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Generating best management practices for Avian conservation with a land-sparing agricultural system

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Abstract Here we provide guidance for the application of a land sparing production system designed to conserve forest-dependent wildlife in coffee growing regions where environmental conditions preclude coffee cultivation with a land-sharing strategy. In an Integrated Open Canopy ("IOC") coffee system, shade trees planted with coffee may be eliminated at the discretion of the farmer to control outbreaks of leaf rust and increase yields, while an adjacent forest patch of equal or greater area than coffee is conserved. Farmers are compensated for the opportunity costs of conserving forest by the sale of carbon credits, as well as ecosystem services provided by forest patches in the form of increased pollination and pest control by forest-associated bees and birds, respectively. Previous studies have shown IOC farms support forest-dependent birds not found in shade coffee farms. To determine whether there are threshold values of IOC forest characteristics below which the conservation value of IOC farms decreases, we surveyed bird communities with point counts within IOC farms and other forest patches in Costa Rica during 2012. We detected 113 bird species, of which 49 were classified as forest-dependent. Cutpoint regression identified an area of 2.6 ha of forest, and a basal area of 25.2 m^2/ha of forest, below which bird conservation value diminished. These values can serve as the foundation of best management practices for the establishment of IOC farms to afford opportunities for coffee producers to conserve biodiversity in regions where land sharing cultivation is impractical.

Keywords Area · Biodiversity · Bird · Central America · Coffee · Edge · IOC · Threshold

Introduction

Shade coffee, in which coffee is grown under remnant or planted tree cover, has established a paradigm for conserving native biodiversity in agricultural landscapes in the tropics because this system supports high species richness on agricultural lands (Moguel and Toledo 1999). Furthermore, the value of shade coffee as habitat for birds may motivate coffee consumers to pay price premiums, which if passed on to the coffee

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farmer, may motivate them in turn to engage in practices that promote biodiversity (Perfecto et al. 2005). Nevertheless, shade coffee may not be practical in some highland areas that are cool, cloudy and wet because these conditions may encourage coffee leaf rust (*Hemileia vastatrix*), and coffee leaf rust outbreaks are exacerbated by some types of shade cover (Avelino et al. 2004; Johnson et al. 2009). Furthermore, some forest-dependent species are scarce or absent from shade coffee farms (Chandler et al. 2013; Şekercioğlu et al. 2019), and the overwinter survival and persistence of at least one priority species, the wood thrush (*Hylocichla mustelina*), is negatively associated with the use of shade coffee (Bailey and King 2019). The wood thrush is a declining species listed as a Tri-National Concern species and is on the 2016 State of North America's Birds Watch List (North American Bird Conservation Initiative 2016).

Integrated Open Canopy ("IOC") is a coffee growing-system in which an area of coffee is cultivated under shade conditions judged suitable by the producer, adjacent to a patch of conserved forest (Arce et al. 2009). As with many agricultural systems that are employed to conserve biodiversity, there are tradeoffs between production and conservation (Power 2010; although see Jezeer et al. 2017), yet the IOC system does offer benefits to producers that compensate them for the opportunity costs associated with leaving uncultivated land on their property. First, the IOC coffee growing system was originally developed to ameliorate coffee leaf rust infestations under the assumption that more sunlight would reduce the rate of infestation and forest buffers would interrupt spread of spores (Arce et al. 2009). Forest buffers also enhance coffee production by protecting coffee plants from wind damage and erosion and providing a source of organic material from leaf drop (Arce et al. 2009). Farmers are able to sell carbon credits from the forest patches on their farms, and coffee yields may be enhanced by pollination services by forest associated bees (Ricketts 2004) and pest control by forest-associated songbirds (Kellermann et al. 2008; Karp et al. 2013).

IOC coffee may also be a valuable component of biodiversity conservation in coffee-growing lands. For instance, Chandler et al. (2013) found that IOC supported as many forest-dependent bird species as forest, including many species that did not occur in shade coffee plantations. Standards and guidelines exist for promoting suitable habitat conditions for birds in shade coffee that farmers can employ to ensure their farms effectively conserve birds and to assure consumers that their coffee purchases benefit biodiversity (Philpott et al. 2007). Although studies by Chandler et al. (2013) show IOC farms support birds not found in agroforestry habitats, they provided only general guidelines for how the IOC system can be employed to conserve forest-dependent species.

The objective of this study was to generate relationships between forest patch characteristics and the richness of forest-dependent birds to serve as quantitative targets for farmers potentially interested in implementing IOC coffee cultivation. Forest on IOC farms typically consists of relatively small forest patches, and patch area and edge, as well as internal structural characteristics, are known to affect suitability for forest birds (Graham and Blake 2001; Ferraz et al. 2007). Thus, quantifying these relationships, particularly with respect to generating threshold conditions, will provide guidance for potential practitioners, and enable consumers or others wishing to gauge the impacts of these practices to understand their impacts. We hypothesized that an increased forest patch area and width and a low amount of edge relative to area would support more forest-dependent species due to decreased area and edge effects. Also, a broader representation of microhabitat features would create more complexity and habitat niches, and thus be positively associated with the species richness of forest-dependent birds (Philpott et al. 2007).

