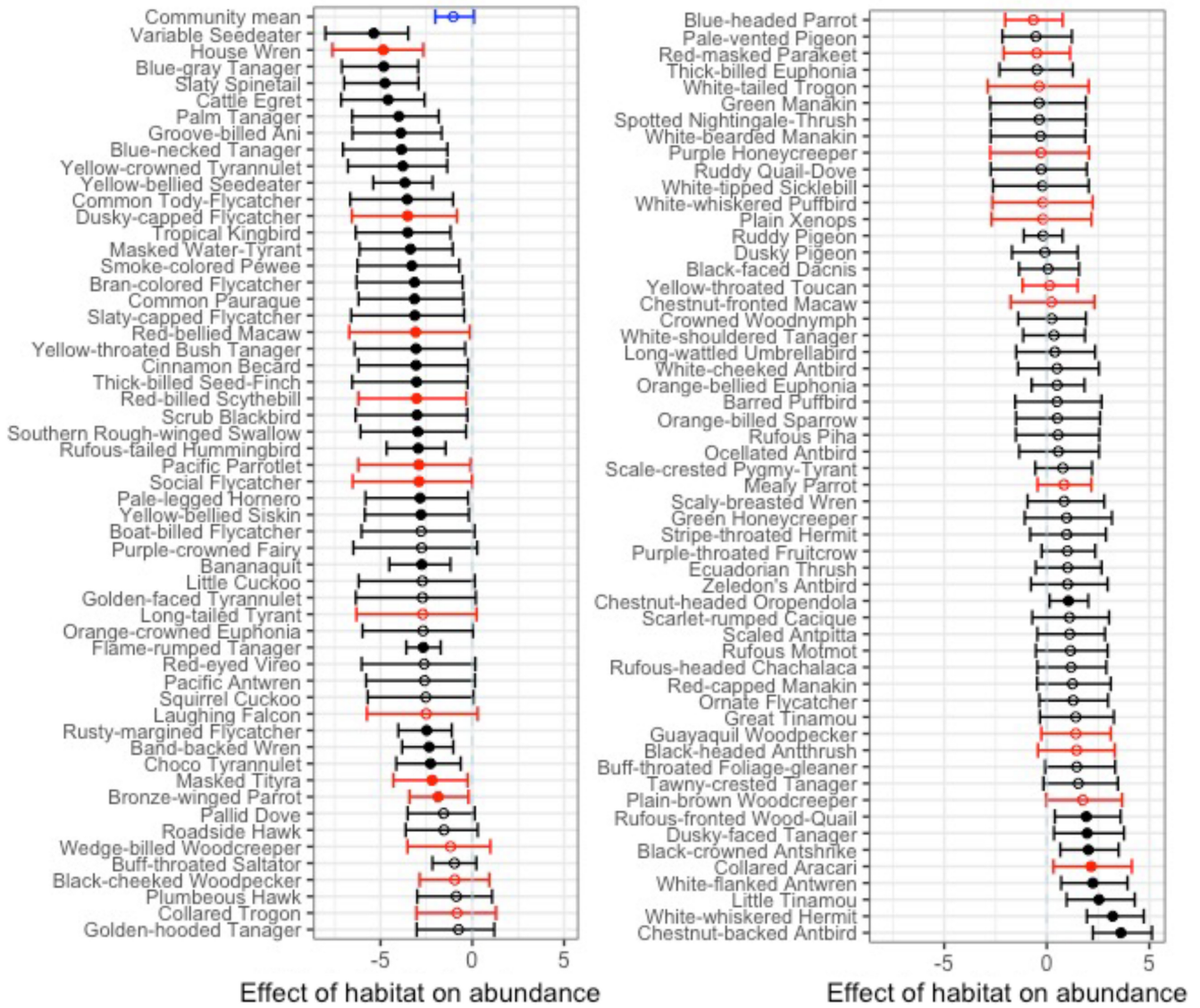


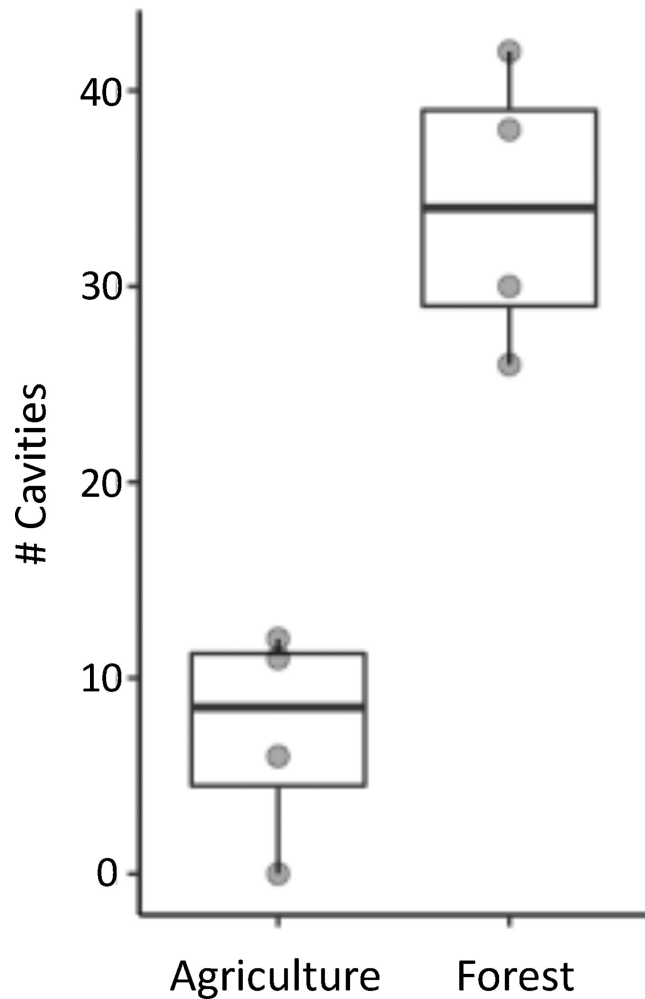
FIGURE 2 N-mixture model estimates and Bayesian Credible Intervals (BCIs) for the effect of land-use type on abundance. Positive values indicate that the species is more abundant in forest than in agriculture. Circles represent posterior means, the blue bar is the estimate of the community mean with a 95% BCI, and all other estimates are for individual species with 90% BCIs. Open circles indicate that the BCI overlaps zero, while closed circles indicate that the BCI does not overlap zero. Red points and bars represent species that nest in cavities.

events, there were 52 nesting attempts in agriculture and 5 in forest. Correspondingly, our Poisson model indicated agriculture had significantly more avian activity events in boxes compared to boxes in forest (Figure 4, Table S2). Smaller nest boxes also had significantly more avian activity events than large boxes (Table 3). Finally, a significant negative interaction was detected between habitat and nest box size, such that the difference in avian activity between forest and agriculture was greater for small nest boxes (Figure 4, Table S2).

Seven bird species laid eggs in nest boxes (six in agriculture and two in forest; Tables 2 and 3). Five nesting attempts could not be attributed to a particular species because eggs disappeared before we could ascertain the species (all in agriculture). No species that used nest boxes were of conservation concern based on the IUCN red list classification. On average, avian nest

success (i.e., successfully fledging at least one young) was 44% in agriculture (out of 52 nesting attempts) and 20% in forest (out of 5 nesting attempts). Out of the 57 total nesting attempts, we presumed that 13 nests had eggs predated and 12 nests had chicks predated because the eggs or chicks disappeared before an appropriate fledging age when chicks develop feathers. In our binomial model, neither box size nor habitat had significant effects on nest success, likely due to the low number of nesting attempts in forest (Table S2).

Unlike birds, mammal activity in experimentally placed nest boxes was more common in forest than in agriculture. In agriculture, there was one instance of mammal activity within a nest box (the brown four-eyed possum; *Metachirus nudicaudatus*) vs. 28 instances in forest (i.e., 22 brown four-eyed possum and 6 red-tailed squirrel



**FIGURE 3** Boxplots of the number of natural cavities found per site in agriculture versus forest. Gray points represent raw data. The solid horizontal bar represents the median, and the box represents the first and quartiles. Whiskers represent the minimum and maximum values that are no further than 1.5 times the interquartile range. Star indicates a significant difference (from a Welch's two-sample  $t$ -test; mean 34 cavities/ha vs. 7.25/ha;  $t = -5.85$ ,  $p$ -value = .0014).

