Title

Land-use Change Effects on Tropical Bird Communities: Abundance Patterns, Behavioral Shifts, and Reproductive Success

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Publication Date

2023

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By

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DISSERTATION

Submitted in partial satisfaction of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

Ecology

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

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2023

ACKNOWLEDGEMENTS

I would like to thank my family, Xin Ke, Jianhong Lin, and Eileen Ke for supporting me throughout my life and academic career.

I would like to thank Daniel Karp for welcoming me into the lab and being the best advisor and mentor for over the last five years. I appreciate everything you have done for me to advance my career and make my graduate experience successful and enjoyable.

I would like to thank my lab mates in the Karp Lab for providing great feedback, serving as mentors, and being so encouraging to me.

I would like to thank my undergraduate mentors, Matthew Luskin, Chevonne Reynolds, Robert Fletcher, Paul Elsen, and Kaitlyn Gaynor for inspiring me to pursue a graduate degree, giving me research opportunities, helping me get into grad school, and helping me get the GRFP.

I would like to thank my field assistants, Mario Loaiza, Manuel Sanchez, Beto Gonzales, and Evaristo Cede*ñ*o. None of my work would have been possible without your knowledge and hard work.

I would like to thank my dissertation committee members, Daniel Karp, Rahel Sollmann, Marcel Holyoak, and Jordan Karubian for taking the time to review my dissertation.

I would like to thank the collaborators on my graduate work and side projects, including The Karp Lab, Rahel Sollmann, Luke Frishkoff, Jordan Karubian, Alejandra Echeverri, Jim Zook, Juan Pablo Gomez, Gustavo Londo*ñ*o, Mario Loaiza, Manuel Sánchez, Luis Carrasco, Beto Gonzales, Fernando Castillo, Evaristo Cedeño, and Frank Fogarty. You have all been important to my research and growth as a scientist.

I would like to thank my cohort mates Deniss Martinez, Jasmin Green, and Frederick Nelson for all the support from day one. I would like to thank my friends from the ecology grad group as well as housemates including Katie Lauck, Jessica Greer, Cody Pham, Susannah Scherer, Bogumila Backiel, Valerie Barreto, and Dmitry Shemetov for all of the good times we've shared.

I would like to thank my climbing friends including Quency Atwood, Kris Hokr, Laura Chen, Austin Cheung, Yohei Iwako, Daniel Coral, Dave Zhou, Ben Baek, Dorothy Wu, Jorge Portillo, Azalie Welsh, and more. I've had so many wonderful memories climbing with you all, which was the main activity keeping me sane during my graduate career.

Abstract

Land-use change currently constitutes the primary driver of modern biodiversity loss. One way that land conversion to agriculture can lead to biodiversity loss is through biotic homogenization where agriculture consistently favors the same species, causing communities to converge in species composition over space or time. Biotic homogenization could also occur phylogenetically, where species from the similar phylogenetic lineages are consistently favored by agriculture. However, whether phylogenetic homogenization occurs across multiple scales and in tropical regions is rarely investigated. In Chapter 1, I leveraged species' phylogeny and traits to understand how land-use change affects tropical bird communities within Costa Rica and Colombia. We conducted bird surveys across Costa Rica and Colombia in 294 sites that varied in levels of local forest cover and annual precipitation. We then analyzed sites in Costa Rica and Colombia together to find that land conversion from forest to agriculture consistently favors the same types of species at a large scale. While most trait-based studies measure effects of global changes on species occurrences or abundances, changes in species abundance or occurrence provide little information about how species actually use the habitats where they occur. For example, a species detected in agriculture could simply be passing through (and not actually resilient to land-use change) or it could be using agriculture to forage, reproduce, or otherwise complete its lifecycle (meaning the species is resilient to land-use change). In Chapter 2, I developed and then validated a statistical model to analyze how species' behavior differs between habitat types using observational data. To our knowledge, this is the first model to measure how animals use different environments while accounting for behavior-specific imperfect detection probability. We compared the model to an alternative model that did not account for imperfect detection probability and found that our new model produced more accurate estimates of the mean and uncertainty of the effects of environmental covariates on behaviors. Thus, this model allows researchers and managers to more accurately assess how species use the environments they are in using observational behavior data. In Chapter 3, I applied this model to over 14,000 behavioral observations across 55 bird species in Northwest Costa Rica to understand how local forest cover and forest protection level affect bird behaviors. We found that birds were more likely to perform reproductive behaviors in protected forest than private forest and agriculture, meaning that protected areas are likely important for bird reproduction and conservation. This chapter also demonstrates the importance of behavioral analyses in conservation planning, as species' behavioral responses were not always consistent with their differences in abundance. Beyond measuring changes in occurrence and behavior, it is also critical to understand if habitats can support sufficient reproductive rates to allow for population persistence. Tropical cavity-nesting birds may be particularly threatened by agricultural land-use change, which removes the tree they rely on for nesting and roosting. In Chapter 4, I aimed to understand how land-use change affects tropical cavity-nesting bird reproduction by measuring nest site availability and conducting a nest-box addition experiment in forest and agriculture Northwest Ecuador. I found that land-use change likely limits the reproduction of cavity-nesting birds in agriculture, as nest boxes in agriculture had much higher levels of avian activity than nest boxes in forest. Nest boxes also had a relatively high rate of chicks fledged, meaning that nest boxes could be a successful conservation strategy for certain species. Overall, my dissertation explores the different effects of agricultural land-use change on tropical bird occurrence, behavior, and reproduction. I found that these effects can differ from each other and across scales. The results highlight the importance of forest conservation, especially in wet regions, and support investigating species' responses beyond occurrence when comparing the conservation value of habitat types

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Introduction

Land conversion from forest to agriculture can cause local extinctions by decreasing population sizes, increasing population isolation, and in turn, increasing the influence of stochastic events (Wiens 1992, Brooks *et al.* 2002). If agricultural land-use change consistently favors the same widespread species in very different regions, then this could cause biotic homogenization, where communities become more similar over space in time and biodiversity is lost across large scales (McKinney & Lockwood 1999, Olden *et al.* 2018). Currently, most studies of biotic homogenization focus on taxonomic diversity and take place in temperate regions at one scale (Olden et al., 2018). Meanwhile, phylogenetic homogenization may occur if agriculture selects species from the same lineages in different regions, resulting in a loss of diversity in key parts of the tree of life (Nowakowski et al., 2018). To address these knowledge gaps, we investigated whether land-use change causes phylogenetic homogenization of tropical bird communities at two scales: regionally (*i.e.,* within the countries of Costa Rica and Colombia) and continentally (*i.e.,* among the two countries). We also determined which traits were associated with species that were most vulnerable to land-use change, and whether or not these traits were consistent across countries. To do so, we conducted parallel bird surveys in forest and agriculture in Costa Rica and Colombia. We recorded all birds seen or heard within 50 m in 294 sites across varying levels of local forest cover and annual precipitation. We found that among both countries, land conversion from forest to agriculture consistently favored birds from similar phylogenetic lineages. However, we did not find the same pattern regionally: within Costa Rica, beta-diversity was highest in agriculture, and, within Colombia, beta-diversity peaked in wetter sites (irrespective of land use). Why then did agriculture cause homogenization among countries? We found that open-habitat associated, more mobile, and seed-eating species thrived in agricultural areas across both countries, and these traits were related to phylogeny, helping to explain the large-scale phylogenetic homogenization. We also found that species with large global ranges tended to occur in agriculture, meaning the same species were more likely to occur in agriculture than in forest between distant sites. Our findings suggest that it is important to measure biotic homogenization at multiple scales, as patterns could differ between scales. It is also important to conserve undisturbed forest, especially in wetter areas, as these habitat types hosted the highest variation in species communities among Costa Rica and Colombia.

While understanding which species are most likely to occur in different habitat types can provide insights on the effects of land-use change on biodiversity, measuring how animals behave in their environment is critical to determining the conservation value of habitats (Luck 2002; Lyons 2005). For example, species must be able to forage and reproduce for populations to persist. However, measuring behaviors often requires a large amount of effort, including capturing and tracking individuals (*e.g.,* Luck 2002; Tremblay et al. 2005). On the other hand, observational surveys can be used to sample behaviors, where an observer records the behaviors performed by any individual within a given time period. However, some behaviors are more difficult to observe than others, which biases results when analyzing raw data. Here, we developed a novel statistical method to account for the fact that the detectability of a behavior depends on the species, behavior performed, and surrounding environment (*e.g.*, a foraging bird is likely easier to detect in an open field versus a dense forest). We developed a Bayesian model, which we call the behavior N-mixture model, to estimate the probability that an individual performs a given behavior in a particular environment while accounting for imperfect detection. We simulated data to validate the model's ability to estimate the probability of a species performing a given behavior, as well as the effect of environmental covariates on behaviors. We compared our model estimates to a naïve model that did not account for imperfect detection. Then, we used our model to estimate behavior probabilities of three species from bird observations in forests and farms in Northwest Costa Rica. We found that the behavior N-mixture model produced more accurate estimates of behaviors and covariate effects on behaviors than the naïve model, which often produced incorrect results about the effects of covariates on behaviors. For example, our model could be used to measure the effect of canopy cover on the probability of a bird foraging. In our case study, we found that Hoffmann's Woodpecker (*Melanerpes hoffmannii)* and Inca Dove (*Columbina inca*) behaved differently in forested versus agricultural habitats, while Turquoise-browed Motmot did not. The behavior N-mixture model can be used to identify habitats that are most important for species' needs while using lower survey effort than more traditional methods.

In Chapter 2, we developed a novel statistical model to estimate behaviors while accounting for imperfect detection. Again, most studies of the effects of land-use change on biodiversity focus on species abundance or occurrence, but animals' first responses to environmental changes are behavioral, and behavioral changes may not reflect differences in abundance or occurrence (Wright et al. 2010; Wong & Candolin 2015; González-Lagos & Quesada 2017). For example, species may be observed in agriculture but may not be able to forage or reproduce in that habitat. The model from Chapter 2 can only applied to one species at a time. This makes it difficult to understand how the behaviors of species communities are changing as a whole, and it requires more observations to estimate covariates for each species separately. Here, we extended the model from Chapter 2 from a single-species model to a community model to investigate how species' abundances and behaviors differed between protected forest, private forest, and agriculture in Northwest Costa Rica, and if their changes in abundance were related to their changes in behavior. We analyzed over 14,000 behavioral observations of 55 bird species and used a novel statistical model (an extension of the model from Chapter 2) to quantify how species differed in their abundances and their foraging, reproductive, and passive (e.g., perching, preening) behaviors between land-use types. We found that on average, birds were more abundant and more likely to perform reproductive behaviors in forest than in agriculture. We also found that on average, birds were more likely to perform reproductive behaviors in protected forest than private forest, despite there being no significant difference in abundance between protected and private forest. Individual species were not always more abundant in the habitats where they were more likely to exhibit foraging or reproductive behaviors, meaning that behavioral surveys and analyses add valuable information to assess habitat quality. Our work also highlights the importance of forest, especially protected forest, for the reproduction of tropical birds.

While understanding how animals behave in different environments can elucidate which resources they may be obtaining from their habitat, most studies of the effects of land-use change on biodiversity do not assess whether habitats contain the resources necessary to sustain species' reproduction. Animals that use or nest in tree cavities may be especially vulnerable to deforestation, which removes their critical nesting habitat (Engblom *et al.* 2002, Cockle *et al.* 2010). Cavity-nesting birds are most diverse in the Neotropics, but little research has been done on the reproductive biology of tropical cavity-nesting birds and how converting forest to agriculture may affect their nesting resources and success (Hoek *et al.* 2017). For example, to our knowledge, there have been no experiments conducted in tropical pastures to understand the effectiveness of nest boxes as a conservation strategy. Here, we aimed to understand how land conversion from forest to agriculture affects the reproductive resources of cavity-nesting birds by comparing cavity-nesting bird abundance, nesting habitat availability, artificial nest box use, and nest success in tropical forests and pastures in Northwest Ecuador. We hypothesized that cavity

limitation would lead to higher rates of artificial nest box use in agriculture as compared to forest. We conducted four rounds of bird surveys at ten sites, half in forest and half agriculture, recording all cavity-nesting birds seen or heard within 50 m and ten minutes. We found more natural cavities and higher levels of avian nest box occupancy in agriculture than forest, which supported our hypothesis that deforestation limits nesting resources for cavity-nesting birds in Neotropical pastures. Retaining trees and adding nest boxes to agriculture could help to conserve certain species, while promoting insectivorous cavity-nesting species in farms could also potentially benefit farmers if the birds consume crop pests.

Land conversion homogenizes tropical bird lineages at continental but not regional scales

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Abstract

Land conversion from forest to agriculture may be a driver of biotic homogenization where communities converge in species composition over space or time, resulting in the loss of biodiversity. This could occur if agricultural habitats consistently favor the same widespread species across distant regions. Currently, there are a lack of studies that investigate homogenization at various scales, measure dimensions of biodiversity other than taxonomic diversity, and take place in tropical regions. Here, we surveyed birds across precipitation gradients in Costa Rica and Colombia to understand how land conversion from forest to agriculture affects the phylogenetic homogenization of tropical bird communities at two scales, regionally (*i.e.,* within the countries of Costa Rica and Colombia) and continentally (*i.e.,* among the two countries). We then explored if species' responses to forest cover were consistently explained by traits related to habitat affinity, global range size, dispersal ability, and diet across regions to understand if traits may explain patterns of phylogenetic homogenization. We found that land-use change drives phylogenetic homogenization at a continental scale, and that phylogenetic homogenization is likely mediated by phylogenetically conserved functional traits, with open-habitat associated, more mobile, and seed-eating species thriving in and homogenizing in agricultural areas across both countries. However, the effects of land-use and climate on phylogenetic beta diversity varied across regions and spatial scales – within Costa Rica, beta-diversity was highest in agriculture, and within Colombia, beta-diversity peaked in wetter sites (irrespective of land use). Our study suggests that it is critical to study homogenization at multiple scales, and that conserving undisturbed forest, preventing forest degradation, and restoring degraded areas, especially in wetter areas, may be critical to preventing phylogenetic homogenization at large spatial scales.

Introduction

Most contemporary biodiversity consists of ecological communities changing in composition over space (*i.e.,* beta-diversity; Anderson et al. 2011). However, it is increasingly recognized that biotic homogenization may be a hallmark of the Anthropocene, whereby global changes cause communities to converge in species composition over space or time (McKinney & Lockwood, 1999; Olden et al., 2018). Indeed, a recent global synthesis reported that half of the studies analyzed found evidence for biotic homogenization as opposed to biotic differentiation or no change (Olden et al., 2018). Land conversion to agriculture is thought to be a major driver of biotic homogenization, as agricultural habitats seem to consistently favor the same widespread, disturbance-adapted, and/or generalist species across distant regions (Nowakowski et al., 2018). Nonetheless, key knowledge gaps persist regarding many facets of homogenization, with effects of land-use change in particular varying considerably among sites, taxonomic groups, and scales (Socolar et al., 2016).

At least three key biases exist in the literature that impede understanding of the homogenization process. First, there has been disproportionate research on terrestrial plants and freshwater fishes in Nearctic regions, with far fewer studies focused on other taxonomic groups and in tropical regions (Olden et al., 2018). Yet land conversion may be especially likely to cause homogenization in the tropics, as tropical species generally exhibit higher sensitivity to ecological change, more specialization, poorer dispersal ability, and less prior experience with climatic variability (Janzen, 1967; Newbold et al., 2020; Sheldon et al., 2018; Wiens, 2016). Second, while many studies examine homogenization within regions, fewer focus on homogenization at continental or global scales (Olden et al., 2018; Socolar et al., 2016). Yet such large-scale studies are crucial to determine whether biodiversity is eroding due to the expansion of widespread species and decline of range-restricted, endemic species (Socolar et al., 2016). In addition, much of the theory for why land conversion may cause homogenization at continental scales assumes that species consistently respond (either positively or negatively) to land-use change across their ranges, which may not be true (Orme et al., 2019; Williams & Newbold, 2021). Indeed, it is harder to imagine how land conversion could cause global homogenization if the same species persists in anthropogenic habitats in some regions but not others (McGill et al., 2015).

Third, and finally, there are multiple facets of biotic homogenization, but taxonomic homogenization is by far the most studied. Over 80% of studies quantify homogenization by comparing taxonomic species overlap over space or time (Olden et al., 2018). However, diversity could also be lost at large spatial scales if the same phylogenetic lineages are favored by land-use change across broad regions and/or if land-use change negatively affects phylogenetically unique lineages characteristic to certain places (Nowakowski et al., 2018). Moreover, phylogenetic analyses provide insight into how communities are ecologically, historically, and evolutionarily structured, and are particularly useful at larger scales if few taxonomic species are shared between distant sites (Graham & Fine, 2008).

Land conversion could favor the same lineages in different regions if the key traits that dictate how species respond to global changes are phylogenetically conserved (Nowakowski et al., 2018). For example, traits that describe the demography, dispersal, habitat usage, and/or biogeography of a species are often used to predict their sensitivity to global change or extinction risk (Henle et al., 2004). If these traits are phylogenetically conserved, then species' traits could provide a predictive framework for understanding why global changes may phylogenetically homogenize communities (Henle et al., 2004). Most trait-based studies, however, only focus on one community or region: without an assessment of the generality of trait-based patterns, it is unknown how reliable the traits can be as proxies to species sensitivity across regions (*e.g.*, Hausner et al. 2003, Cleary et al. 2007). Indeed, analyses have called into question the idea that the same set of traits consistently predict species responses to global change across regions. For example, Kennedy et al. (2010) found that, in Jamaica, ground-nesting birds were less sensitive to forest fragmentation than tree-nesting birds. Yet Davies et al. (2010) and Hausner et al. (2003) found that ground-nesting birds were more adversely affected by land-use change as compared to other groups in Australia and Norway, respectively.

Here, we investigated how land conversion to agriculture affects the phylogenetic homogenization of tropical bird communities at two scales: regionally (*i.e.,* within the countries of Costa Rica and Colombia) and continentally (*i.e.,* between the two countries, with about 20% of taxonomic species present in both countries). We then explored whether traits related to habitat affiliation, global range size, dispersal ability, and diet consistently predict species responses to land conversion across regions. To link traits with phylogeny, we also determined the degree to which different traits are phylogenetically conserved. We surveyed birds across precipitation gradients in both countries, as it is known that Neotropical bird communities change dramatically with precipitation due to changes in vegetation structure and biotic interactions (Gomez et al., 2020; Karp et al., 2018). Land conversion, however, may cause vegetation structure to converge across precipitation gradients and erode this natural turnover, an observation that we have reported previously in Costa Rican birds (Karp et al., 2018).

Our work was guided by three questions. First, how does land conversion from forest to agriculture affect the phylogenetic differentiation of bird communities across precipitation gradients within Costa Rica and Colombia? We hypothesized that agriculture would favor similar lineages of birds in both dry and wet regions, thereby eroding the natural turnover of bird communities across precipitation gradients (Gomez et al., 2020; Karp et al., 2018). Second, how does land conversion affect the phylogenetic differentiation of bird communities between Costa Rica and Colombia? We hypothesized that species' responses to land conversion would be consistent between countries and that similar bird lineages would occupy agriculture in both countries, driving phylogenetic homogenization at the continental scale. Finally, what traits predict species responses to land-use change? Are they consistent across regions, and are they phylogenetically conserved? We predicted that in both countries the species most vulnerable to land-use change would be those adapted to dense habitats, with limited range sizes, low dispersal ability, and specialized diets, and that these traits would be phylogenetically conserved (Kennedy et al., 2010; Newbold et al., 2013).

Methods

Study regions

We investigated how land use shapes bird communities in the Guanacaste Province of Costa Rica and the Magdalena River Valley of Colombia (Figure 1). Our study regions are geographically distant but similar in important ways. First, both regions are a mosaic of tropical forest and agriculture, much of which is cattle pasture. Both regions also contain rainfall gradients, varying from ~1,500 mm to ~3,000 mm over ~60 km in Costa Rica and ~1,300 mm to ~3,600 mm over ~270 km in Colombia. In both regions, elevation (and thus temperatures) remains largely constant between sites, allowing us to isolate the effects of rainfall. Guanacaste experiences a dry season from December to April as well as a mid-rainy season drought in July and August. Similarly, the Magdalena River Valley also has two dry seasons, December-February, and June-July. Summer rainfall in the Guanacaste region is projected to decrease up to 25% over the next century (Rauscher et al., 2008), while the rainfall in the Magdalena River Valley is predicted to increase (World Bank Climate Knowledge Portal).

In Costa Rica, we selected point count locations across a network of five protected areas and 20 farms along the rainfall gradient, and in Colombia, we selected point count locations across a network of 12 farms along the rainfall gradient (Figure 1). The farms in Colombia were more distant from each other, and fewer farms could be included. Moreover, protected areas were absent in our study region in Colombia. All farms were adjacent to forests. On each farm in Costa Rica, birds were surveyed at six-point count locations (N= 150 locations). On each farm in Colombia, birds were surveyed at 12 point-count locations to balance sampling effort across countries (N = 144 locations). At each farm, half of the point counts occurred in agriculture and half occurred in forest, whereas at each protected area, all point counts occurred in forest. Equal numbers of points were placed in 1) forest interiors, 2) forest edges, 3) small forest fragments, 4) agricultural field centers, 5) fields bordering forest, and 6) fields surrounded by forest (Figure 1C). Thus, forest cover in the landscape varied independently from the local land-use.

Bird surveys

We surveyed bird communities in Costa Rica between May-July each year from 2016-2019, and in Colombia between June-August in 2018 and 2019. In Costa Rica, JZ recorded all birds seen and heard in 20 min and within 50 m (excluding fly overs). In Colombia, ML, MS, and AK recorded all birds seen and heard in 10 min within 50 m – the sampling time was shorter because we were required to visit more point count locations per day. In Costa Rica, we repeatedly sampled half of the point-count locations three times within a 1-week period and the other half were surveyed once to increase spatial replication while still allowing us to estimate detection probabilities. Similarly, in Colombia, three quarters of all point-count locations were repeatedly sampled three times with in a 1-week period, and the other quarter were sampled once. We conducted surveys between sunrise and 5 hours after sunrise. During each survey, we recorded time of day, date, ambient noise, number of people within the count radius, and wind speed (using a handheld anemometer) to account for variation in the probability of detection.

Forest cover and precipitation measurements

To quantify surrounding forest cover, we hand-classified tree cover within 1.5 km of all point-count locations, using the most recent cloud-free Google Earth images available closest to 2016 in Costa Rica and 2019 in Colombia (ranging from 2013-2019).

For Costa Rica, we modeled precipitation levels at each site, where site refers to either a farm or protected area, using weather station data collected between 1921 and 2015 from Costa

Rica's Instituto Meteorólogico Nacional; *Inicio - IMN*, N = 8), the Organization for Tropical Studies (http://www.ots.ac.cr/meteoro; N = 1), KNMI Climate Explorer (https://climexp.knmi.nl/; N = 19), and one of our focal farms (http://tiopelon.cr/; N = 1). We filled missing days and months by averaging two previous and subsequent days and averaging the same month in two previous and subsequent years, respectively. We omitted years with over 3 months of missing data. Then, to interpolate the precipitation at sampling sites, we used a general additive mixed model (GAMM) with a spatial thin-plate spline, distance from the coast to each census location along the predominant offshore wind direction (30° North of West chosen based on MERRA re-analysis data (http://globalwindatlas.com/)) as a covariate, and "Year" as a random intercept.

For Colombia, we downloaded monthly precipitation data from 1981-2010 from 404 precipitation stations in the MRV from Instituto de Hidrologia, Meteorologia y Estudios Ambientales (IDEAM, www.ideam.gov.co). We fitted a thin-plate spline to the mean monthly precipitation values and interpolated predicted values using the 'fields' package (Nychka et al., 2015) in R (Team, 2013). Precipitation and forest cover were not correlated (r = -0.023).

Phylogeny and trait data

To quantify phylogenetic dissimilarity between point count locations, we obtained 10,000 phylogenetic trees from http://BirdTree.org (Jetz et al., 2012), using Hackett et al. (2008) as the backbone. We computed a consensus tree from the *phytools* package (Revell, 2012) in R version 4.0.0 (R Core Team 2013). Two species in Colombia were not in the tree and excluded from phylogenetic analyses: Striolated Manakin (*Machaeropterus striolatus,* observed in 4% of visits) and Colombian Chachalaca (*Ortalis columbiana,* observed in 16% of visits). To understand which traits predicted species responses to land-use change, we obtained data on species' diet, habitat affiliation, range size, and dispersal ability. Specifically, we obtained species' diet traits from EltonTraits (Wilman et al., 2014), which includes percentage of diet comprised of invertebrates as well as seeds and grains. We obtained altitudinal range data from Bird et al. (2020) and migration status, hand-wing index, territoriality, habitat affiliation, and range-size data from Sheard et al. (2020).

Occupancy models

We implemented a community occupancy model for each region to estimate the probability of each species occupying each point count location. The occupancy models used spatially and temporally replicated surveys to account for variation in detection probability across species and point count locations (Kery & Schaub, 2011). The observed occupancy of a species (i) at a given point count location (j) in a given visit (k) during a given year (t) was modeled as follows:

$$Y_{i,j,k,t} \sim Bernoulli(\mathrm{Z}_{i,j,t} * \mathrm{P}_{i,j,k,t})$$

Where *Y* represents whether a species was observed (Y = 1 if observed, 0 if not), Z is the true occupancy state (Z = 1 if present, 0 if absent), and P is the probability of detecting a species. The detection process was modeled as follows:

$$\mathrm{logit}(\mathrm{P}_{i,j,k,t}) = \alpha 0_{LU[j]} + \alpha 1 * time_{j,k} + \alpha 2 * noise_{j,k} + \alpha 3 * ppl_{j,k} + \alpha 4 * wind_{j,k} + \theta 1_i * date_{j,k} + \delta 0_i + \delta 1_{i,j,k,t}$$

Here, all α parameters were fixed effects. *LU* (land use) was a binary variable indicating if the point count was in forest or agriculture, *time* was the time at the start of the point count, *noise* represents the presence of loud noise during the survey (cicadas, farm machinery, etc.), *ppl* represents the log number of people within the survey area (e.g., farm workers), and *wind* is the wind speed during the point count. *date* is the day of the year of the survey. The effect of date on detection probability of each species ($\theta 1$) was drawn from a normal distribution estimated from the data, as different species may be more detectable at different parts of the year. The δ parameters were random intercepts drawn from normal distributions with mean 0 and variance estimated from the data. The species-level intercept ($\delta 0$) allowed species to have different detection probabilities, while $\delta 1$ accounted for the remaining variation in detection among point count locations, visits, and years that was not explained by the other effects.

The occupancy process, or the true presence or absence of a species (Z), was modeled as follows:

$$Z_{i,j,t} \sim Bernoulli(\psi_{i,j,t}),$$

where ψ is the occupancy probability. We modelled the occupancy probability as:

$$\text{logit}(\psi_{i,j,t}) = \beta 0_i + \beta 1_i * local_j + \beta 2_i * precip_j + \beta 3_i * landscape_j + \beta 4_i * local_j * precip_j + \gamma 0_{i,j} + \gamma 1_{i,site[j]}$$

Here, each β term was estimated for each species, and was drawn from a normal distribution with hyperparameters estimated from the data. $\beta 0_i$ is a species-specific intercept. Each species was allowed to have a different response to local forest cover within 50 m (*local*), annual precipitation (*precip*), the interaction between local forest cover and precipitation, and landscape forest cover (*landscape*). Landscape forest cover was the area of forest cover within 610 m, subtracting the local forest cover within 50 m. This was the scale found to be most biologically relevant for species on average using the Costa Rica dataset (Frishkoff et al., 2019; Karp et al., 2018). All covariates were scaled prior to analysis. Finally, we included random effects γ to account for additional variation in species-point combinations ($\gamma 0_{i,j}$) and species-site combinations ($\gamma 1_{i,site[j]}$), where site refers to either a farm or protected area. We allow changes in detection but not occupancy between years to simplify model structure.

We implemented models in a Bayesian framework in R Version 4.0.0 using the R2jags Version 0.7-1 package, which runs Markov chain Monte Carlo algorithms (Su & Yajima, 2012; Team, 2013). For each model, we ran three chains starting at random initial values, with 25,000 burn-in iterations, 75,000 post-burn-in iterations, and a thinning rate of 50. We considered the chains to converge if the Gelman-Rubin statistics of the chains of every parameter were ≤ 1.1 (Gelman et al., 2004). We also determined if forest cover had a significant relationship with average species occupancy by assessing whether the 95% Bayesian Credible Interval (BCI) for the community mean of the local land-use slope ($\beta 1$) crossed zero.

To understand if species respond similarly to local land use in different parts of their range, we calculated the Spearman's rank correlation coefficient for the beta values of the effect of forest cover on species' occupancy ($\beta 1$) in Costa Rica and Colombia, only using the shared species among countries.

Quantifying and analyzing pairwise dissimilarity

We quantified phylogenetic pairwise dissimilarity between all point count locations in Costa Rica and Colombia using a simulation method because samples from the posterior distributions in each country were not linked. First, we used our occupancy models to simulate 1000 communities, where the occupancy of each species at each point count location was drawn from a Bernoulli distribution, with the probability determined by the posterior mean of that species' occupancy probability at that point count location. Then, we calculated the turnover component of the Sorensen phylogenetic pairwise dissimilarities among all point count locations, using the *betapart* package Version 1.5.4 (Baselga & Orme, 2012).

Next, we categorized point count locations across countries into three levels of local forest cover (low, intermediate, high) and two levels of rainfall (low, high), resulting in six categories total (*e.g.,* dry/forested, wet/agricultural, etc.). The local forest cover category cutoffs were 40% and 85%, which correspond approximately to the 33% and 66% percentile of forest cover of all point count locations. For the cross-country analyses, we restricted our analysis to point count locations with annual rainfall between 1325 and 3065 mm, which is 200 mm above and below the precipitation range of Costa Rica. This resulted in analyzing 96 out of the 144 point count locations in Colombia in cross-country analyses. The precipitation category cutoff that determined high versus low precipitation was 1826 mm, which corresponds to the 50% percentile of precipitation of all point count locations in the analysis (after removing the 48 Colombian point count locations). To visualize phylogenetic turnover across land-use and precipitation axes, we used non-metric multidimensional scaling. Then, to quantify whether phylogenetic turnover was significant across land-use and precipitation categories, we ran a permutational multivariate analysis of variance (PERMANOVA) with local forest cover and annual precipitation as predictors, constrained by point count locations (*i.e*., farms or protected areas).

To measure homogenization within each country, we measured the phylogenetic turnover between all unique pairs of point count locations for each of the 1000 simulated communities. We then calculated the average distance between each pair of point count locations across the 1000 simulated communities, resulting in one “true” community distance matrix. Within each habitat category (*e.g.*, wet forest, dry agriculture, etc.), we then calculated the mean distance across the pairwise point count location distances within each category. Next, we used a null method to determine if these mean distances were statistically different among habitat categories, while accounting for nonindependence between point count location distances (as the same point count location is incorporated into many distance measurements). In the null method, we shuffled the point count locations of the "true" distance matrix while keeping the country and points within farms/protected areas consistent. Then, we calculated the mean distances within each habitat (as we did for the true matrix). We repeated this procedure for 1000 null communities. To compare two habitat categories (*e.g.*, is the mean distance in wet forest significantly higher than the mean difference in dry agriculture?), we determined whether >95% of the mean distances calculated using the null matrices were greater or less than the true difference. We also repeated this analysis using point count location comparisons within habitat categories but across countries to quantify phylogenetic homogenization among countries.

To account for variation in species richness among point count locations (which may influence beta-diversity metrics), we used an additional null model approach (as in Ponisio et al. 2016, Karp et al. 2018). For each of the 1000 simulated communities from the occupancy models, we shuffled point count location labels, keeping point count locations within countries and point count locations within farms consistent, and then calculated the turnover component of Sorensen phylogenetic pairwise dissimilarities. Then, we took the difference between each of the 1000 true distance matrices and their corresponding null distance matrix. We repeated the method described above to determine if mean distances were statistically different among habitat categories.

Analyzing traits

We quantified each species' response to land-use in each country using the mean of each species' posterior distribution of the beta parameter for the effect of local forest cover on occupancy ($\beta 1$). Higher beta values indicated a species was more likely to occupy more forested areas. We then created the following trait predictor variables according to our hypotheses about which types of traits are related to species' responses to land-use change:

1. % Diet insects: % of diet consisting of invertebrates
2. % Diet seeds: % of diet consisting of seeds and grains
3. Mobility: Linear combination of whether or not a species is migratory (binary), hand-wing index, and the territoriality of a species (3 levels)
4. Biogeography: Linear combination of global range size and altitudinal range
5. Habitat affinity: Habitat scores 1 = dense, 2 = semi-open, 3 = open

Hand-wing index represents the elongation of the wing, and is positively associated with dispersal ability (Arango et al., 2022). The territoriality levels were non-territorial, seasonal or weak territoriality, and year-round territoriality; we hypothesized that more territorial species would be more restricted to one area and exhibit less movement. We used linear combinations for mobility and biogeography to combine relevant but correlated measures. To understand which traits were most related to species' responses to land-use while accounting for phylogenetic non-independence, we ran phylogenetic generalized linear models with a normal error distribution using the five trait predictors and the *ape* Version 5.6-1 package (Paradis et al., 2004). To account for varying amounts of uncertainty associated with forest affiliation scores of each species, we weighted each observation by one divided by the variance of the posterior distribution of the beta parameter for the effect of local forest cover on occupancy ($\beta 1$). We fit one linear model to all species observed in Colombia and one model for all species observed in Costa Rica. To understand whether predictive traits were consistent between countries, we checked if the same traits were significant ($p < 0.05$) in the same direction. To check model fit, we checked whether the residuals were normally distributed and if the variance of error terms was consistent. We also repeated this analysis for each country using only the 66 shared species among countries.

Finally, we calculated Pagel's lambda for each trait using the *phytools* Version 1.0-1 package, which measures the degree to which correlations in traits relate to their shared evolutionary history. We determined the traits to be significantly phylogenetically conserved if the p-value was <0.05. Finally, we measured the average phylogenetic distance among species in each trait category, both within each country and in a phylogeny including all detected species. To do so, we split continuous traits into two categories at the mean value (*e.g.,* cutoff of high vs. low proportion of insect diet at 52%). For the habitat affinity trait, we split the three categories into two to simplify all comparisons to two categories: dense and a combination of semi-open and open. Then, to determine whether phylogenetic distances significantly differed, we compared true differences in phylogenetic distance to 1000 null distances, generated by randomly shuffling tips of the phylogeny while maintaining the number of species in each trait category. We considered distances to be significantly different if the true distance was greater than over 95% of the null distances.

Results

We detected 168 species (20,184 individuals) in Costa Rica and 264 species (8,812 individuals) in Colombia, with 66 species present in both countries (Table S1.1). In Costa Rica, local forest cover had a positive effect on species' occupancy on average (effect size 0.75, 95% BCI [0.36, 1.13]), whereas in Colombia, there was no significant effect of local forest cover on occupancy across species on average (effect size 0.06, 95% BCI [-0.13, 0.25]). All core parameters in the logistic model of occupancy converged (Gelman-Rubin Statistics <1.1). As expected, communities exhibited significant turnover across land-use and precipitation gradients within both countries; however, forest cover was correlated with relatively more community turnover in Costa Rica and precipitation caused relatively more turnover in Colombia (Figure 2; Table S1.2).

In our analyses of pairwise dissimilarities, we found that patterns in the degree of phylogenetic turnover across categories of forest cover and precipitation differed within Costa Rica and Colombia. Surprisingly, in Costa Rica, agricultural habitats had the highest phylogenetic turnover, while forested habitats had the lowest turnover (Figure 3A). This pattern was consistent across the precipitation gradient. Wetter sites generally had lower phylogenetic turnover than dryer sites across all categories of forest cover, though these differences were not statistically significant at any category of forest cover (Figure 3A). On the contrary, phylogenetic turnover was correlated primarily by precipitation and not land-use in Colombia (Figure 3B). Specifically, phylogenetic turnover was highest in wet habitats across all levels of forest cover, while dry forest had the lowest phylogenetic turnover as compared to all other habitat types (Figure 3B).

In contrast, when analyzing Costa Rica and Colombia together (only including across-country comparisons), forested sites had higher phylogenetic turnover than agricultural sites, supporting our hypothesis about agriculture-driven homogenization at the continental scale. This pattern was consistent across the precipitation gradient, though wetter sites generally had higher turnover than dryer sites. However, there was no significant difference in phylogenetic turnover between dry and wet agricultural sites (Figure 3C). Results from the null method to account for variation in species richness among sites matched our findings without accounting for species richness (Figure S1).

Functional traits tended to consistently predict species responses to forest cover across both countries. In Colombia, species that inhabited denser habitats, were less mobile, ate more insects, and ate fewer seeds/grains responded positively to local forest cover (Table 1). Similarly, in Costa Rica, species that inhabited denser habitats, ate more insects, and ate fewer seeds/grains also responded more positively to local forest cover (Table 1). Trends were similar, and effect sizes often even larger, when analyzing the 66 shared species only (Table S1.3). All traits were phylogenetically conserved (Table 1). Importantly, however, the mean phylogenetic distances associated with agricultural traits tended to be smaller than those associated with forest traits. Specifically, within each country, phylogenetic distances were greater for species associated with closed habitats, species that ate insects, and species with smaller ranges (Colombia only; Table 2). Across the entire phylogeny of all detected species, phylogenetic distances were greater for forest-associated birds, species that ate insects, species that were less mobile, and species with smaller ranges (Table 2). The 66 species that occurred in both countries displayed consistent response to land conversion (Figure 4; Spearman's rho = 0.49, $p<0.001$). This correlation was strong despite there being some species with a near-zero effect size in Costa Rica (due to there being few observations of those species in the data).

Because the range metric did not have a statistically significant effect in our full models and it was slightly correlated with other trait metrics (Table S1.4), we also ran a phylogenetic linear model with only global range size as a predictor. When only including global range size as a trait, species with larger global range sizes were more likely to have a positive response to agriculture, though species with large range sizes tended to have smaller residuals, meaning that the relationship could be driven by a few of the widest-ranging species.

Discussion

We found that land-use change drives phylogenetic homogenization at a continental scale, and that phylogenetic homogenization is likely mediated by phylogenetically conserved functional traits. Specifically, species' habitat affiliations, mobility, and diets consistently explained sensitivity to land-use change in Costa Rica and Colombia, with open-habitat associated, more mobile, and seed-eating species thriving in and homogenizing communities in agriculture across both countries. However, the effects of land-use and climate on phylogenetic beta diversity varied across regions and spatial scales. Indeed, within Costa Rica, phylogenetic beta-diversity was highest in agriculture, and within Colombia, phylogenetic beta-diversity peaked in wetter sites (irrespective of land use).

Regional patterns in phylogenetic beta diversity

We were surprised that agriculture did not lower beta-diversity and cause phylogenetic homogenization within Costa Rica or Colombia. Indeed, our prior work in the same Costa Rican study system reported lower taxonomic beta-diversity in agriculture compared to forest (Karp et al., 2018), a pattern that has been replicated in other taxa and study systems (*e.g.*, Solar et al. 2015, Ibáñez-Álamo et al. 2017, Liang et al. 2019, Weideman et al. 2020). One possible explanation for the difference may be temporal replication. Here, we leveraged 4 years of bird survey data versus 1 year in our prior work (Karp et al., 2018). High-intensity agriculture is regularly disturbed, destabilizing species' abundances and driving shifts in community composition among years (Hendershot et al., 2020; Karp et al., 2011). The high temporal beta-diversity in agriculture may thus accentuate differences in community composition among sites over time. Correspondingly, García-Navas and Thuiller (2020) found that phylogenetic diversity was lower in forest than farmland in France, and that phylogenetic diversity of farmland assemblages increased over the study period.

