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# Land-sparing and land-sharing provide complementary benefits for conserving avian biodiversity in coffee-growing landscapes

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## ABSTRACT

Protecting biodiversity while sustaining agricultural production is one of our greatest modern challenges. The dominant conservation paradigm in tropical coffee-growing regions involves *land-sharing*, wherein wildlife-friendly shade trees are integrated into plantations. Meanwhile, the value of *land-sparing* approaches that combine intensified farming with forest preservation has not been fully explored. We surveyed bird communities in forests and coffee plantations in the Sierra Nevada de Santa Marta, Colombia and used community occupancy models to quantify the effects of multi-scale habitat characteristics on distributions of 3 species groups (forest specialists, open area specialists, and generalists). We then predicted avian diversity across simulated landscape mosaics of sun coffee, shade coffee, and forest to compare land-sharing, land-sparing, and hybrid conservation approaches. Simulated land-sharing landscapes supported more open area specialists (16–17% of the community) and up to 17 (95% credible interval 11, 24) more generalist species (53–62% of the community) per point than sparing landscapes. Conversely, the richness of forest specialists (21–30% of the community) was greatest in land-sparing and hybrid simulations. Total community richness was greatest in simulated sparing landscapes during the breeding season but in sharing landscapes during the non-breeding season. Our results demonstrate that land-sharing and land-sparing can be complimentary conservation strategies to support functionally diverse and seasonally variable avian communities in coffee-growing regions. We recommend that eco-certification programs incorporate both conservation models to provide (1) habitat for the greatest diversity of species across the annual cycle, and (2) flexible participation options for farmers exposed to heterogeneous markets, growing conditions, and landscape contexts.

## 1. Introduction

Conversion of native ecosystems to agriculture currently poses the greatest threat to biodiversity (Foley et al., 2005). Although agricultural systems can support diverse biotic communities (Elsen et al., 2018; Karp et al., 2019), responses of individual species to land cover change are variable (Newbold et al., 2016; Frishkoff and Karp, 2019). Community composition also tends to be more homogeneous in agricultural systems than native ones due to habitat simplification (Newbold et al., 2016; Karp et al., 2019). Conservation strategies that counteract such homogenization will be essential for protecting biodiversity in the future (Kremen and Merenlender, 2018).

Balancing biodiversity conservation and agricultural production has been framed as a tradeoff between land-sparing and land-sharing strategies (Matson and Vitousek, 2006; Fischer et al., 2008; Phalan et al., 2011). Agricultural yields are maximized in land-sparing models by intensifying farming in smaller areas and saving more space for biodiversity reserves (Phalan et al., 2011; Edwards et al., 2015). In many regions, land-sparing optimizes tradeoffs between diversity and agricultural yields (Phalan et al., 2011; Balmford et al., 2015). However, agricultural intensification within land-sparing can increase nutrient and pesticide runoff and inadvertently promote agricultural expansion

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(Matson and Vitousek, 2006; Chappell et al., 2009). The alternative land-sharing model integrates food production and biodiversity conservation through wildlife-friendly farming practices such as retention of native, structurally diverse vegetation (Luck and Daily, 2003; Fischer et al., 2008). Proponents of land-sharing emphasize biodiversity protection must occur in human-modified landscapes that increasingly dominate the Earth's surface (Daily, 2001; Pereira and Daily, 2006; Kremen and Merenlender, 2018). Land-sharing, however, can also facilitate agricultural expansion if wildlife-friendly farming practices, such as retention of shade trees in coffee farms, result in lower crop yields that do not meet production needs (Moguel and Toledo, 1999).

Coffee provides a model system to investigate wildlife habitat management in agroforestry landscapes. Coffee is a globally important commodity with nearly 10 billion kilograms consumed annually (ICO, 2022). Currently, coffee is grown on over 1 million km$^2$ of agricultural land worldwide (FAO, 2022), and much of this land is found at mid-elevations in tropical regions that support high levels of biodiversity and endemism (Perfecto et al., 1996; Jha et al., 2014). Over the last 50 years, coffee has increasingly been cultivated as a monoculture with full exposure to the sun; however, when grown under a diverse canopy of native trees, coffee can support high species richness across taxonomic groups (Perfecto et al., 1996; Moguel and Toledo, 1999; Philpott et al., 2007). Shade-grown coffee certifications (e.g., Smithsonian Bird Friendly®, Rainforest Alliance Certified, Jaguar Friendly) are thus widely used for incentivizing land-sharing, and their popularity is increasing, with over 14,900 ha of coffee certified under the Smithsonian Bird Friendly® label alone in 2021 (Smithsonian Institution, 2021). However, shade certifications may have been adopted prematurely without fully exploring the potential benefits of land-sparing (Rappole et al., 2003; Chandler et al., 2013). Indeed, land-sparing approaches that combine sun-grown coffee with equal areas of native forest can support greater biodiversity than shade coffee plantations (Arce et al., 2009; Chandler et al., 2013). Remnant forest tracts positively influence bird diversity (Ruiz-Gutiérrez et al., 2010), and provide pollination and pest control services to farmers (Ricketts et al., 2004; Karp et al., 2013). Further, with agricultural expansion driving most tropical deforestation (Curtis et al., 2018), land-sparing may be necessary to conserve the many tropical species negatively affected by fragmentation (Betts et al., 2019). Land-sparing thus requires further consideration as a conservation model in coffee-growing landscapes.

Integrating forest tracts into coffee-dominated landscapes will likely have complex spatial effects on local (α) species diversity and variability among locations (β diversity), both of which will influence regional (γ) diversity. An increase in the amount of one habitat type, such as forest, should increase the diversity of the species dependent on that habitat. Landscapes with more forest should contain larger, better connected forest patches (Fahrig, 2013), resulting in higher α diversity of forest specialists through increased persistence and colonization rates (MacArthur and Wilson, 1967; Levins, 1969; Hanski, 1998) and curtailment of negative edge effects (Ries et al., 2004). Additionally, environmental heterogeneity within the forest itself can increase with forest area, which could increase β and γ diversity (Stein et al., 2014). Yet for the same-sized landscape, an increase in forest cover will be concordant with a decrease in the cover and contiguity of other landcover types such as coffee plantations. Amount and diversity of habitat for species that prefer open areas is maximized at low forest cover levels, while habitat for edge specialists is maximized at intermediate forest cover with high interspersion of contrasting habitat types. Indeed, heterogeneous landscapes containing a mixture of coffee and forest may have the greatest β diversity and perhaps support the greatest total diversity (sensu Intermediate Disturbance Hypothesis; Connell, 1978).