(*Sciurus granatensis*) activity events across all sites; Table 2). Poisson models indicated that mammal activity was significantly higher in forest than agriculture, but no effects of nest box size were observed (Table S2). Finally, 10 nest boxes were occupied by wasps and bees, half in agriculture and half in forest.

## 4 | DISCUSSION

We conducted a nest box addition experiment in tropical pastures to determine whether cavity-nesting birds experience cavity limitation in tropical agriculture versus forests. We found that bird abundance, including the abundance of cavity-nesting birds, was not significantly higher in forests than in agriculture. There were many more natural cavities in forest than in agriculture. There was

also much more avian activity and nesting in nest boxes in agriculture compared to forest, suggesting that birds might be limited by cavities in agriculture. Finally, we observed very little natural cavity activity in either habitat. There were also very few bird nesting attempts in forest, making it difficult to compare nest success between habitats.

### 4.1 | Trends in bird abundance

On average, birds were not more abundant in forests than agriculture. Cavity-nesting species also did not differ in abundance between habitats, even though natural nest site availability was low in agriculture. One possible explanation is that agriculture may act as a sink habitat, drawing animals out from better habitat but not enabling sufficient reproduction for populations to persist in the absence of continued immigration (Gilroy & Edwards, 2017). If agriculture is a sink habitat, then biologists may be overestimating the ability of cavity-nesting birds to persist in agricultural landscapes and there could be unexpected crashes in populations of cavity-nesting birds if forest loss continues (Delibes et al., 2001). However, we found higher nesting success in agriculture than in forest (though there were few observations in forest), which does not support this hypothesis. Alternatively, the high bird abundances in agriculture may be explained by birds simply moving through agricultural systems and/or using multiple habitats to complete their life cycles; for example, foraging in agriculture and reproducing in forest (Frishkoff et al., 2019). This could mean that agriculture provides certain resources such as food and that increasing nesting habitat would further increase the use of agriculture. Looking forward, behavioral analyses could be used to identify the habitats that species preferentially move through, forage in, and reproduce in Ke et al. (2022), providing a clearer picture of the degree to which cavity-nesting birds rely on forests.

Of the species we observed, 23.4% of them are known to nest in cavities, which is high compared to the percentage of cavity-nesting birds globally (ranging from 10.9% to 19.5% depending on the global realm) (van der Hoek et al., 2017). Eight cavity-nesting species were more abundant in agriculture. All eight species have "Least Concern" conservation status from IUCN and mostly have wide global distributions. Thus, the species that are more abundant in agriculture could generally be more ecologically flexible and could be considered "winners" when forest is converted to agriculture (Järvinen & Ulfstrand, 1980). House Wrens had the most nesting attempts within nest boxes in agriculture (60% of the attempts in agriculture, no nesting attempts in forest) and are also known to readily use nest boxes in temperate agriculture (Baldwin & Bowen, 1928; Willner et al., 1983). Dusky-capped Flycatchers and Pacific Parrotlets each nested once in agriculture, and both have been previously documented using nest boxes (Bock et al., 1992; Collar et al., 2020). On the contrary, Collared Aracaris were significantly more abundant in forest, though they were observed using natural cavities in both forest and agriculture.

TABLE 1 Number of natural cavities found and total avian activity events in natural cavities split by the type of activity at each site.

Land-use	Site	Natural cavities found	Observations at entrance	Observations excavating existing cavity	Observations inside cavity	Total natural cavity activity events	Observations excavating new cavity
Agriculture	1	0	0	0	0	0	0
	2	6	3	2	6	11	1
	3	12	1	5	1	7	4
	4	11	0	1	0	1	2
Forest	1	26	0	2	1	3	0
	2	30	0	0	1	1	3
	3	42	0	1	0	1	0
	4	38	0	0	0	0	7