Within Colombia, we also did not find that agriculture caused phylogenetic homogenization. Instead, phylogenetic beta-diversity was mostly related to precipitation (Table S1.2), with dry forest having the lowest phylogenetic turnover among all habitat types (Figure 3). This could be because dry forests tended to have a unique bird community, but the community was consistently observed across sites. Indeed, many species inhabiting neotropical seasonally dry forests tend to be highly associated with and/or endemic to that habitat (Prieto-Torres et al., 2019). Dry regions in Colombia also had smaller species pools than wetter regions: 135, 139, 182, and 189 species were found in dry forest, dry agriculture, wet forest, and wet agriculture, respectively. Wetter regions may have had higher phylogenetic beta-diversity because of both its larger species pool and low per-species abundances, leading to observations of rarer species that varied more between visits and sites.

Why might have precipitation been correlated with patterns in beta-diversity in Colombia but not Costa Rica? One possibility is that the extent of the study region in Colombia is geographically longer (270 vs. 60 km) and encompasses a wider range of annual precipitation. Thus, habitat filtering and dispersal limitation may be stronger in Colombia if variation in habitat is greater between dry and wet sites than in Costa Rica, causing communities to be more distinct between dry and wet regions regardless of local forest cover (Gómez et al. 2010). On the other hand, in Costa Rica, the precipitation gradient is geographically shorter with a smaller range of annual rainfall, leading to more shared species across the precipitation gradient.

Homogenization at the continental scale

Unlike regional patterns, we found evidence that land conversion to agriculture may cause phylogenetic homogenization at larger spatial scales. That is, when comparing communities across Costa Rica and Colombia combined, wet forests hosted the most phylogenetically distinct communities whereas agriculture (both wet and dry) was significantly more phylogenetically homogenous (Figure 2). At least two potential mechanisms may explain why agriculture seemed to cause homogenization across countries but not within them.

First, if species respond to agriculture consistently across their ranges, and agriculture is more likely to host wide-ranging species, then distant agricultural sites should be more likely to share species than distant forest sites. Correspondingly, we found that the 66 species that occurred in both countries responded similarly to forest cover in each country (Figure 4). Moreover, though our range metric did not significantly explain variation in species' habitat associations when present with all other traits (Table 1), there was a significant negative relationship between species' responses to forest cover and global range size when modeled in isolation (Figure 4). This discrepancy likely arose because range size was correlated with other traits that were even more predictive of species' preferences for forest versus agriculture (Table S1.4). Nonetheless, our work suggests that agriculture may homogenize biodiversity by promoting the same wide-ranging species across large geographic distances.

Second, phylogenetic homogenization could arise if forest-associated species are derived from very distinct lineages in different regions, but agriculture-associated species are not. Correspondingly, we found that forest-affiliated species were less phylogenetically clustered than agriculture-affiliated species across the phylogeny encompassing all detected species (Table 2). However, they were not less clustered than agriculture-affiliated species across the smaller phylogenies of each individual country (Table 2).

These patterns may have been mediated through species' traits. Consistent with other research, we found that, in both countries, agriculture tended to favor species that have a diet consisting of more seeds/grains and fewer insects, are more mobile, have larger ranges, and are affiliated with more open habitats (Hatfield et al., 2018; Kennedy et al., 2010; Newbold et al., 2013). These traits were phylogenetically conserved and tended to be more concentrated in the bird phylogeny (*i.e.,* present in a more limited subset of lineages) than the corresponding traits associated with forest species. That is, the species that occupy forests— specifically, insect-eating species with narrow ranges that are less mobile and more affiliated with closed habitats— are more likely to be from more distant lineages of the bird phylogeny than the species that occupy agriculture (Table 2). Meanwhile, the more limited subset of lineages that contain species with high mobility, that prefer seeds/grains over insects, and that have large range sizes may be a homogenizing force in agriculture.

Limitations

Our core result—that agriculture homogenizes bird lineages across countries—may be conservative. In our study systems, forest sites were often degraded. For example, compared to the protected areas, privately-owned forests in Costa Rica were twice as fragmented as protected areas and more frequently logged, causing significantly lower canopy cover, shorter tree heights, and lower tree richness (Karp et al., 2019). No protected areas were present in our Colombia study system. If the forests studied here have already lost some of the most phylogenetically distinct and range-restricted species (Sykes et al., 2020), then we could be underestimating the degree of phylogenetic differentiation that "should" be present between forested sites. Indeed, only five species we detected in Costa Rica (Great Curassow (*Crax rubra;* 5 observations), Yellow-naped

Parrot (*Amazona auropalliata*; 22 observations), Crested Guan (*Penelope purpurascens*; 1 observation), Keel-billed Toucan (*Ramphastos sulfuratus*; 3 observations), and Eastern Meadowlark (*Sturnella magna*; 21 observations)) and five species in Colombia (Military Macaw (*Ara militaris*; 1 observation), White-mantled Barbet (*Capito hypoleucus*; 1 observation), Crested Guan (*Penelope purpurascens*; 2 observations), Saffron-headed Parrot (*Pyrilia pyrilia*; 1 observation), and Yellow-throated Toucan (*Ramphastos ambiguus*; 6 observations)) that are not listed as "least concern" by IUCN. If forest point count locations were more intact, we would expect to observe more species that are rare, threatened, and phylogenetically distinct, resulting in higher phylogenetic turnover in forest. Moreover, in Colombia, there were some auditory observations that could not be identified, and these events were more common in forest than agriculture (86 vs. 57), meaning we could be further missing some elusive forest species.

Conclusion

We used species traits and phylogenetic relationships to understand the traits associated with species that profit from land conversion to agriculture, those that do not, and what the ensuing consequences are for biotic homogenization. We found that the proliferation of wide-ranging species in agriculture, as well as the concentration of agriculture-associated species in certain lineages within the avian phylogeny, caused phylogenetic homogenization between Costa Rica and Colombia but not within each country. These results suggest it is critical to study homogenization at multiple scales (Olden et al., 2018), because regional patterns may differ from continental ones. They also point to the importance of examining multiple dimensions of homogenization (*i.e.,* taxonomic, functional, and phylogenetic), given that species traits are often non-randomly distributed across phylogenies and agriculture-associated traits may be particularly concentrated in certain lineages (Olden et al., 2018; Soares et al., n.d.).

Tropical forests are one of the most endangered ecosystems in Central and South America due to land conversion to agriculture (Janzen, 1988; Portillo-Quintero & Sánchez-Azofeifa, 2010). In Colombia, the government's recent agreement with The Revolutionary Armed Forces of Colombia brought an end to the decades-long civil conflict but, in doing so, indirectly opened up vast forested areas that people previously avoided to deforestation (Clerici et al., 2016). In contrast, northwest Costa Rica is currently experiencing reforestation; however, climate change is expected to elicit significant regional droughts that may threaten wet forests in the future (Karp et al., 2019; Rauscher et al., 2008). In the face of these ongoing global changes, our study suggests that conserving undisturbed forest (Gibson et al., 2011), preventing forest degradation, and restoring degraded areas (Malhi et al., 2014), especially in wetter areas (Karp et al., 2019), may be critical to preventing phylogenetic homogenization at large spatial scales.

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Table 1: Functional traits are consistently related to species' responses to forest cover in Costa Rica and Colombia. Table shows coefficient estimates, standard errors, t-values, and p-values from phylogenetic least squares models for Colombia and Costa Rica. The response variable is the mean of each species' posterior distribution of the beta parameter for the effect of local forest cover on occupancy ($\beta 1$), where higher values represent higher occupancy as forest increases. Coefficients are associated with traits, which are described in methods. Table also contains an analysis of trait conservatism, reporting Pagel's lambda and the associated p-value for each trait.

	Within Colombia				Within Costa Rica				Pagel's lambda across countries	
Coefficient	Value	Standard error	t-value	p-value	Value	Standard error	t-value	p-value	Pagel's lambda	p-value
Intercept	0.078	0.08	0.93	0.35	0.562	0.38	1.48	0.14		
Habitat	-0.369	0.04	-8.30	<0.01	-0.766	0.15	-5.08	<0.01	0.75	<0.001
Mobility	-0.130	0.04	-2.94	<0.01	-0.238	0.13	-1.87	0.06	0.78	<0.001
Diet-invertebrate	0.075	0.05	1.51	0.13	0.009	0.00	2.11	0.04	0.98	<0.001
Diet-granivore	-0.130	0.04	-2.97	<0.01	-0.012	0.01	-1.95	0.05	0.91	<0.001
Biogeography	-0.022	0.05	-0.46	0.64	-0.137	0.17	-0.81	0.42	0.78	<0.001

Table 2: Mean branch lengths between species grouped by country and traits. "High" and "Low" species' response to forest cover denotes whether the mean of each species' posterior distribution of the beta parameter for the effect of local forest cover on occupancy ($\beta 1$) is positive (High) or negative (Low). Habitat openness is a categorial variable with three categories. Diet, mobility metric, and range metric are split by whether a species has a trait value above or below the mean value of the community. Cells in dark grey denote that there is a significant difference between the branch length categories using a null model method (See SI Methods). For cells in light grey (habitat openness), there was a significant difference between high and medium categories, medium and low categories, but not high and low categories.

	Species' response to local forest cover		Habitat openness		Diet - invertebrate		Diet - seed		Mobility metric		Range metric	
	High	Low	Open/Medium	Closed	High	Low	High	Low	High	Low	High	Low
Across Countries	143.76	138.25	139.84	142.71	149.01	128.42	141.33	138.54	137.36	144.89	139.49	146.32
Significance	0.017		0.136		0.000		0.320		0.004		0.004	
Within Costa Rica	152.14	145.83	141.13	151.91	157.00	132.52	150.54	142.19	148.43	150.28	147.65	151.04
Significance	0.108		0.001		0.000		0.080		0.369		0.187	
Within Colombia	138.54	139.34	136.25	147.83	145.41	124.85	136.49	140.51	135.01	139.20	134.39	145.26
Significance	0.402		0.000		0.000		0.094		0.089		0.000	

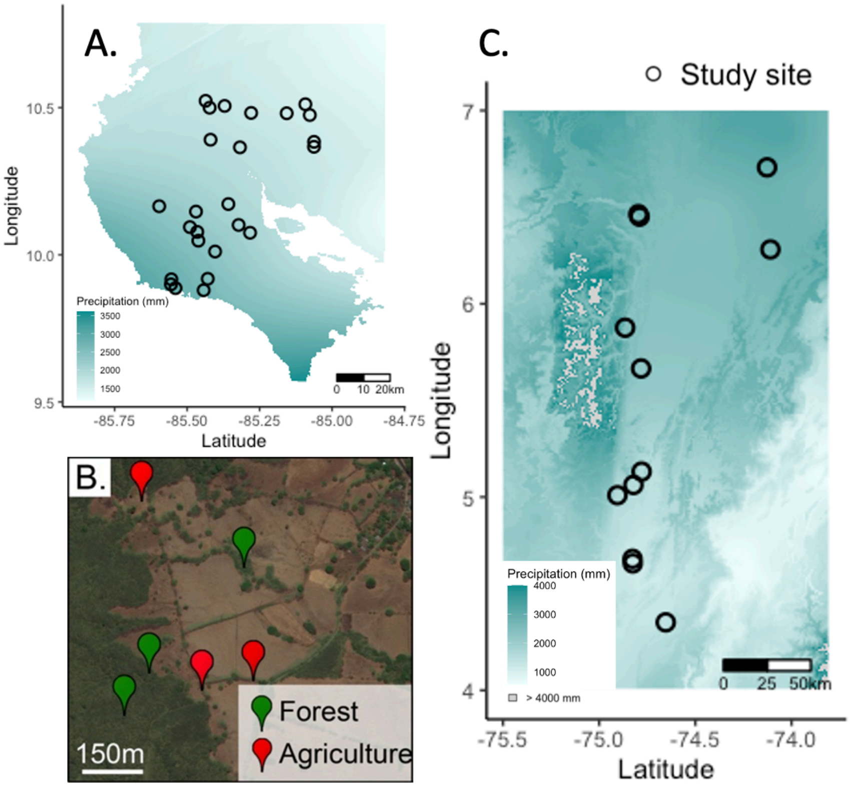

Figure 1: (A) Map of study sites in Costa Rica. Precipitation data are modelled (see Methods). (B) An example study site in Costa Rica, where half of the point-count locations were in forest and the other half were in agriculture. (C) Map of study sites in Colombia. Precipitation data are from WorldClim (Fick & Hijmans, 2017).

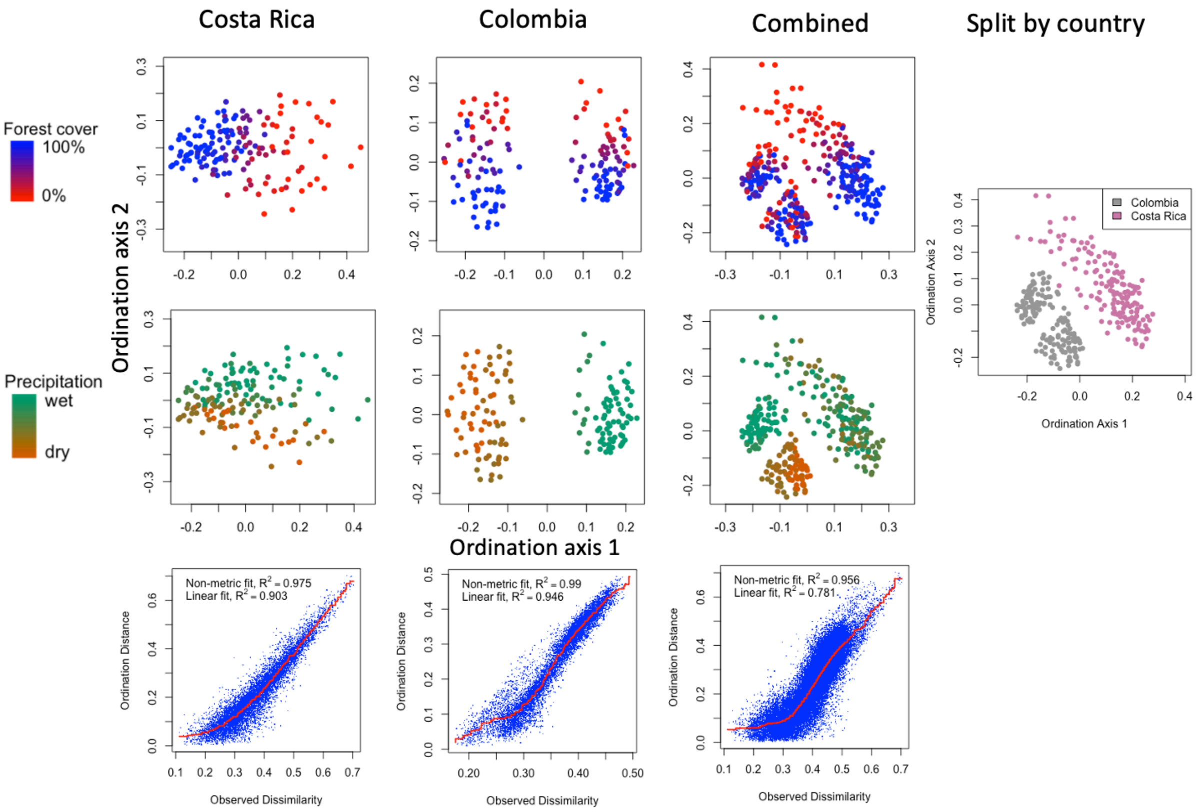

Figure 2: Non-metric multidimensional scaling (NMDS) plots showing bird community phylogenetic turnover along gradients of forest cover (top row), phylogenetic turnover along gradients of precipitation (middle row), and Shepard diagrams (bottom row). Plots show trends within countries (Costa Rica, left panel, stress = 0.16; Colombia, middle panel, stress = 0.13) and for both countries combined (right panels, stress = 0.21). The distance among sites (points) represents the differences in phylogenetic turnover, according to changes in species occupancy (Sorensen similarity). The precipitation gradient ranges from 1525 mm to 2865 mm in Costa Rica and from 1309 mm to 3580 mm in Colombia and the “Combined” plot. In both Costa Rica and Colombia, sites with more similar levels of forest cover (red to blue gradient) and precipitation (orange to green gradient) tended to have more similar bird communities. Nonetheless, forest cover influenced bird community turnover more in Costa Rica, whereas

precipitation influenced bird community turnover in Colombia (Table S1.2). Sites across countries had very phylogenetically distinct communities.

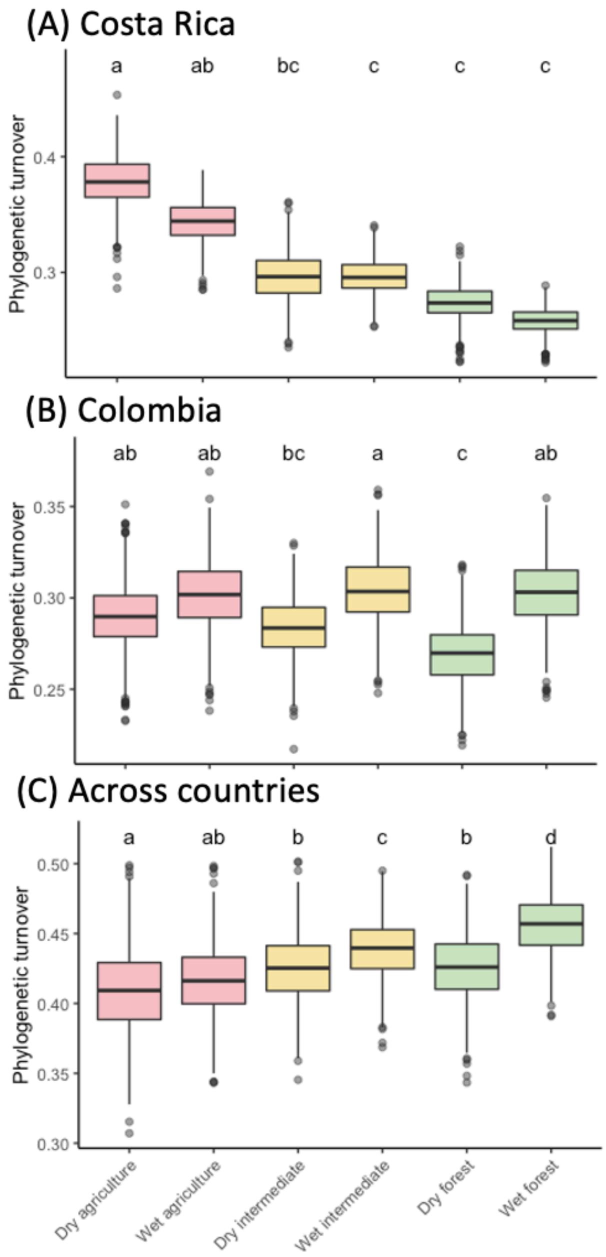

Figure 3: Agriculture elicited phylogenetic homogenization across but not within countries. Boxplots depict phylogenetic turnover in each habitat type (A) within Costa Rica, (B) within Colombia, and (C) between sites in Costa Rica and Colombia. All boxplots depict the median phylogenetic turnover from 1000 simulated communities for each habitat; whiskers are 1.5 times the interquartile range. Different letters denote statistical significance, based on a null shuffling method to account for nonindependence among sites in pairwise comparisons (see Methods).

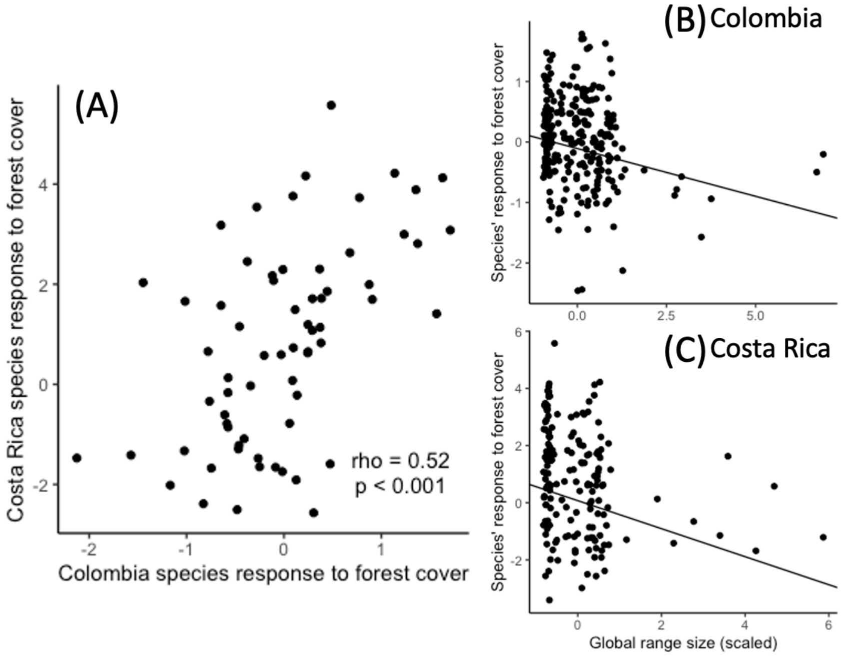

Figure 4: Large-ranged species may contribute to phylogenetic homogenization in agriculture. (A) Shared species responded similarly to local forest cover in Costa Rica and Colombia. The x-axis represents the effect of local forest cover on occupancy in Colombia, and the y-axis represents the same metric in Costa Rica (*i.e.,* the mean $\beta 1$ across each species' posterior distribution). Higher numbers indicated a species was more likely to occupy forested areas. The Spearman's rho correlation and the p-value associated with it are shown. (B and C) Plots of species' response to forest cover and global range size in Colombia (B) and in Costa Rica (C). The x-axes represent scaled global range size, and the y-axis represents responses to forest cover (as in panel A). The line is the predicted relationship between the variables according to a phylogenetic generalized linear model with only range size as a predictor.

Supporting Information 1

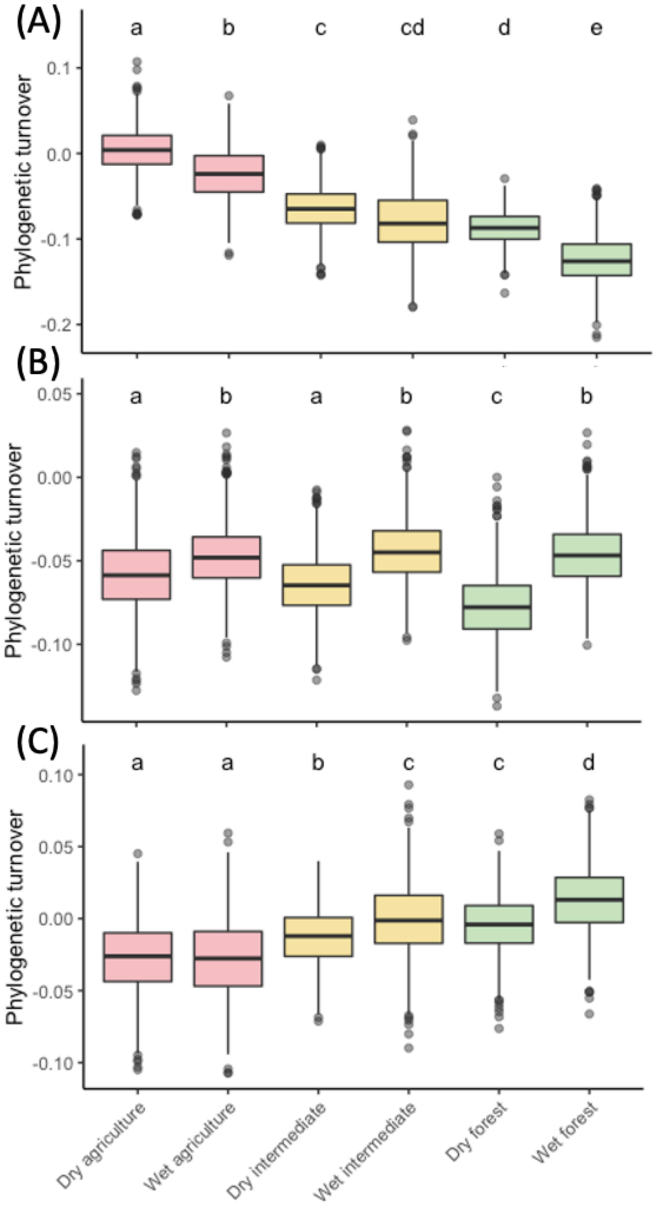

Figure S1: Comparisons of phylogenetic beta-diversity across sites, leveraging a null analysis method to account for variation in species richness between sites. Boxplots depict phylogenetic turnover in each habitat type (A) within Costa Rica, (B) within Colombia, and (C) between sites in Costa Rica and Colombia. All boxplots indicate the median phylogenetic turnover from 1000 simulated communities for each habitat, and whiskers are 1.5 times the interquartile range.

Different letters denote statistical significance, based on a null shuffling method to account for nonindependence among sites in pairwise comparisons (see Methods).

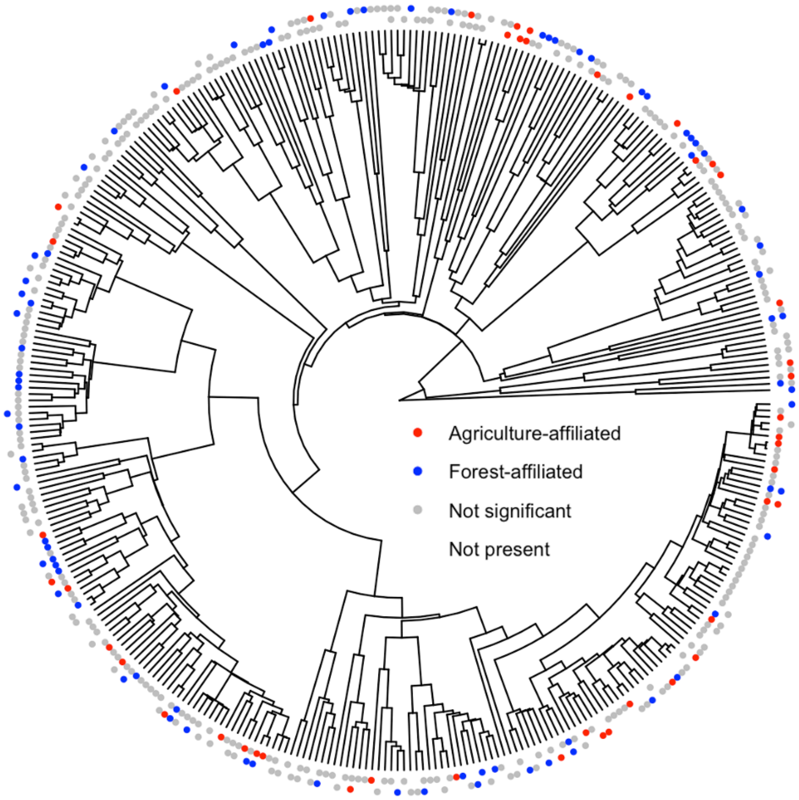

Figure S1.2: Forest cover benefits similar lineages across both Costa Rica and Colombia. Figure depicts a phylogenetic tree of the 366 species detected in Costa Rica and Colombia. The inner circle of points represents species in Colombia, and the outer circle of points represents species in Costa Rica. Species absent from a country were left blank. Points are colored by the species' relationship to local forest cover, where red indicates significantly higher occupancy as forest cover decreases, blue indicates significantly higher occupancy as forest cover increases, and grey indicates no significant differences with changes in forest cover.

Table S1.1: List of species in the study and which country each species was present in.

Species	Present in Colombia	Present in Costa Rica
Agelaius phoeniceus	0	1
Aimophila ruficauda	0	1
Amazilia amabilis	1	0
Amazilia franciae	1	0
Amazilia rutila	0	1
Amazilia saucerrottei	1	1
Amazilia tzacatl	1	1
Amazona albifrons	0	1
Amazona amazonica	1	0
Amazona auropalliata	0	1
Amazona ochrocephala	1	0
Amblycercus holosericeus	0	1
Ammodramus humeralis	1	0
Anthracothorax nigricollis	1	0
Anthracothorax prevostii	0	1
Ara ararauna	1	0
Ara macao	0	1
Ara militaris	1	0
Aramides cajanea	1	1
Aramus guarauna	0	1
Aratinga canicularis	0	1
Ardea alba	1	1
Arremon aurantiirostris	1	0
Arremonops conirostris	1	0
Arremonops rufivirgatus	0	1
Asio clamator	0	1
Atalotriccus pilaris	1	0
Atticora tibialis	1	0
Attila spadiceus	1	1
Baryphthengus martii	1	0
Basileuterus rufifrons	1	1
Brotogeris jugularis	1	1
Bubulcus ibis	1	1
Burhinus bistriatus	0	1
Busarellus nigricollis	1	0

Buteo albonotatus	0	1
Buteo magnirostris	1	1
Buteo nitidus	0	1
Buteogallus anthracinus	0	1
Buteogallus meridionalis	1	0
Butorides striata	1	0
Butorides virescens	0	1
Cacicus cela	1	0
Cairina moschata	0	1
Calocitta formosa	0	1
Campephilus guatemalensis	0	1
Campephilus melanoleucos	1	0
Camptostoma imberbe	0	1
Camptostoma obsoletum	1	0
Campylorhamphus trochilirostris	1	0
Campylorhynchus griseus	1	0
Campylorhynchus rufinucha	0	1
Campylorhynchus zonatus	1	0
Cantorchilus leucotis	1	0
Cantorchilus nigricapillus	1	0
Capito hypoleucus	1	0
Capsiempis flaveola	1	0
Caracara cheriway	1	1
Cathartes aura	1	1
Catharus aurantiirostris	0	1
Celeus loricatus	1	0
Ceratopipra erythrocephala	1	0
Cercomacra nigricans	1	0
Cercomacroides tyrannina	1	0
Certhiaxis cinnamomeus	1	0
Chaetura vauxi	0	1
Chalybura buffonii	1	0
Chiroxiphia lanceolata	1	0
Chiroxiphia linearis	0	1
Chloroceryle amazona	1	1
Chloroceryle americana	1	1
Chlorophanes spiza	1	0
Chlorostilbon canivetii	0	1

Chlorostilbon gibsoni	1	0
Chondrohierax uncinatus	0	1
Claravis pretiosa	1	1
Cnemotriccus fuscatus	1	0
Coccyzus minor	0	1
Coereba flaveola	1	0
Colaptes punctigula	1	0
Colinus cristatus	1	1
Colonia colonus	1	0
Columba livia	1	0
Columbina inca	0	1
Columbina minuta	1	1
Columbina passerina	1	1
Columbina talpacoti	1	1
Conirostrum leucogenys	1	0
Contopus cinereus	1	1
Contopus sordidulus	0	1
Coragyps atratus	1	1
Coryphospingus pileatus	1	0
Crax rubra	0	1
Crotophaga ani	1	0
Crotophaga major	1	0
Crotophaga sulcirostris	1	1
Crypturellus cinnamomeus	0	1
Crypturellus soui	1	1
Cyanerpes caeruleus	1	0
Cyanerpes cyaneus	0	1
Cyanocompsa cyanoides	1	1
Cyanocorax affinis	1	0
Cyclarhis gujanensis	1	1
Dacnis cayana	1	0
Dacnis lineata	1	0
Dendrocincla fuliginosa	1	0
Dendrocincla homochroa	0	1
Dendrocincla tyrannina	1	0
Dendrocolaptes picumnus	1	0
Dendrocolaptes sanctithomae	0	1
Dendrocygna autumnalis	1	1
Dendroplex picus	1	0

Dives dives	0	1
Donacobius atricapilla	1	0
Dryocopus lineatus	1	1
Elaenia flavogaster	1	1
Elanus leucurus	1	1
Electron platyrhynchum	1	0
Epinecrophylla fulviventris	1	0
Eucometis penicillata	1	1
Eumomota superciliosa	0	1
Euphonia affinis	0	1
Euphonia concinna	1	0
Euphonia hirundinacea	0	1
Euphonia laniirostris	1	0
Euphonia luteicapilla	0	1
Euphonia xanthogaster	1	0
Euscarthmus meloryphus	1	0
Falco femoralis	1	0
Falco rufigularis	0	1
Falco sparverius	1	0
Florisuga mellivora	1	0
Fluvicola pica	1	0
Formicivora grisea	1	0
Forpus conspicillatus	1	0
Furnarius leucopus	1	0
Galbula ruficauda	1	0
Geothlypis poliocephala	0	1
Geotrygon montana	1	1
Geranospiza caerulescens	1	1
Glaucidium brasilianum	0	1
Glaucis hirsutus	1	0
Glyphorynchus spirurus	1	0
Gymnocichla nudiceps	1	0
Habia cristata	1	0
Habia gutturalis	1	0
Habia rubica	0	1
Heliomaster constantii	0	1
Hemithraupis flavicollis	1	0
Hemitriccus margaritaceiventer	1	0

Henicorhina leucosticta	1	0
Herpetotheres cachinnans	1	1
Herpsilochmus rufimarginatus	1	0
Himantopus mexicanus	0	1
Hirundo rustica	0	1
Hylophilus decurtatus	1	1
Hylophilus flavipes	1	0
Hypnelus ruficollis	1	0
Icterus auricapillus	1	0
Icterus nigrogularis	1	0
Icterus pectoralis	0	1
Icterus pustulatus	0	1
Icterus spurius	0	1
Ictinia plumbea	1	0
Islerothraupis luctuosa	1	0
Jacana jacana	1	0
Jacana spinosa	0	1
Juliamyia julie	1	0
Laniocera rufescens	1	0
Laterallus albigularis	1	0
Legatus leucophaius	1	1
Leistes militaris	1	0
Lepidocolaptes souleyetii	1	1
Lepidopyga goudoti	1	0
Leptodon cayanensis	0	1
Leptopogon amaurocephalus	1	0
Leptopogon superciliaris	1	0
Leptotila plumbeiceps	0	1
Leptotila verreauxi	1	1
Lonchura malacca	0	1
Machaeropterus regulus	1	0
Machaeropterus striolatus	1	0
Machetornis rixosa	1	0
Malacoptila panamensis	1	0
Manacus manacus	1	0
Megaceryle torquata	1	1
Megarynchus pitangua	1	1
Melanerpes hoffmannii	0	1
Melanerpes pucherani	1	0

Melanerpes pulcher	1	0
Melanerpes rubricapillus	1	0
Micrastur semitorquatus	0	1
Microcerculus marginatus	1	0
Microrhopias quixensis	1	0
Milvago chimachima	1	1
Mimus gilvus	1	0
Mionectes oleagineus	1	1
Mionectes olivaceus	1	0
Molothrus aeneus	0	1
Molothrus bonariensis	1	0
Molothrus oryzivorus	0	1
Momotus aequatorialis	1	0
Momotus momota	0	1
Morococcyx erythropygus	0	1
Mycteria americana	0	1
Myiarchus apicalis	1	0
Myiarchus cephalotes	1	0
Myiarchus nuttingi	0	1
Myiarchus panamensis	1	0
Myiarchus tuberculifer	1	1
Myiarchus tyrannulus	0	1
Myiodynastes chrysocephalus	1	0
Myiodynastes luteiventris	0	1
Myiodynastes maculatus	1	1
Myiopagis gaimardii	1	0
Myiopagis viridicata	1	1
Myiothlypis fulvicauda	1	0
Myiozetetes cayanensis	1	0
Myiozetetes similis	1	1
Myrmeciza immaculata	1	0
Myrmeciza longipes	1	0
Myrmotherula axillaris	1	0
Myrmotherula brachyura	1	0
Myrmotherula pacifica	1	0
Notharchus macrorhynchos	0	1
Notharchus pectoralis	1	0
Notharchus tectus	1	0
Numenius americanus	0	1

Nyctibius grandis	1	0
Nyctibius griseus	1	0
Nycticorax nycticorax	0	1
Nyctidromus albicollis	1	1
Nystalus radiatus	1	0
Odontophorus gujanensis	1	0
Oncostoma cinereigulare	0	1
Oncostoma olivaceum	1	0
Onychorhynchus coronatus	0	1
Ornithion brunneicapillus	1	0
Ortalis columbiana	1	0
Ortalis vetula	0	1
Oryzoborus angolensis	1	0
Oryzoborus crassirostris	1	0
Oryzoborus funereus	1	0
Pachyramphus aglaiae	0	1
Pachyramphus cinnamomeus	1	0
Pachyramphus polychopterus	0	1
Pachyramphus rufus	1	0
Pandion haliaetus	0	1
Pardirallus maculatus	0	1
Passer domesticus	0	1
Passerina caerulea	0	1
Patagioenas cayennensis	1	0
Patagioenas fasciata	1	0
Patagioenas flavirostris	0	1
Patagioenas speciosa	1	0
Patagioenas subvinacea	1	0
Penelope purpurascens	1	1
Phaeomyias murina	1	0
Phaethornis anthophilus	1	0
Phaethornis striigularis	1	1
Phaethornis syrmatophorus	1	0
Pheugopedius fasciatoventris	1	0
Philohydor lictor	1	0
Phimosus infuscatus	1	0
Phyllomyias griseiceps	1	0
Piaya cayana	1	1
Picumnus olivaceus	1	0

Pilherodius pileatus	1	0
Pionus menstruus	1	0
Pitangus sulphuratus	1	1
Platyrinchus cancrominus	0	1
Poecilotriccus sylvia	1	1
Poliocrania exsul	1	0
Polioptila albiloris	0	1
Polioptila plumbea	1	1
Porphyrio martinica	0	1
Progne chalybea	1	1
Psarocolius angustifrons	1	0
Psarocolius decumanus	1	0
Pteroglossus torquatus	1	1
Pygochelidon cyanoleuca	1	0
Pyrilia pyrilia	1	0
Pyrocephalus rubinus	1	0
Pyrrhomyias cinnamomeus	1	0
Quiscalus mexicanus	0	1
Ramphastos ambiguus	1	0
Ramphastos sulfuratus	0	1
Ramphastos vitellinus	1	0
Ramphocaenus melanurus	0	1
Ramphocelus dimidiatus	1	0
Rhynchocyclus olivaceus	1	0
Rostrhamus sociabilis	0	1
Saltator coerulescens	1	0
Saltator grossus	1	0
Saltator maximus	1	0
Saltator striatipectus	1	0
Sarcoramphus papa	1	1
Sayornis nigricans	1	0
Schiffornis turdina	1	0
Sicalis flaveola	1	0
Sittasomus griseicapillus	1	1
Sporophila corvina	0	1
Sporophila intermedia	1	0
Sporophila minuta	1	0
Sporophila nigricollis	1	0
Sporophila schistacea	1	0

Sporophila torqueola	0	1
Stelgidopteryx ruficollis	1	0
Streptoprocne zonaris	0	1
Sturnella magna	0	1
Synallaxis albescens	1	0
Synallaxis brachyura	1	0
Tangara cyanicollis	1	0
Tangara gyrola	1	0
Tangara icterocephala	1	0
Tangara inornata	1	0
Tangara larvata	1	0
Tangara vitriolina	1	0
Tapera naevia	1	1
Terenotriccus erythrurus	1	0
Tersina viridis	1	0
Thalurania furcata	1	0
Thamnophilus atrinucha	1	0
Thamnophilus doliatus	1	1
Thamnophilus multistriatus	1	0
Thamnophilus nigriceps	1	0
Thamnophilus schistaceus	1	0
Thraupis episcopus	1	1
Thraupis palmarum	1	1
Threnetes ruckeri	1	0
Thryothorus modestus	0	1
Thryothorus pleurostictus	0	1
Thryothorus rufalbus	0	1
Tiaris olivaceus	0	1
Tigrisoma mexicanum	0	1
Tityra inquisitor	1	1
Tityra semifasciata	1	1
Todirostrum cinereum	1	1
Todirostrum nigriceps	1	0
Tolmomyias sulphurescens	1	1
Troglodytes aedon	1	0
Trogon caligatus	1	0
Trogon chionurus	1	0
Trogon elegans	0	1
Trogon melanocephalus	0	1

Trogon melanurus	1	0
Trogon violaceus	0	1
Turdus grayi	0	1
Turdus ignobilis	1	0
Turdus leucomelas	1	0
Turdus leucops	1	0
Tyrannulus elatus	1	0
Tyrannus melancholicus	1	1
Tyrannus savana	1	0
Tyto alba	0	1
Vanellus chilensis	1	1
Veniliornis kirkii	1	0
Vireo flavoviridis	0	1
Vireolanius eximius	1	0
Volatinia jacarina	1	1
Xenops minutus	1	0
Xiphorhynchus flavigaster	0	1
Xiphorhynchus susurrans	1	0
Zenaida asiatica	0	1
Zenaida auriculata	1	0
Zenaida macroura	0	1

Table S1.2: PERMANOVA tests of phylogenetic community differentiation along local forest cover and precipitation gradients within Costa Rica and within Colombia.