Diversity patterns in coffee-growing landscapes are thus driven by dynamic biotic processes such as dispersal and habitat selection interacting with spatially explicit distributions of habitat elements (Sánchez-Clavijo et al., 2020). Testing mechanisms shaping biodiversity and evaluating conservation strategies in such dynamic systems requires comparisons of diversity across spatially explicit landscapes. Here, we use community occupancy models to model biodiversity in a region dominated by forest and coffee agriculture. We then use the fitted models to compare conservation approaches in simulated landscapes (Gilroy et al., 2014; Cannon et al., 2019). Using birds as indicators, we test 3 hypotheses. The *land-sparing hypothesis* posits that integrating natural habitats with intensive farming will maximize biodiversity benefits, and species richness should be greatest in landscapes combining tracts of native forest and sun-grown coffee. Alternatively, the *land-sharing hypothesis* postulates that integrating wildlife friendly habitat elements into agricultural lands will maximize biodiversity through increased habitat heterogeneity. If true, species richness should be greatest in landscapes comprised predominantly of shade-grown coffee. Finally, the *hybrid sparing/sharing hypothesis* posits that biodiversity is maximized in landscapes that combine these approaches to include forest tracts embedded in shade-grown coffee plantations. This study assesses support for these three hypotheses within a globally important agricultural system, with the goal of informing conservation practices in hyper-diverse, tropical forest landscapes.

## 2. Materials and methods

### 2.1. Sampling sites

Data collection occurred on the western/northwestern slopes of the Sierra Nevada de Santa Marta in northern Colombia (Fig. 1). This isolated massif supports an avian community with high diversity and endemism (Cracraft, 1985; Jenkins et al., 2013), and has been ranked as the World's most irreplaceable protected area (Le Saout et al., 2013). The massif is also an important stopover and wintering region for Neotropical migratory birds (Gómez et al., 2015; Bayly et al., 2017). Since adoption of intensive coffee production in the 1970s, thousands of hectares of native forest in the Sierra Nevada de Santa Marta have been converted to coffee farms (Guhl, 2008).

We used a stratified random approach to identify bird survey stations (hereafter *sites*). We first built and validated a landcover classification using local landcover data (Supplement S1). We then stratified potential sites across two gradients. The first was site type, with sites distinguished as forest, low-shade coffee (canopy cover $\leq$ 30%), and high-shade coffee (canopy cover $>$ 30%). Sampling this gradient allowed comparing avian diversity among forest sites and heterogeneous coffee sites. Because forest cover around a site can affect local diversity through immigration (Fahrig, 2013), we also sampled across a gradient of forest cover within 2 km of each site type. Quantifying these contextual effects is critical for comparing land-sharing and land-sparing models given that land-sparing incorporates forest patches into a landscape. We chose 2 km because forest cover at this scale was highly correlated ($r > 0.7$) with forest cover measured at scales ranging from 1 km to 5 km (Fig. S2.1), and therefore likely relevant to species with heterogeneous perceptions of landscape context. Full details on site selection are available in Supplement S2. Ultimately, we selected 80 forest points, 62 low-shade points, and 82 high-shade points spaced at least 200 m apart.

### 2.2. Avian and vegetation sampling

Trained observers conducted morning point-count surveys at 202 breeding season sites (5 May–15 July 2018) and 224 non-breeding season sites (9 January–18 February 2019). We conducted multiple surveys per site so we could use occupancy models (Dorazio and Royle, 2005) to account for species-specific detection probabilities. The number of surveys per site (mean = 4, SD = 1) and days between repeated surveys (mean = 5, SD = 13) varied due to weather or logistical issues. Counts lasted 10 min but were extended when necessary to identify all birds present (mean survey length = 10.22 min, SD = 0.84). Observers recorded all birds seen or heard within 50 m of the site, excluding

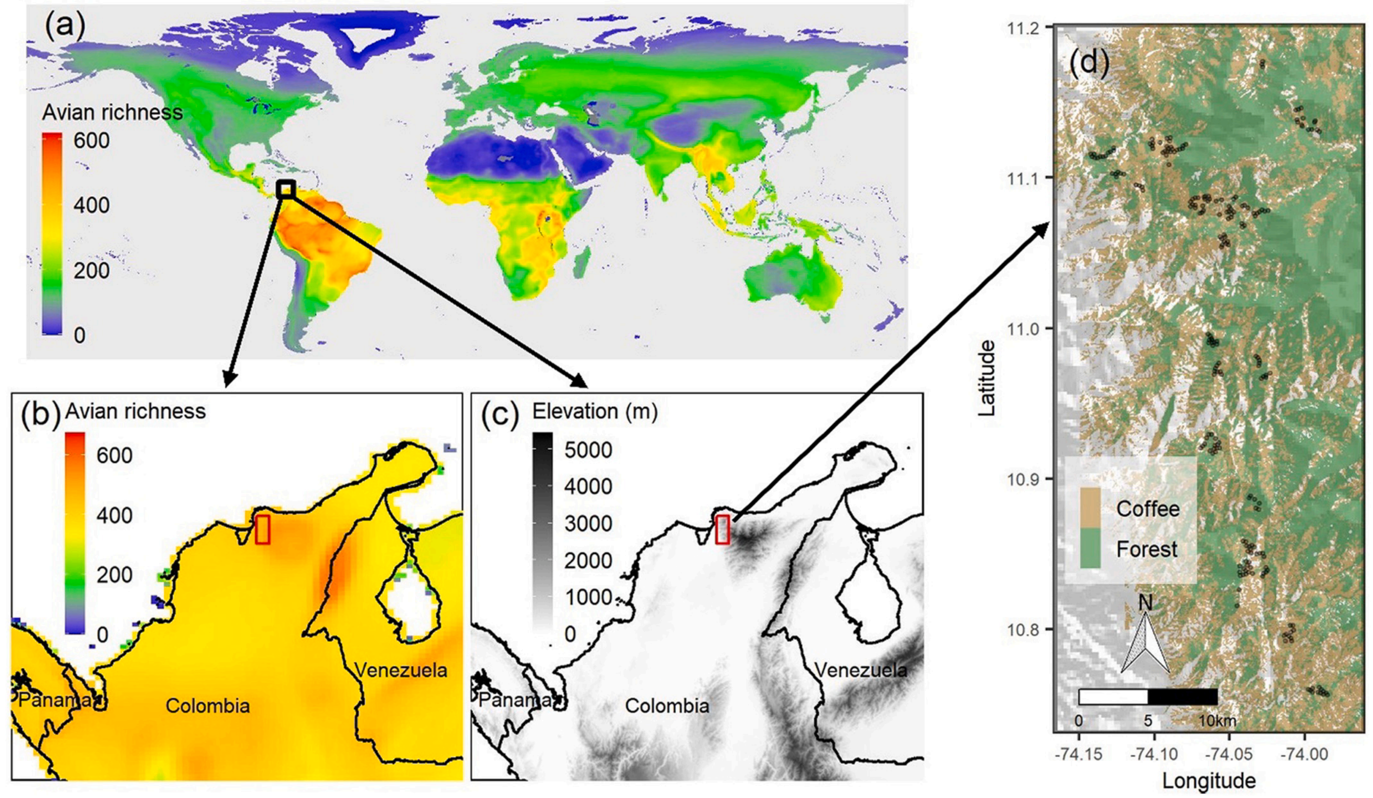

**Fig. 1.** Our study area on the western slope of the Sierra Nevada de Santa Marta is a global hotspot for avian diversity (a, b; data from Jenkins et al., 2013). This isolated massif in northern Colombia (c) was historically dominated by tropical forest, but much of the forest at mid-elevations has been converted to coffee agriculture. Our study sampled avian communities at point-count stations (black symbols, d) across forest and coffee habitats in the region at elevations between 700 and 1800 m.

flyovers. Prior to analysis, we classified the 245 detected species into one of three habitat preference groups: forest specialists, open area specialists, and generalists (Supplement S3).