Land-use	Site	Avian activity, did not lay eggs	Avian nesting attempts (laid eggs)	Mammalian activity
Agriculture	1	21	9	0
	2	18	12	0
	3	11	17	0
	4	1	2	1
	5	6	12	0
Forest	1	0	0	7
	2	0	0	11
	3	0	5	5
	4	0	0	2
	5	0	0	3

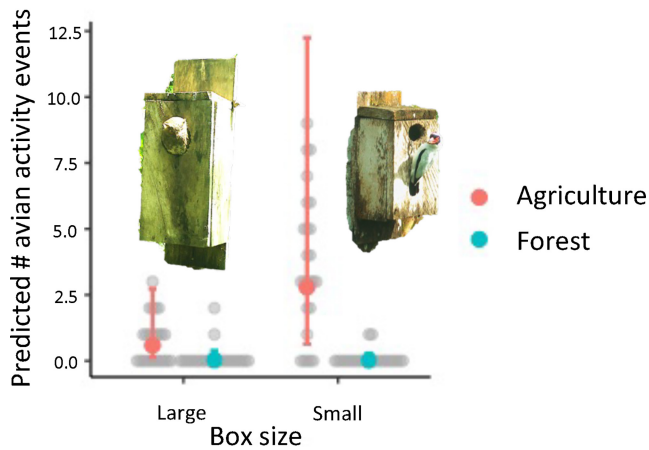
TABLE 2 Total number of avian and mammalian observations in artificial nest boxes at each site.

Note: We monitored 100 nest boxes total (50 in forest and 50 in agriculture). We monitored all nest boxes weekly (60 nest boxes monitored from September 2019 to June 2022 and the remaining 40 nest boxes monitored from February 2020 to June 2022), resulting in 10,837 nest box visits.

TABLE 3 Total number of nesting attempts in artificial nest boxes by species, whether or not species are obligate or facultative cavity-nesters, land use, and nest box size.

Scientific name	Common name	Obligate or Facultative	Nesting attempts in agriculture (small)	Nesting attempts in agriculture (large)	Nesting attempts in forest (small)	Nesting attempts in forest (large)
<i>Dendrocincla fuliginosa</i>	Plain-brown Woodcreeper	Obligate	1	2	0	0
<i>Forpus coelestis</i>	Pacific Parrotlet	Facultative	1	0	0	0
<i>Lepidocolaptes souleyetii</i>	Streak-headed Woodcreeper	Obligate	10	0	2	0
<i>Myiarchus tuberculifer</i>	Dusky-capped Flycatcher	Obligate	1	0	0	0
<i>Tityra semifasciata</i>	Masked Tityra	Obligate	1	0	0	0
<i>Troglodytes aedon</i>	House Wren	Facultative	30	1	0	0
<i>Megascops guatemalae</i>	Choco Screech Owl	Obligate	0	0	0	3
Unknown	Unknown	NA	4	1	0	0





**FIGURE 4** Predicted effect of land use and nest box size on avian activity within artificial nest boxes. Points (mean predicted effects from the mixed-effects model) and lines (95% confidence intervals from the model) are colored according to land-use type (agriculture in red; forest in blue). Gray points represent raw data. Models indicated a significant interaction between land-use type and nest box size, such that difference in avian activity between forest and agriculture was accentuated in small nest boxes. Icons depict a large and small nest box.

#### 4.2 | Natural cavities: Density and frequency of use

We found over four times the density of natural cavities in forest than in agriculture. If anything, this is likely a significant underestimate of the difference because it is difficult to find cavities that are high in the canopy and/or in dense foliage (Koch, 2008). Cockle et al. (2010) recorded over nine times the density of suitable cavities (at least 13 cm deep and 2.5 m high above ground level) in primary forest compared to logged forest in the Atlantic forest of Argentina. They also found that cavities were much more likely to be in large trees (>100 cm DBH). While the height of trees containing cavities was higher in agriculture than in forest, we did not find significant differences in the cavity height, DBH, or orientation of cavities in forest versus agriculture. Nonetheless, our estimates could be biased if we tended to overlook cavities high up in forest canopies. This is in contrast to studies such as White Jr et al. (2006) for example, which found that birds prefer cavities with entrances oriented westward.