	Coefficient	Df	Sum of squares	Mean squares	F	R2	Pr(>F)
Within Costa Rica	Precipitation	1	0.89	0.89	18.60	0.08	0.001
	Forest cover	1	2.99	2.99	62.62	0.27	0.001
	Residuals	147	7.02	0.05		0.64	
	Total	149	10.89			1.00	
Within Colombia	Precipitation	1	2.67	2.67	62.53	0.28	0.001
	Forest cover	1	0.68	0.68	15.99	0.07	0.001
	Residuals	141	6.02	0.04		0.64	
	Total	143	9.37			1.00	

Table S1.3: Functional traits consistently dictate species' responses to forest cover amongst the 66 shared species between Costa Rica and Colombia. Table shows coefficient estimates, standard error, t-value, and p-values from phylogenetic least squares models using only the 66 shared species between Costa Rica and Colombia. The response variable is the mean of each species' posterior distribution of the beta parameter for the effect of local forest cover on occupancy ($\beta 1$), where higher values represent higher occupancy as forest increases. Coefficients represent traits, which are described in methods.

Country	Coefficient	Value	Standard error	t-value	p-value
Colombia, shared species	Intercept	-0.329	0.26	-1.24	0.22
	Habitat	-0.509	0.10	-5.25	<0.01
	Mobility	-0.279	0.12	-2.36	0.02
	Diet-invertebrate	0.071	0.13	0.56	0.58
	Diet-granivore	-0.079	0.10	-0.77	0.45
	Biogeography	-0.332	0.11	-3.06	<0.01
Costa Rica, shared species	Intercept	0.789	0.51	1.55	0.13
	Habitat	-1.239	0.19	-6.37	<0.01
	Mobility	-0.230	0.23	-1.02	0.31
	Diet-invertebrate	0.935	0.27	3.42	<0.01
	Diet-granivore	0.130	0.30	0.44	0.66
	Biogeography	-0.376	0.22	-1.69	0.10

Table S1.4: Correlation between trait predictors in the phylogenetic generalized linear models.

	Colombia					Costa Rica				
	Habitat affiliation	Diet - invertebrate	Diet - seeds	Range metric	Mobility metric	Habitat affiliation	Diet - invertebrate	Diet - seeds	Range metric	Mobility metric
Habitat affiliation	1.00	-0.09	0.21	0.43	0.20	1.00	-0.10	0.16	0.33	0.10
Diet - invertebrate	-0.09	1.00	-0.40	-0.05	0.26	-0.10	1.00	-0.37	0.00	0.16
Diet - seeds	0.21	-0.40	1.00	0.09	-0.13	0.16	-0.37	1.00	0.05	-0.23
Range metric	0.43	-0.05	0.09	1.00	0.32	0.33	0.00	0.05	1.00	0.19
Mobility metric	0.20	0.26	-0.13	0.32	1.00	0.10	0.16	-0.23	0.19	1.00

A hierarchical N-mixture model to estimate behavioral variation and a case study of Neotropical birds

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Open Research: Data and novel code are permanently archived on Dryad:
https://datadryad.org/stash/dataset/doi:10.25338/B8VP85?

Abstract:

Understanding how and why animals use the environments where they occur is both foundational to behavioral ecology and essential to identify critical habitats for species conservation. However, some behaviors are more difficult to observe than others, which can bias analyses of raw observational data. To our knowledge, no method currently exists to model how animals use different environments while accounting for imperfect behavior-specific detection probability. We developed an extension of a binomial N-mixture model (hereafter the behavior N-mixture model) to estimate the probability of a given behavior occurring in a particular environment while accounting for imperfect detection. We then conducted a simulation to validate the model's ability to estimate the effects of environmental covariates on the probabilities of individuals performing different behaviors. We compared our model to a naïve model that does not account for imperfect detection, as well as a traditional N-mixture model. Finally, we applied the model to a bird observation dataset in Northwest Costa Rica to quantify how three species behave in forests and farms. Simulations and sensitivity analyses demonstrated that the behavior N-mixture model produced unbiased estimates of behaviors and their relationships with predictor variables (*e.g.*, forest cover, habitat type). Importantly, the behavior N-mixture model accurately characterized uncertainty, unlike the naïve model which often suggested erroneous effects of covariates on behaviors. When applied to field data, the behavior N-mixture model suggested that Hoffmann's woodpecker (*Melanerpes hoffmanii*) and Inca dove (*Columbina inca*) behaved differently in forested versus agricultural habitats, while turquoise-browed motmot (*Eumomota superciliosa*) did not. Thus, the behavior N-mixture model can help identify habitats that are essential to a species' life cycle (*e.g.*, where individuals nest, forage) that non-behavioral models would miss. Our model can greatly improve the appropriate use of behavioral survey data and conclusions drawn from them. In doing so, it provides a valuable path forward for assessing the conservation value of alternative habitat types.

Introduction

Species responses to environmental conditions are most often assessed by measuring effects on their occurrences or abundances (*e.g.*, Newbold et al. 2013; Hatfield et al. 2018). Yet, changes in incidence provide little information about how species use the environments where they occur (Gilroy and Edwards 2017; Ortega-Álvarez et al. 2021). For example, a species regularly detected in agricultural habitats could simply be passing through, rather than actively using agricultural habitats to forage, reproduce, and complete its lifecycle (Vickery et al. 2001). Variation in the behavioral use of different environments can have cascading implications for individual fitness and population persistence (*e.g.,* Luck 2002; Lyons 2005). For example, a dense habitat may not be necessary for an individual to survive, but still important for population persistence because it contains the necessary substrates for reproduction (*e.g.*, nesting, mating). Therefore, changes in behavior can act as a warning signal that a population is in trouble (Berger-

Tal et al. 2016), and understanding the fitness effects of animals behaving differently in different habitats is critical to conserve species effectively. In contrast, if we base costly, lengthy management actions solely on incidence, without understanding how a species uses that habitat, we may fail to protect habitats that are essential to critical phases of the species' life cycle.

Unfortunately, many behaviors are difficult to observe (Durso, Willson, and Winne 2011), and the detectability of individuals often depends on the behaviors they perform (Crowe and Longshore 2010). Moreover, the detectability of different behaviors may change depending on the surrounding environment. This may be particularly problematic when changes in behaviors are confounded with changes in their detection probability, such as when the same covariate (*e.g.,* vegetation density) influences behaviors and the probability of detecting both individuals and their behaviors. For example, the probability of detecting bird vocalizations may be similar between open areas (*e.g.,* farms) and dense environments (*e.g.,* forests), whereas the probability of detecting behaviors that are observed visually may decline. Meanwhile, it is possible that a species performs behaviors detected visually, such as foraging, more frequently in denser environments. Without accounting for behavior-specific detection, we would risk falsely concluding that open environments are more beneficial to this species because we observe it foraging there more often. To our knowledge, no method currently exists to model how different habitats support different behaviors while accounting for behavior-specific detection probability.

Ecologists have long grappled with the problem of imperfect detection when modeling the abundance of wildlife (Hilborn, Redfield, and Krebs 1976; Seber 1982; M. Kéry and Royle 2008). Failing to account for variation in detection (among species, observers, habitats, *etc.*) can bias estimates of abundances (Kellner and Swihart 2014). One method frequently used to account for imperfect detection in abundance estimation is the N-mixture model (Royle 2004; Marc Kéry

2018). N-mixture models estimate abundance and detection using spatially and temporally replicated surveys where the number of individuals is counted. They assume populations are closed, such that the same number of individuals are present during each visit to a site, and that all individuals have the same detection probability. If there is unmodeled heterogeneity in detection (such as variable detection probabilities between behaviors), N-mixture models are known to underestimate abundance (Marc Kéry and Royle 2015). Therefore, modeling behavior-specific detection probabilities could potentially account for behavior-driven heterogeneity (*e.g.* between individuals, age-sex classes, populations) in detection.

Given a dataset of species observations with spatial and temporal replication, where behaviors are noted for all detected individuals, a conceptually straightforward way to account for behavior-specific detection probabilities is to extend the N-mixture model to estimate abundance of each behavior separately, using repeated counts of behaviors. Then, a species' total abundance is the sum of the abundances of each behavior. This approach allows each behavior to have its own detection probability that can be modelled as a function of covariates. It also allows modeling of covariate effects on the prevalence of a given behavior. However, a major challenge with this method is that the N-mixture model assumes populations are closed, which may be less probable with behavior-specific abundances than overall abundances. Specifically, it is quite possible that, across multiple visits to a single site, the same number of individuals are present but perform different behaviors – we refer to this as a violation of the behavioral closure assumption.

Here, we develop a behavior N-mixture model that estimates the effects of environmental covariates on behavior probabilities (that is, the probability that an individual performs a certain behavior), while accounting for imperfect detection of individuals and behaviors. This method adds another conditional layer to the traditional N-mixture model. Specifically, it estimates the probabilities that individual animals will use one type of habitat for a behavior (*e.g.,* foraging, vocalizing), while accounting for the imperfect and variable detection of those behaviors. We conduct a simulation study to understand how variation in detection, abundance, and violation of the behavioral closure assumption affect our ability to estimate relationships between environmental covariates and behavior probabilities. To assess performance, we compare our model to a naïve model that estimates behavior probabilities without accounting for imperfect detection, as well as a traditional N-mixture model that accounts for overall imperfect detection but neither estimates behavior probabilities nor behavior-specific detection probabilities. Finally, we apply our model to a four-year dataset of bird surveys in Costa Rica, in which behaviors (*e.g.,* vocalizing, eating, passive behaviors) were noted during repeated point counts in agricultural and forested habitats.

Materials and Methods

Formulation of the Behavior N-Mixture Model

We extended the N-mixture model framework to quantify how environmental covariates influence the relative frequency of behaviors performed (behavior probability), while accounting for variation in detection probability among different behaviors in different environments (Royle 2004; Marc Kéry 2018). Under certain assumptions, our new model can also be used as a typical N-mixture model to estimate abundance, though in other cases doing so can be problematic (see below). In typical N-mixture models, the number of individuals observed (Y) at a site (j) and a visit (k) is modeled based on abundance and detection processes such that:

$$Y_{j,k} \sim Binomial(N_j, P_{j,k}) \; ,$$

where *N* is the true number of individuals and *P* is the per-individual detection probability. *P* can be modeled as a function of site and visit-specific covariates. Site-specific abundances, N_j, are modeled as a random count variable (*e.g.,* with a Poisson probability distribution), and expected abundance can be modeled as functions of site-specific covariates. For the behavior N-mixture model, to model the counts (*Y*) and proportion (π) of individuals performing the b^{th} behavior, we modified the typical N-mixture model such that:

$Y_{j,b,k} \sim Binomial(N.b_{j,b}\ , P_{j,b,k})$

$N.b_{j,b} \sim Poisson(\lambda_j * \pi_{j,b})$

$N_j = \sum_{b=1}^{B} N.b_b$.

Here, $Y_{j,b,k}$ is the number of individuals observed performing a certain behavior (*b*) at a site (*j*) and a visit (*k*). $P_{j,b,k}$ is the detection probability of an individual performing a certain behavior at a particular site and visit. $N.b_{j,b}$ is the number of individuals performing a certain behavior at a site, and $\pi_{j,b}$ is the probability that an individual performs a certain behavior at a site. Finally, λ_j is the expected value of the total abundance (N_j) at a site. Note that $\pi_{j,b}$ and $N.b_{j,b}$ are indexed by site and behavior, which implies closure of relative behavior frequencies between visits (*i.e.,* assuming the same number of individuals performs each behavior during each visit). Expected abundance λ_j can be modeled as:

$\log(\lambda_j) = \alpha_0 + \boldsymbol{\alpha}'\mathbf{X_j}$,

where α_0 is the intercept and $\boldsymbol{\alpha}'$ is a vector of coefficients that are multiplied by the covariates **X**.

$B.p_{j,b}$ is modeled as a function of covariates using multinomial logistic regression. For the first behavior,

$$\pi_{j,1} = \frac{1}{1 + \sum_{b=2}^{B} e^{\beta_{0b} + \boldsymbol{\beta}'_{\mathbf{b}} \mathbf{Z}_{\mathbf{j}}}} ,$$

and for the remaining behaviors,

$$\pi_{j,b} = \frac{e^{\beta_{0b} + \boldsymbol{\beta}'_{\mathbf{b}} \mathbf{Z}_{\mathbf{j}}}}{1 + \sum_{b=2}^{B} e^{\beta_{0b} + \boldsymbol{\beta}'_{\mathbf{b}} \mathbf{Z}_{\mathbf{j}}}} .$$

The first behavior serves as a reference category that the other behaviors are compared to; any category can be used as the reference. B is the number of behavior categories. In the multinomial logistic regression, β_{0_b} is a behavior-specific intercept and $\boldsymbol{\beta}'$ is the vector of coefficients that is multiplied by the covariates $\mathbf{Z}$.

Finally, the detection probability of an individual performing a certain behavior at a given site and visit ($P_{j,b,k}$) can be modelled as a function of site- and visit-specific covariates:

$$\text{logit}\left(P_{j,b,k}\right) = \gamma_0 + \boldsymbol{\gamma}'_{\mathbf{b}} \mathbf{V}_{\mathbf{j}} ,$$

where γ_0 is the intercept and $\boldsymbol{\gamma}'$ is the vector of behavior-specific coefficients that are multiplied by the covariates $\mathbf{V}$.

Simulation study

We evaluated the performance of the behavior N-mixture model under five combinations of mean expected abundance (λ) and detection probability (*P*). For each scenario, we applied the behavior N-mixture model to 100 sets of simulated observations of behaviors and abundances for one species across 50 sites (indexed by *j*), with five visits to each site (indexed by *k*). In all scenarios, individuals could perform one of three behaviors (indexed by *b*), with intercepts of the behavior probabilities fixed at 0.6, 0.15, and 0.25 (β_0 = [0, -1.38, -0.87]). The intercepts of the behavior probabilities must sum to 1, and the first behavior served as the reference level. First, we tested model performance with a detection probability intercept fixed at 0.2 (a realistic value for bird communities; Karp et al. 2018) and three levels of abundance intercepts representing 1, 2.7, and 7.4 individuals per site. Second, we tested model performance with an abundance intercept fixed at 2.7 individuals per site ($\alpha_0 = 1$) and two additional levels of detection probability intercepts: 0.5 and 0.8 ($\gamma_0 = 0$ and 1.38).

In all cases, the abundance intercept α_0 was added to the product of one site-specific covariate X and an abundance coefficient α'. The behavior probability intercept β_0 was added to the product of a behavior-specific coefficient β'_b and one site-specific covariate Z for two behaviors, while the first behavior served as the reference level. The number of individuals performing each behavior at each site and visit was determined using a multinomial random distribution with size n = N_j and cell probabilities $\boldsymbol{\pi}_{1:3,j}$. This case reflects behavioral closure, where the numbers of individuals performing each behavior at each site is constant across visits. Finally, we generated detection probabilities by adding the intercept γ_0 and the product of a behavior-specific detection coefficient and the covariate Z. For each replicate, the abundance coefficient and detection intercept were drawn from a normal distribution with mean 0 and variance 0.25, while the behavior-specific coefficients were drawn from a normal distribution with mean 0 and variance 1. We wanted to explore more of the parameter space of the behavior-specific coefficients in contrast to abundance and detection parameters, which we aimed to control for in each simulation scenario. Site-specific covariates were also drawn from a normal distribution with mean 0 and variance 1 so that we did not have to standardize environmental covariates prior to analysis.

Assuming behavioral closure could be problematic in practice, as animals can change behaviors frequently. To explore how the behavior N-mixture model performs under complete violation of behavioral closure, we applied it to an additional dataset paired with each simulated dataset described above, where the number of individuals performing each behavior was re-sampled from the same multinomial distribution for each visit. This way, the number of individuals was constant across visits, but the number of them engaging in each behavior could change. Next, to understand model performance under intermediate levels of violation of the behavioral closure assumption, we applied the behavior N-mixture model to more paired datasets where the numbers of individuals performing each behavior each visit were determined by re-sampling 0, 25, 50, 75, and 100% of the total abundance while holding the detection intercept at 0.2 and abundance intercept at 2.7 (see above). When the behavioral closure assumption was violated, we expected abundance to be overestimated and detection probability to be underestimated. This is because when an individual is observed performing different behaviors between visits, it contributes to overall abundance estimates multiple times.

Alternative models

To compare how the behavior N-mixture model estimated total abundance to an alternative model, we applied a traditional N-mixture model to every simulated dataset where we retained covariates for estimating abundances and detection probabilities. Under behavioral closure, we expected the traditional N-mixture model to underestimate abundance due to unmodeled variation in detection probabilities. When behavioral closure was violated, we expected the behavior N-mixture model to produce more biased abundance estimates than the traditional N-mixture model.

We also sought to compare the behavior N-mixture model's estimates of behavior parameters to a naïve model that did not account for imperfect detection. To do so, we applied a multinomial regression model to every simulated dataset, where we aggregated behavioral observations across visits for each simulation replicate. This was the most straightforward way to model behavior frequencies without accounting for imperfect detection. We expected the naïve model to produce biased relationships with covariates, especially when the same covariate affected detection and behavior.

We assessed model estimates for abundance (N, α_0, α'), detection ($P_{j,b,k}$, γ_0, γ'_b), and behavior ($\pi_{j,b}$, β_0, β'_b) parameters. For each replicate, we calculated the absolute bias of the posterior means and 95% Bayesian credible interval (BCI hereafter) coverage, which represents how often the range between the 2.5 and 97.5th percentiles of the posterior distribution contains the true value. We compared bias and BCI coverage across levels of mean detection, abundance, and violation off behavioral closure. We also compared bias and BCI coverage of parameters between the behavior N-mixture model, traditional N-mixture model, and naïve multinomial regression model.

Implementation

We implemented all models in R Version 4.0.0 using the package *nimble,* which runs Markov chain Monte Carlo (MCMC) algorithms (Team 2013; de Valpine et al. 2017). For each simulation replicate, we ran three chains starting at random initial values and 5,000 burn-in iterations. We included 150,000, 100,000, and 50,000 burn-in iterations and thinning rates of 75, 50, and 25 for the behavior N-mixture, traditional N-mixture, and naïve multinomial regression models, respectively. We considered models to converge if all chains for abundance, detection probabilities, behavior probabilities, and intercept and slope parameters had Gelman-Rubin statistics ≤1.1 (Gelman et al. 2004). If any chains did not converge, we excluded the entire replicate (*i.e.*, all models fit to that dataset) from further analysis.

Case Study: Effects of Agriculture on Bird Behavior in Northwest Costa Rica

We applied the behavior N-mixture model to behavioral observations of Hoffmann's woodpecker (*Melanerpes hoffmannii*), Inca dove (*Columbina inca*), and turquoise-browed motmot (*Eumomota superciliosa*) in adjacent agricultural and forested sites in northwest Costa Rica. All species are regularly observed both in forest and agricultural habitats; our objective was to determine whether species changed behavior frequencies between habitats.

At twenty forest-adjoining farms and five protected areas, birds were surveyed at six sites each, half in agricultural sites and half in forest (N=150 sites total). At each site, the same expert observer (J. Zook) surveyed all birds seen or heard in 20-min, 50-m fixed radius point counts in May – July from 2016-2019. Half of the point counts were sampled three times within a 1-week period and the other half were surveyed once to increase spatial replication while still being able to estimate detection probabilities. One farm or protected area (6 sites) was surveyed each day, beginning at sunrise and continuing for ~5 hr. The observer recorded species identity, number of individuals observed, time of day, and ambient noise, which we considered to be noise levels that were above typical background noises and were thought by the observer to interfere with his ability to detect bird vocalizations. Each observation of a species was associated with one of 32 behaviors (Appendix S1: Table S2.2) that we classified into three categories: vocalizing, eating/foraging, and other. When an individual performed more than one behavior during a point count (10.5% of observations), we randomly selected one of the behaviors from those recorded by the observer.

We modeled annual abundance of each species at each site as a function of an intercept, a coefficient multiplied by the fraction of forest cover within 50 meters, and random effects for farm, point, and year. We modeled behavior probability as a function of a behavior-specific intercept and a behavior-specific coefficient multiplied by a binary habitat covariate (agriculture vs. forest).

We modeled detection probability as a function of an intercept, a behavior-specific coefficient multiplied by a binary noise variable (no noise vs. noise; *e.g.,* machinery, cicadas), a behavior-specific coefficient multiplied by the binary habitat covariate, and a coefficient multiplied by the time of day.

We considered the composition of behaviors to differ between habitats when the BCIs for any behavior coefficients did not include zero. Because the values of behavior coefficients are relative to the reference behavior, their values do not necessarily reflect how a behavior probability differs between habitats. Thus, we considered a behavior probability to be significantly different between forested and agricultural habitats when the BCI for the predicted difference in the behavior probability between habitats did not include zero. We compared estimates of behavior probabilities and coefficients to the naïve model and compared estimates of abundance to the traditional N-mixture model (See Supporting Information 2). For all models, we ran three chains of 5,000 burn-in iterations and 150,000 post burn-in iterations and thinned chains by 75. We implemented models in R Version 4.0.0 using the package *nimble* and checked for convergence as described above (Team 2013; de Valpine et al. 2017).

Results

Model convergence

Chains for every parameter within the behavior N-mixture, traditional N-mixture, and naïve models converged for 60-85% of the simulation replicates when the detection intercept was 0.2 and 0.5 across all levels of abundance. When the detection intercept was 0.8, all chains converged in only 14% of replicates (Appendix S1: Table S2.1). When we adjusted the levels of violation of the behavioral closure assumption, all chains from 15 models (three models applied to five levels of closure violation) converged in 23% of replicates.

Behavior parameters

Overall, we found that the behavior N-mixture model better estimated behavior probabilities and effects of covariates (*e.g.,* land-use type) on behavior compared to the naïve model. Specifically, the mean estimate of behavior probabilities was 0.96-3.34 times more likely to be less biased under the behavior N-mixture model than under the naïve model across scenarios (Appendix S1: Table S2.3). When data met the behavioral closure assumption, BCIs from the behavior N-mixture model captured the true value of the behavior probabilities 90-95% of the time across all scenarios of abundance and detection (Table 3). The naïve model, however, only captured the true value 42-74% of the time.

The mean absolute bias of estimates of behavior probability and behavior probability coefficients (*i.e.,* the effect of a covariate on each behavior; β'_b) from the behavior N-mixture model were small (-0.001 to 0.03 and -0.01 to 0.21, respectively; true β'_b values ranged from -4.11 to 3.06; Table 3). When the detection intercept was 0.2 or 0.5, the behavior N-mixture model's BCI coverage of the behavior probability coefficients was 91-95%. However, when mean detection was 0.8, the behavior N-mixture model's BCI coverage was only 82% (Appendix S1: Table S2.3). Again, coverage of behavior probability coefficients was always higher for the behavior N-mixture model than the naïve model (Figure 5). Further, the behavior N-mixture model's mean estimate of behavior probability coefficients was 1.33-6.14 times more likely to be less biased than the naïve model (Appendix S1: Table S2.3). For behavior probabilities and coefficients, BCIs from the behavior N-mixture model were about 50% wider than BCIs from the naïve model, which clearly underestimated uncertainty. Therefore, the better coverage of the behavior N-mixture model can be attributed to a combination of both lower bias and wider BCIs.

Abundance parameters

Under behavioral closure, the mean absolute bias of the behavior N-mixture model's estimate of abundance (*N)* ranged from 0.03 to 0.22 (true values ranged from 0-47, with three outlier values of 88) across all scenarios (Appendix S1: Table S2.4). The mean absolute bias of the traditional N-mixture model's abundance estimate ranged from -1.23 to -0.02 across scenarios (Appendix S1: Table S2.6). The behavior N-mixture model's BCI coverage of abundance was 98-99% (Appendix S1: Table S2.4), and across scenarios, the behavior N-mixture model's estimate of abundance was 1.17-2.13 times more likely to be less biased than the traditional N-mixture model (Appendix S1: Table S2.3).

The mean absolute bias of the behavior N-mixture model's estimate of the abundance coefficient (α') ranged from -0.03 to 0.02 across scenarios, which was similar to that from the traditional N-mixture model (-0.02 to 0.02; Appendix S1: Table S2.3, Table S2.6). The behavior N-mixture model's BCI coverage of the true value of α' was 84-100%, and the highest coverage occurred were when the detection intercept was 0.2 (Appendix S1: Table S2.4). The behavior N-mixture model's mean estimate of the abundance coefficient was 0.59-3.35 times more likely to be less biased than the traditional N-mixture model across trials (Appendix S1: Table S2.3), so for some simulation scenarios, the behavior N-mixture model resulted in more bias than the traditional N-mixture model.

Detection parameters

Under behavioral closure, mean absolute bias of the behavior N-mixture model's estimate of detection probability ($P_{j,b,k}$) ranged from -0.01 to 0.00, and the BCI coverage of the true value was 88-97% (Appendix S1: Table S2.4). Mean absolute bias of the detection probability coefficient (γ'_b) ranged from -0.10 to 0.07 (true values ranged from -3.90 to 2.67) (Appendix S1: Table S2.4), and the BCI coverage of the true value was 90-96%. The worst-performing scenario for detection parameters was when the mean detection probability was 0.8 (Appendix S1: Table S2.4). There was no alternative model that estimated behavior-specific detection probabilities for comparison, as the naïve model did not estimate detection probabilities and the traditional N-mixture model did not estimate behavior-specific parameters.

Violation of the behavioral closure assumption

When the behavioral closure assumption was violated, the behavior N-mixture model still outperformed the naïve model in estimating behavioral frequencies (and effects of covariates on behaviors) but performed worse than the traditional N-mixture model at estimating abundances. Specifically, when the behavioral closure assumption was fully violated (*i.e.,* 100% of the behaviors re-sampled each visit), the mean absolute bias of behavior probability coefficients (β'_b) for the behavior N-mixture model ranged from -0.10 to 0.25 (Appendix S1: Table S2.4). Although the range of absolute bias increased when the behavioral closure assumption was violated, BCI coverage for the behavior N-mixture model (74-91%) was still much greater than the naïve model (28-67%). The only scenario where the BCI coverage for the naïve model was greater was when the detection intercept was 0.8 (Figure 5). With violation of the behavioral closure assumption, the variance of the bias of behavior and detection parameters increased, but the mean absolute bias was close to zero (Appendix S1: Table S2.4). Across intermediate levels of behavioral closure violation, there was little variation in the BCI coverage of behavior probability coefficients (Figure 6).

With increasing violation of the behavioral closure assumption, bias in total abundance (*N*) became increasingly positive and bias of detection probability (*P*) became increasingly negative (Figure 7; Appendix S1: Table S2.4). At low levels of behavioral closure violation, such as when 25% of the behaviors were re-sampled, mean absolute bias of *N* was still rather low (*i.e.,* 0.51; Figure 7; true values ranged from 0 to 13). However, at higher levels of mean abundance, mean absolute bias increased (Appendix S1: Table S2.4). Meanwhile, the traditional N-mixture model underestimated *N* on average – mean absolute bias ranged from -0.27 to -0.15 across all levels of behavioral closure violation. When the behavioral closure assumption was violated, the mean absolute bias of the behavior N-mixture model's estimates of the abundance and detection coefficients (α' and γ') were not consistently positive or negative, ranging from -0.01 to 0.05 and -0.10 to 0.07, respectively (Appendix S1: Table S2.4). In addition, when mean detection was 0.2 or 0.5, at the behavior N-mixture model's estimates of α' were 1.04-2.44 times more likely to be less biased than the naïve and traditional N-mixture models across replicates (Appendix S1: Table S2.3).

Application: bird behavior variation between forest and agricultural habitats

We estimated the effects of land use on the probabilities of eating and vocalizing for three focal species, using the behavior N-mixture model and a naïve model. In some cases, predictions from the behavior N-mixture and naïve model largely aligned. The behavior N-mixture and naïve models both estimated higher probabilities of eating in agricultural habitats and vocalizing in forest for Inca dove, a species often found foraging in agricultural fields ("Inca Dove - Columbina Inca

- Birds of the World" n.d.; though they differed in which behavior coefficients were statistically significant; Figure 8). In other cases, the models produced very distinct results. For example, for Hoffmann's woodpecker, a species known to occupy both forest and open areas (Stiles, Skutch, and 1904- 1989), the behavior N-mixture model only found that the probability of the "other" behavior was significantly higher in agricultural land than in forest, whereas the naïve model suggested that the woodpecker was less likely to vocalize and more likely to perform the "other" behavior category in agricultural land than in forest (Figure 8). Similarly, for turquoise-browed motmot, a species that has been observed foraging and nesting in both forested and anthropogenic landscapes (Snow and Kirwan 2020), the behavior N-mixture model did not find significant effects of land use on behavior; however, the naïve model indicated a marginally significant higher probability of vocalizing and lower probability of "other" in forest as compared to agricultural habitats (Figure 8), where the BCI bordered 0.00. Additionally, the behavior N-mixture model suggested that loud noises reduced the likelihood of detecting vocalizations of all three species, Hoffmann's woodpecker was harder to detect later in the day, and forest cover increased the likelihood of observing turquoise-browed motmots eating (Appendix S1: Fig. S1). The behavior N-mixture model also suggested that forest cover increased the abundance of Hoffmann's woodpecker and turquoise-browed motmot but not Inca dove.

Discussion

We developed and applied a novel hierarchical model to assess shifts in animal behavior across environments. Data on how animals behave can be used to understand how local management activities and global changes affect species, quantify habitat suitability (*e.g.,* by identifying potential source/sink habitats), and identify conservation interventions (Ortega-

Álvarez et al. 2021). Indeed, behavior data can reveal trends that census data cannot. For example, urban parks may appear to be high quality habitat for wildlife based on the presence and abundance of individuals, even as human activity reduces the availability of foraging resources, thereby decreasing fitness and increasing the probability of future extirpations (Jokimäki et al. 2011). Most studies of animal behavior, however, rely on intensively monitoring animals (*e.g.,* Luck 2002; Tremblay et al. 2005), and are thus limited to few individuals because they are labor-intensive and restricted to certain species (*e.g.,* those that can carry tracking equipment).

Here, we present a novel method that allows researchers to leverage survey-type behavioral data while accounting for imperfect detection, thereby enabling scientists or practitioners to analyze behaviors for many individuals of multiple species and better assess the conservation value of alternative habitat types. When the behavioral closure assumption was met, our behavior N-mixture model produced unbiased estimates of behavior probabilities, their relationships with predictor variables, and abundance, even when the same covariate affected both behavior and detection probability. When the behavioral closure assumption was violated, the behavior N-mixture model still produced unbiased estimates of behavior probabilities and the effects of covariates on behaviors, but it overestimated total abundance. Further, the behavior N-mixture model had better BCI coverage than the naïve model when estimating behavior probabilities in all scenarios, except when the behavioral closure assumption was completely violated and the mean detection probability was high (Note: Figure 9 provides a decision tree of which models to choose in different circumstances).

Behavior parameters

The behavior N-mixture model produced unbiased estimates of covariates affecting behavior probability and accurate estimates of uncertainty. As mentioned, the only scenario in which the behavior N-mixture model performed worse than the naïve model was when mean detection probability was 0.8 and the behavioral closure assumption was violated. In reality, a mean detection probability of 0.8 or greater is rare (Marc Kéry 2018; Kellner and Swihart 2014), and if detection probability is near-perfect, a naïve model may be sufficient (Figure 9). While the naïve model is a simpler alternative that does not make assumptions about closure, the behavior N-mixture model produced similar or less biased estimates of behavior parameters in all cases when there was behavioral closure, and at mean detection probabilities of 0.5 or lower when the behavioral closure assumption was violated (Table 3).

A critical disadvantage of the naïve model is that it underestimated uncertainty, causing it to make incorrect inferences about how covariates affected behaviors. In the most egregious cases the naïve model returns significant results suggesting that a behavior increases in probability in an environment, when in fact it decreases. For example, under behavioral closure, when the naïve model was applied to the scenario with mean detection probability of 0.2 and mean abundance of 2.7 (Figure 5a), 14% of the significant coefficients affecting behavior (*i.e.,* where BCI did not include 0) were in the opposite direction of the true value. This type of error could be problematic if naïve model results are applied to management decisions, as we may fail to protect essential habitats for a species' life cycle, and potentially protect non-important habitats instead. In contrast, the behavior N-mixture model did not estimate any statistically significant coefficients affecting behavior in the wrong direction in the same scenario.

Abundance parameters

The behavior N-mixture model produced unbiased estimates of abundance parameters, as well as accurate estimates of uncertainty, when the data conformed to the behavioral closure assumption. In this case, it outperformed the traditional N-mixture model, which tended to underestimate abundance. When the behavioral closure assumption was violated, however, the behavior N-mixture model performed poorly (Figure 7), which we expected based on what is known about N-mixture models (Rota et al. 2009). Therefore, when the behavioral closure assumption is violated, the behavior N-mixture model should not be used to estimate abundances or detection probabilities. However, when mean detection probability is around 0.5 or lower, the behavior N-mixture model can still be used to estimate coefficients affecting abundance and detection (Table 3).

When the behavioral closure assumption is violated, the traditional N-mixture model can still be used to estimate abundance and detection in most cases. Although there was a negative bias in abundance estimates, BCI coverage was at least 93% across all scenarios. Bias was greatest when mean abundance was high (average of 7.4 individuals per site), when the traditional N-mixture model consistently overestimated detection and underestimated abundance (Appendix S1: Table S2.6).

In practice, it may be hard to determine whether the behavioral closure assumption is violated, so caution is warranted before using the behavior N-mixture model to estimate abundances. To assess behavioral closure, users could potentially contrast abundance estimates under both models and, if similar, solely use the behavior N-mixture model. Overall, we recommend using the traditional N-mixture model to estimate abundances, but to use the behavior N-mixture model to measure changes in behavior (Figure 9).

Bird behavior variation in Northwest Costa Rica

The behavior N-mixture model produces important insights into the effects of environmental conditions on behaviors. As illustrated in the simulation study, these effects can be incorrectly determined when not accounting for imperfect and varying detection.

Among our case studies, the turquoise-browed motmot and Hoffmann's woodpecker highlight scenarios where the behavior N-mixture model suggests that birds do not behave differently in forest and agricultural habitats, while the naïve model suggests that they do. This is likely because the naïve model underestimates the uncertainty around coefficients (as seen in the simulation study), and the detectability of some of these behaviors differed between habitats (Appendix S1: Fig. S1). In contrast, the Inca dove highlights that sometimes both models can produce consistent estimates of important effects on behaviors. This may occur when there are large differences in behaviors performed between habitats that are apparent even without correcting for detection.

The results of the behavior N-mixture and naïve models seemed to differ the most when there was more heterogeneity in the effects of habitat on the detection probability of each behavior (Figure 8; Appendix S1: Fig. S1). That is likely because the naïve model confounds effects of habitat on detection of behaviors with effects on the behaviors themselves. For example, for the turquoise-browed motmot, the naïve model likely estimated a larger effect of forest on the probability of vocalizing than the behavior N-mixture model because it did not account for the fact that vocalizing is relatively easier to detect in forest than foraging, which becomes more difficult to see when there is dense cover (Appendix S1: Fig. S1). Thus, a potential consequence of using the naïve model is falsely concluding that turquoise-browed motmots vocalize more frequently in forest. Because vocalization is essential for reproduction, this could lead to incorrect conclusions about the importance of forest habitat for reproduction. Indeed, turquoise-browed motmots are known to breed in human-dominated areas and even exploit nesting opportunities created by human infrastructure (Snow and Kirwan 2020). In contrast, for Hoffmann's woodpecker, the effects of habitat on detection probability of each behavior were near zero (Appendix S1: Fig. S1), likely because the foraging behavior of Hoffmann's woodpecker is often audible. Because habitat did not have a large effect on detection probability, the behavior N-mixture and naïve models produced similar coefficient estimates (Figure 8). More generally, this suggests that our model is especially critical in scenarios where there is heterogeneity in the detection probabilities of different behaviors and their relationships with the environment. For example, when conducting visual surveys of amphibians, it is important to account for the variation in detection probability depending on the activity level of individuals (Hammond et al. 2021).

The behavior N-mixture model provided useful information on how birds utilize different habitats. For the turquoise-browed motmot and Hoffmann's woodpecker, the behavior N-mixture model estimated a positive effect of forest cover on abundance, but no significant differences in the probability of eating and vocalizing between habitats (Appendix S1: Fig. S1; Table 4). This implies that there may be higher densities of individuals in more forested habitats, but individuals have similar probabilities of eating and vocalizing in forest and in agricultural habitats. This could mean that these species indeed perform important behaviors for their life history in agricultural habitats, but that forest habitat can support more individuals performing these key behaviors. In contrast, the Inca dove was estimated to eat more and vocalize less in agricultural habitats than in forest. This makes biological sense because they primarily eat seeds from grains, weeds, and grasses, which are more abundant in agricultural habitats (Johnston 1960). Interestingly, the behavior N-mixture model did not find an effect of forest cover on abundance. This implies that agricultural habitats provide better foraging resources for the Inca dove than forest, and that certain types of agriculture may boost populations of Inca doves. Without accounting for behaviors, managers may assume forest and agricultural habitats are equally beneficial for Inca doves, while in reality, agricultural habitats support more foraging resources. Thus, the behavior N-mixture model can add insights to abundance information that could lead to novel conservation strategies and ecological understanding; for example, by identifying where animals obtain resources to survive and reproduce.

Limitations

There are several limitations to applying the behavior N-mixture model in practice. First, there is currently no method to determine whether data meet the behavioral closure assumption. A potential method to measure the degree of behavioral closure is to model the abundance of each behavior category separately using an N-mixture model that allows for temporary emigration (Chandler, Royle, and King 2011). An animal switching behaviors between visits could result in a higher estimate of the probability of temporary emigration that indicates more violation of the behavioral closure assumption, but we have not explored this further. Based on our simulation, another sign of behavioral non-closure could be when estimates of abundance from the behavior N-mixture model are consistently higher than estimates from a traditional N-mixture model. An issue we did not explore is that not only may the behaviors performed differ between visits, but the probabilities of behaviors an individual performs could change across visits, which could worsen the violation of the closure assumption.