We also surveyed vegetation at each site, estimating shrub cover and three tree-related metrics: canopy cover, canopy height, and basal area. Tree metrics were highly correlated (Table S4.1) and were reduced to a single covariate (representing 77% of the variation among them) using a principal components analysis (Table S4.2). See Supplement S4 for full vegetation sampling protocols.

### *2.3. Data analyses*

We analyzed data for the breeding and non-breeding season separately using Bayesian hierarchical community occupancy models (Dorazio and Royle, 2005; Iknayan et al., 2014). This approach allowed us to model the distributions of all recorded species (even rare ones) while accounting for imperfect detection and to generate an unbiased estimate of the richness of the regional community (Iknayan et al., 2014; Tingley et al., 2020). We chose species richness over other biodiversity metrics (e.g., functional, genetic, and phylogenetic diversity) because it is most comparable with results from previous land-sharing studies in shade-grown coffee systems (e.g., Philpott et al., 2007; Chandler et al., 2013).

Our occupancy models had multiple, nested hierarchical levels. Individual species were nested within habitat preference groups, repeated surveys were nested within sites, and sites were nested within seven spatial regions to account for spatial autocorrelation. In the following equations: g indexes the three habitat preference groups; s(g) indexes unique species nested within each preference group g; r indexes the seven spatial regions; i(r) indexes unique sites nested within each region r; and j(r,i) indexes unique surveys conducted at site i in region r.

We reformatted our survey data so that there was a single binary observation for each species on each survey. This observation variable, $y_{g,s(g),r,i(r),j(r,i)}$, took a value of 1 if the species was detected and 0 otherwise. Under this modeling framework, a species can only be recorded during a survey if (1) it is part of the regional community, (2) it occupies the sampling site, and (3) the observer detects it. All 245 detected species were considered part of the regional community. We also added between 150 and 200 additional species to each habitat preference group to represent hypothetical species that may have been part of the community but were never detected (Iknayan et al., 2014; Tingley et al., 2020). We supplemented the dataset with a value of 0 for each $y_{g,s(g),r,i(r),j(r,i)}$, for the augmented species.

Following precedent (Dorazio and Royle, 2005; Iknayan et al., 2014), we specified our community occupancy model such that:

$$y_{g,s(g),r,i(r),j(r,i)} \sim \text{Bernoulli}\left(p_{g,s(g),r,i(r),j(r,i)} \times z_{g,s(g),r,i(r)}\right)$$

$$z_{g,s(g),r,i(r)} \sim \text{Bernoulli}\left(\psi_{g,s(g),r,i(r)} \times w_{g,s(g)}\right)$$

$$w_{g,s(g)} \sim \text{Bernoulli}\left(\Omega_{(g)}\right)$$

The value $p_{g,s(g),r,i(r),j(r,i)}$ represents the conditional probability a species is detected on the survey given it uses the site; $\psi_{g,s(g),r,i(r)}$ represents the conditional probability a species uses a site given it is a member of the community; and $\Omega_g$ is the probability the species is part of the community. The variable $z_{g,s(g),r,i(r)}$ takes a value of 1 if the site is used by the species and 0 otherwise, and $w_{g,s(g)}$ takes a value of 1 if the species is a member of the community and 0 if it is not. Because individuals may not be detected even when they are present, both $z_{g,s(g),r,i(r)}$ and $w_{g,s(g)}$ are imperfectly observed. Under these models, a species cannot be detected if it is not present at a site and cannot be present at the site if it is not a member of the community. These models also assume the community is consistent across sites and that species-specific site use is consistent across surveys to ensure all probabilities are identifiable (Iknayan et al., 2014; Tingley et al., 2020).

Within the model, we linked $p_{g,s(g),r,i(r),j(r,i)}$ with covariates that could impact detection probability using logistic regression:

$$\mathrm{logit}\left(p_{g,s(g),r,i(r),j(r,i)}\right) = \alpha 0_{g,s(g)} + \alpha 1_{g,s(g)}\mathrm{Coffee}_{r,i(r)} + \alpha 2_{g,s(g)}\mathrm{Length}_{r,i(r),j(r,i)} + \alpha 3_{g,s(g)}\mathrm{Time}_{r,i(r),j(r,i)} + \alpha 4_{g,s(g)}\mathrm{Time}^2_{r,i(r),j(r,i)} \tag{1}$$

Here, *Coffee* is an indicator specifying whether the site was in coffee or forest. *Length* represents survey duration (minutes), and *Time* represents time of day that the survey was conducted (recorded in minutes since midnight). We similarly used logistic regression to model $\psi_{g,s(g),r,i(r)}$ as a function of covariates that could influence site use:

$$\begin{aligned}\mathrm{logit}\left(\psi_{g,s(g),r,i(r)}\right) = {} & \beta 0_{g,s(g)} + \mathrm{Region}_{g,r} + \beta 1_{g,s(g)}\mathrm{Coffee}_{r,i(r)} + \beta 2_{g,s(g)}\mathrm{Elevation}_{r,i(r)} \\ & + \beta 3_{g,s(g)}\mathrm{Elevation}^2_{r,i(r)} + \beta 4_{g,s(g)}\mathrm{Tree}_{r,i(r)} \\ & + \beta 5_{g,s(g)}\mathrm{Tree}_{r,i(r)}\mathrm{Coffee}_{r,i(r)} + \beta 6_{g,s(g)}\mathrm{Shrub}_{r,i(r)} \\ & + \beta 7_{g,s(g)}\mathrm{Shrub}_{r,i(r)}\mathrm{Coffee}_{r,i(r)} + \beta 8_{g,s(g)}\mathrm{Forest500m}_{r,i(r)} \\ & + \beta 9_{g,s(g)}\mathrm{Forest500m}_{r,i(r)}\mathrm{Coffee}_{r,i(r)} + \beta 10_{g,s(g)}\mathrm{Forest2km}_{r,i(r)} \\ & + \beta 11_{g,s(g)}\mathrm{Forest2km}_{r,i(r)}\mathrm{Coffee}_{r,i(r)}\end{aligned} \tag{2}$$

*Region* is a group-specific regional effect to account for spatial autocorrelation and *Elevation* represents site elevation in meters above sea level. *Forest500m* and *Forest2km* are percent forest cover measured at bird territory (500 m) and landscape (2 km) scales, respectively. *Tree* represents the tree metric principal component, and *Shrub* is percent shrub cover at the site. We included an interaction between each of these latter four covariates and *Coffee* to allow effects to vary between coffee and forest sites.