Materials and methods

Study area

Our study area is a mosaic of forest, agriculture, and human settlements on the Pacific slope of the Tilarán mountain range in Costa Rica (N10°13′ W84°39′; Fig. 1). Forest types of the study area can be classified as montane wet forest (often referred to as cloud forest) above 1200 m, and a premontane moist forest below 1000 m, with a transition zone in between (Holdridge 1947). Land use is dominated by cattle pastures, where famers produce either beef or dairy, resulting in a mosaic of mostly pasture and forest patches. There are also small (2–5 ha) family operated coffee farms, which under the classification system of

Fig. 1 Spatial configuration of forest patches on the Pacific slope of the Tilarán mountain range in Costa Rica with point count locations indicated by red dots (left). A view of our study area (right). The forested ridge is part of the Monteverde Reserve Complex

Moguel and Toledo (1999) would be considered "commercial polyculture systems", which is the only commonly used shade-coffee system in our study region in Costa Rica (Somarriba et al. 2004). Other practices include the raising of pigs, chickens, sugar cane (*Saccharum* spp.), and vegetables such as chayote (*Sechium edule*).

Field methods

To estimate the richness of forest-dependent species, we conducted 100-m fixed radius point count surveys in IOC and other forest patches from February 13 to April 6, 2012. A total of 9 farms were identified as practicing IOC with at least as much forest as coffee under cultivation. To increase sample size, an additional 6 farms were added, featuring a forest patch surrounded by pasture rather than coffee. We anticipated that the inclusion of forest patches that were not part of the IOC system would result in an overestimate of bird area requirements, since edge avoidance is believed to be at least in part the cause of area-sensitivity (Banks-Leite et al. 2010), and edge effects are ameliorated in forest patches to some degree by a matrix with complex structure (Koh et al. 2010) such as shade coffee that occurs adjacent to IOC farms. For this reason, we included a term in the models for "IOC" versus "non-IOC forest", but this term was not included in any of the supported models. Forest patches ranged in size from 1.4 to 26.1 ha. We maximized the number of points in each patch, while keeping them spaced 200 meters apart to minimize the occurrence of individuals at multiple points. In total, counts were conducted at 25 points on 15 farms distributed across an approximately 35 km^2 area, with 15 points on farms practicing IOC. Each point was surveyed three times, during which all individuals detected during a 10-min interval were recorded by species.

The following variables, believed a priori to affect the richness of forest-dependent bird species, were recorded at each point: average canopy height, percent canopy cover, and elevation (Leyequién et al. 2010). Within 50 meters we recorded a complexity index for vines: none, some vines but no "tangles" (where vine stems were concentrated enough to create distinct masses of vines and collected fallen leaves and debris), 1–2 tangles, > 2 tangles), dead hanging leaves (0, < 100, 100–1000, > 1000), and epiphytes (none, moss < 2 cm thick and few bromeliads, moss 2–5 cm and few bromeliads, moss > 5 cm and many bromeliads). These variables were identified as important habitat features by Chandler and King (2011). The abundance of large trees is known to affect bird biodiversity in coffee farms (Bakermans et al. 2012), and we measured the diameter at breast height of all trees as selected by a 10-factor cruising prism to estimate basal area. In cases where point count radii extended into adjacent non-forest, we estimated the extent of each habitat category within 100 meters (primary forest, secondary forest, pasture, or coffee). We mapped the perimeter of each site with a handheld global positioning system (GPS) unit and calculated the area of each patch, the edge/area ratio, and the width of each patch (defined as the shortest line that bisects the polygon midpoint) with ArcGIS 10.2 (ESRI 2012). Although we did not have access to aerial imagery suitable for creating a landscape classification due to heavy and persistent cloud cover, we were able to incorporate the influence of large forest blocks by including the distance from each patch to the edge of the Monteverde Reserve Complex (MRC), which influenced the richness of forest-depended birds in the study by Chandler et al. (2013).

Statistical methods

We based our classification of forest-dependent species on Stiles (1985), and included species designated with a score of 1, referring to species that require "almost solid forest" and a score of 2, which refers to species that require "at least patchy forest" (Stiles 1985). Ruiz Gutierrez et al. (2010) reported a higher level of forest use by species in Costa Rica that are not conventionally considered forest species, hence, the classification we used is likely conservative (Chandler et al. 2013). We used an adjusted richness of forest-dependent bird species as the response variable. Observed richness is sensitive to the number of individuals sampled and sampling repetitions. Therefore, we adjusted for different sample sizes by performing rarefaction on the raw species counts using the function rarefy from package vegan in program R (Oksanen et al. 2013). For point counts where the radius overlapped the patch boundary, rarefied values were standardized by including the amount of forest within each 100-m point count radius as an offset in the analyses, following Chandler et al. (2009). From here forward, this adjusted response variable will be referred to as "richness". Explanatory variables were also standardized by the amount of forest when appropriate. Despite some points being in the same forest patch, we treated each as an independent sample. We screened for possible spatial dependence among points by examining variograms and by plotting the standardized residuals from GLM models versus their spatial coordinates and found no evidence of high spatial autocorrelation.