Finally, all model chains converged in over 50% of the simulation trials except for when mean detection was 0.8, when there were often convergence issues. The reasons for non-convergence of chains were unclear. For abundance estimates that did not converge, the chains were often at zero most of the time with a few non-zero values. For other parameters that did not converge, the chains appeared to be in different locations of parameter space. Splitting observations into behavior classes as is necessary for the behavior N-mixture model leads to sparse data and it is possible that increasing the number of observations could improve model convergence. Because of this, we chose frequently observed species and behaviors for our case study, and this model would work best for animals and behaviors that are more easily detectable so that there is sufficient data to estimate detection probabilities. For example, in a camera trap study of mammals, it would likely be difficult to detect and analyze reproductive behaviors, but easier to observe foraging behaviors (Abu Baker, Emerson, and Brown 2015). A useful extension of the behavior N-mixture model could be to develop it into a multi-species community model so that behaviors of many species can be analyzed when data is sparse (Ovaskainen and Soininen 2011).

Conclusions

Measuring behavior is important to understanding the ecology and conservation of species because behavioral changes are often an animal's first response to human-induced environmental changes (Wong and Candolin 2015). The behavior N-mixture model advances the study of behavior because it accurately estimates behavior probabilities and the effects of covariates on behavior probabilities using observational surveys. In doing so, the model facilitates a low-cost method to monitor many individuals' behavior changes simultaneously. Under the behavioral closure assumption, the model can also be used to estimate abundance by modeling heterogeneity in detection between behaviors, though when the behavioral closure assumption is broken, it should not be used for abundance (Figure 9). Behavior-driven heterogeneity in detection is likely present in many taxa, and information on individual behavior can be obtained from many different survey types beyond the point-count data analyzed in our case study (*e.g.*, camera traps for mammals, transects/area searches for herpetofauna, *etc.*) (Burton et al. 2015). Thus, scientists should attempt to collect behavioral observations and incorporate them into analyses whenever possible.

Acknowledgements

We would like to thank the many people involved in collecting the bird survey data we used from Northwest Costa Rica, including J. Zook, A. Echeverri, K. Chan, P. Juárez, X. Campos, E. Rodrígues, L. Bogantes, the FuturAgua team, staff from SINAC, and the landowners who supported our work. Funding was provided by an NSF GRF to A.K. and grants from the National Geographic Society (#9977-16; #67543R-20). All work was conducted with approval from the Costa Rican government (permits: SINAC-SE-CUS-PI-R-036-2016, SINAC-SE-CUS-PI-R-030-2017, SINAC-PNI-ACAT-043-2019, and SINAC-PNA-ACAT-039-2021).

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Table 3: Mean and 2.5 and 97.5th percentiles of absolute bias, and 95% Bayesian credible interval coverage across replicates where all chains converged (see Appendix S1: Table S2.1) for each scenario (defined by input values of mean detection and abundance) for the behavior N-mixture model from the simulation study. The first values in each cell correspond to when the behavioral closure assumption was met, and the values in parentheses correspond to the model under complete violation of behavioral closure, such that 100% of the behaviors were re-sampled each visit. The first column contains the "baseline" levels of the simulation, where we fixed mean detection at 0.2 and mean abundance at 2.7.

Parameter	**Measure**	**detection 0.2, abundance 2.7**	**detection 0.5, abundance 2.7**	**detection 0.8, abundance 2.7**	**detection 0.2, abundance 1**	**detection 0.2, abundance 7.4**
Behavior probability coefficient β'_b	Mean absolute bias	0.21 (-0.04)	0.06 (-0.03)	0.03 (-0.10)	0.07 (-0.04)	-0.01 (0.25)
	2.5 and 97.5th percentile, absolute bias	-1.28, 1.56 (-3.34, 1.88)	-0.63, 0.82 (-2.03, 1.89)	-0.74, 0.59 (-1.65, 2.00)	-1.14, -0.94 (-2.16, 1.58)	-0.70, 0.62 (-1.38, 1.60)
Behavior probability $B.p_{j,b}$	Mean absolute bias	-0.001 (0.01)	0.008 (0.02)	0.003 (0.02)	0.03 (0.03)	0.00 (-0.01)
	2.5 and 97.5th percentile, absolute bias	-0.17, 0.19 (-0.29, 0.30)	-0.12, 0.12 (-0.33, 0.33)	-0.15, 0.13 (-0.36, 0.32)	-0.28, 0.27 (-0.36, 0.35)	-0.11, 0.12 (-0.27, 0.24)

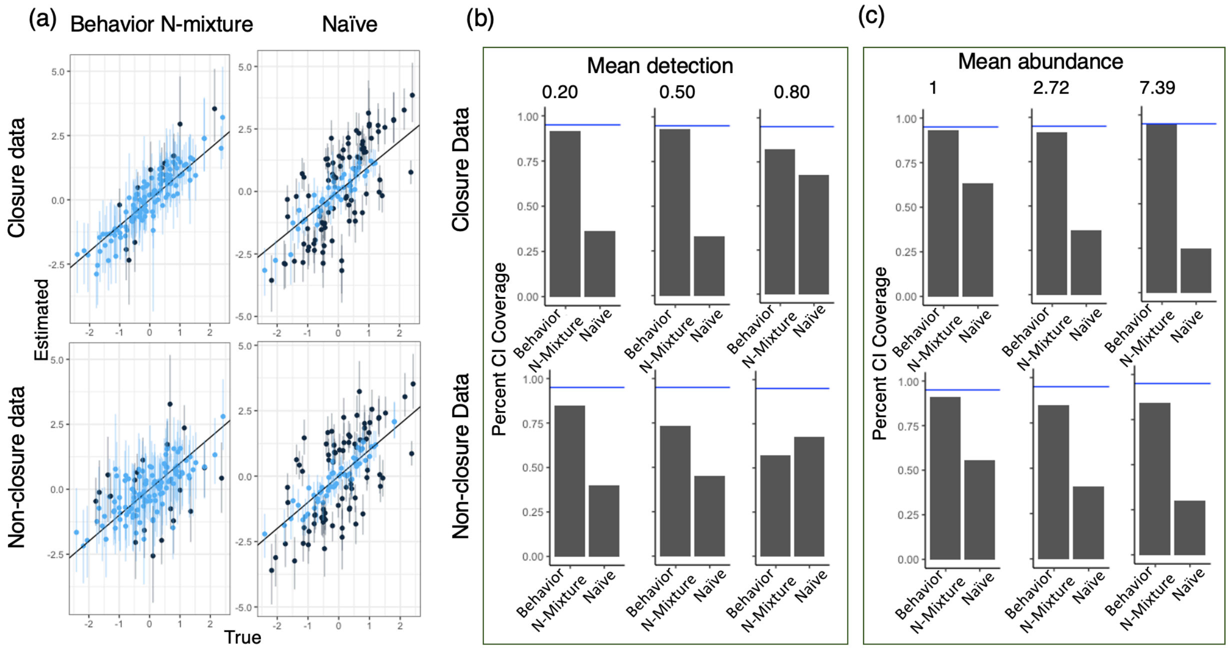

Figure 5: (a) Estimated vs. true input values and 95% Bayesian credible intervals for β'_b, (the effect of a covariate on the probability of an individual performing a behavior) based on a simulation study exploring the effectiveness of the behavior N-mixture model across varying levels of detection and abundance. Dark blue points and lines indicate Bayesian credible intervals (BCIs) that did not capture the true simulated values; light blue points and lines indicate BCI coverage of true values. (b) Percentage of 95% BCIs that captured the true input values for β'_b across all simulation replicates at varying levels of mean detection. The mean abundance is fixed at 2.7 and the blue lines mark 0.95. (c) Percentage of 95% BCIs that capture the simulated values for β'_b across all iterations at varying levels of mean abundance. The mean detection is fixed at 0.2 and the blue lines mark 0.95. Only replicates where all chains converged were used for analysis (Appendix S1: Table S2.1).

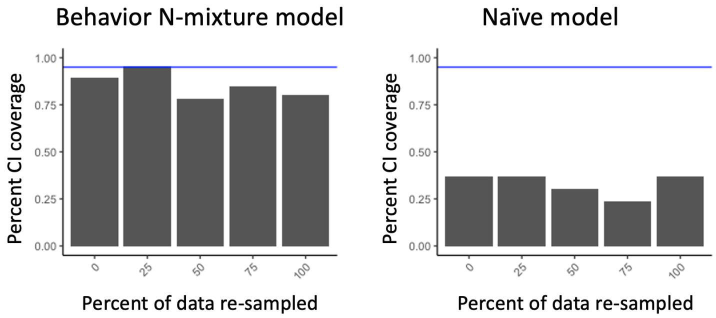

Figure 6: Percentage of 95% Bayesian credible intervals that captured the simulated values for β'_b, (*i.e.,* the effect of a covariate on behaviors) across all replicates where all chains converged (Appendix S1: Table S2.1) of the simulation study where the level of the violation of the behavioral closure assumption (*i.e.,* percent of data resampled) varied from 0 to 100%. The blue lines mark 0.95.

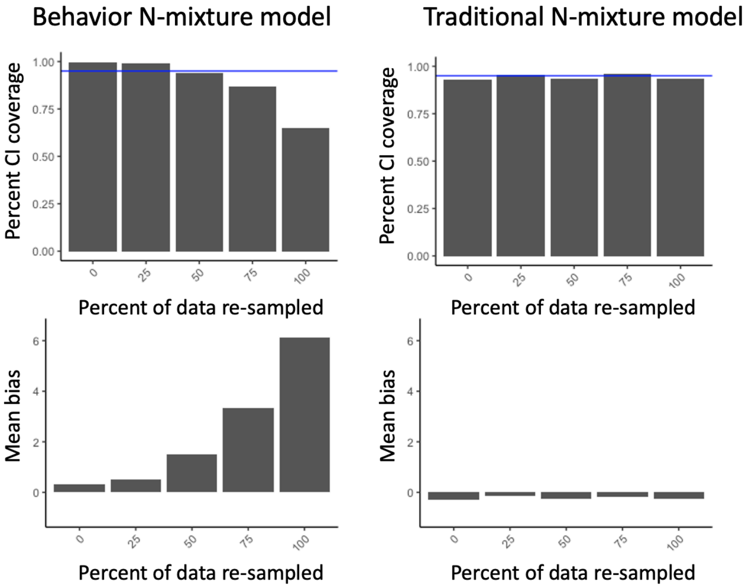

Figure 7: Percentage of 95% Bayesian credible intervals that captured the simulated values for *N* and the mean absolute bias of *N* across all replicates where all chains converged (Appendix S1: Table S2.1) of the simulation study where the level of the violation of the behavioral closure assumption (*i.e.,* percent of data resampled) varied from 0 to 100%. The blue lines mark 0.95.

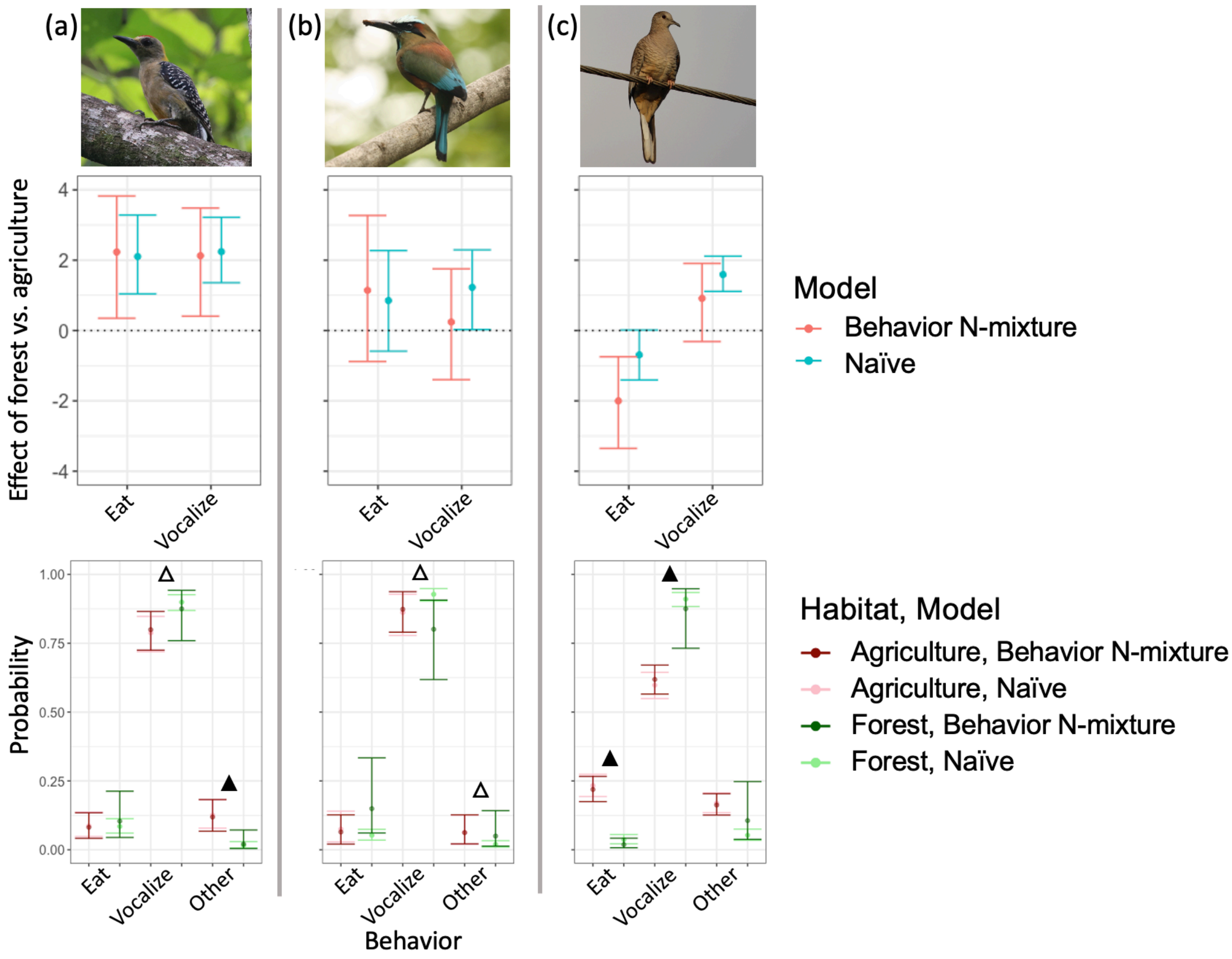

Figure 8: Top row: Behavior N-mixture model and naïve model estimates and 95% Bayesian credible intervals for the effect of land use, where positive values correspond to higher probabilities in forest and negative values correspond to higher probabilities in agriculture, on the probability of eating and vocalizing for (a) Hoffmann's woodpecker, (b) turquoise-browed motmot, and (c) Inca dove. Bottom row: The behavior N-mixture model and naïve model's predictions of the probabilities that an individual performs each behavior in each habitat type. Significant differences between habitats according to only the naïve model are marked with "△"; significant differences according to both models are marked with "▲".

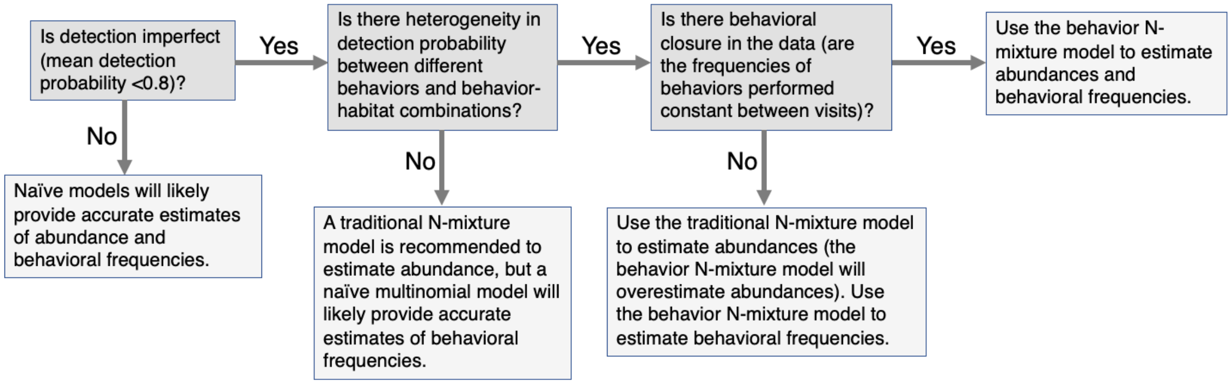

Figure 9: Decision tree to help determine when behavior N-mixture, naïve, and traditional N-mixture models should be used to estimate abundance and behavioral frequencies from wildlife survey data across various scenarios of imperfect detection and population closure.

Supporting Information 2

Table S2.1: Percent of iterations of the behavior N-mixture model per simulation scenario where all chains converged out of 100 trials, such that all estimates of abundance, detection probabilities, behavior probabilities, intercepts, and slope parameters had Gelman-Rubin statistics ≤1.1.

		Detection Mean		
		0.2	0.5	0.8
Abundance mean	1	60%		
	2.7	65%	85%	14%
	7.4	66%		

Table S2.2: Categorization of behaviors.

Recorded behavior	**Behavior category**
Aerial Foraging Bark Gleaning Berry Plucking Foliage Gleaning Flower Visiting Sit-And-Wait Foraging Stalking Hawking Eating Ground Rummaging Plant shoot eating Fruit/flower/seed eating Seed plucking Searching Other Foraging	Eat
Alarm Calling Singing	Vocalize
Courtship Feeding young Mating Nest building Nest sitting Intraspecific aggression Interspecific aggression Mobbing Preening Perching Roosting Fly over	Other

Table S2.3: Percent of the iterations of each scenario for which mean estimates from the behavior N-mixture model were less biased than the alternative model. Each column represents a different parameter. Respective alternative models are specified in parentheses.

Mean detection and abundance levels	**Data type**	**Behavior probability coefficient (Naïve)**	**Behavior probability (Naïve)**	**Abundance coefficient (Naïve)**	**Abundance coefficient (Traditional N-Mixture)**	**Abundance (Traditional N-Mixture)**
Detection 0.2, Abundance 2.7	**Closure**	71%	68%	62%	58%	54%
	Non-closure	58%	53%	52%	51%	5%
Detection 0.5, Abundance 2.7	**Closure**	76%	49%	69%	77%	56%
	Non-closure	49%	42%	62%	53%	1%
Detection 0.8, Abundance 2.7	**Closure**	57%	58%	29%	43%	68%
	Non-closure	25%	28%	43%	43%	0%
Detection 0.2, Abundance 1	**Closure**	58%	63%	47%	37%	62%
	Non-closure	71%	55%	50%	53%	0%
Detection 0.2, Abundance 7.4	**Closure**	86%	77%	77%	53%	58%
	Non-closure	62%	59%	70%	71%	8%

Table S2.4: Mean absolute bias, the 2.5 and 97.5th percentiles of absolute bias, and 95% Bayesian credible interval coverage across 100 trials for each scenario (defined by input values of detection and abundance) of the behavior N-mixture model.

Parameter	**Measure**	**Data type**	**detection 20%, abundance 2.7**	**detection 50%, abundance 2.7**	**detection 80%, abundance 2.7**	**detection 20%, abundance 1**	**detection 20%, abundance 7.4**
Behavior probability coefficient β'_b	Mean absolute bias	Closure	0.21	0.06	0.03	0.07	-0.01
	2.5 and 97.5th percentile, absolute bias		-1.28, 1.56	-0.63, 0.82	-0.74, 0.59	-1.14, -0.94	-0.70, 0.62
	95% CI coverage		92%	93%	82%	93%	95%
	Mean absolute bias	Non-closure	-0.04	-0.03	-0.10	-0.04	0.25
	2.5 and 97.5th percentile, absolute bias		-3.34, 1.88	-2.03, 1.89	-1.65, 2.00	-2.16, 1.58	-1.38, 1.60
	95% CI coverage		85%	74%	57%	91%	84%
Behavior probability $B.p_{j,b}$	Mean absolute bias	Closure	-0.001	0.01	0.003	0.03	0.00
	2.5 and 97.5th percentile, absolute bias		-0.17, 0.19	-0.12, 0.12	-0.15, 0.13	-0.28, 0.27	-0.11, 0.12
	95% CI coverage		95%	93%	90%	94%	95%
	Mean absolute bias	Non-closure	0.01	0.02	0.02	0.03	-0.01
	2.5 and 97.5th percentile, absolute bias		-0.29, 0.30	-0.33, 0.33	-0.36, 0.32	-0.36, 0.35	-0.27, 0.24
	95% CI coverage		90%	82%	67%	94%	88%
Abundance coefficient α'	Mean absolute bias	Closure	0.01	0.02	0.00	-0.03	0.00
	2.5 and 97.5th percentile, absolute bias		-0.69, 0.74	-0.28, 0.19	-0.12, 0.15	-0.40, 0.27	-0.09, 0.09
	95% CI coverage		94%	84%	86%	100%	100%
	Mean absolute bias	Non-closure	-0.01	0.02	0.00	0.05	-0.01
	2.5 and 97.5th percentile, absolute bias		-0.19, 0.18	-0.23, 0.25	-0.10, 0.10	-0.37, 0.50	-0.13, 0.11
	95% CI coverage		94%	76%	86%	83%	98%
Abundance N_j	Mean absolute bias	Closure	0.22	0.03	0.03	0.22	0.08
	2.5 and 97.5th percentile, absolute bias		-2.50, 2.79	-2.01, 1.39	-0.73, 0.38	-1.66, 1.80	-4.55, 4.51
	95% CI coverage		99%	99%	99%	99%	98%
	Mean absolute bias	Non-closure	7.85	7.08	6.59	3.65	14.61
	2.5 and 97.5th percentile, absolute bias		0.57, 35.82	1.34, 18.75	0.83, 20.26	-0.29, 12.91	-0.54, 60.61
	95% CI coverage		63%	25%	17%	15%	41%
Detection probability coefficient γ'	Mean absolute bias	Closure	0.03	-0.01	-0.09	0.10	0.00
	2.5 and 97.5th percentile, absolute bias		-0.69, 0.74	-0.47, 0.56	-1.44, 0.52	-1.17, 2.14	-0.51, 0.69
	95% CI coverage		95	96	90	96	95
	Mean absolute bias	Non-closure	0.01	-0.05	-0.05	0.07	-0.10
	2.5 and 97.5th percentile, absolute bias		-1.52, 1.66	-1.52, 2.36	-1.72, 2.29	-2.32, 1.81	-1.70, 1.67
	95% CI coverage		80	45	33	84	72
Detection probability $P_{j,b,k}$	Mean absolute bias	Closure	0.00	0.00	-0.01	0.00	0.00
	2.5 and 97.5th percentile, absolute bias		-0.11, 0.15	-0.09, 0.11	-0.13, 0.12	-0.16, 0.22	-0.09, 0.09
	95% CI coverage		94	97	88	96	97
	Mean absolute bias	Non-closure	-0.14	-0.33	-0.50	-0.14	-0.12
	2.5 and 97.5th percentile, absolute bias		-0.49, 0.04	-0.67, 0.03	-0.75, -0.07	-0.58, 0.10	-0.47, 0.05
	95% CI coverage		28	10	4	37	29

Table S2.5: Mean absolute bias, the 2.5 and 97.5th percentiles of absolute bias, and 95% Bayesian credible interval coverage across 100 trials for each scenario (defined by input values of detection and abundance) of the naïve model.

Parameter	**Measure**	**Data type**	**detection 20%, abundance 2.7**	**detection 50%, abundance 2.7**	**detection 80%, abundance 2.7**	**detection 20%, abundance 1**	**detection 20%, abundance 7.4**
Behavior probability coefficient β'_b	Mean absolute bias	Closure	0.03	0.22	-0.06	0.18	0.13
	2.5 and 97.5th percentile, absolute bias		-1.90, 1.84	-1.61, 2.27	-0.72, 0.43	-2.15, 3.37	-1.56, 2.13
	95% CI coverage		36%	33%	68%	63%	25%
	Mean absolute bias	Non-closure	-0.03	0.17	-0.04	0.02	0.04
	2.5 and 97.5th percentile, absolute bias		-2.20, 2.02	-1.35, 1.96	-0.60, 0.55	-3.57, 2.54	-1.54, 2.12
	95% CI coverage		40%	45%	68%	56%	30%
Behavior probability $B.p_{j,b}$	Mean absolute bias	Closure	0.01	0.01	0.003	0.01	0.01
	2.5 and 97.5th percentile, absolute bias		-0.31, 0.32	-0.31, 0.32	-0.12, 0.12	-0.39, 0.35	-0.30, 0.33
	95% CI coverage		55%	47%	62%	70%	42%
	Mean absolute bias	Non-closure	0.01	-0.01	0.001	0.03	0.01
	2.5 and 97.5th percentile, absolute bias		-0.32, 0.33	-0.31, 0.28	-0.12, 0.10	-0.41, 0.43	-0.31, 0.32
	95% CI coverage		60%	67%	79%	71%	45%
Abundance coefficient α'	Mean absolute bias	Closure	0.00	0.01	0.00	-0.06	0.00
	2.5 and 97.5th percentile, absolute bias		-0.20, 0.27	-0.32, 0.22	-0.15, 0.08	-0.40, 0.23	-0.19, 0.14
	95% CI coverage		68%	62%	86%	85%	76%
	Mean absolute bias	Non-closure	0.00	0.01	-0.01	0.03	-0.01
	2.5 and 97.5th percentile, absolute bias		-0.24, 0.26	-0.27, 0.24	-0.10, 0.08	-0.37, 0.56	-0.22, 0.14
	95% CI coverage		77%	56%	71%	80%	67%

Table S2.6: Mean absolute bias, the 2.5 and 97.5th percentiles of absolute bias, and 95% Bayesian credible interval coverage across 100 trials for each scenario (defined by input values of detection and abundance) of the traditional N-mixture model.

Parameter	**Measure**	**Data type**	**detection 20%, abundance 2.7**	**detection 50%, abundance 2.7**	**detection 80%, abundance 2.7**	**detection 20%, abundance 1**	**detection 20%, abundance 7.4**
Abundance coefficient α'	Mean absolute bias	Closure	0.00	0.02	-0.01	-0.02	-0.01
	2.5 and 97.5th percentile, absolute bias		-0.23, 0.22	-0.33, 0.22	-0.14, 0.11	-0.35, 0.26	-0.14, 0.08
	95% CI coverage		94%	84%	86%	100%	100%
	Mean absolute bias	Non-closure	-0.01	0.01	0.00	0.05	-0.01
	2.5 and 97.5th percentile, absolute bias		-0.19, 0.20	-0.31, 0.23	-0.10, 0.07	-0.31, 0.42	-0.14, 0.11
	95% CI coverage		94%	76%	86%	83%	98%
Abundance N_j	Mean absolute bias	Closure	-0.06	-0.16	-0.04	-0.02	-1.23
	2.5 and 97.5th percentile, absolute bias		-3.16, 2.92	-2.78, 1.49	-0.97, 0.52	-2.05, 1.48	-7.32, 3.58
	95% CI coverage		96%	94%	98%	99%	89%
	Mean absolute bias	Non-closure	0.35	0.06	-0.02	0.36	0.05
	2.5 and 97.5th percentile, absolute bias		-2.73, 4.51	-1.80, 1.65	-0.97, 0.45	-1.59, 1.74	-6.02, 7.05
	95% CI coverage		98%	98%	99%	99%	93%

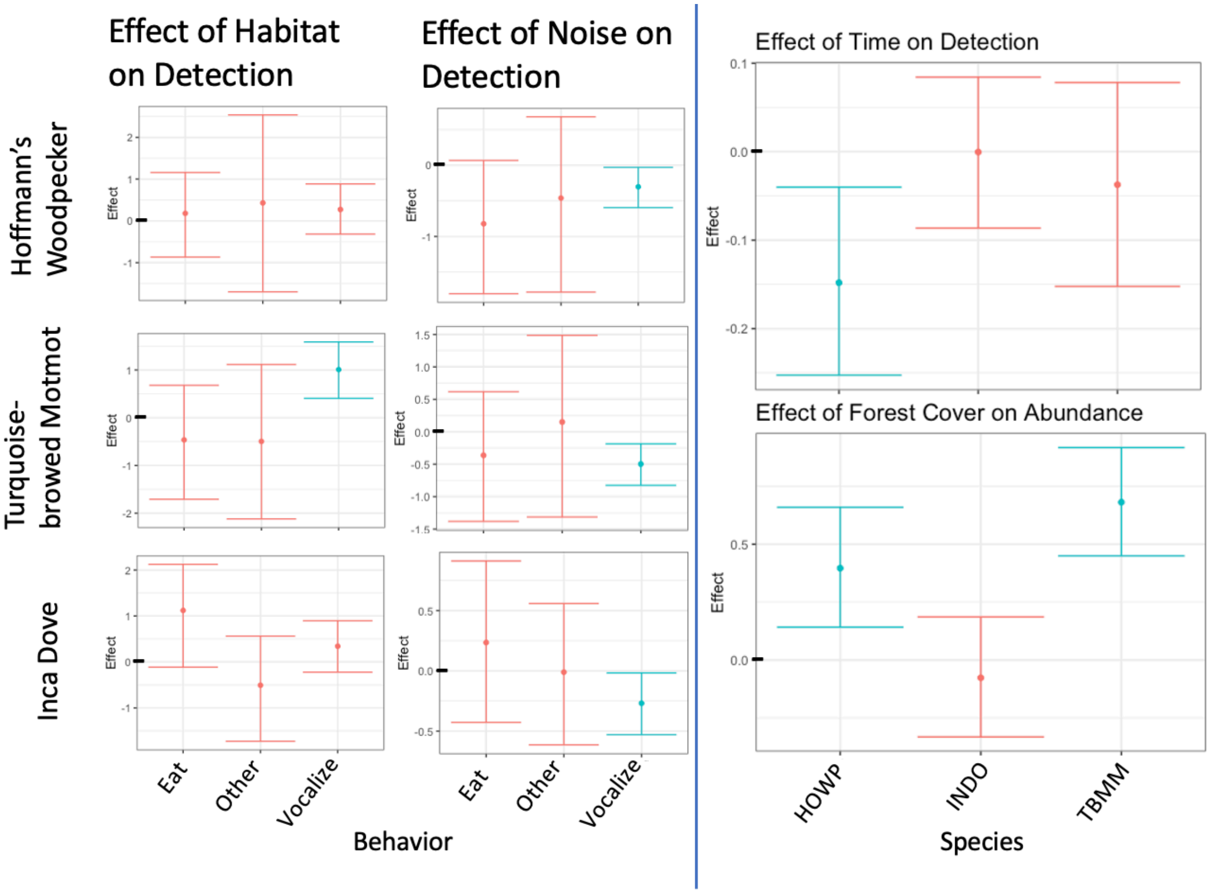

Figure S1.1: The behavior N-mixture model's estimates of the effects of habitat (binary variable where forest = 1 and agriculture = 0), noise, and time on detection probability and the effect of forest cover on abundance for Hoffmann's Woodpecker (HOWP), Turquoise-browed Motmot (TBMM), and Inca Dove (INDO). Effects are in blue when the 95% Bayesian credible interval does not overlap zero.

Applying the traditional N-mixture model to birds in Northwest Costa Rica

When we applied the traditional N-mixture model to each species, the mean differences between the abundance estimates from the traditional N-mixture model and the behavior N-mixture model were -1.41, 2.56, and 0.43 for Inca Dove, Hoffmann's Woodpecker, and Turquoise-browed Motmot, respectively.

On average, the behavior N-mixture model's abundance estimates of Hoffmann's Woodpecker and Turquoise-browed Motmot were higher than the traditional N-mixture model, which could indicate violation of the behavioral closure assumption. Meanwhile, the behavior N-mixture model's abundance estimates of Inca Dove were lower than the traditional N-mixture model's estimates, which could mean that there is a large amount of unmodeled heterogeneity in *P* in the traditional N-mixture model (Kéry and Royle, 2015).

Differences in avian behavior between forest and agriculture in Northwest Costa Rica

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Authorship: AK, DK, and AE conceived the study. DK acquired funding for the study. JZ collected the data. AK, RS, LF, and DK conceived of the analysis. AK analyzed the data and wrote the manuscript. All authors provided feedback on the manuscript.

Acknowledgements: We thank the many people who helped collect bird survey data from Northwest Costa Rica, including K. Chan, P. Juárez, X. Campos, E. Rodrígues, L. Bogantes, the FuturAgua team, staff from SINAC, and the landowners who provided access to field sites. This work was supported by an NSF GRFP to A.K. and grants from the National Geographic Society (#9977-16; #67543R-20). All work was conducted with approval from the Costa Rican government (permits: SINAC-SE-CUS-PI-R-036-2016, SINAC-SE-CUS-PI-R-030-2017, SINAC-PNI-ACAT-043-2019, and SINAC-PNA-ACAT-039-2021).

Abstract

Behavioral changes are often animals' first responses to environmental change and may act as a bellwether for population viability. Nonetheless, most studies of habitat conversion focus on changes in species occurrences. We analyzed >14,000 behavioral observations across 55 bird species in communities within Northwestern Costa Rica to understand how land-use affects reproductive, foraging, and other 'passive' kinds of behaviors not associated with either foraging or reproduction. Specifically, we quantified differences in behaviors between farms, privately-owned forests, and protected areas, implementing a novel modeling framework to account for variation in detection. Birds were 1.3 times more likely to exhibit reproductive behaviors in forest than in agriculture, and 1.1 times more likely to exhibit reproductive behaviors in protected areas than in private forests. Moreover, species were not always most abundant in the habitats where they were most likely to exhibit foraging or reproductive behaviors. Finally, species of higher conservation concern were less abundant in agriculture than in forest. Together, our results highlight the importance of behavioral analyses for elucidating the conservation value of different habitat types.

Introduction

Habitat loss and fragmentation are restructuring wildlife communities, especially in tropical regions where rates of biodiversity loss and land conversion peak (Gibbs et al. 2010; von Essen & Lambin 2021; Winkler et al. 2021). While biodiversity is often higher in intact protected areas than human-dominated landscapes (Newbold et al. 2015), 'working landscapes' can be managed to provide for human needs while sustaining wildlife (Kremen and Merenlender 2018, Frishkoff et al. 2019). For example, Frishkoff et al. (2014) found that diversified farms in Costa Rica with multiple crop types and natural habitat patches sustained similar levels of species richness as tropical forest reserves (though reserves supported more phylogenetic diversity).

In most studies of land-use change, changes in species occurrences and/or abundances are used to quantify species' tolerances for anthropogenic landscapes (*e.g.*, Newbold et al. 2013, Hatfield et al. 2018, Ehlers Smith et al. 2018). Such studies, however, provide little information about how species actually use the habitats where they occur (Kleijn et al. 2011; Gilroy & Edwards 2017; Ortega-Álvarez et al. 2021). For example, a species regularly detected in agriculture may be passing through or spilling over from nearby natural habitats (and thus not actually resilient to land-use change; Vickery et al. 2001, Brudvig et al. 2009, Frishkoff et al. 2019). Alternatively, the species could use working landscapes to forage and reproduce, meaning it is resilient to or can even benefit from land-use change. Finally, a species may use working landscapes, but with suboptimal demographic rates such that populations are subject to source-sink dynamics (Pulliam 1988), buffer effects (Gill et al. 2001), spill-over effects (Brudvig et al. 2009), ecological traps (Gates & Gysel 1978), and/or extinction debt (Tilman et al. 1994). For example, urban areas in Southern Arizona acted as ecological traps for Cooper's Hawks (*Accipiter cooperii*), which resided and nested in cities but suffered over 50% nest failure, primarily from trichomoniasis acquired from feeding on urban doves (Boal & Mannan 1999). Therefore, looking beyond species occurrence is critical for quantifying the conservation value of anthropogenic habitats.

One way to assess how animals use their environments is by examining behavior. Behavioral changes are often an animal's first response to human-induced environmental changes, and can indicate whether individuals are able to cope with land-use change (Wright et al. 2010; Wong & Candolin 2015; González-Lagos & Quesada 2017). For example, some species can adapt their acoustic signals to maximize transmission in new environments, thus maintaining communication between individuals (Graham et al. 2017). Alternatively, land-use change can result in behaviors and physiological responses that decrease an individual's fitness, such as reducing foraging due to higher risk of predation (Desrochers *et al.* 2002), altering their acoustic signals (Slabbekoorn & Peet, 2003), or decreasing their body mass (Liker, et al. 2008). Because behavior can often be linked to demographic parameters (*e.g.,* birth, death, migration), variation in behavior across different environments can have cascading implications for population persistence (Luck 2002, Lyons 2005). For example, male bird song rate can be used as a proxy for superior male quality and territory defense (Møller 1991; Gil & Gahr 2002), and Pillay et al. (2019) measured male per-capita song rate to explore the potential mechanisms underlying tropical bird distributions in selectively logged forest. Therefore, observing changes in behavior can help identify species that are able to exploit anthropogenic resources and act as an early warning signal for populations in trouble (Wong & Candolin 2015; Berger-Tal et al. 2016). If, however, management decisions rely only on occurrence data, ignoring how species use different habitats, then areas essential to phases of the species' life cycle may not be protected (Ke et al. 2022).

Most studies that measure variation in behavioral use of different environments are limited to few individuals and species because they require labor-intensive animal-monitoring methods (*e.g.*, focal observations or telemetry; Luck 2002, Tremblay et al. 2005). In contrast, survey-type data require fewer resources to collect, can capture a larger portion of the population, and are often suitable for multiple species simultaneously. However, some behaviors are difficult to observe (*e.g.*, sedentary, ambush-oriented feeding behavior in snakes; Durso et al. 2011). Moreover, the detectability of individuals often depends on the behaviors they perform (Crowe & Longshore 2010), which could lead to underestimating the frequency of hard-to-detect behaviors. The detectability of different behaviors may also vary across environments. For example, the probability of observing visually detected behaviors may be lower in dense vegetation compared to open areas. Without accounting for behavior-specific detection, we could risk falsely concluding, for example, that a species forages more often in agriculture than forests, simply because the species is more apparent in open environments.

Here, we evaluate how land-use affects the likelihood of birds exhibiting reproductive, foraging, and passive behaviors (e.g., perching, preening, roosting; Table S3.1; See SI for details), using four years of bird surveys in Northwest Costa Rica, encompassing >14,000 behavioral observations of 55 species across 150 sites. We extended a single-species behavior N-mixture model (Ke *et al.* 2022) to a community model to quantify differences in behaviors between farms, privately-owned forest patches, and formal nature reserves, accounting for variation in detection between behaviors, species, and habitats.

Our work was guided by three core questions. First, how do bird communities vary in abundance and behavior between land-uses? We hypothesized that because high-intensity agricultural habitats contain fewer trees and fewer bird species that utilize the habitat (Luck & Daily 2003), birds would be less abundant and perform foraging and reproductive behaviors less frequently in agriculture as compared to forest. Based on prior work (Karp et al. 2019), we also hypothesized that protected areas would have similar bird abundances but higher probabilities of exhibiting reproductive behaviors than privately-owned forests, due to higher rates of disturbance from logging, fires, and hunting in private forests. Second, do species that peak in abundance in one habitat also forage and/or reproduce there more often? We predicted that most species would exhibit reproductive and foraging behaviors in the habitats where they peak in abundance (as long as they are selecting their habitats correctly and not subject to ecological traps; Gates & Gysel 1978). However, we predicted that some species would have "inconsistent responses" in abundance and behavior, for example, if individuals are more likely to perform reproductive behaviors in one habitat but are equally or less abundant in that habitat. That is, a species could have equal abundances in forest and agriculture, but perform more reproductive behaviors in forest. Finally, do species of higher conservation concern (*i.e.,* range-restricted and/or declining species) react differently than less sensitive species? Given prior research documenting the sensitivity of range-restricted species to habitat conversion (Karp et al. 2019; Sykes et al. 2020), we predicted that species of higher conservation concern would be more abundant and perform foraging and reproductive behaviors more frequently in protected areas than in agriculture and private forests.