We standardized all covariates to facilitate model convergence. Pearson's correlation among all covariate pairs in the models was $r \leq 0.48$ (Table S4.1). Each species-specific parameter ($\alpha 0_{g,s(g)}$ through $\alpha 4_{g,s(g)}$ and $\beta 0_{g,s(g)}$ through $\beta 11_{g,s(g)}$) was assumed to come from a normal distribution governed by community-level hyperparameters. Specifying these hyperdistributions allows information to be shared across species, improving the precision and accuracy of parameter estimates (Iknayan et al., 2014). We specified parameter-specific hyperdistributions as:

$$\theta_{g,s(g)} \sim \mathrm{Normal}\left(\mu_{\theta g}, \sigma^2_{\theta g}\right), \quad \text{for } \theta = \beta 0, \beta 1, \ldots, \beta 11$$

$$\theta_{g,s(g)} \sim \mathrm{Normal}\left(\mu_{\theta}, \sigma^2_{\theta}\right), \quad \text{for } \theta = \alpha 0, \alpha 1, \ldots, \alpha 4$$

$$\mathrm{Region}_{g,r} \sim \mathrm{Normal}\left(0, \sigma^2_{\mathrm{Region}}\right)$$

We derived species richness (N) from the fitted model by summing the species in each habitat preference group:

$$N_g = \sum_{s(g)} w_{g,s(g)}$$

We fit models in JAGS (v. 4.3.0; Plummer, 2003) using the 'jagsUI' package (v. 1.5.1; Kellner, 2019) in R (v. 3.6.1) operating on the Smithsonian's computing cluster (https://doi.org/10.25572/SIHPC). We used vague priors on community hyperparameters and ran three MCMC chains for 410,000 iterations, burning the first 210,000 and retaining every 100th estimate. We assessed convergence by ensuring the Gelman-Rubin statistic (Rc) for monitored parameters was Rc < 1.1 (Gelman et al., 2004) and by visually inspecting traceplots. The full model specification and fit assessment is in Supplement S5.

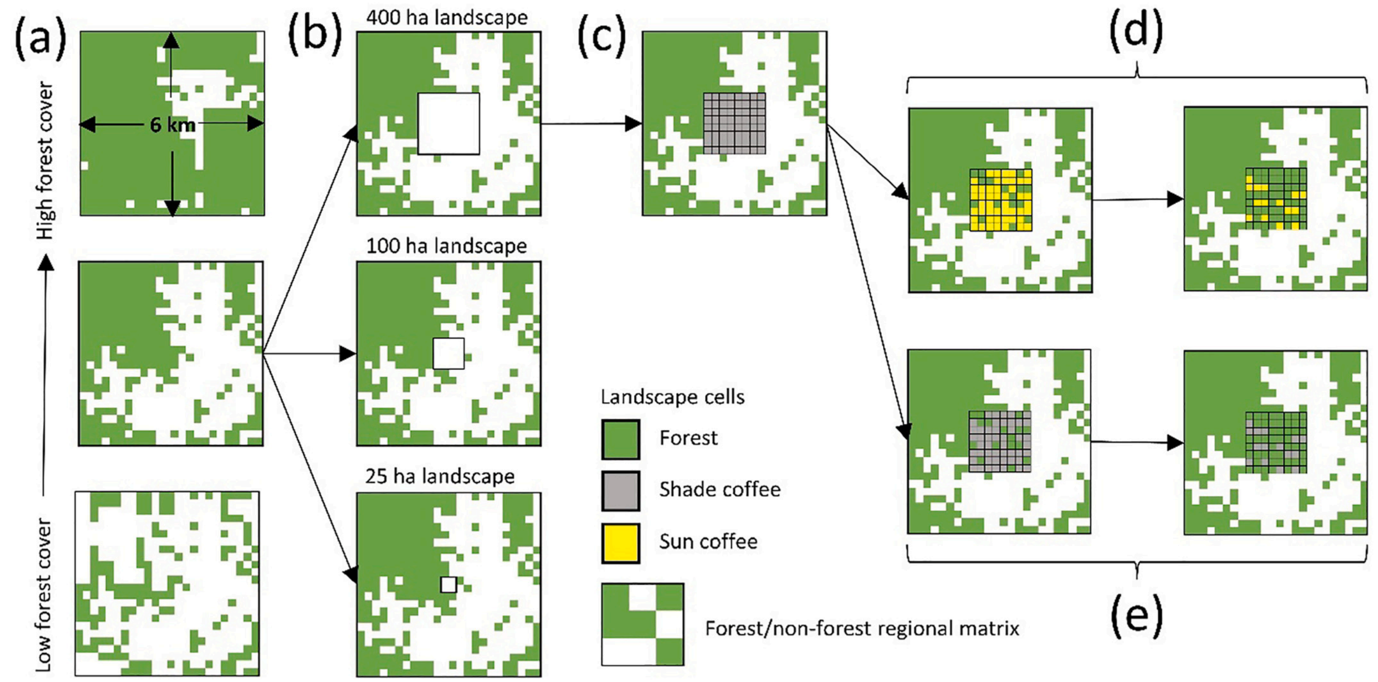

**Fig. 2.** A visual depiction of the simulation process used to compare hypotheses regarding the importance of land-sharing and land-sparing for conserving avian biodiversity in a tropical region dominated by forest and coffee agriculture. (a) We first simulated regional forest cover in 36 km$^2$ regions using parameters that created a gradient in forest cover and configuration among regions. (b) In each simulated region, we inserted landscapes of 3 different sizes in parallel. (c) Within each landscape, we created a land-sharing scenario where all 250 m grid cells in the landscape are assumed to be shade coffee (≥40% canopy cover). We simulated species assemblages in each grid cell using a community occupancy model fit to an empirical dataset and calculated mean alpha, beta, and gamma diversity for the landscape. (d) We created land-sparing scenarios for comparison by converting all cells to sun coffee (≤10% canopy cover) and iteratively adding more forest cells into the landscape and calculating diversity metrics at each iteration. (e) To create hybrid sharing/sparing scenarios, we took the same approach as in (d), though we replaced sun coffee cells with shade coffee cells. For comparison, we subtracted diversity metrics in the land-sharing landscape (c) from the analogous metrics recorded in each land-sparing (d) and hybrid (e) landscape in the same simulated region.