Within the natural cavities that we did observe, bird activity tended to be quite low. Many of these cavities may not have been suitable for birds. Cavities that are too low in the canopy might be subject to higher predation risk and thus avoided (Nilsson, 1984). Additionally, cavities must also be large enough to satisfy species' needs. For example, Cockle et al. (2010) found that, among 86 cavities found through ground surveys, only 19% of them exceeded minimal size requirements for birds (at least 13 cm deep and 2.5 m high above ground level), and birds only occupied 25% of those suitable cavities. Similarly, Lima and Garcia (2016) found that birds occupied 26% of natural cavities in Mexico. Our natural cavity occupancy rate was even lower (6.6% with observations of a bird at the entrance or

inside) and thus more similar to values reported from the Peruvian Amazon forest (2%; Brightsmith, 2005). This low activity rate made it challenging to achieve an adequate sample size to compare cavity occupancy between land-use types. Across the board, it seems that occupancy rates in tropical forests may be much lower than in northern temperate forests (e.g., 67% in Ingold and Ingold (1984); 57% in Peterson and Gauthier (1985)).

#### 4.3 | Nest boxes occupancy and reproductive success

Nest boxes were used much more often by birds in agriculture and by mammals in forest. Mammals were likely not outcompeting birds for forest nest boxes because nest box occupancy in forest was relatively low (32 out of 100 nest boxes had activity). Prior studies have also observed low avian activity in tropical forest nest boxes. For example, in Mexico, no nest boxes were occupied in mature forest, whereas 14% of 80 nest boxes were occupied in young forests (Lima & Garcia, 2016). Similarly, only 2% of nest boxes were occupied in an undisturbed Peruvian forest (Brightsmith, 2005), and only four of 16 nest boxes were used by Yellow-shouldered Parrots (*Amazona barbadensis*) over 3 years in Venezuela (Sanz et al., 2003). These numbers stand in stark contrast to studies conducted in temperate forests. In temperate regions, many nest box addition experiments have been shown to increase cavity-nesting bird and mammal populations (Aitken & Martin, 2012; Lindenmayer et al., 2009; Norris et al., 2018). This may be because tropical forests have much higher cavity density than temperate forests (e.g., mean 34 cavities/ha in our study vs. mean 2.4 cavities/ha in Swedish boreal forest (Andersson et al., 2018); mean 12.5 cavities/ha in Polish coniferous forest (Walankiewicz et al., 2014). Low nest box occupancy rates may occur if natural cavities are both ubiquitous and advantageous. For example, unlike artificial boxes, natural cavities can be found higher in the canopy and in live wood (Cockle et al., 2015; Nilsson, 1984; Wesołowski, 2002). Together, these studies and our work suggest that cavity-nesting birds may not be limited by nesting habitat in tropical forests, with other factors like competition, food resources, or predation constraining population sizes (Dhondt, 2012; Nilsson, 1984; Wiebe, 2011).

On the contrary, avian nest box activity was high in agriculture, and six species were observed using experimentally placed nest boxes in agriculture compared to two in forests (though sample size was low in forest). As a comparison, only two species were found occupying nest boxes in primary and logged forests in Argentina (Cockle et al., 2010). Similarly, only two species were found in nest boxes distributed across old growth forest, secondary forest, and coffee plantations in Costa Rica (Saker, 2015). Perhaps because tropical pastures have so few trees, populations of cavity-nesting birds may be especially limited by nesting habitat as compared to populations in selectively logged forests or coffee plantations. It is possible that bird activity was higher in agriculture than forest due to less mammal activity and thus less predation pressure from

mammals. Smaller nest boxes also had significantly more avian activity events than large boxes, potentially because smaller bird species are more willing to use artificial nest boxes that are also at a lower height above ground. Importantly, there are not more small species compared to large cavity-nesting species in the community—out of 86 species that could nest in cavities, 42 were 20 cm or less in body length. The larger species may simply be more unlikely to use artificial nest boxes as a substrate and/or might prefer nesting higher in the canopy (e.g., trogons and parrots).