Methods

Study area

We investigated how land use affects bird behavior and abundance in the Guanacaste Province of northwest Costa Rica (Figure S3.1). Our study region is a mosaic of tropical forest ranging from coastal wet forests to inland dry forests (protected and privately-owned forests) and agriculture (pastures and crop fields). Guanacaste experiences a dry season from December to April, two rainy seasons (May to June and September to November), as well as a mid-summer dry period in July and August (Hund et al. 2021). We selected sites across a network of 5 formally protected areas and 20 farms, which were composed of pasture (N=12), rice (N=6), sugarcane (N=1), and Taiwan grass (a forage crop, N=1). These agricultural types were representative of the broad study region, and we selected sites so that local forest cover within 50m varied, with sites located in forest interiors, forest edges, small forest fragments, agricultural field centers, fields bordering forest, and fields surrounded by forest. The most common tree species in our study region were *Guazuma ulmifolia, Semialarium mexicanum, Ardisia revoluta, Lysiloma divaricatum,* and *Luehea candida.* Protected areas were under government administration, and human activity is not excluded from them as they are visited by tourists and illegal hunting still occurs.

On each farm or protected area, birds were surveyed at six point-count locations (150 points total). On farms, half of the point-count locations were in agriculture and the other half in privately-owned forests. All point counts in protected areas occurred in forest. Privately-owned forests were twice as fragmented as protected areas (measured using total forest edge length);

they are also regularly logged, leading to significantly shorter tree heights than in protected areas (Karp et al. 2019).

Bird surveys

At each point count location, the same expert observer (J. Zook) surveyed all birds seen or heard in 20-min, 50-m fixed radius point counts in from 2016-2019 during the breeding season for most bird species in the region, May-July. The length of point counts allowed us to detect more rare behaviors, and the observer has a high level of expertise allowing him to precisely identify individuals. Zook sampled half of the point-count locations three times within a 1-2 week period. The other half were sampled once to increase spatial replication while still providing sufficient replication to estimate detection probabilities (see below). One farm or protected area (6 points) was surveyed each day, beginning at sunrise and continuing for ~5 hr. Information concerning species identity, number of individuals observed, time of day, and whether noise exceeded typical background levels (*e.g.*, farm machinery, cicadas) was recorded.

Each observation was also associated with one of 32 behaviors that we classified into three categories: reproductive, foraging, and passive behaviors (Table S3.1; See SI for details). Observations that were heard only were classified as "singing" or "calling" behaviors. When an individual performed more than one behavior during a point count (~10.5% of observations), we randomly selected one of the behaviors observed because the structure of our model only allowed for one behavior per individual (See "Modeling behavior"). This could slightly bias results for a given behavior category for the species with the fewest observations, but we did not expect it to affect results on average given only 10% of observations had more than one behavior. To ensure we had enough observations of each species for the model to estimate behaviors, we restricted analyses to species that were observed at least 20 times and had at least one observation in each behavior category, resulting in 55 species for the analysis using all sites and 40 species for the analysis only using forest sites.

Covariates

To quantify local forest cover, we hand-classified tree cover within 50m of all point count locations using cloud-free Google Earth images available from 2013-2017. Because many Neotropical species are understudied and population sizes are often uncertain, we assessed multiple dimensions of rarity. We obtained species' range sizes from ("BirdLife Data Zone") and global population trend information (*i.e.,* whether each species is declining, stable, or increasing) from the IUCN ("The IUCN Red List of Threatened Species" 2022).

Modeling behavior

To quantify how birds change their behavioral use of habitats, we developed a community extension of a behavior N-mixture model (Ke *et al.* 2022). N-mixture models use spatially and temporally replicated surveys where the number of individuals is counted to estimate abundance while accounting for detection probability (Royle, 2004; Kéry, 2018). Behavior N-mixture models quantify the probability of individuals exhibiting different behaviors, while accounting for variation in detectability among different behaviors in different environments (Ke *et al.* 2022). We extended the single-species behavior N-mixture model such that the probabilities of many species exhibiting different behaviors can be estimated jointly. Species-specific parameters were derived from community-wide hyperdistributions governed by (community-level) hyperparameters estimated from the data. This parameterization allows estimating parameters of rare species by sharing information among species in the community, and rare species' parameters tend to shrink towards the community mean (Dorazio & Royle 2005; Kéry & Royle 2015).

In summary, the number of individuals of species (i) performing a certain behavior (b) at site (j) was modeled using a Poisson distribution, where the expected abundance $\lambda_{i,j}$ was modelled as:

$$\log(\lambda_{i,j}) = \alpha 0_i + \alpha 1_i * \mathrm{TreeCover}_\mathrm{j} + \delta 0_{i,farm[j]} + \delta 1_{i,\mathrm{year}[k]} + \delta 2_{i,point[j]}$$

"TreeCover" is the local forest cover within 50m. Parameters in the α family were estimated for each species, and the δ terms represent random effects that were included to account for spatial and temporal autocorrelation in bird abundances and explain variation among species, point-count locations, farms, or years that was not explained by the other parameters. We modeled the probabilities of species performing each behavior as a function of habitat, using multinomial logistic regression. Finally, we modelled the detection probability of an individual of a certain species performing a certain behavior at a given site and visit ($P_{i,j,b,k}$) as:

$$\mathrm{logit}(P_{i,j,b,k}) = \gamma 0_{i,b} + \gamma 1_b * \mathrm{Noise}_\mathrm{j,k} + \gamma 2_{i,b} * \mathrm{Habitat}_\mathrm{j} + \gamma 3 * \mathrm{Time}_\mathrm{j,k} ,$$

where "Noise" is a binary variable indicating if noise levels exceeded typical background noises and "Time" is the time of day of the point count. Parameters $\gamma 0$ and $\gamma 2$ were species-level random effects, while parameters $\gamma 1$ and $\gamma 3$ were constant over species and behaviors. See SI for detailed modelling methods.

To compare shifts in behaviors between protected areas and private forests (Questions 1, 2), we conducted a second analysis omitting all sites in agriculture and replacing the "Habitat" and "TreeCover" variables with a binary variable indicating whether the forest site was in a protected area or not. We also excluded $\gamma 2_{i,b}$ (*i.e.,* habitat type) from the detection process, as all sites were in forests.

Behavioral N-mixture models can be used to estimate effects of environmental covariates on abundance, but the actual abundance estimates generated from them can be biased because when an individual is observed performing different behaviors between visits, it contributes to overall abundance estimates multiple times (Ke *et al.* 2022). Thus, to model abundances (Questions 1, 2), we constructed a traditional N-mixture model for each analysis (forest vs. agriculture and protected vs. private forest; Royle 2004, Kéry 2018). The models retained all parameters above, but removed the behavior index and the behavior components involving π.

All models were implemented in R Version 4.0.0 using the package *nimble,* which runs Markov chain Monte Carlo (MCMC) algorithms (RC Team, 2013; de Valpine et al., 2017). We ran three chains starting at random initial values and 10,000 burn-in iterations. We included 50,000 post burn-in iterations thinned at a rate of 50. We assessed convergence by examining Gelman-Rubin statistics of the chains of every parameter, and considered chains to converge if Gelman-Rubin statistics were ≤ 1.1 (Gelman et al. 2004).

Interpreting behavioral coefficients

We combined parameters to calculate the probability of performing a behavior, as well as the number of individuals performing each behavior in each habitat. We compared the resulting Bayesian Credible Intervals (BCIs) to assess significance (using a 90% BCI cut off because each parameter is estimated with less data than the community means; see SI for detailed methods). To understand how bird communities change in abundance and behavior with changes in land-use (Question 1), we extracted community-wide mean effects of tree cover (or protection status) on abundance ($\alpha 1$) and the mean predicted differences in behavior between habitats using the community-wide means for the behavior probability intercept ($\beta 0$) and the effect of habitat on behavior ($\beta 1$). For community-wide effects, we used a BCI cutoff of 95% to determine statistical significance because we had more data available to estimate them (Kruschke 2014; McElreath 2020). For the effects of forest cover and protected area on abundance, we calculated their statistical significance using MCMC p-values from the *MCMC.qpcr* package (Matz 2020).

To understand how individual species' abundance responses to forest cover (or protection status) related to their behavioral responses (Question 2), we compared differences in abundance across tree cover (or protection levels) to differences in behavior between habitats and measured the strength of relationships using Spearman's correlation coefficient. We then categorized species based on their abundance response to local forest cover (or protection status) and their behavioral response to habitat. For example, when individuals of a species were more likely to exhibit reproductive or foraging behaviors in one habitat (*e.g.*, forests), but they were equally or less abundant in that habitat, we termed this an "inconsistent response." Here, this is because the abundance pattern indicates that forest is not more important than agriculture for the species, but the behavior information implies the opposite. Because passive behaviors were considered as the least important for survival and reproduction, we considered species that were more likely to exhibit passive behaviors in one habitat, but were equally or more abundant in that habitat, to have an "inconsistent response."

In contrast, we considered responses "consistent" when a species was more abundant in one habitat and was also more or equally likely to exhibit reproductive or foraging behaviors (or less likely to exhibit passive behaviors) in that habitat. We labeled these species as "affiliated" with a habitat. Finally, species with no significant differences in abundance or behavior between habitats were labeled "non-significant response." These species could have BCIs that were too wide to be considered statistically significant or be species that have similar abundance and behavioral use in different habitats (*i.e.,* habitat generalists).

Finally, to understand whether species of higher conservation concern exhibited greater sensitivity to agriculture and/or privately-owned forests (Question 3), we calculated Spearman's correlation coefficients between species' global range sizes and differences in abundance across tree cover (or protection levels), as well as differences in behavior between habitats. We also used pairwise Wilcoxon rank sum tests to understand whether differences in abundance across tree cover (or protection levels), as well as differences in behavior between habitats, differed between categories of global population trends (decreasing, stable, or increasing). We used the more conservative non-parametric tests because linear model assumptions were not met.

Results

After filtering out rare species (see methods), we retained 14,051 behavioral observations of 55 species for our analysis comparing forest and agriculture and 9,145 behavioral observations of 40 species when comparing protected and private forests (Table S3.2). Thirty species were passerines and the others were non-passerines (*e.g.*, Columbiformes, Apodiformes). Chains for all parameters of the protected status analysis, and all but 4 (out of 1382) parameters for the land-use analysis converged (Gelman-Rubin statistics <1.1). The four parameters that did not converge had Gelman-Rubin statistics <1.25.

Abundance and behavior trends between land-use types

We found evidence to support our hypothesis that the community-average species abundance significantly increased with forest cover (effect size = 0.37, pMCMC = 0.002, 95% BCI [0.13, 0.61], Figure S3.2, Table S3.7). However, there was no significant effect of protection status on average abundance (effect size = 0.11, pMCMC = 0.34, 95% BCI [-0.12, 0.35]) or abundance of any species (Figure S3.3, Table S3.8).

We also found evidence to support our predictions that, on average across all species, individuals were 1.3 times more likely to perform reproductive behaviors in forest than agriculture (statistically significant, Figure 10A, Table S3.3). Likewise, models predicted 3.3 times more individuals performing reproductive behaviors in forest than agriculture (statistically significant, Figure 10B, Table S3.3). On average, individuals were more likely to perform foraging and passive behaviors in agriculture than in forest; however, we observed no significant differences between land-use types in the number of individuals performing these behaviors (Figure 10A, B, Table S3.3). At the species level, many more species had significantly higher probabilities and numbers of individuals exhibiting reproductive behaviors in forest than agriculture (*e.g.,* Elegant Trogon [*Trogon elegans*]; Table 4, Figure S3.4, Table S3.7, Table S3.9).

Conforming to our expectations, when comparing protected and privately-owned forest, the average species was significantly more likely to perform reproductive behaviors and less likely to perform passive behaviors in protected forest (Figure 10C, Table S3.3). Correspondingly, eleven species had higher probabilities of exhibiting reproductive behaviors in protected forest than in private forest (*e.g.*, Stripe-throated Hermit [*Phaethornis striigularis*]), while only one species had a higher probability of exhibiting reproductive behaviors in private forest (White-winged dove [*Zenaida asiatica*], Table 4, Figure S3.5, Table S3.8). However, the total number of individuals performing reproductive behaviors was not significantly different between protected and privately-owned forest, both across all species and at the species level (Table 4, Figure 10D, Figure S3.7, Table S3.3, Table S3.10).

Relationships between abundance and behavioral responses to land-use

We did not find evidence to support our second hypothesis. Specifically, species were not always more likely to forage or reproduce in the habitats where they were most abundant. Although most species had consistent abundance and behavioral responses, species' abundance responses to forest cover (or protection status) were not statistically correlated with their behavioral responses Table S3.4). This can happen because many species had a significant abundance response but no significant behavioral response to habitat, and these responses were considered to be consistent.

At the species level, 37 species had consistent abundance and reproductive responses to forest versus agriculture (29 affiliated with forest and 8 affiliated with agriculture), 8 had inconsistent responses, and 10 species had non-significant responses (Table 5; Figure 11; see methods for definitions). Species exhibiting inconsistent responses were more likely to perform reproductive behaviors in forest but were either less or equally abundant as local forest cover increased (*e.g.*, Great Kiskadee [*Pitangus sulphuratus*]). In the protected area analysis, there were 12 species with inconsistent responses but no species with consistent responses (likely because no species had a significant abundance response to protected forest vs. private forest; Figure S3.8). In terms of foraging behavior, four species exhibited inconsistent responses. These species were more likely to forage in agriculture but were either less or equally abundant as local forest cover increased (*e.g.*, Yellow-green Vireo [*Vireo flavoviridis*]; Figure 12). In terms of passive behavior, 6 species exhibited inconsistent responses. These species performed passive behaviors more frequently in agriculture but were either less or equally abundant with increasing forest cover (Figure 13).

Species of conservation concern

Our hypothesis that species of higher conservation concern would disproportionately rely on forest and protected areas was partially supported. Based on correlation analyses, species with smaller range sizes and decreasing global population trends tended to be more abundant in forest (Table S3.5, Table S3.6). There were negative relationships between range size (and global population trends) and the numbers of individuals performing each behavior in forest versus agriculture, likely driven by the strong negative relationships with the abundance response (Table S3.5; Table S3.6). However, we observed no significant relationships between species' range sizes (or global population trends) and the probability of individuals exhibiting any behavior between any habitats (Table S3.5, Table S3.6).

Discussion

Our community behavioral N-mixture model elucidated how bird communities and individual species vary in abundance and behavior across land-use types, while accounting for differences in detection probability between species, behaviors, and habitats. On average, we found that Costa Rican bird species were both more abundant and more likely to perform reproductive behaviors in forest than agriculture. Species were also more likely to perform reproductive behaviors in protected forest, despite there being no significant abundance differences between protected versus privately-owned forest. Moreover, abundance and behavioral responses to land-use were largely uncorrelated and sometimes inconsistent at the species-level. These results highlight the importance of behavioral analyses for elucidating the conservation value of different habitat types, as well as identifying species which may have the least behavioral flexibility for coping with human-induced changes (Wong & Candolin 2015).

Behavior and abundance differences between forest and agriculture

Across the community, we found that Costa Rican birds on average increased in abundance, were more likely to perform reproductive behaviors, and were less likely to forage in forest than in agriculture. We also estimated over 3 times as many individuals engaging in reproductive behaviors in forest than in agriculture (Figure 11). This implies that forests host better reproductive territories and resources for the average bird species, which is unsurprising given that Costa Rica was forested historically (Sader & Joyce 1988).

At the species-level, some behavioral responses to habitat were consistent with their abundance responses. For example, "agriculture specialist" species that both occurred and foraged more in agriculture tended to be granivorous (*e.g.*, White-collared Seedeater [*Sporophila torqueola*], Common Ground-Dove [*Columbina passerine*], Crested Bobwhite [*Colinus cristatus*]). Meanwhile, "forest specialist" species tended to be those known to primarily occur and nest in forest (*e.g.*, Lesson's Motmot [*Momotus lessonii*], Elegant Trogon; del Hoyo et al. 2020; Kunzmann et al. 2020). Importantly, there were very few species that increased their reproduction or decreased their foraging behaviors in agriculture – even the species with "consistent" responses primarily showed no significant differences in behavior but with the majority of the posterior density being in favor of forest for reproduction and agriculture for foraging. As such, most of the species with inconsistent responses were agriculture affiliates that reproduce in forest, and some (but fewer) species were forest affiliates that forage in agriculture.

Correlations between species' abundance and behavioral responses to land-use were often low (Table S3.4) and, for some species, abundances did not peak where the species was most likely to exhibit reproductive or foraging behaviors. Thus, combining abundance and behavior information proved essential to understanding how species respond to land-use. For example, Tropical

Kingbirds *(Tyrannus melancholicus*) were more abundant in agriculture and were more likely to perform reproductive behaviors in forest. The greater number of individuals in agriculture was balanced by a greater fraction of individuals performing reproductive behaviors in forest, leading to a similar number of individuals engaging in reproductive behaviors between the two habitat types. On the other hand, Inca Doves (*Columbina inca*) were equally abundant across habitat types but had a higher likelihood and number of individuals foraging in agriculture. This indicates that Inca Doves can likely find more food resources in agriculture but may still need forest for other reasons (*e.g.,* nesting).

Finally, for several species, our analyses suggested the possibility that agriculture may act as an ecological trap (Robinson et al. 1995). Specifically, we found that Common Ground-Dove, Masked Tityra (*Tityra semifasciata*), and Tropical Kingbird showed more reproductive behaviors in forest and more passive behaviors in agriculture, despite being more or equally abundant in agriculture. Interestingly, there is already evidence that land-use change causes declines in Common Ground-Dove: the species used to be highly abundant in gardens and open areas in San José, Costa Rica until the late 1990s but has now almost disappeared from urban areas in this region (Biamonte et al. 2011). Ecological traps have been observed through behavioral studies of other species. For example, Ben-Aharon et al. (2020) tracked the territories of mourning wheatears (*Oenanthe lugens*) to find that roads in southern Israel reduced survival and acted as an ecological trap. Rufous Treecreepers (*Climacterus rufus*) had significantly lower density but significantly higher reproductive success in ungrazed habitats compared to grazed and fragmented habitats in southwestern Australia (Luck 2003), suggesting that habitat quality may be higher in ungrazed areas and that the other habitats may act as ecological traps.

That said, more data is needed before conclusively determining that agriculture is acting as an ecological trap for the species surveyed here. Another possibility is that one habitat is insufficient to fulfill all the needs of a species (*e.g.*, Fiss et al. 2021). For example, a species may forage in agriculture and reproduce in forest. This could be the case for Great Kiskadee and Inca Dove. In this scenario, a mosaic of land-use types could result in larger populations than if only one habitat was present. Conversely, it is also possible that ecological traps are present, even for species that we deemed to have 'consistent responses' to land-use. For example, a species may exhibit more reproductive behaviors in a habitat but reproduction in that habitat may still be unsuccessful. Thus, to truly understand habitat quality for foraging and reproduction, more data would be needed, ideally from experiments that manipulate food availability, nest site locations, or reproductive success between habitat types to see how birds change their behaviors and habitat selection (Bélisle 2005; Knowlton & Graham 2010).

Behavior and abundance differences between privately-owned and protected forest

Consistent with our prior work (Karp et al. 2019), we found that species did not differ in abundance between protected and privately-owned forests, and, as such, the predicted number of individuals performing each behavior did not differ either. Nonetheless, species were, on average, more likely to perform reproductive behaviors and less likely to perform passive behaviors in protected forest. At the species-level, 11 species were more likely to exhibit reproductive behaviors in protected areas versus only one for which reproductive behaviors were more likely in private forests. These differences may result from differences in habitat quality. In our study system, privately-owned forests are embedded in more fragmented landscapes and have less canopy cover, shorter tree heights, lower tree richness, and less dense understories than protected forests, likely due to regular logging, fires, hunting, and other disturbances (Karp et al. 2019). Thus, while bird abundances weren't different between privately-owned forests and protected areas in Northwest Costa Rica in our prior work (Karp et al. 2019), here we show that the behaviors may differ between protection levels.

Species of conservation concern

We found that species with smaller geographic range sizes and decreasing global populations tended to be more abundant in forest (as in Karp *et al*. 2019). Smaller range sizes are especially related to higher extinction vulnerability, lower dispersal ability, and heightened sensitivity to land-use change (Böhning-Gaese et al. 2006; Sykes et al. 2020). This suggests that habitat conversion to agriculture is most likely to threaten species that are already declining, while favoring the species that are more adapted to different or novel food resources. However, we found little evidence that species of conservation concern were more dependent on protected areas than privately owned forests.

Limitations

Like any other study of behavior, it is important to acknowledge that that the frequency a species performs a behavior during surveys may not reflect the behaviors that it performs consistently. Animal behavior is known to vary based on seasons, time of day, which other species are present, and individual personalities (Bailey et al. 2004; Chambert et al. 2012; Veech et al. 2016; Merrick & Koprowski 2017). This limitation could be reduced with more behavioral observations, potentially spread throughout the day. Another assumption that we made is that if animals are spending more time foraging (or engaging in reproductive behaviors) in one location, then they have selected a habitat with more abundant food (or reproductive) resources. However, it is also possible that areas with fewer food resources force individuals to forage more often, or that the individuals foraging may be less skilled at finding food (Lescroël et al. 2010). In this case, the ecological trap may be actually where individuals spend more time foraging.

Another caveat is that because we had to restrict analyses to the most easily observed species, we could be missing the rarest and/or most forest-restricted species. Indeed, compared to included species, species excluded from analyses were observed three times more often in each forested site than in each agriculture site on average, and 1.5 times more often in each protected area site than each private forest site on average. Thus, if anything, our finding that species are more likely to exhibit reproductive behaviors in forests (especially protected areas) is likely conservative.

Conclusions

Our results suggest that habitat conversion to agriculture can have strong effects on avian behavior. These changes may have cascading implications for individual fitness and future population viability, given the strong negative effects on reproductive behavior. Moreover, our finding that reproductive behaviors are, on average, more likely in protected areas than private forests suggest that studying behaviors can unmask differences in habitat value, even when community composition and abundance exhibit little differences between habitat types. Another benefit of the community behavior N-mixture model is that it can be used to identify the species that are most likely to shift their behaviors across land-use types, and, as such, most likely to be caught in ecological traps, unable to adjust to anthropogenic changes, or alternatively, be able to exploit novel resources and thrive in new environments (Sih et al. 2011; Tuomainen & Candolin

2011). Looking forward, we recommend that scientists incorporate behavioral observations into survey protocols and analyses when possible. Doing so could not only help provide early warning signals for species in trouble but may also point towards some of the mechanisms underlying species' habitat selection as well as the ecological and evolutionary consequences of behavioral changes.

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Tables and Figures

Table 4: Number of species that had a positive, negative, or non-significant (NS) behavioral response to habitat, where rows specify which behavior is being measured and which habitats are being compared, and columns specify whether the species' responses were positive, non-significant, or negative, as well as whether the response was the probability of exhibiting a behavior or the number of individuals exhibiting a behavior.

		Prob. of exhibiting a behavior			# Individuals exhibiting a behavior		
		Positive	NS	Negative	Positive	NS	Negative
Effect of forest (relative to agriculture)	Reproductive Behavior	20	34	1	26	25	4
	Foraging Beheavior	0	47	8	14	29	12
	Passive Behavior	2	38	15	10	37	8
Effect of protected areas (relative to private forest)	Reproductive Behavior	11	28	1	0	40	0
	Foraging Beheavior	1	36	3	0	38	2
	Passive Behavior	1	31	8	0	39	1

Table 5: Number of species in each behavior category, where rows specify agriculture vs. forest analyses or private vs. protection forest analyses and columns represent behavior categories. Species were categorized based on their abundance response to local forest cover (or protection status) and their behavioral response to habitat. For example, species exhibited inconsistent responses when individuals were more likely to exhibit reproductive or foraging behaviors in one habitat (*e.g.*, forests), but were equally or less abundant in that habitat. In contrast, responses were "consistent" and "affiliated" with a habitat when a species was both more abundant and more or equally likely to exhibit reproductive or foraging behaviors in the same habitat. Species with no significant differences in abundance or behavior between habitats were labeled "non-significant response."

		Reproductive Behavior	Foraging Beheavior	Passive Behavior
Forest v. agriculture analysis	Forest-affiliated	29	27	29
	Agriculture-affiliated	8	12	10
	Non-significant Response	10	12	10
	Inconsistent Response	8	4	6
Protected v. private forest analysis	Protected-area affiliated	0	0	0
	Private-forest affiliated	0	0	0
	Non-significant Response	28	36	31
	Inconsistent Response	12	4	9

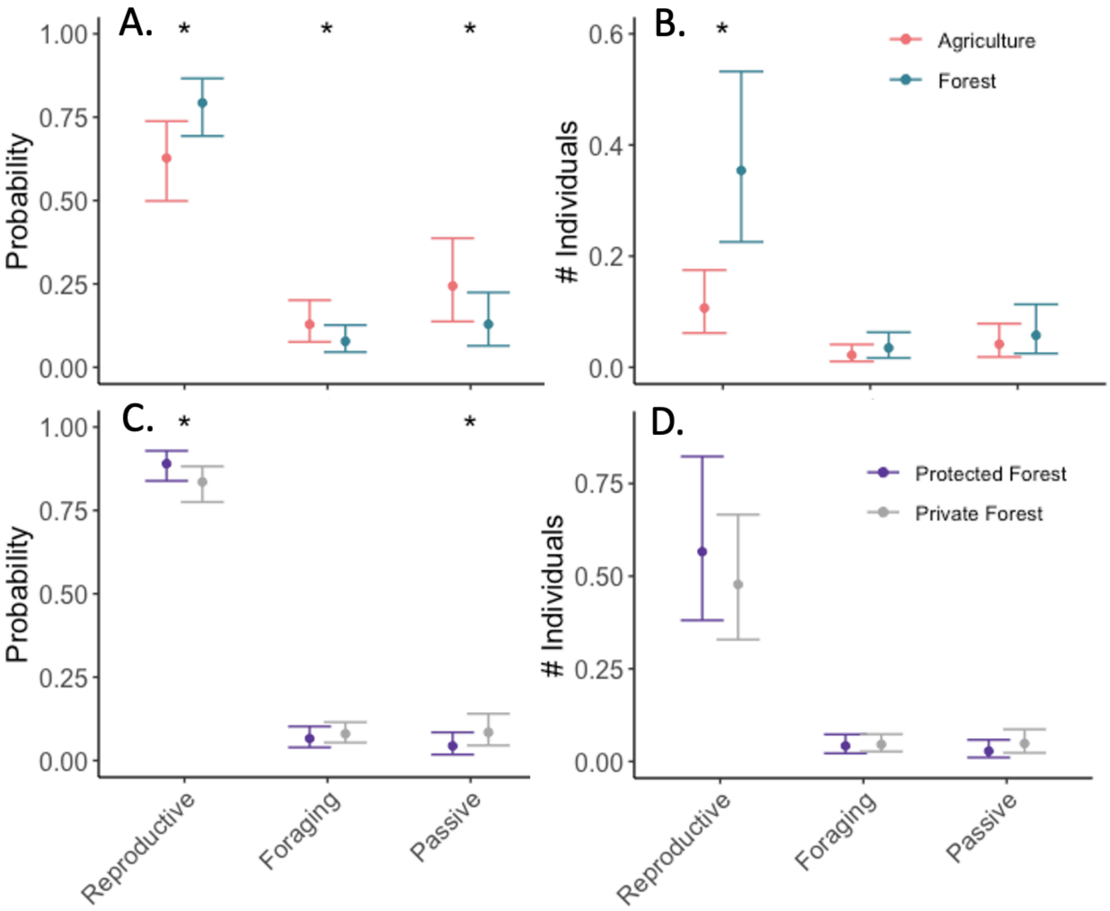


Figure 10: Reproductive, foraging, and passive behavior probabilities differ between forest and agriculture (A), and reproductive behavior probabilities differ between private and protected forest (C). Panels depict mean predicted probabilities (A, C) and expected numbers of individuals (B, D) performing foraging, passive, and reproductive behaviors in agriculture versus forest (A, B) and in protected versus private forest (C, D), using community-wide mean parameters. Uncertainty for probabilities is shown by 95% Bayesian credible intervals and uncertainty for numbers of individuals is the 95% percentile interval of the simulated posterior. Stars denote significant differences between habitats, such that the 95% intervals do not overlap zero.

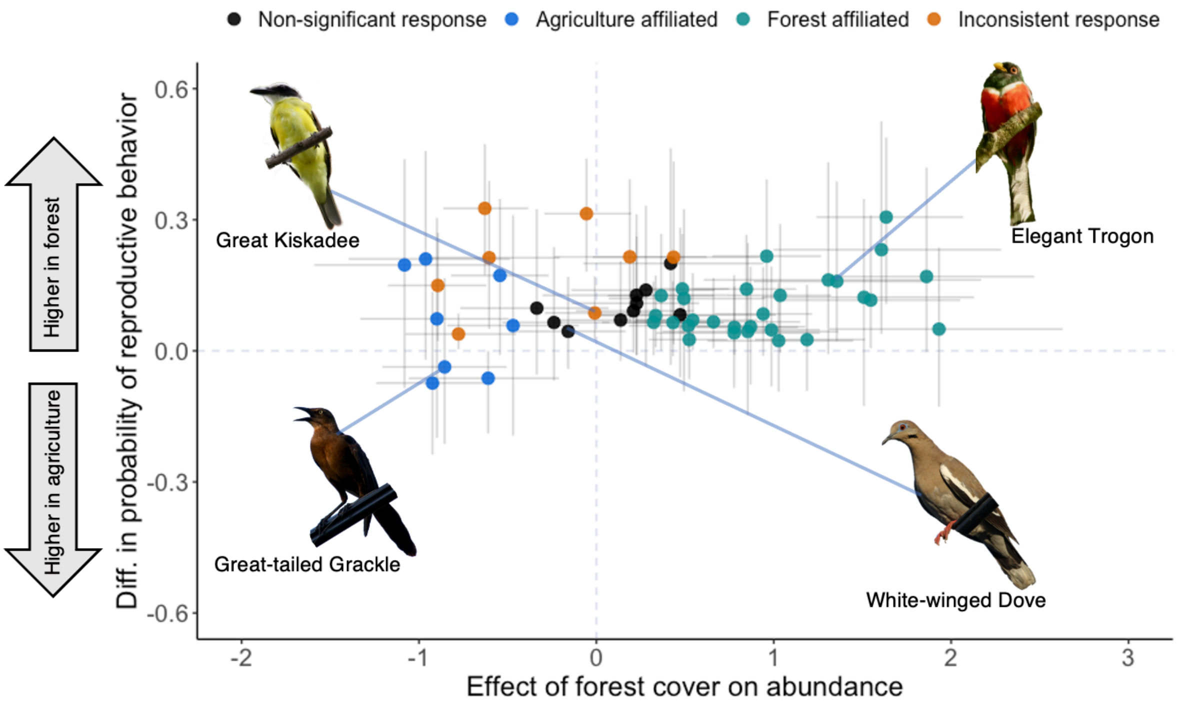


Figure 11: Relationship between the effect of local forest cover on a species' abundance and the predicted difference in species' probability of performing reproductive behaviors between habitats. Grey lines indicate 90% Bayesian credible intervals. Positive values on the y-axis represent a higher probability (on the probability scale) of performing reproductive behaviors in forest than agriculture. Colors represent whether species were classified as habitat generalists (black), agriculture affiliated (blue), or forest affiliated (green). Species with inconsistent responses (orange) preferentially exhibited reproductive behaviors in forest but did not significantly increase in abundance with forest cover. Representative species in each category are pictured and labeled.

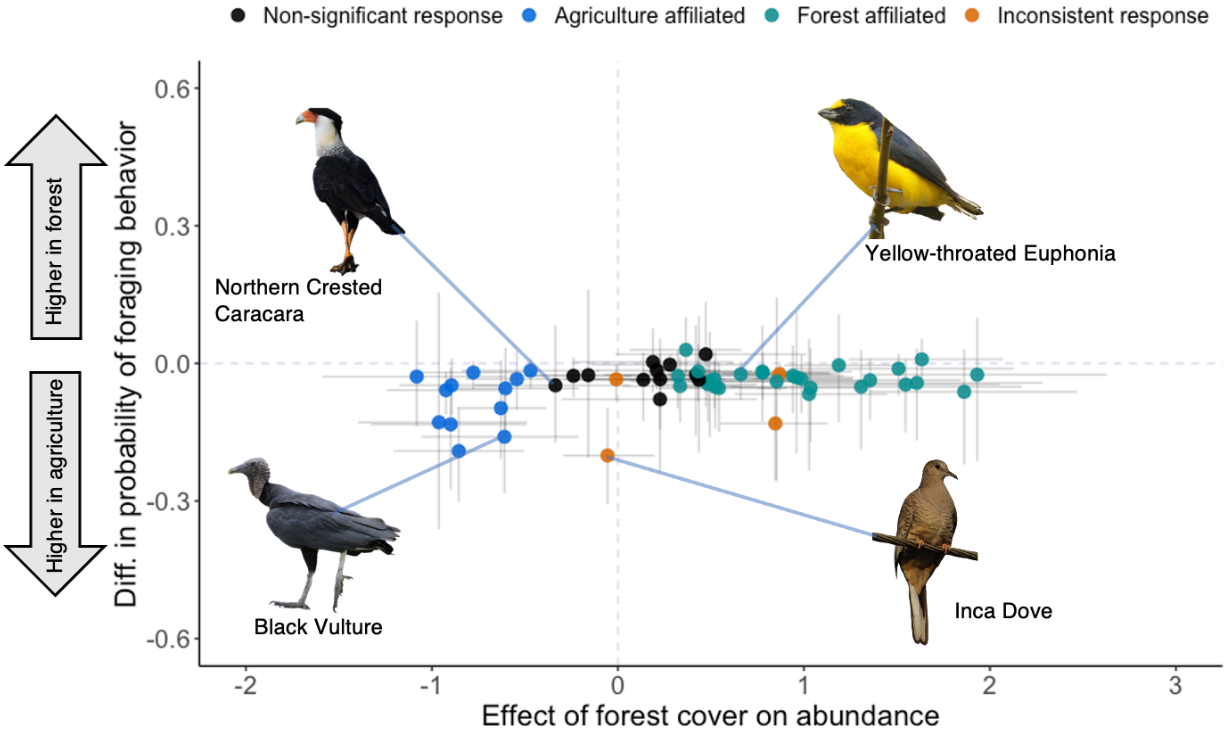


Figure 12: Relationship between the effect of local forest cover on a species' abundance and the predicted difference in a species' probability of performing foraging behaviors between habitats. Grey lines indicate 90% Bayesian credible intervals. Positive values on the y-axis represent a higher probability (on the probability scale) of performing foraging behaviors in forest than agriculture. Colors represent whether species were classified as habitat generalists (black), agriculture affiliated (blue), or forest affiliated (green). Species with inconsistent responses (orange) preferentially exhibited foraging behaviors in agriculture but did not significantly decrease in abundance with forest cover. Representative species in each category are pictured and labeled.

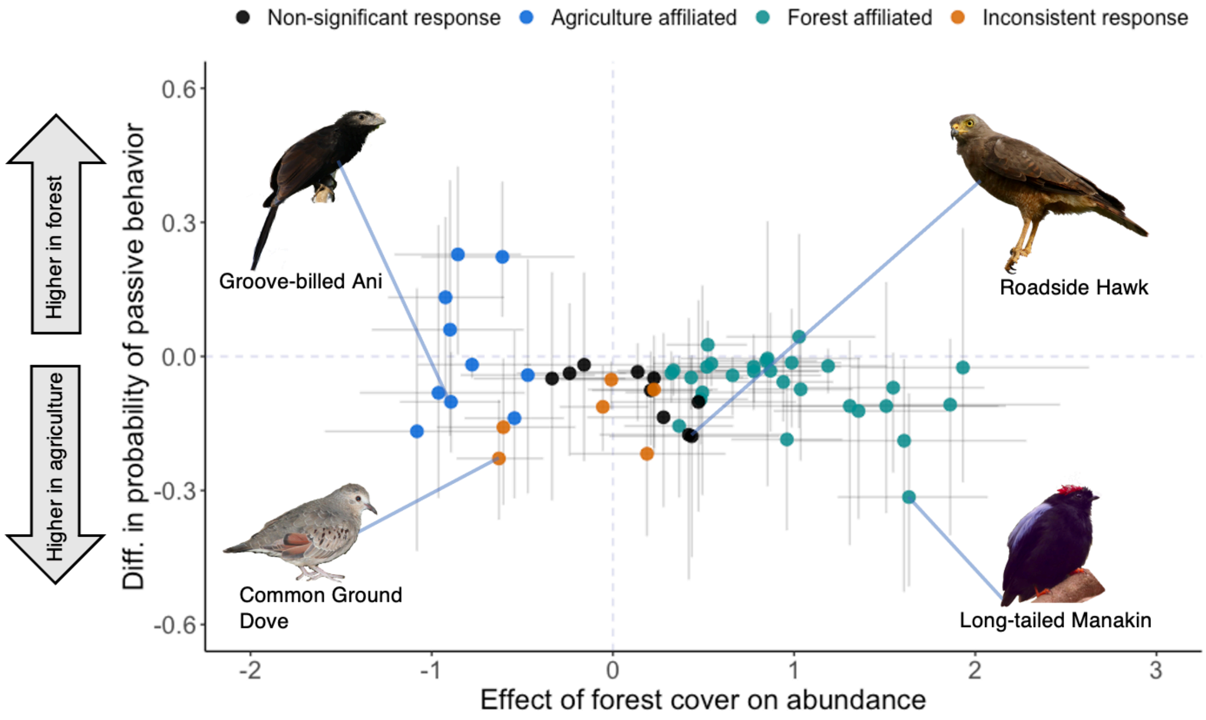


Figure 13: Relationship between the effect of local forest cover on a species' abundance and the predicted difference in a species' probability of performing passive behaviors between habitats. Grey lines indicate 90% Bayesian credible intervals. Positive values on the y-axis represent a higher probability (on the probability scale) of performing passive behaviors in forest than agriculture. Colors represent whether species were classified as habitat generalists (black), agriculture affiliated (blue), or forest affiliated (green). Species with inconsistent responses (orange) preferentially exhibited passive behaviors in agriculture but did not significantly increase in abundance with forest cover. Representative species in each category are pictured and labeled.

Supporting Information 3

Bird surveys

Each observation was also associated with one of 32 behaviors that we classified into three categories: reproductive, foraging, and passive behaviors (*e.g.*, perching; Table S3.1; See Supporting Information for details). We categorized vocalizing behaviors into the reproductive or passive category depending on the species' life history, as determined by expert ornithologist and co-author JZ (Table S3.11). For example, to defend their reproductive territories, some species sing (*e.g.,* Banded Wren [*Thryophilus pleuostictus*]; Catchpole and Slater 2003), while others call (*e.g.*, Lesser Greenlet [*Hylophilus decurtatus*]). We excluded six species from our analysis, as it was not possible to determine whether calling constituted a reproductive behavior: Orange-chinned Parakeet [*Brotogeris jugularis*], Orange-fronted Parakeet [*Aratinga canicularis*], Squirrel Cuckoo [*Piaya cayana*], White-fronted Amazon [*Amazona albifrons*], White-throated Magpie-jay [*Calocitta formosa*], Yellow-naped Amazon [*Amazona auropalliata*]. Aggressive behavior was sometimes placed in the reproductive category, depending on the context of the actual observation. Finally, mobbing, alarm calls, and non-reproductive aggression (~1% of observations combined) were placed into the passive category.