### 2.4. *Simulating sharing and sparing landscapes*

To test our hypotheses, we compared simulated diversity within land-sharing, land-sparing, and hybrid sharing/sparing landscapes. We first generated 3600 ha (6 km squared) *regions* with a grain of 6.25 ha (250 m squared; Fig. 2a). These regions were large enough to provide a 2 km buffer around all sides of the largest landscapes (400 ha) in which we would simulate diversity (Fig. 2b) so we could measure forest cover within 2 km of any point in the landscape. Next, we generated realistic forest cover in these regions by binarizing midpoint displacement neutral landscape models (Peitgen and Saupe, 1988) using the NLMR (v. 1.0) and landscapetools (v. 0.5.0) packages in R (Sciaini et al., 2018). Simulations used binarization break and roughness values ranging from 0 to 1 in increments of 0.1 to vary the composition and configuration of those landscapes, respectively (Fig. 2a), and ensure our results were generalizable across contexts. We generated 100 regions for each of the 101 combinations of simulation parameters.

We centered *landscapes* of three sizes (25, 100, and 400 ha) in each region in parallel simulations (Fig. 2b) to compare conservation approaches across farms areas of variable size. All landscape cells were initially shade-grown coffee, representing a land-sharing scenario (Fig. 2c). We then changed all landscape cells into sun coffee and incrementally converted them into forest to simulate land-sparing scenarios with increasing amounts of forest habitat (Fig. 2d). We similarly simulated hybrid sharing/sparing scenarios using landscapes comprised of shade coffee cells with increasing amounts of forest (Fig. 2e).

In each iteration, we simulated α diversity from our fitted occupancy models at points centered in each landscape cell. We determined the presence of each species at a point using a draw from a Bernoulli distribution where the species' occupancy probability was calculated by inserting point-specific covariates into Eq. (2). These covariates included amount of forest within 500 m and 2 km, which we measured based on the regional context of the point on each landscape simulation. Input values for tree and shrub cover were unique to each point type (forest, sun coffee, shade coffee) and based on data collected at field sites. For forest points, our covariate inputs were the mean tree and shrub cover values recorded across forested field sites; for sun and shade coffee points, these inputs were the mean values recorded across coffee sites with canopy cover $\leq 10\%$ and canopy cover $\geq 40\%$, respectively (Figs. S4.1 and S4.2). We propagated uncertainty from the occupancy model into the simulation by using a random draw from the posterior distribution of the model parameters for each simulated region. We repeated this process using landscapes at the minimum (686 m), maximum (1763 m), and mean (1265.2 m) elevation of our sites.

For each simulation we recorded mean α diversity, mean Bray-Curtis dissimilarity among point pairs (β diversity), and total richness (γ diversity) in the landscape. We treated land-sharing (100% shade coffee) landscapes as the baseline for comparison given this is the current conservation standard. In each simulated region, we subtracted land-sharing diversity metrics from those recorded in land-sparing and hybrid landscapes to estimate differences relative to this standard (Fig. 2). Supplement S6 contains simulation code and a simulation flowchart.

## 3. Results

### 3.1. *Community occupancy models*

We detected 245 unique species over the two seasons (Supplement S3). Estimated bird community richness was 266 species (95% credible interval [CI]: 227, 348) in the breeding season and 328 (95% CI: 268, 431) species in the non-breeding season. Generalists dominated the community (Table 1), comprising 53.7% (95% CI: 40.9%, 62.2%) of breeding and 62.2% (95% CI: 47.2%, 72.5%) of non-breeding species. Consequently, even covariates that had a small influence on the average generalist could have large influences on total species diversity. For example, in breeding season coffee sites, the positive effect of tree cover on forest specialists was 1.5 times larger than the estimated effect on generalists (Table 1). Yet because generalists were much more common, expected richness increased by nearly 30 species from low to high tree cover coffee sites, while expected richness of forest specialists increased by fewer than 10 species (Fig. 3).

**Table 1**

We fit community occupancy models to avian point count data recorded in the Sierra Nevada de Santa Marta to quantify the effects of habitat type (coffee or forest site) and habitat covariates (elevation, tree cover, shrub cover, and amount of forest within 500 m and 2 km) on species-specific occupancy probabilities. Parameter estimates for each species were assumed to come from a normal distribution distinct to their habitat preference group (forest specialists, open area specialists, or generalists), and the estimated mean effects for each group are presented on the logit scale. We also report the estimated number of species comprising each group.

| | Breeding season | | | Non-breeding season | | |
|---|---|---|---|---|---|---|
| | Forest specialists | Open area specialists | Generalists | Forest specialists | Open area specialists | Generalists |
| Model parameter estimates | | | | | | |
| All sites | | | | | | |
| Elevation | −0.04 (−0.52, 0.42) | −0.56 (−1.00, −0.16) | −0.11 (−0.35, 0.11) | 0.13 (−0.44, 0.70) | −0.12 (−0.77, 0.50) | −0.19 (−0.39, 0.02) |
| Elevation$^2$ | 0.20 (−0.10, 0.46) | −0.29 (−0.52, −0.07) | −0.11 (−0.23, 0.01) | −0.19 (−0.41, 0.03) | −0.56 (−0.94, −0.25) | −0.19 (−0.29, −0.10) |
| Forest sites | | | | | | |
| Intercept | −4.71 (−8.09, −2.85) | −5.26 (−7.79, −3.66) | −2.80 (−4.16, −1.75) | −4.80 (−8.56, −2.77) | −7.84 (−14.77, −4.13) | −3.87 (−5.61, −2.55) |
| Tree PC[a] | −0.13 (−0.43, 0.15) | −0.09 (−0.54, 0.32) | −0.20 (−0.35, −0.05) | 0.39 (0.13, 0.66) | −1.10 (−1.84, −0.40) | −0.07 (−0.20, 0.06) |
| Shrub | −0.05 (−0.38, 0.27) | 0.51 (0.00, 1.13) | 0.09 (−0.08, 0.26) | −0.06 (−0.34, 0.22) | 0.53 (−0.24, 1.40) | 0.01 (−0.12, 0.14) |
| Forest 500 m | −0.06 (−0.45, 0.30) | 0.10 (−0.43, 0.62) | −0.01 (−0.20, 0.18) | 0.13 (−0.17, 0.43) | −0.33 (−1.16, 0.47) | 0.06 (−0.09, 0.21) |
| Forest 2 km | −0.18 (−0.60, 0.23) | 0.21 (−0.38, 0.77) | −0.21 (−0.41, −0.01) | −0.14 (−0.50, 0.22) | 0.01 (−0.78, 0.82) | 0.04 (−0.13, 0.22) |
| Coffee sites | | | | | | |
| Intercept | −7.87 (−11.50, −5.77) | −3.01 (−5.34, −1.62) | −2.70 (−4.07, −1.66) | −6.16 (−9.96, −4.07) | −4.82 (−11.54, −1.52) | −3.08 (−4.82, −1.75) |
| Tree PC[a] | 0.41 (−0.07, 0.94) | −0.07 (−0.62, 0.51) | 0.27 (0.09, 0.45) | 0.57 (0.16, 1.00) | 0.00 (−0.43, 0.45) | 0.67 (0.51, 0.83) |
| Shrub | 0.82 (0.30, 1.41) | 0.13 (−0.14, 0.42) | 0.22 (0.09, 0.36) | 0.08 (−0.30, 0.51) | −0.07 (−0.38, 0.27) | 0.05 (−0.07, 0.16) |
| Forest 500 m | 0.00 (−0.62, 0.61) | 0.16 (−0.23, 0.53) | −0.01 (−0.21, 0.20) | 0.03 (−0.44, 0.51) | −0.07 (−0.52, 0.37) | −0.15 (−0.30, 0.01) |
| Forest 2 km | 0.18 (−0.38, 0.74) | −0.20 (−0.68, 0.27) | −0.08 (−0.30, 0.14) | −0.07 (−0.58, 0.43) | −0.20 (−0.71, 0.30) | 0.12 (−0.08, 0.31) |
| Species in the community | 80.80 (55, 156) | 43.56 (35, 65.03) | 142.14 (123, 179) | 70.49 (50, 132.03) | 54.95 (31, 139.03) | 202.92 (167, 272) |