Importantly, we found that nest success was relatively high in artificial nest boxes (~50% fledging at least one young) compared to rates reported from other tropical studies. For example, nesting success of birds nesting in natural cavities has been estimated to be ~25% in lowland Panamanian forests (Brawn et al., 2011; Robinson et al., 2000). 55% of the 62 Puerto Rican parrot fledglings monitored survived to fledging, but this rate excludes nest failure in the egg stage (White Jr et al., 2014). Moreover, many studies of non-cavity nesting birds report lower nest success in fragmented versus natural land uses (Borges & Marini, 2010; Newmark & Stanley, 2011; Rangel-Salazar et al., 2008; Young et al., 2008). Other studies report increased nest success in areas with less canopy connectivity (Britt et al., 2014) and in older cavities (Brightsmith, 2005). If anything, we found that birds nesting in agricultural nest boxes were more successful than in forests; however, the difference was not significant, likely due to the very few nesting attempts we observed in forest. That said, it is possible that we could have slightly overestimated nest success if we missed nest failures near fledging. Specifically, we assumed a bird had fledged if we observed nestlings near fledging age on one visit and then found an empty nest on the next visit. Nevertheless, the nest success that we observed was sufficiently high that it seems that artificial nest boxes in agriculture provide suitable conditions to successfully rear tropical birds.

## 5 | CONCLUSIONS

Overall, we found that nesting habitat seems to limit reproduction by cavity-nesting bird populations in tropical agriculture but not in forest, even though cavity-nesting birds are abundant in tropical agriculture. Retaining forest patches and remnant trees in tropical agriculture may thus provide critical nesting habitat for birds (Cockle et al., 2015; White & Jiménez, 2017). Large trees may be especially important because they are more likely to have cavities, persist for many years, and may be more attractive to cavity-nesting birds (Cockle et al., 2015; Koenig et al., 2007; Lima & Garcia, 2016). However, large trees are declining globally and are particularly threatened by selective logging in ecosystems worldwide, including in agricultural landscapes (Lindenmayer et al., 2012).

Our results also suggest that adding nest boxes to tropical agricultural systems could be a good conservation strategy for certain species. Different species occupied different boxes; thus, while small nest boxes were used more frequently, a mixture of box sizes could be deployed to benefit more species. That said, our study did not

rule out the possibility that nest boxes could lead to source-sink or ecological trap dynamics, drawing species out of forest and leading to lower overall fitness. Putting up nest boxes in more isolated trees with less vines and less contact with adjacent trees may reduce this risk by mitigating nest predation rates (Koenig et al., 2007; Rajeev et al., 2018).

While deploying nest boxes in agriculture is unlikely to benefit species of conservation concern, species that provide valuable ecosystem services may benefit. We found that small insectivorous birds dominated nest boxes in agriculture (e.g., House Wrens), suggesting nest boxes might be useful in helping farmers control insect pests. Indeed, nest boxes are commonly deployed in temperate agricultural systems to attract insectivorous birds and predatory raptors, which, in turn, can help control insect pests, (e.g., Benayas et al., 2017; Jedlicka et al., 2011, 2014; Olmos-Moya et al., 2022), rodents (e.g., Kross et al., 2016), and even pest birds (e.g., Shave et al., 2018). Prior work has shown that House Wrens rapidly occupy nest boxes in Chilean vineyards and feed on insects nearby, causing elevated predation rates on sentinel insect prey near boxes (Olmos-Moya et al., 2022). Beyond pest-control benefits, cavity-nesting birds also play important roles in ecosystems by dispersing seeds (Da Silva & Tabarelli, 2000) and pollinating plants (Saker, 2015). These ecosystem services could increase tree regeneration (though they could promote spread of weedy species) and the economic and biodiversity value of tropical forests (Sethi & Howe, 2009). Even low nest box occupancy levels could increase bird presence and ecosystem services on farms (Hannay et al., 2022). Ultimately, coupling farmer education campaigns about ecosystem services provided by cavity-nesting birds with incentives for maintaining remnant trees and installing nest boxes could help mitigate cavity limitation and bolster bird populations in tropical agricultural systems.

## AUTHOR CONTRIBUTIONS

AK, DK, and JK conceptualized the study. EC, BG, LC, FC, and AK collected the data. AK conducted analyses and wrote the manuscript. All authors reviewed and edited the manuscript.

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## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in Dryad at <https://doi.org/10.25338/B8DS85>.

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## SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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