Interpreting behavioral coefficients

Because the values of behavior coefficients are relative to the reference behavior, they do not necessarily reflect how the probabilities of exhibiting behaviors differ between habitats. Thus, we considered the probability of a species performing a behavior to be significantly different between forested and agricultural habitats (or privately-owned versus protected forest) when the 90% Bayesian credible interval (BCI) for the predicted difference in the behavior probability between habitats did not include zero. We calculated this BCI by predicting the probability of each species performing each behavior in landscapes with 0% and 100% forest cover for each posterior sample. Then, we used the 5% and 95% percentiles of the posterior difference between the predicted values to obtain the 90% BCI. We used a 90% BCI for species-level analyses because each parameter is estimated with less data than the community means, and 90% BCIs are recommended when effective sample sizes are lower (Kruschke 2014; McElreath 2020).

To estimate the number of individuals performing each behavior between habitats (Question 1), we multiplied the posterior samples of predicted behavior probabilities (from the behavior N-mixture model) by the posterior samples of predicted abundance (from the traditional N-mixture model), randomly ordering the samples before multiplication. To estimate uncertainty and statistical significance, we used the 2.5th and 97.5th percentile of the multiplied posterior samples for community-wide effects and the 5th and 95th percentile for species-specific effects. Because these quantities come from two different models, the calculations are technically not BCIs and cannot account for the possible covariance of the two quantities. They are therefore likely to overestimate uncertainty.

Modeling behavior

The number of individuals of species (i) performing a certain behavior (b) at site (j) ($N.b_{i,j,b}$) was modeled using a Poisson distribution. The detection probability ($P_{i,j,b,k}$) of an individual of species (i) performing a certain behavior (b) at site (j) and visit (k) was modeled assuming the number of individuals observed is a binomial random variable, with the number of trials equal to $N.b_{i,j,b}$ and success probability as the detection probability:

$$Y_{i,j,b,k} \sim Binomial(N.b_{i,j,b}\ , P_{i,j,b,k})$$

$$N.b_{i,j,b} \sim Poisson(\lambda_{i,j} * \pi_{i,j,b})$$

The true number of individuals across all behavior classes, N, was derived as $N_{i,j} = \sum_{b=1}^{B} N.b_{i,b}$. Here, $\pi_{i,j,b}$ is the probability that an individual of a certain species performs a certain behavior at a site, and $\lambda_{i,j}$ is the expected value of the total abundance ($N_{i,j}$) at a site. We used point-level covariates to explain variation in expected abundance $\lambda_{i,j}$ and in multinomial logistic regression to model behavior probabilities $\pi_{i,j,b}$. Finally, we used point and visit-level covariates to explain variation in the detection probability of an individual of a given species, behavior, site, and visit $P_{i,j,b,k}$.

To capture variation in expected abundance across habitats (Questions 1, 2), we modeled $\lambda_{i,j}$ as

$$\log(\lambda_{i,j}) = \alpha 0_i + \alpha 1_i * \mathrm{TreeCover_j} + \delta 0_{i,farm[j]} + \delta 1_{i,\mathrm{year}[k]} + \delta 2_{i,point[j]}$$

where "TreeCover" is the local forest cover within 50m. Parameters in the α family were estimated for each species, where each species term was drawn from a normal hyperdistribution with a community-level mean and variance. The δ terms represent random effects (normally distributed with mean of zero and variance estimated from the data) that were included to account for spatial and temporal autocorrelation in bird abundances and explain variation among species, point-count locations, farms, or years that was not explained by the other parameters. To understand how bird communities vary in behavior between habitats (Questions 1, 2), we modeled $\pi_{i,j,b}$ as a function of habitat, using multinomial logistic regression. For the first behavior,

$$\pi_{i,j,1} = \frac{1}{1 + \sum_{b=2}^{B} e^{\beta 0_{i,b} + \beta 1_{\mathrm{i,b}} * \mathrm{Habitat}}},$$

and for the remaining behaviors,

$$\pi_{i,j,b} = \frac{e^{\beta 0_{i,b} + \beta 1_{i,b} * \text{Habitat}}}{1 + \sum_{b=2}^{B} e^{\beta 0_{i,b} + \beta 1_{i,b} * \text{Habitat}}} .$$

The first behavior is a reference category that other behaviors are compared to. B is the number of behavior categories; here, B=3 (for reproductive, foraging, and passive behaviors). "Habitat" is a binary variable indicating whether the survey was in forest or agriculture. Parameters in the β family were species-level random effects, which were drawn from a normal distribution with behavior-specific means and variances. Finally, we modelled the detection probability of an individual of a certain species performing a certain behavior at a given site and visit ($P_{i,j,b,k}$) as:

$$\text{logit}(P_{i,j,b,k}) = \gamma 0_{i,b} + \gamma 1_{b} * \text{Noise}_{\text{j,k}} + \gamma 2_{i,b} * \text{Habitat}_{\text{j}} + \gamma 3 * \text{Time}_{\text{j,k}} ,$$

where "Noise" is a binary variable indicating if noise levels exceeded typical background noises and "Time" is the time of day of the point count. Parameters $\gamma 0$ and $\gamma 2$ were species-level random effects, drawn from a normal distribution with behavior-specific means and variances. Parameters $\gamma 1$ and $\gamma 3$ were constant over species and behaviors because we assumed noise would equally affect detectability of behaviors, and that most birds would become less active (and less detectable) later in the day (Robbins 1981).

Table S3.1: Categorization of behavior observations.

Recorded behavior	Behavior category
Aerial Foraging Bark Gleaning Berry Plucking Foliage Gleaning Flower Visiting Sit-And-Wait Foraging Stalking Hawking Eating Ground Rummaging Plant shoot eating Fruit/flower/seed eating Seed plucking Searching Other Foraging	Eat
Alarm Calling (species-dependent) Singing (species-dependent) Mobbing Preening Perching Roosting Fly over Intraspecific aggression (context-specific) Interspecific aggression (context-specific)	Passive
Calling (species-dependent) Singing (species-dependent) Courtship Feeding young Mating Nest building Nest sitting Intraspecific aggression (context-specific) Interspecific aggression (context-specific)	Reproductive

Table S3.2: List of species uses in behavior analyses including the English common name, scientific name, order, and whether species were included in the protected area analysis, where “1” indicates that the species was included and “0” indicates that the species was not included.

Common name	Scientific name	Family	Order	Protected area analysis
Boat-billed Flycatcher	*Megarynchus pitangua*	*Tyrannidae*	*Passeriformes*	0
Blue-black Grassquit	*Volatinia jacarina*	*Emberizidae*	*Passeriformes*	0
Brown-crested Flycatcher	*Myiarchus tyrannulus*	*Tyrannidae*	*Passeriformes*	1
Lesson’s Motmot	*Momotus lessonii*	*Momotidae*	*Coraciiformes*	1
Black-headed Trogon	*Trogon melanocephalus*	*Trogonidae*	*Trogoniformes*	1
Blue Grosbeak	*Passerina caerulea*	*Emberizidae*	*Passeriformes*	0
Black Vulture	*Coragyps atratus*	*Cathartidae*	*Accipitriformes*	0
Banded Wren	*Thryothorus pleurostictus*	*Troglodytidae*	*Passeriformes*	1
Fork-tailed Emerald	*Chlorostilbon canivetii*	*Trochilidae*	*Apodiformes*	1
Clay-coloured Thrush	*Turdus grayi*	*Turdidae*	*Passeriformes*	1
Collared Aracari	*Pteroglossus torquatus*	*Ramphastidae*	*Piciformes*	1
Common Ground-dove	*Columbina passerina*	*Columbidae*	*Columbiformes*	1
Crested Bobwhite	*Colinus cristatus*	*Odontophoridae*	*Galliformes*	0
Crested Caracara	*Caracara cheriway*	*Falconidae*	*Falconiformes*	0
Elegant Trogon	*Trogon elegans*	*Trogonidae*	*Trogoniformes*	1
Ferruginous Pygmy-owl	*Glaucidium brasilianum*	*Strigidae*	*Strigiformes*	1
Groove-billed Ani	*Crotophaga sulcirostris*	*Cuculidae*	*Cuculiformes*	1
Green Kingfisher	*Chloroceryle americana*	*Alcedinidae*	*Coraciiformes*	1
Great Kiskadee	*Pitangus sulphuratus*	*Tyrannidae*	*Passeriformes*	1
Grey-headed Tanager	*Eucometis penicillata*	*Thraupidae*	*Passeriformes*	1
Great-tailed Grackle	*Quiscalus mexicanus*	*Icteridae*	*Passeriformes*	0
Hoffmann's Woodpecker	*Melanerpes hoffmannii*	*Picidae*	*Piciformes*	1
Inca Dove	*Columbina inca*	*Columbidae*	*Columbiformes*	1
Lesser Greenlet	*Hylophilus decurtatus*	*Vireonidae*	*Passeriformes*	1
Lesser Ground-cuckoo	*Morococcyx erythropygus*	*Cuculidae*	*Cuculiformes*	1
Stripe-throated Hermit	*Phaethornis striigularis*	*Trochilidae*	*Apodiformes*	1
Long-tailed Manakin	*Chiroxiphia linearis*	*Pipridae*	*Passeriformes*	1
Masked Tityra	*Tityra semifasciata*	*Cotingidae*	*Passeriformes*	0
Nutting's Flycatcher	*Myiarchus nuttingi*	*Tyrannidae*	*Passeriformes*	1
Plain-capped Starthroat	*Heliomaster constantii*	*Trochilidae*	*Apodiformes*	0
Rufous-and-white Wren	*Thryothorus rufalbus*	*Troglodytidae*	*Passeriformes*	1

Red-billed Pigeon	*Patagioenas flavirostris*	*Columbidae*	*Columbiformes*	1
Ruddy Ground-dove	*Columbina talpacoti*	*Columbidae*	*Columbiformes*	0
Red-legged Honeycreeper	*Cyanerpes cyaneus*	*Thraupidae*	*Passeriformes*	1
Rufous-naped Wren	*Campylorhynchus rufinucha*	*Troglodytidae*	*Passeriformes*	1
Roadside Hawk	*Buteo magnirostris*	*Accipitridae*	*Accipitriformes*	1
Rose-throated Becard	*Pachyramphus aglaiae*	*Cotingidae*	*Passeriformes*	1
Rufous-tailed Hummingbird	*Amazilia tzacatl*	*Trochilidae*	*Apodiformes*	1
Ruddy Woodcreeper	*Dendrocincla homochroa*	*Dendrocolaptidae*	*Passeriformes*	1
Red-winged Blackbird	*Agelaius phoeniceus*	*Icteridae*	*Passeriformes*	0
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	*Tyrannidae*	*Passeriformes*	1
Streak-backed Oriole	*Icterus pustulatus*	*Icteridae*	*Passeriformes*	0
Scrub Euphonia	*Euphonia affinis*	*Thraupidae*	*Passeriformes*	1
Stripe-headed Sparrow	*Aimophila ruficauda*	*Emberizidae*	*Passeriformes*	0
Social Flycatcher	*Myiozetetes similis*	*Tyrannidae*	*Passeriformes*	1
Streaked Flycatcher	*Myiodynastes maculatus*	*Tyrannidae*	*Passeriformes*	1
Steely-vented Hummingbird	*Amazilia saucerrottei*	*Trochilidae*	*Apodiformes*	1
Turquoise-browed Motmot	*Eumomota superciliosa*	*Momotidae*	*Coraciiformes*	1
Tropical Kingbird	*Tyrannus melancholicus*	*Tyrannidae*	*Passeriformes*	0
White-collared Seedeater	*Sporophila torqueola*	*Emberizidae*	*Passeriformes*	1
White-tipped Dove	*Leptotila verreauxi*	*Columbidae*	*Columbiformes*	1
White-winged Dove	*Zenaida asiatica*	*Columbidae*	*Columbiformes*	1
Yellow-green Vireo	*Vireo flavoviridis*	*Vireonidae*	*Passeriformes*	1
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	*Tyrannidae*	*Passeriformes*	1
Yellow-throated Euphonia	*Euphonia hirundinacea*	*Thraupidae*	*Passeriformes*	0

Table S3.3: Mean predicted probabilities and expected numbers of individuals performing foraging, passive, and reproductive behaviors in agriculture versus forest and in protected versus private forest, using community-wide mean parameters. Uncertainty for probabilities is shown by 95% Bayesian credible intervals and uncertainty for numbers of individuals is the 95% percentile interval of the simulated posterior.

Behavior	Habitat	Mean probability of performing behavior	Mean abundance of individuals of performing behavior
Reproductive	Forest	0.792 (0.693, 0.866)	0.354 (0.224, 0.532)
Reproductive	Agriculture	0.627 (0.498, 0.738)	0.106 (0.06, 0.171)
Eating	Forest	0.078 (0.045, 0.126)	0.034 (0.017, 0.062)
Eating	Agriculture	0.128 (0.076, 0.201)	0.021 (0.01, 0.04)
Passive	Forest	0.129 (0.064, 0.224)	0.057 (0.025, 0.112)
Passive	Agriculture	0.243 (0.137, 0.387)	0.041 (0.018, 0.079)
Reproductive	Protected forest	0.89 (0.838, 0.928)	0.566 (0.38, 0.822)
Reproductive	Privately-owned forest	0.835 (0.775, 0.882)	0.477 (0.328, 0.666)
Eating	Protected forest	0.066 (0.039, 0.102)	0.041 (0.021, 0.073)
Eating	Privately-owned forest	0.08 (0.053, 0.114)	0.045 (0.026, 0.073)
Passive	Protected forest	0.043 (0.017, 0.084)	0.027 (0.01, 0.058)
Passive	Privately-owned forest	0.084 (0.045, 0.14)	0.048 (0.023, 0.086)

Table S3.4: Spearman's correlations between species' abundance responses to forest cover and effect of habitat on the probability of performing each behavior (first row), and Spearman's correlations between species' abundance responses to protection status and effect of protection status on the probability of performing each behavior (second row). Abundance responses are positive when species' abundances increase with higher levels of forest cover or in protected forests versus private forests.

	Reproductive	Foraging	Passive
Forest cover	0.02 (*P*=0.90)	0.22 (*P* =0.10)	-0.07 (*P*=0.61)
Protection status	0.15 (*P*=0.37)	-0.09 (*P*=0.59)	-0.12 (*P*=0.47)

Table S3.5: Spearman's correlations between species' global range sizes and their responses to habitat. Responses to habitat include the effects of forest cover and protection status on overall abundance, the predicted difference in probabilities and number of individuals performing each behavior between forest and agriculture, and the predicted difference in probabilities and number of individuals performing each behavior between protected and private forest. Positive correlations indicate that the corresponding response to habitat increases with range size in more forested and protected areas.

Comparison	Response	Rho	P-value
Forest/Agriculture	Abundance	-0.370	0.01
	Probability Reproductive	0.154	0.26
	Probability Foraging	-0.198	0.15
	Probability Passive	-0.138	0.32
	Number Reproductive	-0.293	0.03
	Number Foraging	-0.336	0.01
	Number Passive	-0.378	<0.01
Protected/Private Forest	Abundance	0.085	0.60
	Probability Reproductive	0.113	0.49
	Probability Foraging	0.054	0.74
	Probability Passive	-0.192	0.24
	Number Reproductive	-0.306	0.06
	Number Foraging	0.146	0.37
	Number Passive	0.159	0.33

Table S3.6: Difference between group means and P-values for pairwise Wilcoxon rank sum tests to understand whether differences in abundance across tree cover (or protection levels), as well as differences in behavior between habitats differed between categories of global population trends (decreasing, stable, or increasing). Response variables include the effects of forest cover and protection status on overall abundance, the predicted difference in probabilities and number of individuals performing each behavior between forest and agriculture, and the predicted difference in probabilities and number of individuals performing each behavior between protected and private forest. Positive estimates indicate larger values of corresponding response variables in more forested and protected areas.

Comparison	Response	Contrast	Difference between group means	P-value
Forest/Agriculture	Abundance	Decreasing - Increasing	1.132	<0.001
	Abundance	Decreasing - Stable	0.523	0.05
	Abundance	Increasing - Stable	-0.610	0.05
	Probability Reproductive	Decreasing - Increasing	-0.009	1.00
	Probability Reproductive	Decreasing - Stable	0.001	1.00
	Probability Reproductive	Increasing - Stable	0.010	1.00
	Probability Foraging	Decreasing - Increasing	0.033	0.23
	Probability Foraging	Decreasing - Stable	0.015	0.93
	Probability Foraging	Increasing - Stable	-0.017	0.28
	Probability Passive	Decreasing - Increasing	-0.024	1.00
	Probability Passive	Decreasing - Stable	-0.017	1.00
	Probability Passive	Increasing - Stable	0.007	1.00
	Number Reproductive	Decreasing - Increasing	0.439	0.09
	Number Reproductive	Decreasing - Stable	0.214	0.78
	Number Reproductive	Increasing - Stable	-0.225	0.46
	Number Foraging	Decreasing - Increasing	0.169	<0.001
	Number Foraging	Decreasing - Stable	0.058	0.22
	Number Foraging	Increasing - Stable	-0.111	0.15
	Number Passive	Decreasing - Increasing	0.323	<0.001
	Number Passive	Decreasing - Stable	0.128	0.03
	Number Passive	Increasing - Stable	-0.195	0.02

Protected/Private Forest	Abundance	Decreasing - Increasing	0.167	0.17
	Abundance	Decreasing - Stable	-0.195	0.13
	Abundance	Increasing - Stable	-0.362	0.03
	Probability Reproductive	Decreasing - Increasing	0.016	1.00
	Probability Reproductive	Decreasing - Stable	0.025	1.00
	Probability Reproductive	Increasing - Stable	0.009	1.00
	Probability Foraging	Decreasing - Increasing	-0.011	0.99
	Probability Foraging	Decreasing - Stable	-0.007	1.00
	Probability Foraging	Increasing - Stable	0.004	1.00
	Probability Passive	Decreasing - Increasing	-0.005	1.00
	Probability Passive	Decreasing - Stable	-0.018	0.63
	Probability Passive	Increasing - Stable	-0.013	1.00
	Number Reproductive	Decreasing - Increasing	0.052	0.24
	Number Reproductive	Decreasing - Stable	0.046	0.77
	Number Reproductive	Increasing - Stable	-0.006	0.77
	Number Foraging	Decreasing - Increasing	0.008	1.00
	Number Foraging	Decreasing - Stable	-0.028	1.00
	Number Foraging	Increasing - Stable	-0.035	1.00
	Number Passive	Decreasing - Increasing	-0.060	0.50
	Number Passive	Decreasing - Stable	-0.018	0.73
	Number Passive	Increasing - Stable	0.042	0.79

Table S3.7: Species-level behavior analyses in forest versus agriculture. Column 2 contains the effect of local forest cover on the abundance of each species, as well as the community mean effect. 90% Bayesian credible intervals (BCIs) are shown for each species, and the 95% BCI is shown for the community mean. Columns 3-5 contain the difference in probability of each behavior between forest and agriculture for each species with 90% Bayesian credible intervals (BCIs). Positive values indicate a higher probability in forest, and negative values indicate a higher probability in agriculture.

Species	Effect of local forest cover on abundance	Difference in prob. of reproductive behavior between forest and agriculture	Difference in prob. of eating behavior between forest and agriculture	Difference in prob. of passive behavior between forest and agriculture
Community mean	0.372 (0.131, 0.612)			
Boat-billed Flycatcher	0.519 (0.183, 0.849)	0.057 (0.005, 0.141)	-0.034 (-0.098, 0.004)	-0.023 (-0.073, 0)
Blue-black Grassquit	-0.925 (-1.24, -0.6)	-0.073 (-0.236, 0.134)	-0.058 (-0.11, -0.019)	0.132 (-0.091, 0.311)
Brown-crested Flycatcher	0.323 (0.031, 0.639)	0.065 (-0.009, 0.158)	-0.027 (-0.097, 0.028)	-0.037 (-0.102, 0.01)
Lesson's Motmot	1.617 (0.999, 2.281)	0.231 (0.039, 0.524)	-0.042 (-0.167, 0.032)	-0.188 (-0.526, -0.005)
Black-headed Trogon	0.871 (0.564, 1.178)	0.055 (-0.076, 0.191)	-0.023 (-0.06, -0.001)	-0.032 (-0.167, 0.097)
Blue Grosbeak	-0.469 (-0.84, -0.099)	0.057 (-0.193, 0.31)	-0.016 (-0.055, 0.007)	-0.041 (-0.306, 0.217)
Black Vulture	-0.62 (-1.057, -0.212)	-0.062 (-0.188, -0.001)	-0.16 (-0.281, -0.071)	0.222 (0.088, 0.391)
Banded Wren	0.992 (0.73, 1.259)	0.047 (-0.08, 0.192)	-0.034 (-0.107, 0.017)	-0.013 (-0.158, 0.106)
Fork-tailed Emerald	-0.158 (-0.49, 0.165)	0.044 (-0.041, 0.169)	-0.025 (-0.206, 0.16)	-0.018 (-0.234, 0.187)
Clay-coloured Thrush	0.365 (0.063, 0.663)	0.126 (0, 0.267)	0.029 (-0.034, 0.099)	-0.155 (-0.315, 0)
Collared Aracari	0.497 (0.069, 0.949)	0.119 (-0.092, 0.323)	-0.039 (-0.159, 0.067)	-0.08 (-0.309, 0.158)
Common Ground-dove	-0.628 (-0.863, -0.384)	0.325 (0.173, 0.472)	-0.097 (-0.208, 0.005)	-0.228 (-0.365, -0.097)
Crested Bobwhite	-0.903 (-1.33, -0.492)	0.073 (-0.198, 0.303)	-0.132 (-0.275, -0.01)	0.059 (-0.177, 0.394)
Crested Caracara	-0.344 (-0.767, 0.068)	0.097 (-0.054, 0.323)	-0.048 (-0.172, 0.081)	-0.049 (-0.321, 0.188)

Elegant Trogon	1.357 (0.887, 1.844)	0.158 (0.022, 0.387)	-0.036 (-0.122, 0.009)	-0.122 (-0.363, -0.003)
Ferruginous Pygmy-owl	0.225 (-0.302, 0.747)	0.127 (-0.009, 0.312)	-0.078 (-0.236, 0.019)	-0.048 (-0.216, 0.046)
Groove-billed Ani	-0.896 (-1.174, -0.62)	0.149 (0.022, 0.27)	-0.047 (-0.112, 0.01)	-0.101 (-0.214, 0.009)
Green Kingfisher	0.418 (-0.073, 0.941)	0.199 (-0.032, 0.463)	-0.024 (-0.157, 0.083)	-0.175 (-0.499, 0.085)
Great Kiskadee	0 (-0.288, 0.326)	0.086 (0.025, 0.169)	-0.034 (-0.082, -0.002)	-0.052 (-0.118, -0.011)
Grey-headed Tanager	1.516 (0.933, 2.128)	0.122 (-0.125, 0.347)	-0.011 (-0.069, 0.02)	-0.111 (-0.35, 0.165)
Great-tailed Grackle	-0.855 (-1.205, -0.507)	-0.036 (-0.212, 0.166)	-0.191 (-0.301, -0.096)	0.228 (0.004, 0.424)
Hoffmann's Woodpecker	0.486 (0.224, 0.745)	0.141 (0.04, 0.267)	-0.045 (-0.126, 0.018)	-0.095 (-0.196, -0.028)
Inca Dove	-0.052 (-0.292, 0.195)	0.313 (0.181, 0.439)	-0.2 (-0.306, -0.097)	-0.112 (-0.211, -0.02)
Lesser Greenlet	1.193 (0.894, 1.512)	0.025 (-0.091, 0.15)	-0.004 (-0.127, 0.106)	-0.021 (-0.082, 0.016)
Lesser Ground-cuckoo	0.13 (-0.261, 0.509)	0.07 (-0.022, 0.204)	-0.035 (-0.125, 0.023)	-0.034 (-0.144, 0.028)
Stripe-throated Hermit	1.945 (1.313, 2.627)	0.049 (-0.127, 0.235)	-0.024 (-0.212, 0.099)	-0.024 (-0.281, 0.286)
Long-tailed Manakin	1.642 (1.241, 2.067)	0.305 (0.107, 0.487)	0.008 (-0.045, 0.053)	-0.314 (-0.514, -0.082)
Masked Tityra	0.194 (-0.236, 0.62)	0.215 (0.064, 0.392)	0.002 (-0.062, 0.076)	-0.217 (-0.401, -0.071)
Nutting's Flycatcher	1.546 (1.045, 2.049)	0.116 (0.006, 0.309)	-0.046 (-0.149, 0.007)	-0.069 (-0.259, 0.007)
Plain-capped Starthroat	0.479 (-0.012, 1.011)	0.082 (-0.06, 0.281)	0.019 (-0.093, 0.133)	-0.102 (-0.346, 0.125)
Rufous-and-white Wren	1.885 (1.352, 2.467)	0.17 (-0.002, 0.419)	-0.061 (-0.22, 0.03)	-0.108 (-0.4, 0.039)
Red-billed Pigeon	0.273 (-0.141, 0.666)	0.138 (-0.033, 0.331)	-0.002 (-0.03, 0.018)	-0.136 (-0.336, 0.051)
Ruddy Ground-dove	-0.952 (-1.396, -0.486)	0.21 (-0.019, 0.457)	-0.128 (-0.36, 0.153)	-0.081 (-0.316, 0.293)
Red-legged Honeycreeper	0.789 (0.337, 1.259)	0.04 (-0.084, 0.172)	-0.017 (-0.127, 0.082)	-0.023 (-0.119, 0.048)
Rufous-naped Wren	0.521 (0.296, 0.738)	0.025 (-0.064, 0.12)	-0.051 (-0.14, 0.024)	0.025 (-0.02, 0.079)
Roadside Hawk	0.436 (-0.02, 0.917)	0.214 (0.015, 0.432)	-0.035 (-0.194, 0.102)	-0.178 (-0.449, 0.002)
Rose-throated Becard	0.428 (0.133, 0.718)	0.064 (-0.011, 0.158)	-0.017 (-0.082, 0.041)	-0.047 (-0.118, -0.004)
Rufous-tailed Hummingbird	1.031 (0.626, 1.447)	0.023 (-0.093, 0.155)	-0.066 (-0.233, 0.052)	0.043 (-0.159, 0.273)
Ruddy Woodcreeper	1.336 (0.605, 2.168)	0.162 (-0.007, 0.431)	-0.051 (-0.187, 0.028)	-0.111 (-0.422, 0.035)
Red-winged Blackbird	-1.083 (-1.589, -0.596)	0.196 (-0.084, 0.437)	-0.028 (-0.136, 0.093)	-0.167 (-0.435, 0.152)
Sulphur-bellied Flycatcher	0.209 (-0.114, 0.549)	0.091 (-0.003, 0.214)	-0.015 (-0.056, 0.013)	-0.075 (-0.198, 0.01)

Streak-backed Oriole	0.337 (0.024, 0.65)	0.08 (0.008, 0.171)	-0.049 (-0.128, 0.012)	-0.031 (-0.087, -0.001)
Scrub Euphonia	0.55 (0.222, 0.907)	0.07 (0.001, 0.177)	-0.054 (-0.148, 0.001)	-0.016 (-0.066, 0.013)
Stripe-headed Sparrow	-0.773 (-1.076, -0.452)	0.038 (0.004, 0.084)	-0.019 (-0.055, 0.004)	-0.018 (-0.048, 0)
Social Flycatcher	0.224 (-0.138, 0.578)	0.108 (-0.009, 0.261)	-0.034 (-0.143, 0.054)	-0.074 (-0.204, 0)
Streaked Flycatcher	0.782 (0.427, 1.135)	0.053 (-0.009, 0.147)	-0.02 (-0.079, 0.021)	-0.033 (-0.102, 0.001)
Steely-vented Hummingbird	0.858 (0.373, 1.364)	0.044 (-0.146, 0.246)	-0.039 (-0.256, 0.142)	-0.004 (-0.289, 0.302)
Turquoise-browed Motmot	0.941 (0.669, 1.215)	0.084 (-0.011, 0.191)	-0.027 (-0.107, 0.038)	-0.057 (-0.145, 0.003)
Tropical Kingbird	-0.601 (-0.97, -0.207)	0.212 (0.05, 0.388)	-0.054 (-0.157, 0.033)	-0.158 (-0.331, -0.004)
White-collared Seedeater	-0.543 (-0.818, -0.27)	0.172 (-0.009, 0.347)	-0.034 (-0.1, 0.026)	-0.138 (-0.317, 0.057)
White-tipped Dove	0.959 (0.654, 1.265)	0.216 (0.039, 0.392)	-0.03 (-0.195, 0.112)	-0.185 (-0.388, -0.038)
White-winged Dove	-0.233 (-0.53, 0.071)	0.064 (-0.067, 0.236)	-0.027 (-0.072, 0.011)	-0.037 (-0.222, 0.118)
Yellow-green Vireo	0.846 (0.549, 1.125)	0.141 (0.034, 0.264)	-0.131 (-0.255, -0.026)	-0.01 (-0.037, 0.005)
Yellow-olive Flycatcher	1.036 (0.744, 1.322)	0.126 (-0.004, 0.289)	-0.053 (-0.17, 0.031)	-0.073 (-0.232, 0.031)
Yellow-throated Euphonia	0.668 (0.21, 1.148)	0.066 (0.006, 0.166)	-0.023 (-0.077, 0.003)	-0.042 (-0.131, -0.001)

Table S3.8: Species-level behavior analyses in private versus protected forest. Column 2 contains the effect of protected forest (versus privately-owned forest) on the abundance of each species, as well as the community mean effect. 90% Bayesian credible intervals (BCIs) are shown for each species, and the 95% BCI is shown for the community mean. Columns 3-5 contain the difference in probability of each behavior between privately-owned and protected forest for each species with 90% Bayesian credible intervals (BCIs). Positive values indicate a higher probability in protected forest, and negative values indicate a higher probability in privately-owned forest.

Species	Mean effect of protection level on abundance	Difference in prob. of reproductive behavior between protected and private forest	Difference in prob. of eating behavior between protected and private forest	Difference in prob. of passive behavior between protected and private forest
Community mean	0.114 (-0.119, 0.351)			
Brown-crested Flycatcher	-0.328 (-1.019, 0.309)	0.009 (-0.079, 0.079)	0.007 (-0.054, 0.091)	-0.016 (-0.054, 0.012)
Lesson’s Motmot	0.577 (-0.045, 1.259)	0.058 (-0.001, 0.143)	-0.028 (-0.088, 0.02)	-0.03 (-0.099, 0.003)
Black-headed Trogon	-0.179 (-0.799, 0.408)	0.079 (0.005, 0.165)	0 (-0.023, 0.028)	-0.079 (-0.165, -0.004)
Banded Wren	-0.334 (-0.99, 0.28)	0.111 (0.037, 0.195)	-0.011 (-0.05, 0.032)	-0.099 (-0.177, -0.036)
Fork-tailed Emerald	0.006 (-0.64, 0.643)	0.047 (-0.136, 0.221)	-0.011 (-0.105, 0.096)	-0.036 (-0.188, 0.133)
Clay-coloured Thrush	0.245 (-0.363, 0.866)	0.131 (0.02, 0.249)	0.059 (0, 0.142)	-0.191 (-0.315, -0.07)
Collared Aracari	0.057 (-0.588, 0.706)	-0.136 (-0.35, 0.028)	-0.006 (-0.072, 0.072)	0.143 (-0.022, 0.372)
Common Ground-dove	-0.331 (-0.988, 0.273)	0.058 (-0.025, 0.142)	-0.013 (-0.079, 0.066)	-0.044 (-0.098, -0.004)
Elegant Trogon	0.56 (-0.039, 1.202)	0.023 (-0.033, 0.086)	-0.003 (-0.047, 0.044)	-0.02 (-0.065, 0.003)
Ferruginous Pygmy-owl	0.496 (-0.159, 1.197)	0.052 (-0.026, 0.161)	-0.009 (-0.062, 0.047)	-0.042 (-0.153, 0.005)
Groove-billed Ani	-0.063 (-0.705, 0.55)	-0.086 (-0.238, 0.028)	0.06 (-0.013, 0.185)	0.025 (-0.063, 0.151)
Green Kingfisher	0.388 (-0.253, 1.069)	0.117 (0, 0.288)	-0.012 (-0.075, 0.055)	-0.105 (-0.288, 0.006)
Great Kiskadee	-0.088 (-0.736, 0.503)	-0.011 (-0.073, 0.033)	0 (-0.033, 0.044)	0.01 (-0.013, 0.053)
Grey-headed Tanager	0.399 (-0.225, 1.05)	0.093 (-0.057, 0.246)	-0.011 (-0.04, 0.011)	-0.082 (-0.238, 0.078)

Hoffmann's Woodpecker	0.007 (-0.553, 0.547)	0.058 (0.009, 0.112)	-0.048 (-0.097, -0.005)	-0.009 (-0.033, 0.013)
Inca Dove	-0.259 (-0.87, 0.329)	0.009 (-0.057, 0.07)	0.005 (-0.031, 0.052)	-0.015 (-0.067, 0.042)
Lesser Greenlet	0.323 (-0.255, 0.909)	0.081 (0.012, 0.161)	-0.065 (-0.144, 0.001)	-0.015 (-0.047, 0.003)
Lesser Ground-cuckoo	-0.275 (-0.966, 0.359)	0.029 (-0.043, 0.102)	-0.014 (-0.066, 0.042)	-0.015 (-0.066, 0.024)
Stripe-throated Hermit	0.613 (-0.017, 1.315)	0.192 (0.027, 0.369)	0.036 (-0.015, 0.108)	-0.228 (-0.407, -0.054)
Long-tailed Manakin	0.447 (-0.15, 1.078)	0.03 (-0.053, 0.109)	-0.001 (-0.031, 0.032)	-0.029 (-0.111, 0.055)
Nutting's Flycatcher	-0.128 (-0.735, 0.469)	0.009 (-0.063, 0.066)	-0.014 (-0.058, 0.031)	0.004 (-0.026, 0.058)
Rufous-and-white Wren	0.542 (-0.03, 1.158)	0.072 (-0.003, 0.162)	-0.025 (-0.082, 0.028)	-0.047 (-0.127, 0.012)
Red-billed Pigeon	-0.309 (-1.099, 0.352)	0.318 (0.095, 0.538)	0.013 (-0.017, 0.066)	-0.331 (-0.559, -0.096)
Red-legged Honeycreeper	0.376 (-0.269, 0.997)	0.081 (0.011, 0.165)	-0.054 (-0.123, 0.001)	-0.026 (-0.078, 0.008)
Rufous-naped Wren	0.02 (-0.579, 0.578)	0.071 (0.004, 0.14)	-0.013 (-0.065, 0.043)	-0.058 (-0.111, -0.019)
Roadside Hawk	0.062 (-0.591, 0.712)	0.031 (-0.066, 0.124)	-0.008 (-0.082, 0.082)	-0.022 (-0.088, 0.019)
Rose-throated Becard	0.137 (-0.455, 0.736)	0.042 (-0.008, 0.098)	-0.033 (-0.088, 0.014)	-0.009 (-0.032, 0.005)
Rufous-tailed Hummingbird	0.281 (-0.338, 0.92)	0.021 (-0.162, 0.198)	0.023 (-0.026, 0.09)	-0.044 (-0.229, 0.148)
Ruddy Woodcreeper	0.199 (-0.478, 0.869)	0.03 (-0.057, 0.121)	-0.023 (-0.082, 0.026)	-0.007 (-0.082, 0.068)
Sulphur-bellied Flycatcher	-0.129 (-0.779, 0.494)	0.037 (-0.017, 0.099)	-0.013 (-0.055, 0.026)	-0.024 (-0.074, 0.011)
Scrub Euphonia	-0.046 (-0.67, 0.552)	0.032 (-0.008, 0.08)	-0.021 (-0.061, 0.013)	-0.011 (-0.037, 0.007)
Social Flycatcher	-0.15 (-0.83, 0.477)	0.034 (-0.028, 0.097)	-0.023 (-0.08, 0.035)	-0.011 (-0.041, 0.006)
Streaked Flycatcher	0.316 (-0.283, 0.935)	0.034 (-0.007, 0.084)	-0.026 (-0.071, 0.012)	-0.008 (-0.031, 0.004)
Steely-vented Hummingbird	0.48 (-0.174, 1.177)	-0.024 (-0.218, 0.151)	0.022 (-0.058, 0.131)	0.002 (-0.181, 0.197)
Turquoise-browed Motmot	0.078 (-0.492, 0.656)	0.026 (-0.042, 0.088)	-0.003 (-0.058, 0.059)	-0.023 (-0.061, 0.007)
White-collared Seedeater	-0.27 (-0.992, 0.381)	0.068 (-0.102, 0.234)	0.033 (-0.028, 0.145)	-0.101 (-0.267, 0.06)
White-tipped Dove	0.399 (-0.202, 1)	-0.072 (-0.169, 0.018)	0.117 (0.035, 0.211)	-0.045 (-0.102, 0.002)
White-winged Dove	-0.001 (-0.662, 0.641)	-0.294 (-0.458, -0.131)	-0.035 (-0.075, -0.008)	0.329 (0.154, 0.502)
Yellow-green Vireo	0.296 (-0.295, 0.872)	0.074 (0.021, 0.141)	-0.066 (-0.132, -0.015)	-0.008 (-0.026, 0.002)
Yellow-olive Flycatcher	0.187 (-0.381, 0.765)	0.071 (-0.002, 0.152)	-0.024 (-0.079, 0.03)	-0.047 (-0.112, -0.001)

Table S3.9: The difference in abundance of individuals performing each behavior between forest and agriculture for each species, with 90% Bayesian credible intervals (BCIs). Positive values indicate a higher abundance in forest, and negative values indicate a higher abundance in agriculture.