[a] Principal component combining canopy cover, canopy height and basal area.

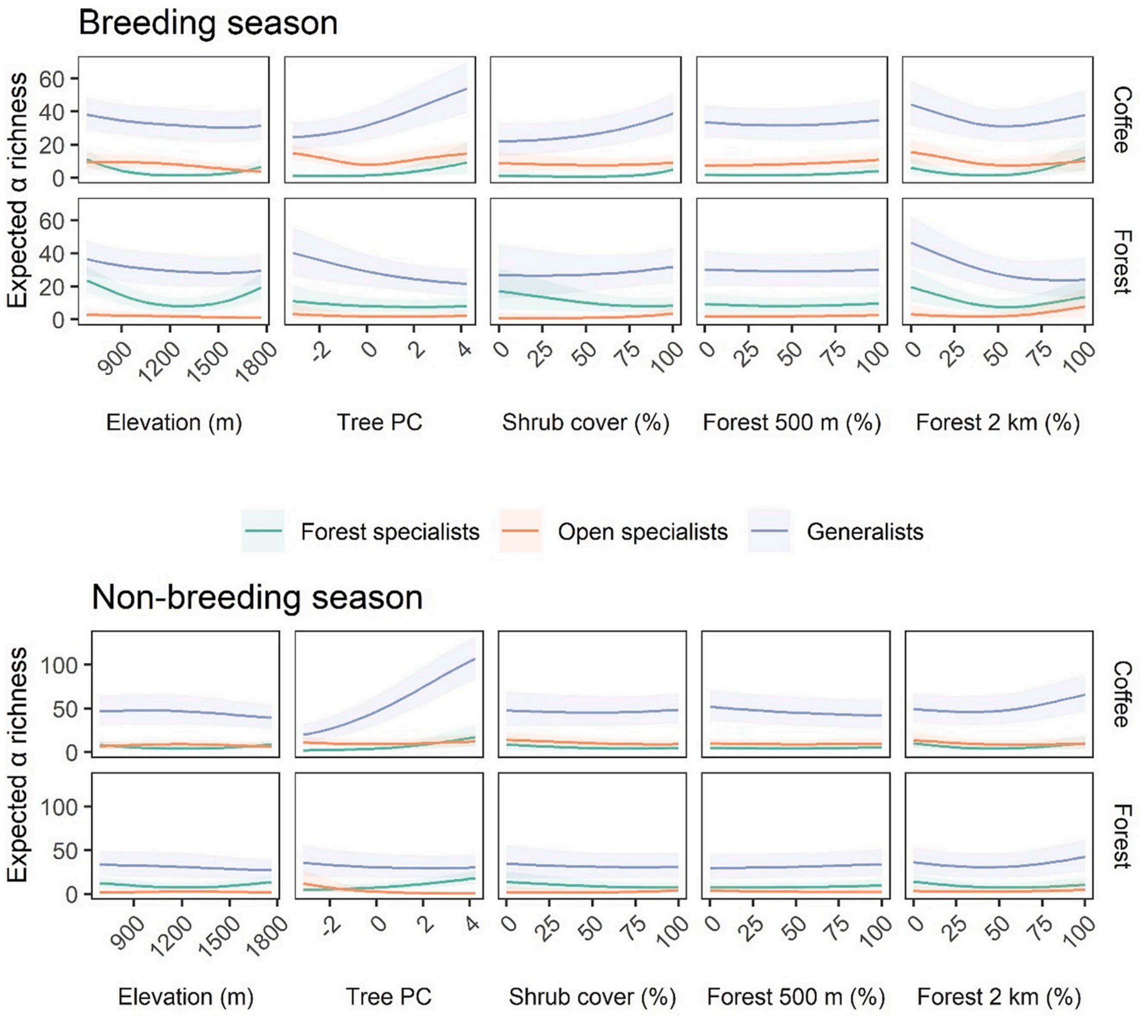

**Fig. 3.** Using fitted community occupancy models, we simulated avian diversity at points in land-sharing and land-sparing landscapes that varied with five habitat characteristics (elevation, tree cover, shrub cover, and the amount of forest within 500 m and 2 km). These plots demonstrate how expected point-level (α) richness (i.e., the sum of occupancy probabilities across species) in three habitat preference groups (forest specialists, open area specialists, and generalists) varies as a function of each habitat characteristics. We held values of all other covariates at their mean when generating expected richness values. Relationships are plotted separately for forest and coffee sites. Error ribbons represent 95% credible intervals.

All three groups were more likely to occupy coffee sites in the non-breeding season than the breeding season. Community hyper-parameter estimates revealed that the average, breeding, open area specialist was 10.2 (95% CI: 3.4, 25.4) times more likely to occupy a coffee than a forest site, while in the non-breeding season it was 27.8 (95% CI: 4.7, 98.5) times more likely. Generalist breeding season occupancy probability was 1.1 (95% CI: 0.7, 1.6) times greater in coffee than forest sites, increasing to 2.2 (95% CI: 1.5, 3.1) times greater in the non-breeding season. Forest specialists showed significant preference for forest sites in both seasons, with occupancy probability being 27.8 (95% CI: 8.5, 78.8) times greater in forest than coffee in the breeding season, although this decreased to only 4.2 (95% CI: 1.8, 8.9) times greater during the non-breeding season.