Species	Difference in # individuals reproductive between forest and agriculture	Difference in # individuals eating between forest and agriculture	Difference in # individuals passive between forest and agriculture
Boat-billed Flycatcher	1.266 (0.251, 2.735)	0.021 (-0.045, 0.104)	-0.001 (-0.038, 0.033)
Blue-black Grassquit	-0.305 (-0.633, -0.082)	-0.089 (-0.196, -0.025)	-0.579 (-1.248, -0.105)
Brown-crested Flycatcher	0.723 (-0.14, 2.015)	0.03 (-0.068, 0.159)	0.002 (-0.064, 0.08)
Lesson’s Motmot	0.394 (0.156, 0.813)	0.026 (0.003, 0.074)	0.022 (0, 0.077)
Black-headed Trogon	2.443 (0.824, 5.175)	0.025 (-0.016, 0.089)	0.403 (0.057, 1.053)
Blue Grosbeak	-0.074 (-0.253, 0.064)	-0.008 (-0.03, 0.002)	-0.108 (-0.326, 0.053)
Black Vulture	-0.073 (-0.243, 0)	-0.145 (-0.352, -0.036)	-0.373 (-1.062, 0.129)
Banded Wren	1.321 (0.636, 2.269)	0.07 (0.006, 0.173)	0.207 (0.054, 0.435)
Fork-tailed Emerald	-0.023 (-0.122, 0.043)	-0.109 (-0.318, 0.023)	-0.165 (-0.467, 0.03)
Clay-coloured Thrush	0.055 (-0.009, 0.14)	0.015 (-0.009, 0.048)	0.037 (-0.15, 0.208)
Collared Aracari	0.181 (0.006, 0.512)	0.028 (-0.012, 0.109)	0.087 (-0.023, 0.283)
Common Ground-dove	-1.164 (-2.972, 0.043)	-0.823 (-1.772, -0.219)	-1.266 (-2.593, -0.405)
Crested Bobwhite	-0.15 (-0.415, 0)	-0.085 (-0.217, -0.014)	-0.085 (-0.248, 0.01)
Crested Caracara	0.003 (-0.064, 0.08)	-0.014 (-0.06, 0.022)	-0.047 (-0.223, 0.109)
Elegant Trogon	0.554 (0.264, 0.993)	0.019 (0.002, 0.055)	0.017 (-0.002, 0.057)
Ferruginous Pygmy-owl	0.035 (-0.04, 0.123)	0 (-0.021, 0.016)	0 (-0.016, 0.014)
Groove-billed Ani	-3.061 (-6.134, -1.037)	-0.563 (-1.24, -0.174)	-1.075 (-2.3, -0.345)
Green Kingfisher	0.038 (-0.025, 0.124)	0.002 (-0.015, 0.021)	0 (-0.048, 0.043)
Great Kiskadee	0.585 (-1.485, 2.859)	-0.048 (-0.222, 0.076)	-0.083 (-0.281, 0.039)
Grey-headed Tanager	0.116 (0.027, 0.3)	0.006 (0, 0.02)	0.211 (0.057, 0.482)
Great-tailed Grackle	-0.2 (-0.509, -0.014)	-0.188 (-0.42, -0.059)	-0.268 (-0.706, 0.028)
Hoffmann's Woodpecker	2.34 (0.634, 4.672)	0.154 (-0.072, 0.478)	-0.015 (-0.186, 0.162)
Inca Dove	1.043 (-1.645, 4.049)	-0.888 (-2.112, -0.014)	-0.514 (-1.518, 0.252)
Lesser Greenlet	0.827 (0.432, 1.39)	0.143 (0.054, 0.278)	0.018 (-0.001, 0.06)
Lesser Ground-cuckoo	0.019 (-0.243, 0.252)	-0.007 (-0.045, 0.019)	-0.007 (-0.045, 0.018)
Stripe-throated Hermit	0.179 (0.031, 0.497)	0.085 (0.019, 0.22)	0.582 (0.199, 1.264)

Long-tailed Manakin	0.626 (0.296, 1.121)	0.055 (0.017, 0.125)	0.614 (0.284, 1.143)
Masked Tityra	0.22 (-0.09, 0.667)	0.014 (-0.02, 0.068)	-0.033 (-0.118, 0.025)
Nutting's Flycatcher	0.799 (0.332, 1.602)	0.03 (0.003, 0.092)	0.021 (0, 0.067)
Plain-capped Starthroat	0.023 (-0.01, 0.09)	0.01 (-0.006, 0.04)	0.054 (-0.053, 0.196)
Rufous-and-white Wren	0.491 (0.236, 0.881)	0.042 (0.01, 0.103)	0.044 (0.009, 0.108)
Red-billed Pigeon	0.05 (-0.01, 0.144)	0.001 (-0.004, 0.008)	0.064 (-0.103, 0.255)
Ruddy Ground-dove	-0.068 (-0.269, 0.06)	-0.155 (-0.387, -0.015)	-0.12 (-0.315, -0.002)
Red-legged Honeycreeper	0.332 (0.049, 0.809)	0.043 (-0.004, 0.128)	0.018 (-0.006, 0.069)
Rufous-naped Wren	1.259 (0.4, 2.344)	0.114 (-0.048, 0.331)	0.109 (0.018, 0.257)
Roadside Hawk	0.075 (-0.01, 0.221)	0.01 (-0.014, 0.05)	0 (-0.034, 0.035)
Rose-throated Becard	0.614 (0.014, 1.409)	0.031 (-0.033, 0.125)	-0.007 (-0.052, 0.031)
Rufous-tailed Hummingbird	0.09 (0.008, 0.25)	0.055 (0.004, 0.15)	0.397 (0.128, 0.868)
Ruddy Woodcreeper	0.193 (0.047, 0.5)	0.013 (0, 0.047)	0.017 (-0.001, 0.064)
Red-winged Blackbird	-0.108 (-0.318, 0.003)	-0.037 (-0.107, -0.002)	-0.134 (-0.366, -0.019)
Sulphur-bellied Flycatcher	0.248 (-0.282, 0.841)	0 (-0.034, 0.033)	-0.019 (-0.115, 0.057)
Streak-backed Oriole	0.582 (0.005, 1.445)	0.018 (-0.048, 0.107)	-0.004 (-0.033, 0.024)
Scrub Euphonia	0.889 (0.107, 2.058)	0.022 (-0.055, 0.122)	0.012 (-0.023, 0.067)
Stripe-headed Sparrow	-2.277 (-4.73, -0.708)	-0.105 (-0.271, -0.016)	-0.076 (-0.201, -0.01)
Social Flycatcher	0.112 (-0.138, 0.388)	0.002 (-0.049, 0.052)	-0.011 (-0.053, 0.017)
Streaked Flycatcher	0.951 (0.267, 2.05)	0.036 (-0.006, 0.116)	0.007 (-0.016, 0.046)
Steely-vented Hummingbird	0.064 (0, 0.188)	0.042 (-0.001, 0.12)	0.112 (0.012, 0.29)
Turquoise-browed Motmot	1.727 (0.819, 3.049)	0.161 (0.036, 0.364)	0.068 (-0.012, 0.198)
Tropical Kingbird	-0.158 (-0.481, 0.061)	-0.05 (-0.143, 0)	-0.105 (-0.266, -0.013)
White-collared Seedeater	-0.226 (-0.607, 0.059)	-0.059 (-0.156, -0.002)	-0.265 (-0.596, -0.038)
White-tipped Dove	1.748 (0.754, 3.225)	0.518 (0.159, 1.076)	0.188 (-0.017, 0.508)
White-winged Dove	0.06 (-0.216, 0.465)	-0.028 (-0.114, 0.041)	-0.053 (-0.933, 1.042)
Yellow-green Vireo	1.105 (0.497, 1.959)	0.118 (0.012, 0.298)	0.008 (-0.003, 0.031)
Yellow-olive Flycatcher	0.689 (0.361, 1.105)	0.063 (0.012, 0.148)	0.05 (0.003, 0.132)
Yellow-throated Euphonia	0.564 (0.108, 1.46)	0.009 (-0.004, 0.038)	0.005 (-0.009, 0.03)

Table S3.10: The difference in abundance of individuals performing each behavior between privately-owned and protected forest for each species, with 90% Bayesian credible intervals (BCIs). Positive values indicate a higher abundance in protected forest, and negative values indicate a higher abundance in privately-owned forest.

Species	Difference in # individuals reproductive between protected and private forest	Difference in # individuals eating between protected and private forest	Difference in # individuals passive between protected and private forest
Brown-crested Flycatcher	0.007 (-0.841, 0.865)	0.005 (-0.099, 0.13)	-0.012 (-0.061, 0.029)
Lesson’s Motmot	0.034 (-0.627, 0.706)	-0.016 (-0.099, 0.054)	-0.017 (-0.077, 0.016)
Black-headed Trogon	0.167 (-2.052, 2.514)	0 (-0.117, 0.121)	-0.166 (-0.65, 0.204)
Banded Wren	0.131 (-0.866, 1.17)	-0.013 (-0.119, 0.095)	-0.117 (-0.29, 0.009)
Fork-tailed Emerald	0.009 (-0.168, 0.191)	-0.002 (-0.059, 0.058)	-0.008 (-0.093, 0.072)
Clay-coloured Thrush	0.056 (-0.149, 0.284)	0.025 (-0.026, 0.098)	-0.082 (-0.361, 0.166)
Collared Aracari	-0.06 (-0.599, 0.446)	-0.002 (-0.083, 0.077)	0.065 (-0.122, 0.346)
Common Ground-dove	0.038 (-0.6, 0.724)	-0.008 (-0.124, 0.111)	-0.028 (-0.1, 0.02)
Elegant Trogon	0.019 (-0.834, 0.882)	-0.002 (-0.083, 0.081)	-0.016 (-0.071, 0.019)
Ferruginous Pygmy-owl	0.014 (-0.383, 0.419)	-0.002 (-0.041, 0.035)	-0.011 (-0.059, 0.015)
Groove-billed Ani	-0.058 (-0.811, 0.653)	0.04 (-0.072, 0.204)	0.017 (-0.117, 0.18)
Green Kingfisher	0.029 (-0.3, 0.366)	-0.003 (-0.042, 0.034)	-0.026 (-0.122, 0.034)
Great Kiskadee	-0.021 (-2.141, 2.1)	0.001 (-0.145, 0.161)	0.017 (-0.06, 0.129)
Grey-headed Tanager	0.042 (-0.27, 0.389)	-0.004 (-0.031, 0.016)	-0.036 (-0.402, 0.306)
Hoffmann's Woodpecker	0.16 (-2.743, 3.128)	-0.134 (-0.509, 0.182)	-0.026 (-0.144, 0.08)
Inca Dove	0.022 (-2.227, 2.312)	0.013 (-0.204, 0.266)	-0.036 (-0.297, 0.227)
Lesser Greenlet	0.101 (-0.887, 1.155)	-0.081 (-0.315, 0.119)	-0.019 (-0.076, 0.022)
Lesser Ground-cuckoo	0.008 (-0.345, 0.362)	-0.003 (-0.038, 0.031)	-0.004 (-0.031, 0.019)
Stripe-throated Hermit	0.183 (-0.384, 0.918)	0.033 (-0.07, 0.168)	-0.215 (-0.998, 0.436)
Long-tailed Manakin	0.041 (-0.723, 0.836)	-0.001 (-0.098, 0.097)	-0.041 (-0.712, 0.622)
Nutting's Flycatcher	0.005 (-0.685, 0.681)	-0.008 (-0.065, 0.048)	0.002 (-0.034, 0.048)
Rufous-and-white Wren	0.048 (-0.541, 0.661)	-0.016 (-0.101, 0.059)	-0.031 (-0.13, 0.04)
Red-billed Pigeon	0.089 (-0.165, 0.417)	0.003 (-0.014, 0.03)	-0.092 (-0.314, 0.069)
Red-legged Honeycreeper	0.052 (-0.798, 0.906)	-0.036 (-0.169, 0.061)	-0.017 (-0.082, 0.028)
Rufous-naped Wren	0.144 (-1.5, 1.793)	-0.025 (-0.269, 0.243)	-0.116 (-0.294, 0.003)
Roadside Hawk	0.006 (-0.315, 0.315)	-0.002 (-0.046, 0.045)	-0.004 (-0.027, 0.013)

Rose-throated Becard	0.048 (-1.268, 1.36)	-0.037 (-0.185, 0.087)	-0.01 (-0.055, 0.023)
Rufous-tailed Hummingbird	0.013 (-0.325, 0.385)	0.013 (-0.051, 0.095)	-0.027 (-0.458, 0.387)
Ruddy Woodcreeper	0.009 (-0.434, 0.47)	-0.006 (-0.047, 0.031)	-0.002 (-0.044, 0.041)
Sulphur-bellied Flycatcher	0.027 (-0.785, 0.883)	-0.009 (-0.076, 0.055)	-0.017 (-0.077, 0.028)
Scrub Euphonia	0.044 (-1.459, 1.556)	-0.027 (-0.145, 0.074)	-0.015 (-0.074, 0.029)
Social Flycatcher	0.018 (-0.646, 0.698)	-0.012 (-0.093, 0.06)	-0.006 (-0.033, 0.013)
Streaked Flycatcher	0.043 (-1.405, 1.597)	-0.031 (-0.159, 0.084)	-0.011 (-0.06, 0.021)
Steely-vented Hummingbird	-0.01 (-0.405, 0.378)	0.009 (-0.078, 0.11)	0.001 (-0.221, 0.23)
Turquoise-browed Motmot	0.045 (-1.468, 1.596)	-0.006 (-0.251, 0.236)	-0.039 (-0.154, 0.051)
White-collared Seedeater	0.015 (-0.193, 0.235)	0.007 (-0.022, 0.049)	-0.024 (-0.114, 0.046)
White-tipped Dove	-0.211 (-2.767, 2.243)	0.351 (-0.406, 1.326)	-0.133 (-0.53, 0.182)
White-winged Dove	-0.201 (-0.665, 0.143)	-0.024 (-0.08, 0.009)	0.226 (-0.341, 0.931)
Yellow-green Vireo	0.095 (-1.074, 1.297)	-0.086 (-0.28, 0.057)	-0.01 (-0.044, 0.016)
Yellow-olive Flycatcher	0.061 (-0.652, 0.769)	-0.02 (-0.114, 0.072)	-0.04 (-0.124, 0.022)

Table S3.11: Table describes how species' singing and calling behaviors were categorized. 'Singing reproductive territory defense' indicates whether or not singing represents a reproductive activity (e.g. attracting mates) or reproductive territory defense (Y=Yes, N=No, M=Maybe). 'Calling reproductive' indicates whether or not calling represents a reproductive activity (e.g. attracting mates; Y=Yes, N=No, M=Maybe, NA=Not applicable as calling not in dataset). 'Calling Territory Defense' indicates whether or not calling represents a reproductive territory defense (Y=Yes, N=No, M=Maybe, NA=Not applicable as calling not in dataset). We excluded species with "Maybe" categorizations from the analysis.

Common name	Scientific name	Singing Reproductive Territory Defense	Calling Reproductive	Calling Territory Defense
Red-winged Blackbird	*Agelaius phoeniceus*	Y	Y	Y
Stripe-headed Sparrow	*Aimophila ruficauda*	Y	Y	Y
Steely-vented Hummingbird	*Amazilia saucerrottei*	Y	N	N
Rufous-tailed Hummingbird	*Amazilia tzacatl*	Y	N	Y
Roadside Hawk	*Buteo magnirostris*	Y	NA	NA
Rufous-naped Wren	*Campylorhynchus rufinucha*	Y	NA	NA
Crested Caracara	*Caracara cheriway*	Y	N	N
Long-tailed Manakin	*Chiroxiphia linearis*	Y	N	N
Green Kingfisher	*Chloroceryle americana*	Y	NA	NA
Fork-tailed Emerald	*Chlorostilbon canivetii*	Y	N	N
Crested Bobwhite	*Colinus cristatus*	Y	N	N
Inca Dove	*Columbina inca*	Y	NA	NA
Common Ground-dove	*Columbina passerina*	Y	NA	NA
Ruddy Ground-dove	*Columbina talpacoti*	Y	NA	NA
Black Vulture	*Coragyps atratus*	NA	NA	NA
Groove-billed Ani	*Crotophaga sulcirostris*	Y	NA	NA
Red-legged Honeycreeper	*Cyanerpes cyaneus*	Y	NA	NA

Ruddy Woodcreeper	*Dendrocincla homochroa*	Y	Y	Y
Grey-headed Tanager	*Eucometis penicillata*	Y	N	N
Turquoise-browed Motmot	*Eumomota superciliosa*	Y	Y	Y
Scrub Euphonia	*Euphonia affinis*	Y	Y	Y
Yellow-throated Euphonia	*Euphonia hirundinacea*	Y	NA	NA
Ferruginous Pygmy-owl	*Glaucidium brasilianum*	Y	Y	Y
Plain-capped Starthroat	*Heliomaster constantii*	Y	N	N
Lesser Greenlet	*Hylophilus decurtatus*	Y	NA	NA
Streak-backed Oriole	*Icterus pustulatus*	Y	Y	Y
White-tipped Dove	*Leptotila verreauxi*	Y	NA	NA
Boat-billed Flycatcher	*Megarynchus pitangua*	Y	NA	NA
Hoffmann's Woodpecker	*Melanerpes hoffmannii*	Y	NA	NA
Lesson’s Motmot	*Momotus lessonii*	Y	N	Y
Lesser Ground-cuckoo	*Morococcyx erythropygus*	Y	Y	Y
Nutting's Flycatcher	*Myiarchus nuttingi*	Y	Y	Y
Brown-crested Flycatcher	*Myiarchus tyrannulus*	Y	NA	NA
Sulphur-bellied Flycatcher	*Myiodynastes luteiventris*	Y	NA	NA
Streaked Flycatcher	*Myiodynastes maculatus*	Y	NA	NA
Social Flycatcher	*Myiozetetes similis*	Y	NA	NA
Rose-throated Becard	*Pachyramphus aglaiae*	Y	NA	NA
Blue Grosbeak	*Passerina caerulea*	Y	N	N
Red-billed Pigeon	*Patagioenas flavirostris*	Y	NA	NA
Stripe-throated Hermit	*Phaethornis striigularis*	Y	N	N
Great Kiskadee	*Pitangus sulphuratus*	Y	NA	NA
Collared Aracari	*Pteroglossus torquatus*	Y	NA	NA
Great-tailed Grackle	*Quiscalus mexicanus*	Y	N	N
White-collared Seedeater	*Sporophila torqueola*	Y	N	N
Banded Wren	*Thryothorus pleurostictus*	Y	N	N
Rufous-and-white Wren	*Thryothorus rufalbus*	Y	N	N
Masked Tityra	*Tityra semifasciata*	Y	NA	NA

Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	Y	Y	Y
Elegant Trogon	*Trogon elegans*	Y	Y	Y
Black-headed Trogon	*Trogon melanocephalus*	Y	N	N
Clay-coloured Thrush	*Turdus grayi*	Y	M	M
Tropical Kingbird	*Tyrannus melancholicus*	Y	NA	NA
Yellow-green Vireo	*Vireo flavoviridis*	Y	Y	Y
Blue-black Grassquit	*Volatinia jacarina*	Y	N	N
White-winged Dove	*Zenaida asiatica*	Y	NA	NA

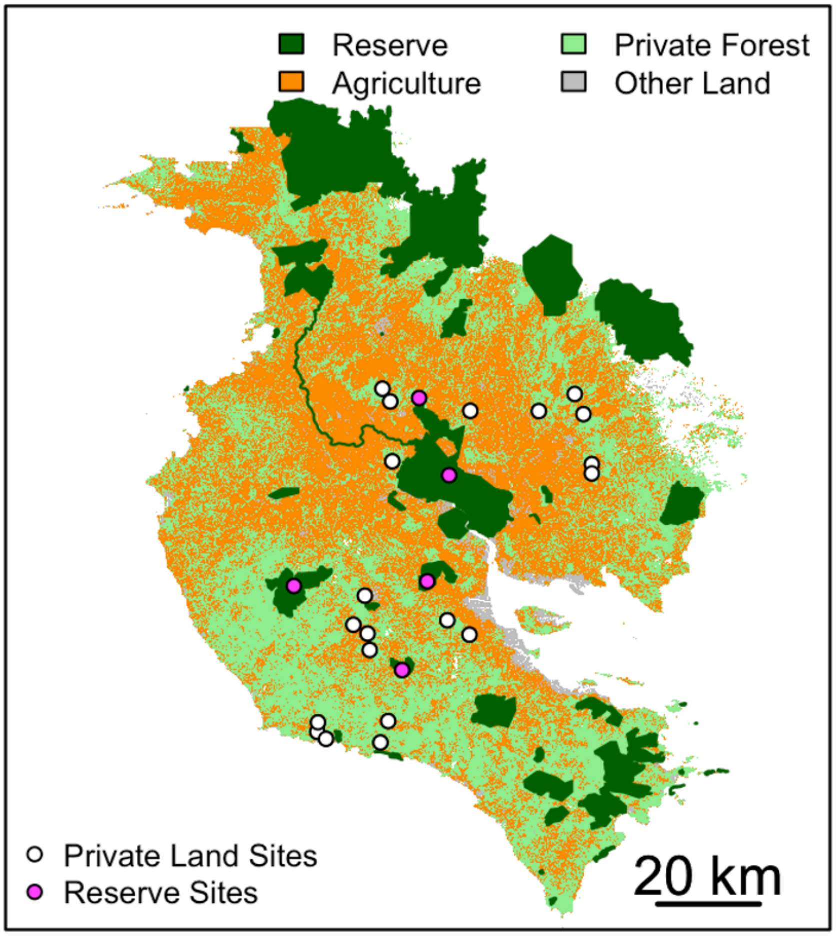


Figure S3.1: Map of 25 study sites, with private land and protected areas denoted by color.

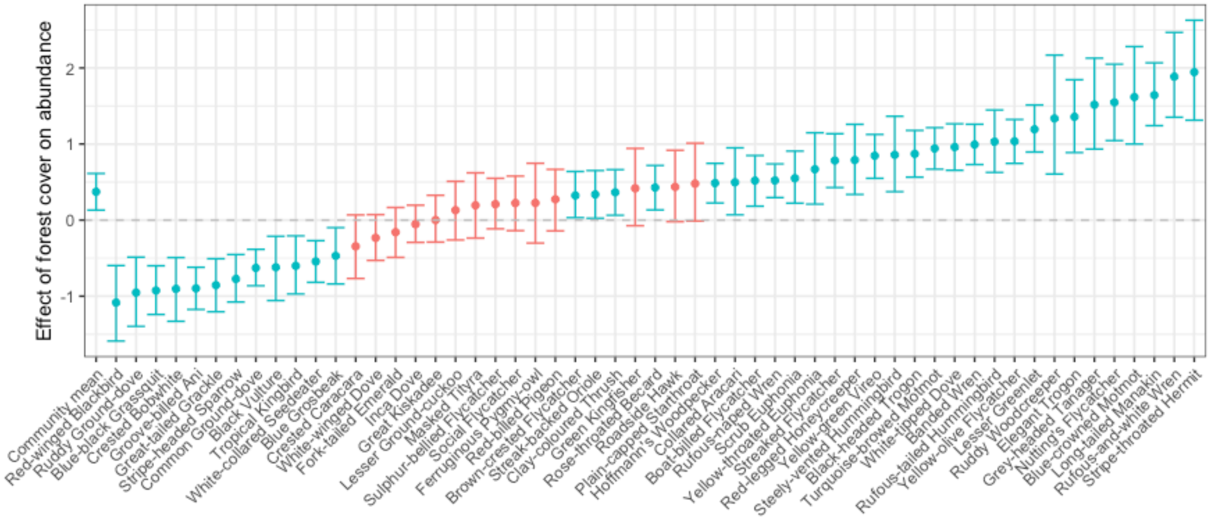


Figure S3.2: Effect of local forest cover on the abundance of each species, as well as the community mean effect. 90% Bayesian credible intervals (BCIs) are shown for each species, and the 95% BCI is shown for the community mean. Blue lines indicate BCIs that do not overlap zero.

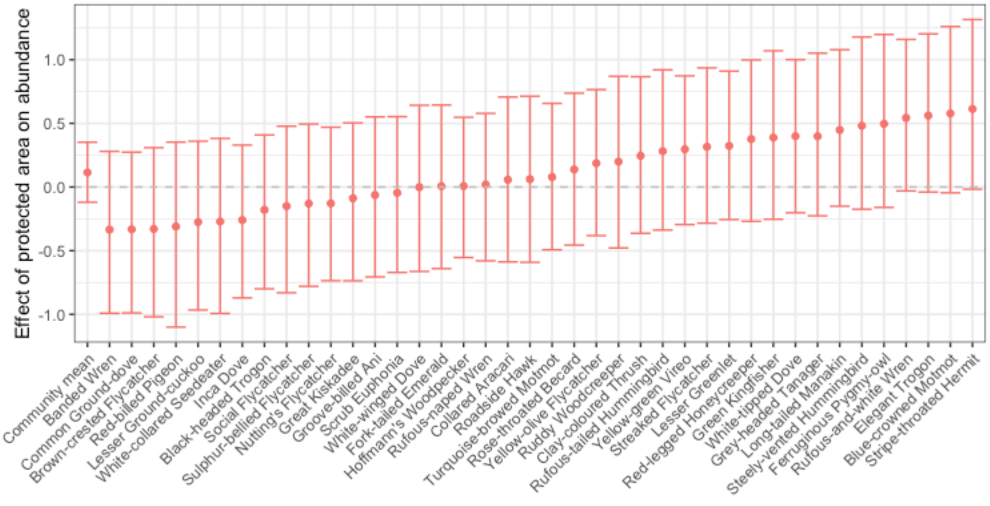


Figure S3.3: Effect of protected forest (versus privately-owned forest) on the abundance of each species, as well as the community mean effect. 90% Bayesian credible intervals (BCIs) are shown for each species, and the 95% BCI is shown for the community mean. Blue lines indicate BCIs that do not overlap zero.

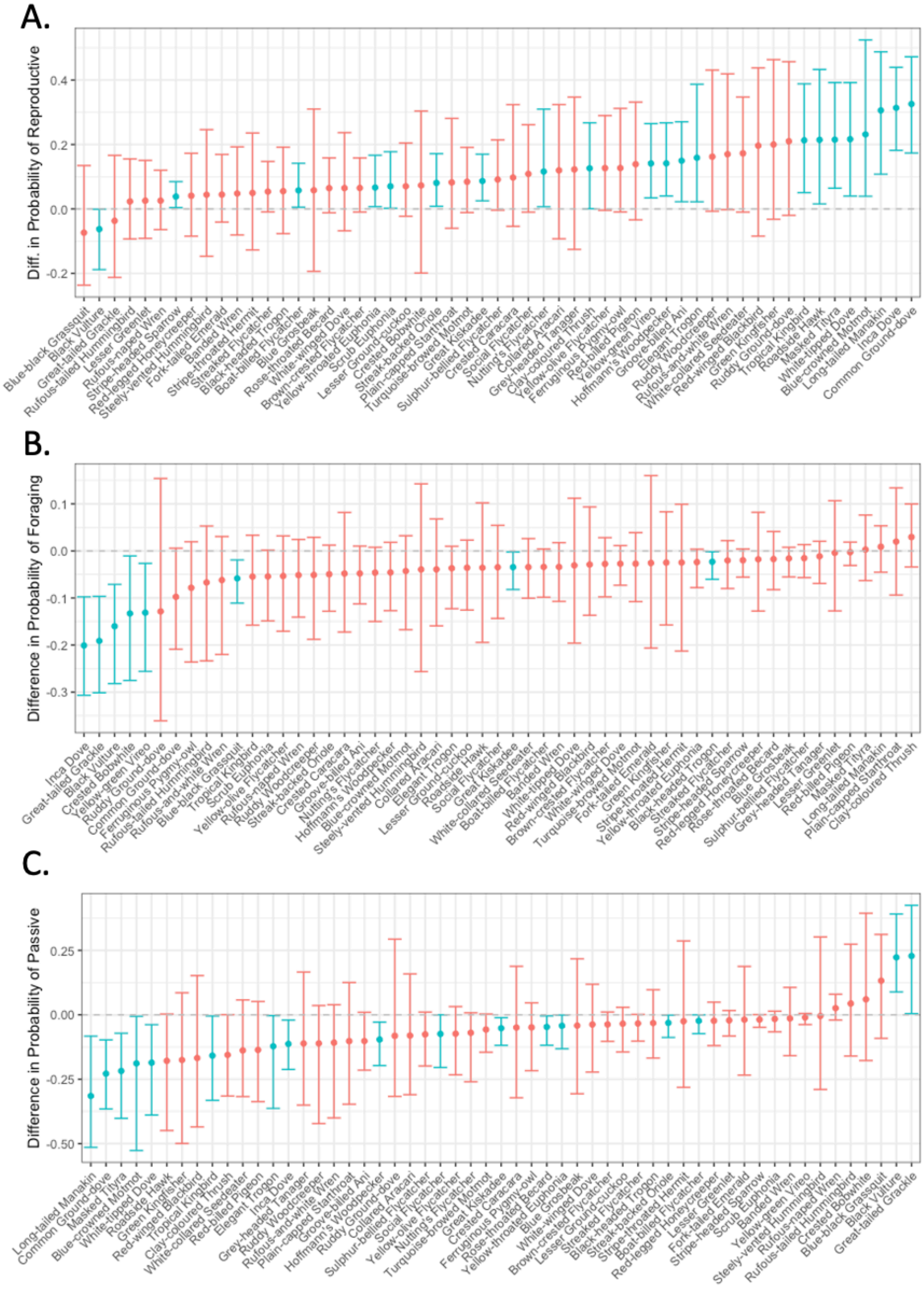


Figure S3.4: Difference in probability of each behavior between forest and agriculture for each species with 90% Bayesian credible intervals (BCIs). Positive values indicate a higher probability in forest, and negative values indicate a higher probability in agriculture. Blue lines indicate BCIs that do not overlap zero.

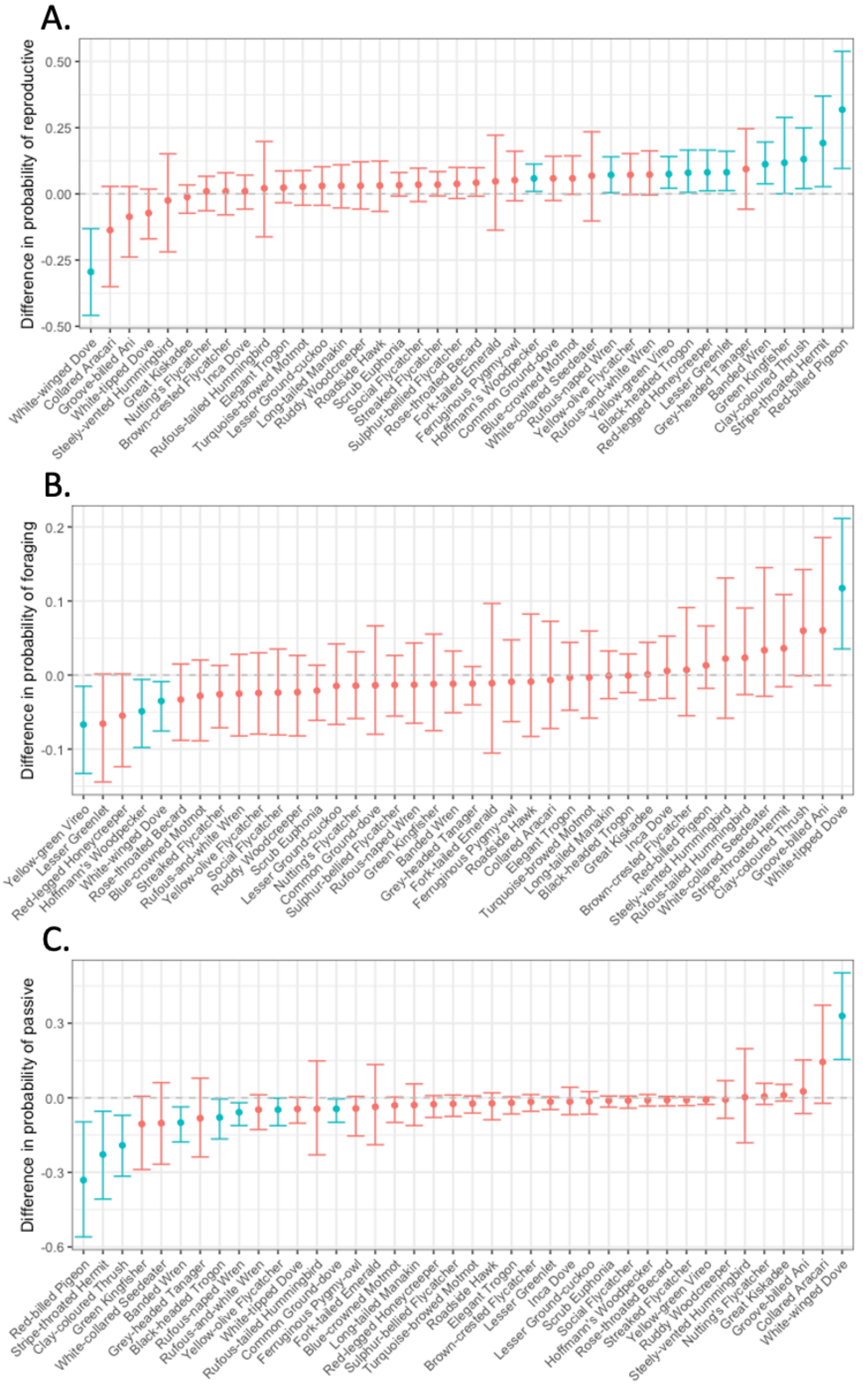


Figure S3.5: Difference in probability of each behavior between privately-owned and protected forest for each species with 90% Bayesian credible intervals (BCIs). Positive values indicate a higher probability in protected forest, and negative values indicate a higher probability in privately-owned forest. Blue lines indicate BCIs that do not overlap zero.

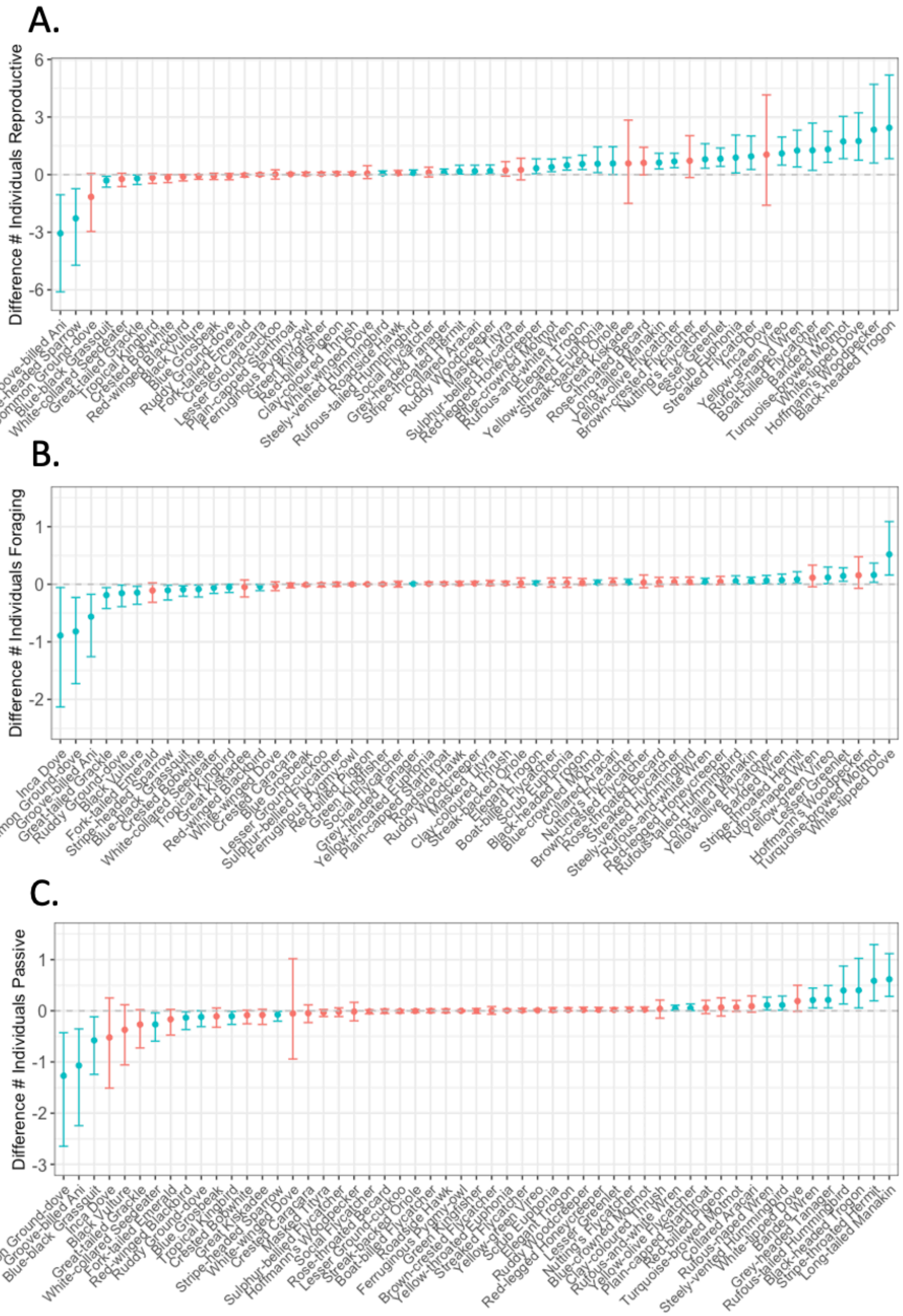


Figure S3.6: Difference in numbers of individuals performing each behavior between forest and agriculture for each species with the 90% percentile interval of the simulated posterior. Positive values indicate a higher number in forest, and negative values indicate a higher number in agriculture. Blue lines indicate intervals that do not overlap zero.

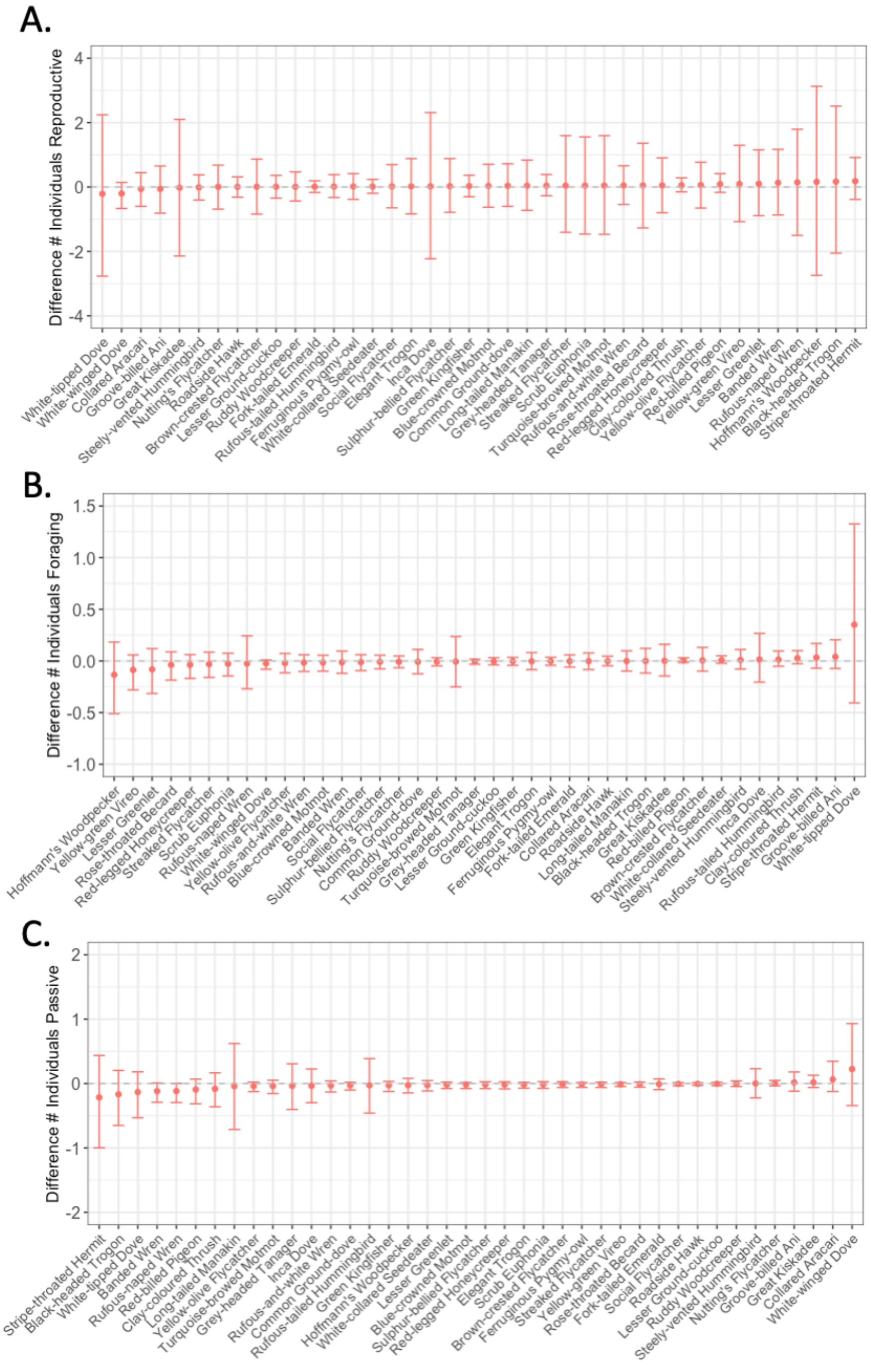
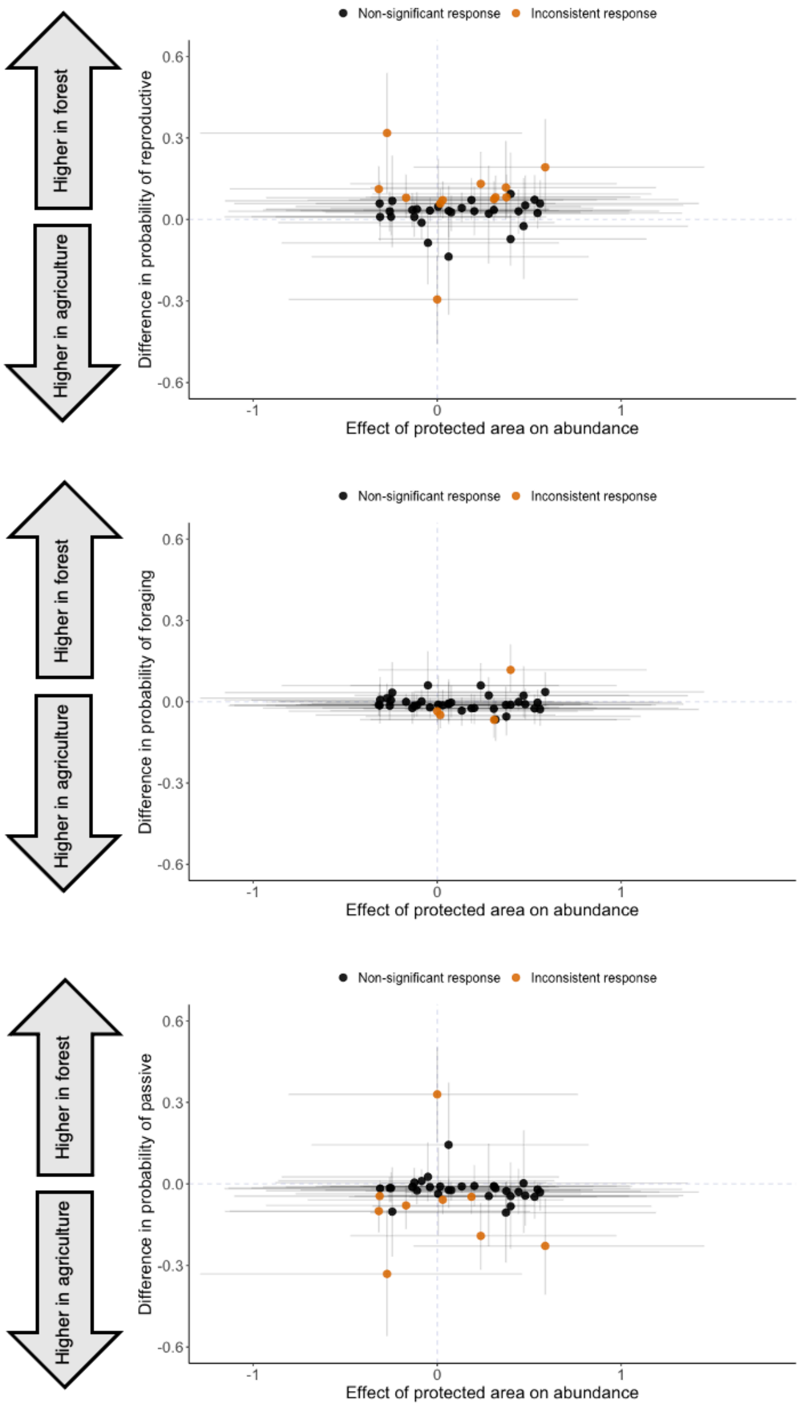


Figure S3.7: Difference in numbers of individuals performing each behavior between privately-owned and protected forest for each species with the 90% percentile interval of the simulated posterior. Positive values indicate a higher number in protected forest, and negative values indicate a higher number in privately-owned forest. Blue lines indicate intervals that do not overlap zero.



Figures S3.8-3.10: Relationship between the effect of protection status on species' abundance and the predicted difference in species' probabilities of performing reproductive behaviors between protected and privately-owned forest. Grey lines indicate 90% Bayesian credible intervals. Positive values on the y-axis represent a higher probability of performing reproductive behaviors in protected forest than privately-owned forest. Colors represent whether species were classified as habitat generalists (black), or inconsistent responses (red), which preferentially exhibited reproductive behaviors in one habitat but did not significantly increase in abundance in that habitat.

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 if cavity limitation in agriculture would elicit higher use of artificial nest boxes than in forest. 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.

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 (Wiens 1992, Brooks *et al.* 2002). 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., Sekercioglu et al. 2007, Newbold et al. 2013). 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.

A major consequence of habitat conversion to agriculture is deforestation, which may make organisms that use or nest in tree cavities especially threatened due to the loss of their nesting sites. These organisms include many mammal species (*e.g.*, bats, squirrels, mice; Czeszczewik et al. 2008), as well as cavity-nesting birds, which depend on tree cavities to breed and roost (Martin & Eadie 1999). Worldwide, 26% of land bird species nest or roost in tree cavities (Newton 1998). Researchers have found that these species tend to decline in areas where humans remove cavities, for example, in forests that are selectively logged (Engblom *et al.* 2002, Cockle *et al.* 2010). 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 (Cornelius *et al.* 2008). However, like other taxa, cavity-nesting bird diversity is highest in the tropics, and it peaks in the Neotropics, where 678 cavity-nesting bird species occur (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 other hand, Goldingay et al. (2015) found that native birds very rarely used nest boxes in eastern Australia. However, in tropical regions, while there are some studies evaluating whether nest boxes could be used for particular species (*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. To our knowledge, no 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 cavity-nesting bird abundances compare between forest and pastures. We hypothesized that, due to a lack of large trees, there would be lower cavity-nesting bird abundances, lower cavity availability, and higher cavity occupancy rates in agriculture than in forest. Then, we conducted an experiment, adding artificial nest boxes to forest and pastures to understand how artificial 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 will 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).

Methods

Study sites

We studied cavity-nesting bird communities in Northwest Ecuador, around the Mache-Chindul Ecological Reserve (0◦ 470N, 79◦ 780W; elevation 390-510 m in our study site) in the Esmeraldas Province (Figure 14). 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 (Sierra 1999, Orme *et al.* 2005). The Mache-Chindul Ecological Reserve was created in 1996 and consists of pristine and secondary forest fragments with agricultural lands, and it has experienced rapid agricultural expansion in the last 50 years. About 6500 people live in the reserve, typically on farms of 20-50 ha with agriculture including cacao, pasture for cattle, corn, beans, rice, plantain, and oil palm (Carrasco *et al.* 2013). Dominant forest types include humid evergreen and sub-humid evergreen forests, with canopy heights in primary forest spanning 30-40 m. Average monthly temperatures range from 26 to 28°C, and total annual precipitation ranges from 2 to 3.5 m in the region with the majority of the rainfall occurring between January and May. To study bird communities and cavity limitation, we identified fourteen 0.5-ha plots (100 m x 50 m), half within forest and half in agriculture, consisting mostly of pasture but also with occasional cacao or plantain plants. All plots were separated by at least 150 m (mean distance between plots: 178 m).

Bird surveys

To survey bird communities, FC and LC conducted 10-minute point counts during in February 2020, July 2020, May 2021, and July 2021 at five agriculture sites and five forest sites (Figure 14). There are two peaks of breeding activities in our 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 a stationary observer. Within each of the four survey periods, each site was sampled three times over the course of a week to estimate bird abundances while accounting for imperfect detection (see N-mixture modeling section below). Point counts took place between 6:00 and 11:30am (with 97% taking place between 6:00 and 10:00am). We recorded the survey time, wind conditions (qualitative 0-3 scale), and fog conditions (qualitative 0-3 scale) to help account for variation in detection probabilities between species, conditions, and habitats. No surveys were conducted in the rain. Finally, we used existing databases to identify cavity-nesting species (*e.g.*, del Hoyo 2015).

Modelling bird communities

To estimate the abundance of each bird species at each site, we implemented an N-mixture model, where the number of individuals is counted during spatially and temporally replicated surveys to estimate abundance while accounting for imperfect detection (Royle 2004, Kéry 2018). We combined an N-mixture model with a community modeling framework where species-specific parameters are 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 modelled as:

$$\log(\lambda_{i,j}) = \alpha0_i + \alpha1_i * \mathrm{LU_j} + \alpha2 * \mathrm{cavity_i} + \alpha3 * \mathrm{cavity_i} * \mathrm{LU_j} + \delta0_j + \delta1_{\mathrm{year}[survey[j]]}$$

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. $\alpha0$ and $\alpha1$ were estimated for each species, and $\alpha 2$ was a fixed effect representing the interaction between cavity-nesting species and land-use type. The δ 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 ($\delta 1$).

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

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

where "time" represents time of day, "wind" is the level of wind from 0-3, "fog" is the level of fog from 0-3, 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, because we believed that wind and fog 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 (Su & Yajima 2012, Team 2013). 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 ≤ 1.1 (Gelman *et al.* 2004).

We expected the bird community on average to be positively associated with forest habitat (*i.e.,* $\alpha 1 > 0$); and 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 is estimated with fewer data than the community means, and 90% BCIs are recommended when effective sample sizes are lower (Kruschke 2014, McElreath 2020).

Natural cavity availability and use

In 2019, we searched each tree within four of the agricultural and four of the forest plots (Figure 14) for natural cavities (entrance hole diameter >2 cm, >2.5 m high) by scanning each tree using binoculars (Cockle *et al.* 2010). We noted the height and orientation of each cavity, as well as the tree's height (using a hypsometer) and diameter at breast height (DBH). 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, from September 2019 to April 2020, we conducted weekly observations of each natural cavity for 15 minutes, noting any cavity-nesting bird activity observed. We considered cavity-nesting bird activity 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-minute 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 cavity activity in forest versus agriculture.

Nest box addition experiment

To quantify use of and fledging success from artificial nest boxes, we constructed and placed ten nest boxes in each of the five agricultural and five forest plots (100 nest boxes total; Figure 14). Specifically, we placed nest boxes on trees in six of the plots in September 2019 and the remaining four plots several months later (February 2020). Boxes were located 10-20 m apart within a plot 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 x 12-cm depth x 24-cm height, with a 4-cm diameter entrance hole), and the other half were large (18-cm width x 18-cm depth x 38-cm height, with a 10-cm diameter entrance hole). Because nest box studies are rare in tropical ecosystems and we wanted to cater to a wide variety of species, nest box sizes were based on standard dimensions for attracting Western Bluebirds (*Sialia mexicana*) (Jedlicka *et al.* 2011) and then ~1.5x those dimensions 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, defining new activity as evidence of new materials in a nest box that was inactive for several weeks or a different material than what was present from the previous species occupying the box. Bird nesting materials were often sticks, bark, and leaves; mammal nesting materials were often leaves (opossum) and dried grasses (squirrel). We considered an activity 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, with the response variable as 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 also included a random effect of 'site' to account for both spatial autocorrelation (*i.e.,* multiple nest boxes at the same site) and 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. The interaction between land-use type and nest box size was not included in the model of mammalian activity 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 or not at least one chick fledged during each avian nesting attempt.

Results

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 S4.1). Out of 4440 abundance estimates (N), 38 did not converge (3%; all had R-hat $\leq$ 1.25, 88% of which had R-hat < 1.2), $\gamma 0_{LU[2]}$ had an R-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 15), meaning that, on average, species were not more abundant in agriculture or forests. Eight cavity-nesters 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*; Bronze-winged Parrot, *Pionus chalcopterus*) whereas one cavity-nester 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]), suggesting that cavity-nesting species did not differ from non-cavity nesting species in their response to land use.

Natural cavity availability and use

As expected, there were significantly more natural cavities in forest than agriculture (mean 34 cavities/ha versus 7.25/ha; t = -5.85, p-value = 0.0014; Figure 16). The mean cavity height in forest and agriculture were similar (13.8 [range 3-43 m] and 13.9 m [range 4-34 m], respectively) and natural cavities did not tend to be oriented in any cardinal direction (Figure S4.1). Mean DBH of trees with cavities in forest and agriculture were 42.9 cm (range 7-200 cm) and 33.7 cm (range 10-63 cm) respectively, and mean tree height for forest and agriculture cavities were 22.0 m (range 3-46 m) and 21.6 m (range 6-35 m) respectively. 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 6). Five of the seven observations of a bird inside a cavity in agriculture were of the Collared Aracari using the same cavity, while there was one observation of the 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 rates between forest versus agriculture.

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. There were 109 total avian activity events in agriculture from 8 species and 5 in forest from 2 species. Of those activity 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 than forest (Figure 17, Table S4.2). Smaller nest boxes also had significantly more avian activity events than large boxes, and a significant negative interaction was found between habitat and nest box size, such that difference in avian activity between forest and agriculture was greater for small nest boxes (Figure 17, Table S4.2). Ten nest boxes were occupied by wasps and bees, half in agriculture and half in forest.

Seven bird species laid eggs in nest boxes (six in agriculture and two in forest; Table 7). 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 the 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 0.44 in agriculture (out of 52 nesting attempts) and 0.2 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 a significant effect on nest success, likely due to the low number of nesting attempts in forest (Table S4.2).

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*) versus 28 instances in forest (*i.e.,* 22 brown four-eyed possum and 6 red-tailed squirrel (*Sciurus granatensis*) activity events across all sites; Table 7). As such, Poisson models indicated that mammal activity was significantly higher in forest than agriculture, but no effects of nest box size were observed (Table S4.2).

Discussion

To our knowledge, this was the first nest box addition experiment conducted in tropical pastures to determine if cavity-nesting birds experience cavity limitation in tropical forest versus agriculture. We found that bird abundance, including cavity-nester abundance, was not significantly higher in forests than in agriculture. There were many more natural cavities in forest than in agriculture and much more avian activity and nesting in nest boxes placed 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, and there were very few bird nesting attempts in forest, making it difficult to compare nest success between habitats.

Trends in bird abundance

On average, birds were not more abundant in forests than agriculture. Cavity-nesting species were also not more abundant in either habitat, 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 cavity-nesting bird populations if forest loss reaches a certain threshold (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 rates of 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 already provides certain key resources such as food and increasing nesting habitat would further increase the usage of agriculture by birds. 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), allowing us to understand how reliant species are on forest for populations to persist.

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) (Hoek *et al.* 2017). Eight cavity-nesting species were more abundant in agriculture, which all have "Least Concern" conservation status from IUCN and are mostly species with wide global distributions. 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 agriculture in temperate regions (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 other hand, Collared Aracaris were significantly more abundant in forest, though they were observed using natural cavities in both forest and agriculture.

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 between habitat types because it is difficult to find cavities that are high in the canopy and/or in dense foliage (Koch 2008). For example, Cockle et al. (2010) recorded over nine times the density of suitable cavities (at least 13 cm deep and 2.5 m high) 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). We did not find significant differences in the tree height, cavity height, DBH, or orientation of cavities in forest versus agriculture; however, our estimates could be biased if we tended to overlook cavities high up in forest canopies.

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), 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 get a good sample size to understand cavity occupancy. Overall, 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)).

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 in forest nest boxes because overall 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 and Garcia, 2016). Similarly, only 2% of nest boxes were occupied in an undisturbed Peruvian forest (Brightsmith, 2005). These numbers stand in stark contrast to studies conducted in temperate forests, where many nest box addition experiments have been shown to increase cavity-nesting bird and mammal populations (Lindenmayer *et al.* 2009, Aitken & Martin 2012, 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 versus 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, which may be preferable for tropical birds (Nilsson 1984, Wesolowski 2002, Cockle *et al.* 2015). 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 (Nilsson 1984, Wiebe 2011, Dhondt 2012).

On the other hand, 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), and 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, cavity-nesting bird populations may be especially limited by nesting habitat as compared to populations in selectively logged forests or coffee plantations.

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 (Robinson *et al.* 2000, Brawn *et al.* 2011). Moreover, many studies of non-cavity nesting birds report lower nest success in fragmented versus natural land uses (Rangel-Salazar *et al.* 2008, Young *et al.* 2008, Borges & Marini 2010, Newmark & Stanley 2011). Other studies report increased nest success in areas with more 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). It is possible that we could have slightly overestimated nest success if we missed nest failures near fledging in the cases that we observed nestlings near fledging age on one visit, and then found an empty nest on the next visit. Nevertheless, the nest success we observed was sufficiently high that it seems that artificial nest boxes in agriculture provide suitable conditions to successfully rear tropical birds.

Conclusions

Overall, we found that nesting habitat seems to limit reproduction by cavity-nesting bird populations in tropical agriculture but not forest, even though cavity-nesting birds are abundant in tropical agricultural systems. Retaining forest patches and remnant trees in tropical agriculture may thus provide critical nesting habitat for birds (Cockle *et al.* 2015). Large trees may be especially important because they are more likely to have cavities and persist for many years (Cockle *et al.* 2015, 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, though this could potentially lead to a source-sink or ecological trap dynamic, drawing species out of forest and leading to lower fitness (Robertson & Hutto 2006). 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. While deploying nest boxes in agriculture is unlikely to benefit species of conservation concern, we found that small insectivorous birds dominated nest boxes in agriculture (e.g., House Wrens), indicating 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., Jedlicka et al. 2011, 2014, Benayas et al. 2017, 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 temperate and tropical forests alike (Sethi & Howe 2009). Even low nest box occupancy levels could increase bird presence and ecosystem services on farms (Hannay *et al.* 2022), so 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.

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Table 6: 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

Table 7: Total number of avian and mammalian observations in artificial nest boxes at each site.

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 8: 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 (small versus large).

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)
Dendrocincla fuliginosa	Plain-brown Woodcreeper	Obligate	1	2	0	0
Forpus coelestis	Pacific Parrotlet	Facultative	1	0	0	0
Lepidocolaptes souleyetii	Streak-headed Woodcreeper	Obligate	10	0	2	0
Myiarchus tuberculifer	Dusky-capped Flycatcher	Obligate	1	0	0	0
Tityra semifasciata	Masked Tityra	Obligate	1	0	0	0
Troglodytes aedon	House Wren	Facultative	30	1	0	0
Megascops guatemalae	Choco Screech Owl	Obligate	0	0	0	3
Unknown	Unknown	NA	4	1	0	0

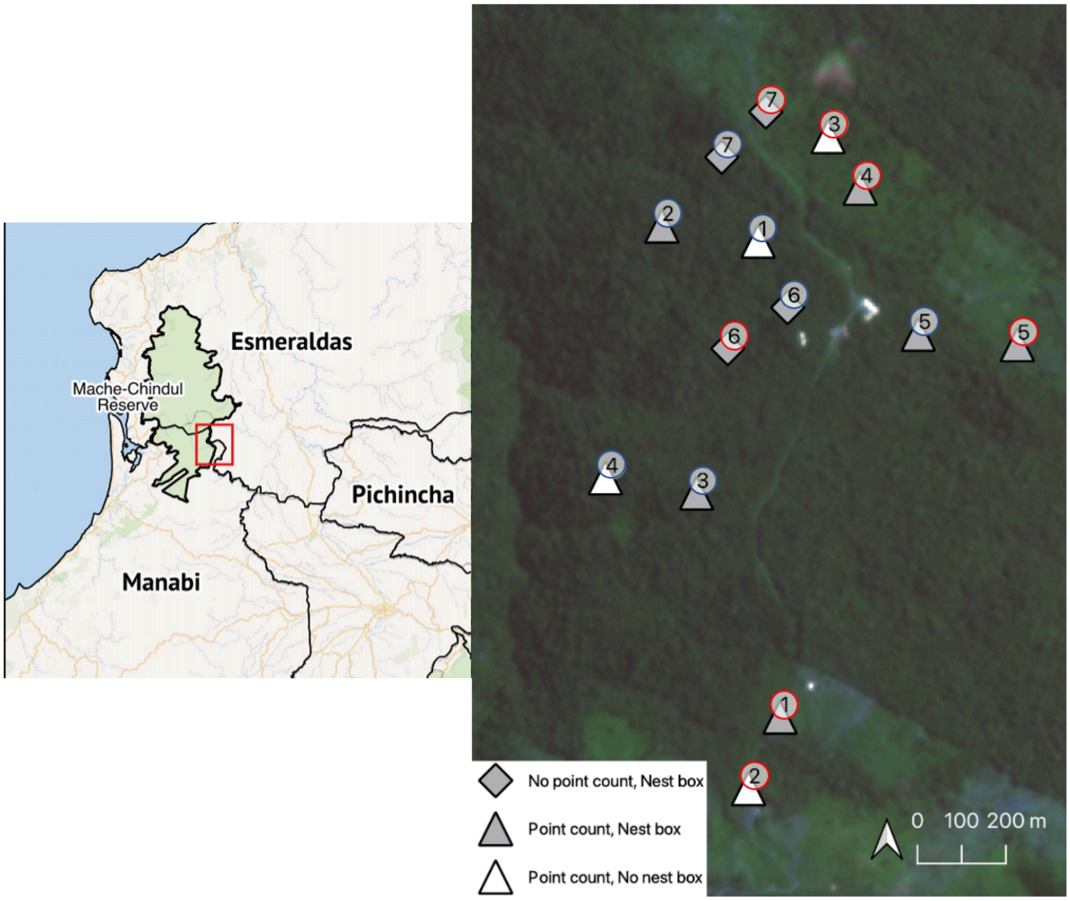

Figure 14: Map of study region (left) and map of study sites (right). In map of study sites, labels outlined in red represent agriculture and labels outlined in blue represent forest. Shapes and colors indicate if sites were surveyed for bird communities ("point count") and/or had nest boxes. Natural cavity surveys and monitoring occurred at points 1-4 in agriculture and forest.

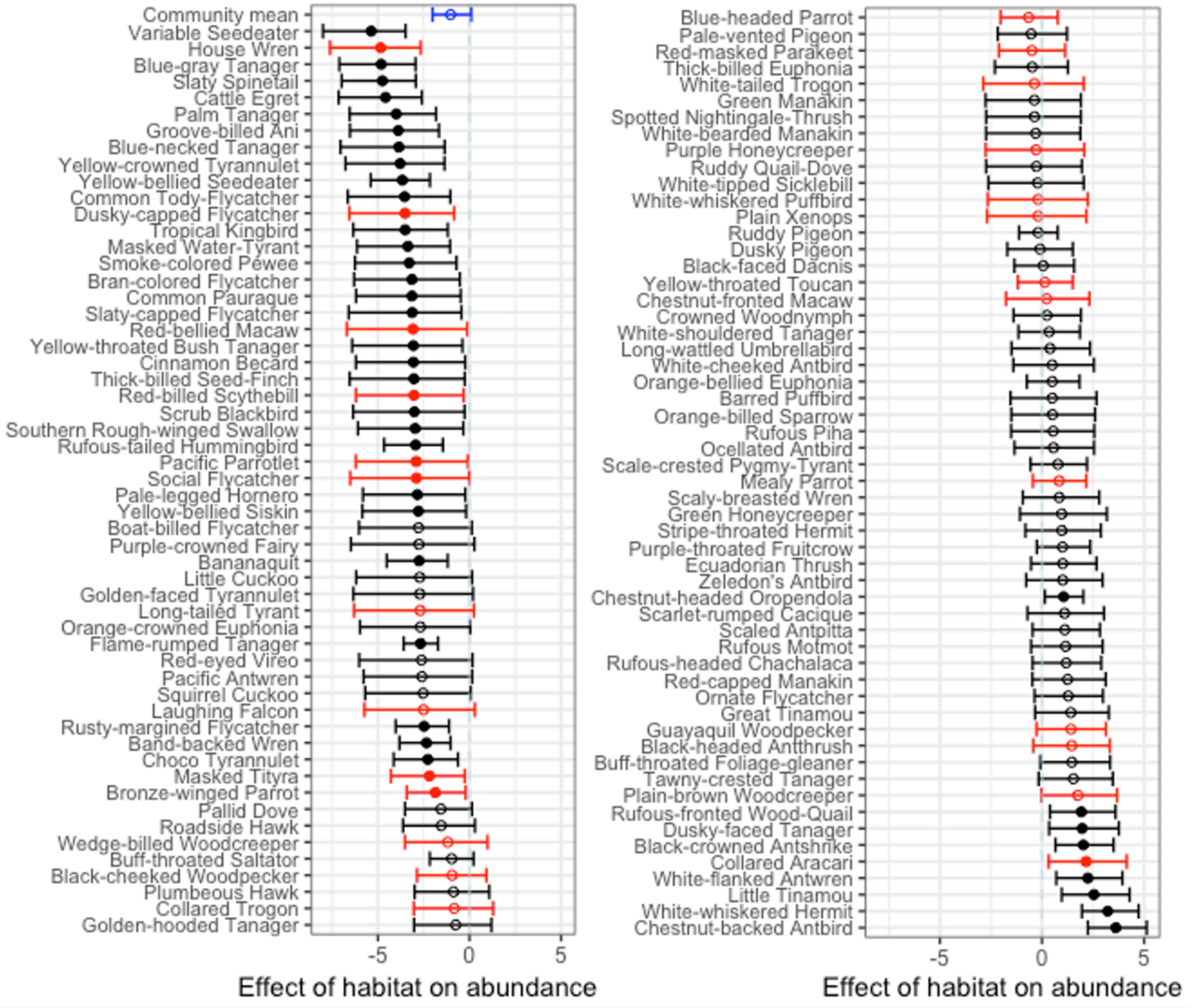

Figure 15: N-mixture model estimates and Bayesian Credible Intervals (BCIs) for the effect of land-use type on abundance. Positive values indicate that the species is more abundant in forest than in agriculture. Circles represent posterior means, the blues bar is the estimate of the community mean with 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.

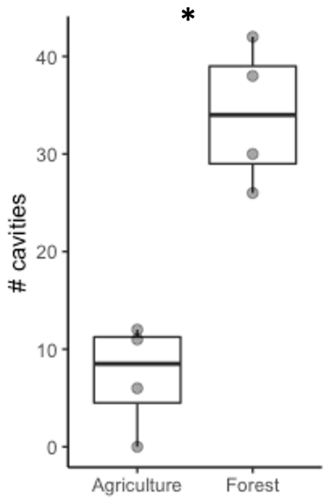

Figure 16: Boxplots of the number of natural cavities found per site in agriculture versus forest. Gray points represent raw data. The solid horizontal bar represents the median and the box represents the first and quartiles. Whiskers represent the minimum and maximum values that are no further than 1.5 times the interquartile range. Star indicates a significant difference (from a Welch's two-sample t-test).

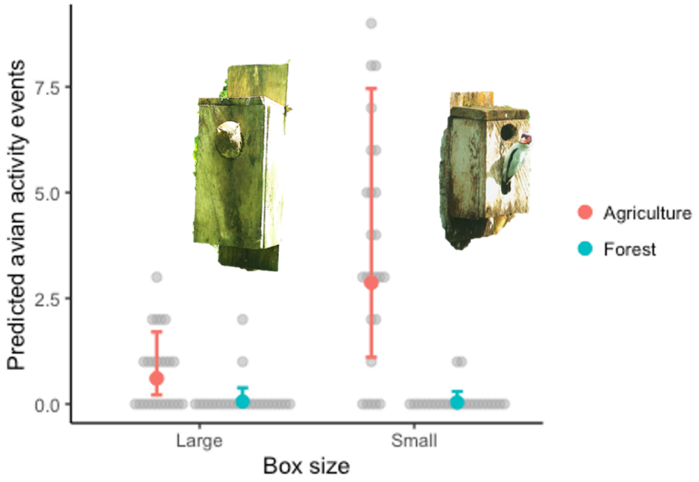

Figure 17: Predicted effect of land use and nest box size on avian activity within artificial nest boxes. Points (mean predicted effects from the mixed-effects model) and lines (95% confidence intervals from the model) are colored according to land-use type (agriculture in red; forest in blue). Gray 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.

Supporting Information 4

Common name	Scientific name	Cavity-nesting	Total observations in agriculture	Total observations in forest
Bananaquit	*Coereba flaveola*	0	13	1
Band-backed Wren	*Campylorhynchus zonatus*	0	15	2
Barred Puffbird	*Nystalus radiatus*	0	0	2
Black-cheeked Woodpecker	*Melanerpes pucherani*	1	4	2
Black-crowned Antshrike	*Thamnophilus atrinucha*	0	1	16
Black-faced Dacnis	*Dacnis lineata*	0	3	4
Black-headed Antthrush	*Formicarius nigricapillus*	1	0	5
Blue-gray Tanager	*Thraupis episcopus*	0	34	0
Blue-headed Parrot	*Pionus menstruus*	1	16	10
Blue-necked Tanager	*Tangara cyanicollis*	0	7	0
Boat-billed Flycatcher	*Megarynchus pitangua*	0	1	0
Bran-colored Flycatcher	*Myiophobus fasciatus*	0	2	0
Bronze-winged Parrot	*Pionus chalcopterus*	1	15	3
Buff-throated Foliage-gleaner	*Automolus ochrolaemus*	0	0	5
Buff-throated Saltator	*Saltator maximus*	0	7	4
Cattle Egret	*Bubulcus ibis*	0	23	0
Chestnut-backed Antbird	*Poliocrania exsul*	0	0	46
Chestnut-fronted Macaw	*Ara severus*	1	0	6
Chestnut-headed Oropendola	*Psarocolius wagleri*	0	8	34
Choco Tyrannulet	*Zimmerius albigularis*	0	7	1
Cinnamon Becard	*Pachyramphus cinnamomeus*	0	2	0
Collared Aracari	*Pteroglossus torquatus*	1	0	8
Collared Trogon	*Trogon collaris*	1	1	1
Common Pauraque	*Nyctidromus albicollis*	0	2	0
Common Tody-Flycatcher	*Todirostrum cinereum*	0	4	0
Crowned Woodnymph	*Thalurania colombica*	0	1	3
Dusky Pigeon	*Patagioenas goodsoni*	0	2	3
Dusky-capped Flycatcher	*Myiarchus tuberculifer*	1	5	0
Dusky-faced Tanager	*Mitrospingus cassinii*	0	0	6
Ecuadorian Thrush	*Turdus maculirostris*	0	1	5
Flame-rumped Tanager	*Ramphocelus flammigerus*	0	71	7

Golden-faced Tyrannulet	*Zimmerius chrysops*	0	1	0
Golden-hooded Tanager	*Tangara larvata*	0	1	1
Great Tinamou	*Tinamus major*	0	0	4
Green Honeycreeper	*Chlorophanes spiza*	0	0	4
Green Manakin	*Cryptopipo holochlora*	0	0	1
Groove-billed Ani	*Crotophaga sulcirostris*	0	10	0
Guayaquil Woodpecker	*Campephilus gayaquilensis*	1	1	11
House Wren	*Troglodytes aedon*	1	35	0
Laughing Falcon	*Herpetotheres cachinnans*	1	1	0
Little Cuckoo	*Coccycua minuta*	0	1	0
Little Tinamou	*Crypturellus soui*	0	0	14
Long-tailed Tyrant	*Colonia colonus*	1	1	0
Long-wattled Umbrellabird	*Cephalopterus penduliger*	0	0	2
Masked Tityra	*Tityra semifasciata*	1	7	1
Masked Water-Tyrant	*Fluvicola nengeta*	0	4	0
Mealy Parrot	*Amazona farinosa*	1	23	74
Ocellated Antbird	*Phaenostictus mcleannani*	0	0	2
Orange-bellied Euphonia	*Euphonia xanthogaster*	0	3	7
Orange-billed Sparrow	*Arremon aurantiirostris*	0	0	2
Orange-crowned Euphonia	*Euphonia saturata*	0	1	0
Ornate Flycatcher	*Myiotriccus ornatus*	0	0	4
Pacific Antwren	*Myrmotherula pacifica*	0	1	0
Pacific Parrotlet	*Forpus coelestis*	1	2	0
Pale-legged Hornero	*Furnarius leucopus*	0	2	0
Pale-vented Pigeon	*Patagioenas cayennensis*	0	2	2
Pallid Dove	*Leptotila pallida*	0	3	1
Palm Tanager	*Thraupis palmarum*	0	10	0
Plain Xenops	*Xenops minutus*	1	0	1
Plain-brown Woodcreeper	*Dendrocincla fuliginosa*	1	0	6
Plumbeous Hawk	*Cryptoleucopteryx plumbea*	0	1	1
Purple Honeycreeper	*Cyanerpes caeruleus*	1	0	1
Purple-crowned Fairy	*Heliothryx barroti*	0	1	0
Purple-throated Fruitcrow	*Querula purpurata*	0	2	9
Red-bellied Macaw	*Orthopsittaca manilatus*	1	2	0
Red-billed Scythebill	*Campylorhamphus trochilirostris*	1	2	0
Red-capped Manakin	*Ceratopipra mentalis*	0	0	4
Red-eyed Vireo	*Vireo olivaceus*	0	1	0

Red-masked Parakeet	*Psittacara erythrogenys*	1	5	4
Roadside Hawk	*Rupornis magnirostris*	0	3	1
Ruddy Pigeon	*Patagioenas subvinacea*	0	12	14
Ruddy Quail-Dove	*Geotrygon montana*	0	0	1
Rufous Motmot	*Baryphthengus martii*	0	0	5
Rufous Piha	*Lipaugus unirufus*	0	0	2
Rufous-fronted Wood-Quail	*Odontophorus erythrops*	0	0	8
Rufous-headed Chachalaca	*Ortalis erythroptera*	0	0	4
Rufous-tailed Hummingbird	*Amazilia tzacatl*	0	18	1
Rusty-margined Flycatcher	*Myiozetetes cayanensis*	0	17	2
Scale-crested Pygmy-Tyrant	*Lophotriccus pileatus*	0	2	7
Scaled Antpitta	*Grallaria guatimalensis*	0	0	4
Scaly-breasted Wren	*Microcerculus marginatus*	0	0	4
Scarlet-rumped Cacique	*Cacicus uropygialis*	0	0	3
Scrub Blackbird	*Dives warczewiczi*	0	2	0
Slaty Spinetail	*Synallaxis brachyura*	0	36	0
Slaty-capped Flycatcher	*Leptopogon superciliaris*	0	2	0
Smoke-colored Pewee	*Contopus fumigatus*	0	3	0
Social Flycatcher	*Myiozetetes similis*	1	2	0
Southern Rough-winged Swallow	*Stelgidopteryx ruficollis*	0	2	0
Spotted Nightingale-Thrush	*Catharus dryas*	0	0	1
Squirrel Cuckoo	*Piaya cayana*	0	1	0
Stripe-throated Hermit	*Phaethornis striigularis*	0	0	3
Tawny-crested Tanager	*Tachyphonus delatrii*	0	0	5
Thick-billed Euphonia	*Euphonia laniirostris*	0	2	2
Thick-billed Seed-Finch	*Sporophila funerea*	0	2	0
Tropical Kingbird	*Tyrannus melancholicus*	0	6	0
Variable Seedeater	*Sporophila corvina*	0	58	0
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*	1	2	1
White-bearded Manakin	*Manacus manacus*	0	0	1
White-cheeked Antbird	*Gymnopithys leucaspis*	0	0	2
White-flanked Antwren	*Myrmotherula axillaris*	0	0	9
White-shouldered Tanager	*Tachyphonus luctuosus*	0	2	4
White-tailed Trogon	*Trogon chionurus*	1	0	1
White-tipped Sicklebill	*Eutoxeres aquila*	0	0	2
White-whiskered Hermit	*Phaethornis yaruqui*	0	0	53
White-whiskered Puffbird	*Malacoptila panamensis*	1	0	1
Yellow-bellied Seedeater	*Sporophila nigricollis*	0	28	1

Yellow-bellied Siskin	*Spinus xanthogastrus*	0	2	0
Yellow-crowned Tyrannulet	*Tyrannulus elatus*	0	6	0
Yellow-throated Bush Tanager	*Chlorospingus flavigularis*	0	2	0
Yellow-throated Toucan	*Ramphastos ambiguus*	1	16	24
Zeledon's Antbird	*Hafferia zeledoni*	0	0	3

Table S4.1: List of species observed in point count surveys, whether each species nests in cavities, and total number of observations in agriculture and forest.

		Estimate	Std. Error	z value	Pr(>|z|)
Avian activity	Intercept	-0.50	0.53	-0.95	0.34
	Habitat	-2.39	1.09	-2.18	0.03
	Box size	1.56	0.25	6.16	<0.01
	Habitat x Box size	-1.96	0.95	-2.07	0.04
Mammalian activity	Intercept	-4.22	1.19	-3.55	<0.01
	Habitat	4.23	1.26	3.36	<0.01
	Box size	0.00	0.59	0.00	1.00
Avian nest success	Intercept	0.09	1.05	0.09	0.93
	Habitat	-1.51	1.51	-1.00	0.32
	Box size	-0.19	1.11	-0.17	0.87

Table S4.2: Estimates, standard errors, z-values, and p-values of predictors from mixed effects models with the response variables as the total number of avian activities at each nest box, the total number of mammalian activities at each nest box, and avian nest success (among nests where at least one egg was laid). Predictor variables include habitat (larger values indicate higher activities/success in forest) and nest box size (larger values indicate higher activities/success in small nest boxes).

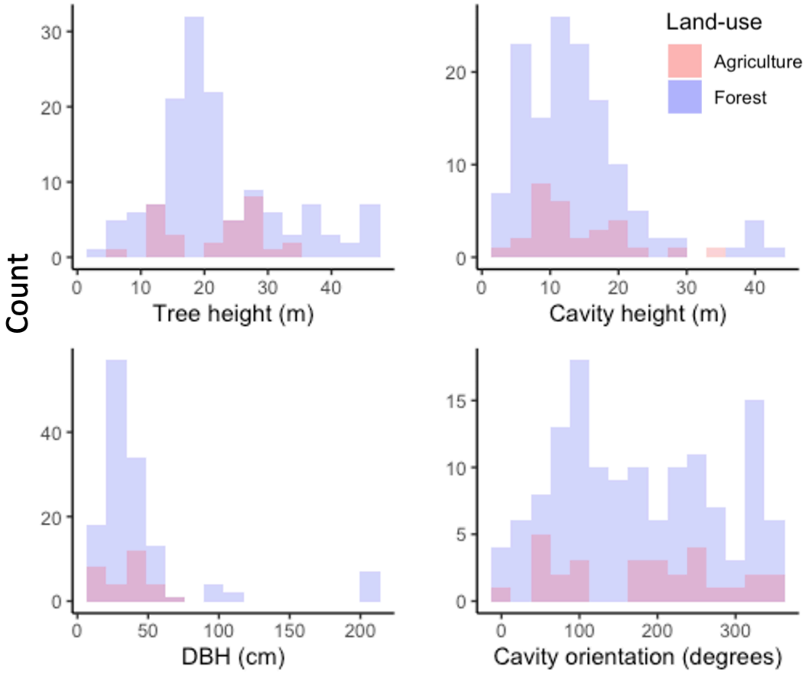

Figure S4.1: Histograms of tree height, cavity height, diameter at breast height (DBH), and orientation of natural cavities found in agriculture (red) and forest (blue).