We found no evidence for lack of fit in either our breeding (Bayesian *p*-value = 0.63) or non-breeding (Bayesian p-value = 0.58) season models. That is, our models could generate datasets that were statistically like the empirical data (Kéry and Royle, 2016), and should thus generate realistic bird communities in simulated landscapes. Full model results are in Supplement S7.

### 3.2. Simulated landscape diversity

Diversity patterns were remarkably similar among different-sized landscapes and across elevations. Therefore, we focus on comparing conservation approaches in intermediate (100 ha) landscapes at mean elevations (1265 m). Results from alternative landscape sizes and elevations are in Figs. S7.1–S7.4.

Forest specialists benefited more from land-sparing than land-sharing; mean α diversity increased in both seasons as landscapes were converted from sun coffee to forest, while mean β diversity decreased, indicating convergence towards forest specialist communities across points (Fig. 4). Consequently, total richness of forest specialists was greater in land-sparing than land-sharing landscapes regardless of the amount of forest retained, and significantly greater when at least 50% of the landscape was comprised of forest (Fig. 4).

Conversely, open area specialists benefited slightly more from land-sharing compared to land-sparing. When forest cover was low in land-sparing landscapes, point-level α and β diversity was similar between sparing, sharing, and hybrid sparing-sharing models. As forest cover increased, average α diversity decreased while average β diversity increased (Fig. 4). When scaled up, these opposite patterns had relatively little effect on landscape-level γ diversity. Total richness of open area specialists was generally lower in land-sparing than land-sharing landscapes, although these differences were small and not statistically significant.

Generalists fared poorly in land-sparing landscapes compared to

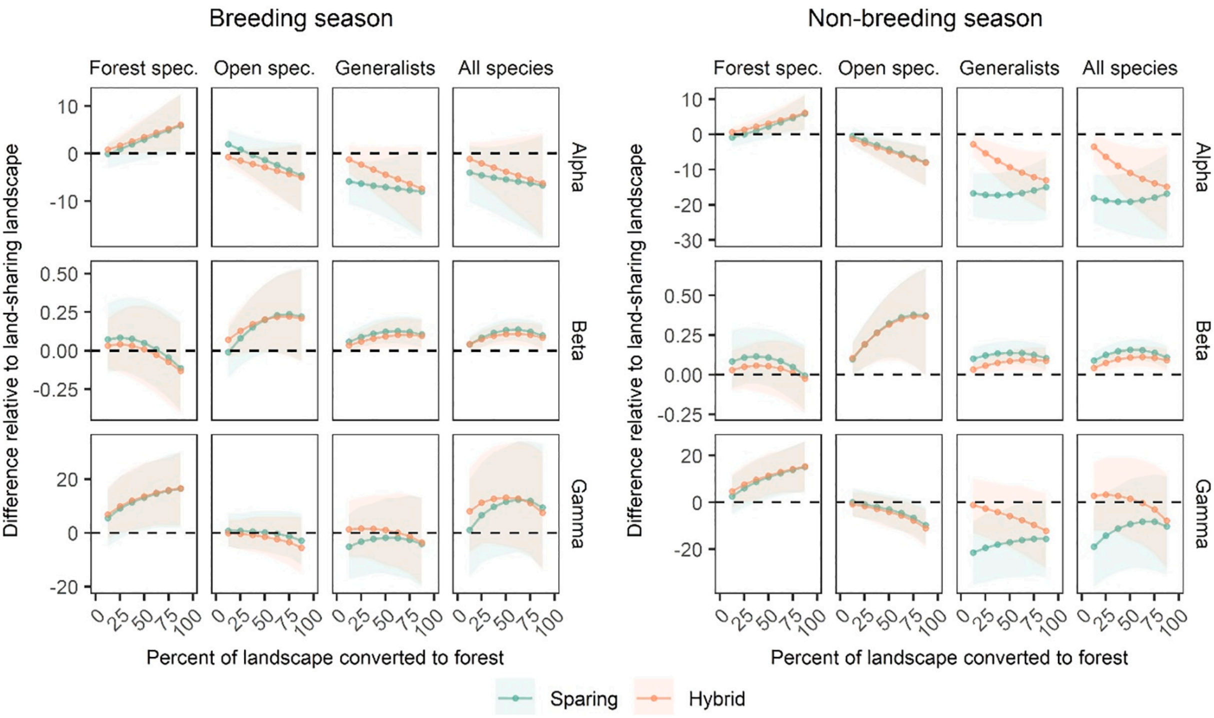

**Fig. 4.** A comparison of simulated diversity metrics in land-sharing landscapes relative to land-sparing and hybrid sharing/sparing landscapes (100 ha) for birds in three habitat preference groups (forest specialists, open area specialists, and generalists) and for all groups combined. Land-sharing landscapes were comprised of 100% shade coffee and represent the standard conservation model in coffee agroforestry systems. Sparing and hybrid landscapes were comprised of both forest and either sun or shade coffee, respectively. Diversity metrics are measured and plotted relative to a land-sharing landscape in an identical region. Values above the dashed line indicate that diversity was greater in land-sparing or hybrid landscapes than land-sharing landscapes and vice versa. The alpha, beta, and gamma diversity metrics represent mean species per point, mean dissimilarity per point, and total landscape richness, respectively. Error ribbons represent 1 SD.

land-sharing landscapes. Mean α diversity of generalists was significantly lower in sparing landscapes for nearly all levels of forest cover, particularly during the non-breeding season where up to 17.21 (95% CI: 24.19, 11.00) fewer generalists used each point (Fig. 4). This occurred due to the significant, positive relationship between tree cover and generalist occupancy patterns (Table 1; Fig. 3). Because coffee habitat in sparing landscapes had almost no tree cover, coffee plots supported many fewer generalist species than shade coffee plots in sharing landscapes. Total generalist richness was also lower in sparing than sharing landscapes across forest cover levels, with differences most pronounced during the non-breeding season (Fig. 4).

When we aggregated species groups, land-sparing supported greater diversity than land-sharing during the breeding season, while the opposite pattern was true in the non-breeding season. Sparing led to diversity gains in forest specialists that were similar between seasons, but the diversity losses of generalists and open area specialists were greater in the non-breeding season. The gains in forest specialist diversity more than compensated for the losses of generalist and open area species during the breeding season, but not the non-breeding season.

Hybrid landscapes tended to support greater generalist diversity than sparing landscapes, particularly at low levels of forest cover (Fig. 4). Again, this difference was driven by an increase in generalist diversity with tree cover in coffee plots; shade coffee in hybrid landscapes supported more generalists than sun coffee in sparing landscapes. Differences in diversity between sparing and hybrid landscapes were typically small and non-significant for other species groups (Fig. 4).

## 4. Discussion

Across agricultural systems, the species that benefit from land-sharing conservation are often not those of greatest conservation concern, or even those found in the original native vegetation (Phalan, 2018). Results from our study bolster previous evidence that shade-grown coffee does not support the same bird community as the native forest habitat it typically supplants (Arce et al., 2009; Chandler et al., 2013; Sánchez-Clavijo et al., 2020). Although shade-grown coffee can support similar species richness and abundance as nearby forest (Perfecto et al., 2003; Moguel and Toledo, 1999; Philpott et al., 2007), the composition differs between these communities. Our results suggest that land-sparing conservation models designed to protect networks of native forest tracts within coffee plantations could help support more forest specialists and greater overall species diversity, particularly during the breeding season.

We nonetheless caution against discounting the conservation value of shade coffee. Endemic and IUCN listed species in our study area were split between forest specialist and generalist categories (Table S3.1), groups that provide complementary ecological functions in tropical systems. Generalist avian pollinators and seed-dispersers, for example, accelerate tropical forest regeneration (Carlo and Morales, 2016) and provide resilience to local foraging networks (Palacio et al., 2016) in communities where forest-dependent frugivores, understory insectivores, and nectarivores are absent or scarce (Gómez et al., 2021). Because forest specialists tend to be at greatest risk of extinction due to degradation of tropical forests (Betts et al., 2019; Gómez et al., 2021), providing habitat via shade-grown coffee for generalists and open-area specialists may conserve functional and taxonomic diversity in highly disturbed regions (Jha et al., 2014).

All species groups in our study relied more on shade coffee during the non-breeding season than the breeding season, implying the utility of shade coffee as habitat varies seasonally. Previous research in the region found that breeding performance of avian habitat generalists was generally higher in forest patches compared to shade-grown coffee (Sánchez-Clavijo et al., 2020). Both resident and Neotropical migrant birds are known to track resource availability across the annual cycle

(Tellería and Pérez-Tris, 2003), suggesting that resources (e.g., insect prey) may be more abundant in shade coffee during the non-breeding season. Seasonal differences could further be driven by the influx of generalist Nearctic-Neotropical migrants during the non-breeding season (Petit et al., 1995; Bennett et al., 2018). Regardless of the mechanisms, our results suggest combining land-sparing and land-sharing conservation models will maximize the conservation value of coffee-growing landscapes across the annual cycle.

### 4.1. Land-sparing and coffee certification programs

Coffee is one of the most widely traded tropical products and supports 25 million households in more than 50 lower- and middle-income countries worldwide (FAO, 2022; ICO, 2022). Integrative conservation approaches are therefore essential to sustain coffee production while supporting wildlife in the Earth's generally biodiverse coffee-growing regions (Perfecto et al., 1996). Eco-certifications and voluntary sustainability standards represent one such conservation mechanism that is increasing in prevalence within the coffee sector as global demand for specialty coffee increases (FAO, 2022; Meemken et al., 2021). The historical promotion of shade-grown coffee within such programs grew intuitively from the crop's evolution as an understory shrub but tends to neglect the landscape scale processes that shape local biodiversity (Tscharntke et al., 2015; Grass et al., 2019). Therefore, we recommend promoting land-sparing conservation models, in addition to shade-grown coffee, within such programs. This will provide habitat for a greater diversity of species and maximize opportunities for farmers to participate in these programs.

Land-sparing conservation approaches assume that areas subject to intensive farming practices will produce greater crop yields and revenue than those that incorporate wildlife-friendly practices (Karp et al., 2013). However, coffee farm profitability is mediated by spatial variability in yield-shade relationships (DaMatta, 2004; Arce et al., 2009) and access to specialty markets based on product quality, direct-trade relationships, and certifications (Perfecto et al., 2005; Hernandez-Aguilera et al., 2018). Low-input shade coffee can sometimes be more profitable than high-yielding, intensified sun-grown coffee (Perfecto et al., 2005; Jeezer et al., 2017). Proximal forest tracts can also confer economic benefits to farmers via pest control and increased pollination rates (Ricketts et al., 2004; Karp et al., 2013). Thus, where opportunities exist to pair high-yielding shade coffee with protection or restoration of forest tracts, hybrid sparing/sharing models are likely to be highly effective for integrating conservation and farming. In other regions, one option may be more feasible or economically favorable than the other. Certifications that incorporate both options create alternatives for farmers exposed to heterogeneous local markets, growing conditions, and landscape contexts.

Most certification programs operate at the farm scale, and our findings were consistent across spatial extents relevant to coffee cooperatives, large industrial farms, and estate farms (25–400 ha). At these scales, retaining native forest on 10–25% of the landscape can provide habitat for an equal or greater number of breeding bird species (particularly forest specialists) as shade coffee farms with 40% canopy cover (Figs. 4, S7.1–S7.4). Programs such as Smithsonian Bird Friendly already certify shade coffee farms with at least 40% canopy cover but would need to create new options to evaluate and certify farms with forest set-asides or in landscapes with forest reserves (Tscharntke et al., 2015). However, most coffee farmers globally manage less than 10 ha of coffee (Jha et al., 2014), emphasizing that conservation actions aimed at protecting larger forest tracts may require partnerships with public land managers or collective action among landowners (Tscharntke et al., 2015). Certification standards could also consider small landholders who can set aside at least 2.6 ha of contiguous forest. Below this threshold, the conservation value of forest stands in coffee landscapes appears to diminish (Ritterson et al., 2021), suggesting that 2.6 ha is also a useful target for individual forest stands on larger properties.

Ultimately, the optimal management approach will be dictated by idiosyncrasies in species habitat requirements, coffee growing conditions, landscape context, and stakeholder values. No single strategy is likely to work in all systems. We argue for flexible coffee certification models that allow producers to decide if land-sparing, land-sharing, or a hybrid approach is the best option given their financial and environmental constraints. We also recommend models that can prioritize farms based on habitat and management criteria that help meet regional conservation goals and that encourage engagement with multi-owner partnerships to protect larger forest tracts. These actions are essential for engaging coffee farmers in voluntary conservation programs and to sustain the complimentary avian communities that exist within coffee-growing landscapes.

## CRediT authorship contribution statement

**Jonathon J. Valente:** Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Ruth E. Bennett:** Investigation, Project administration, Resources, Writing – original draft, Writing – review & editing. **Camila Gómez:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Nicholas J. Bayly:** Conceptualization, Data curation, Investigation, Methodology, Project administration, Writing – original draft, Writing – review & editing. **Robert A. Rice:** Conceptualization, Funding acquisition, Investigation, Methodology, Resources, Supervision, Writing – review & editing. **Peter P. Marra:** Conceptualization, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing. **T. Brandt Ryder:** Conceptualization, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing. **T. Scott Sillett:** Conceptualization, Funding acquisition, Investigation, Project administration, Resources, Supervision, Writing – review & editing.

## Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2022.109568.

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