We examined the variables described above for breakpoints at which the richness of forest-dependent bird species exhibited a change in response. We used a loess smoother on each univariate relationship and if a breakpoint was suggested, we continued with piecewise regression using the following model:

$$y_i = \begin{cases} \beta_0 + \beta_1 x_i + e_i & for \;\; x_i \leq \alpha \\ \beta_0 + \beta_1 x_i + \beta_2 (x_i - \alpha) + e_i & for \;\; x_i > \alpha \end{cases}$$

where y_i is the value for the ith observation, x_{i} is the value of the independent variable, α is the breakpoint, and e_i are assumed to be independent with homogeneous variance (Toms and Lesperance 2003). We identified the breakpoint value by calculating the model deviance along a range of the independent variable. The value minimizing the deviance indicates the breakpoint location. Finally, we generated confidence intervals for the breakpoint location with a bootstrap technique, nonparametric resampling of the errors (Davison and Hinkley 1997; Toms and Lesperance 2003). The errors are sampled with replacement and added to the fitted values to create a new set of "observations" from which the breakpoint is estimated. After repeating many times, the 2.5th and 97.5th percentiles of the breakpoint distribution give a 95% confidence interval for the point estimate.

Richness of forest-dependent bird species was also modeled as a function of the explanatory variables described above using multiple linear regression. We began by examining the distribution of each variable and decided to log transform area, width, and distance to MRC to meet the assumption of normally distributed residuals. We then screened for collinearity among variables with correlations $|r| > 0.6$ being unacceptable. We continued by examining variance inflation factors among variables, with an acceptable value being ≤ 3 (Zuur et al. 2009). The variables of log10 width, edge and log10 Area were highly collinear. However, these variables describe the shape of the forest patch and are important for making management recommendations. We therefore ran the proceeding analysis three times, rotating which shape variable was included. After assessing the full model for heterogeneity of variance, we took two model selection approaches, both yielding similar results. We first performed a manual backwards selection by conducting likelihood ratio tests on nested models, successively removing terms until all were significant. In the second approach, we examined all subsets of models nested within the full model and ranked them according to AICc.

Results

We detected 113 species during three repetitions of 25 point counts, 49 of which are considered forest-dependent species (Table 1). A loess smoother suggested that the variables log10 area and basal area have a nonlinear relationship with the species richness of forest-dependent birds. A breakpoint at the value of log10 area = 4.42, 95% [CI = 4.16, 4.87] was identified, corresponding to back-transformed value of 2.6 ha (Fig. 2). For basal area, a value of 25.1 m^2/ha, 95% [CI = 5.51, 45.0] was identified as the breakpoint (Fig. 2).

The top multiple regression models included either log10 area, log10 width, or edge (whichever shape variable was in the model; Table 2). Also included were basal area, vine, and for the model with log10 area, canopy height was included. The models predict that the richness of forest-dependent species will increase with (1) an increase in forest patch area, (2) an increase in patch width, (3) a decrease in the amount of edge, (4) an increase in vine complexity, and (5) an increase in the basal area of trees. Each model, containing either log10 area, log10 width, or edge, explained of 80.4%, 80.5%, and 78.1% of the variation, respectively.

Discussion

The identification of habitat thresholds for IOC coffee cultivation given here represents a key advancement in the implementation of land-sparing agriculture for biodiversity conservation. We found that species richness of forest birds did not change across a range of forest patch sizes from 1.4 to 2.6 ha, and increased monotonically thereafter. Although this relationship does not identify a threshold value for area of IOC forest patches, it does show that there is no significant variation within the range of patch areas shown by Chandler et al. (2013) to support significantly higher numbers of forest dependent species (1.51–3.53 ha). Thus, any forest patch size within this range is expected to support more forest-dependent species than other coffee growing systems, as reported by Chandler et al. (2013). Increases in species richness in patches greater than 2.6 ha at least up to 26.1 ha confirms what would be anticipated based on established patch-area relationships from the tropics (e.g. Graham and Blake 2001; Ferraz et al. 2007), that is, larger patches are preferable.

Since the analyses included patches that were irregularly shaped, the area values we present are probably conservative, because rounder and less complex patches of the same area would probably support more species (Graham and Blake 2001). This is supported by the multiple regression models including forest patch width and edge. Thus, it would not satisfy the objectives of IOC if practitioners conserved > 2.6 ha in a narrow elongated or highly linear strip of forest. We were unable to unambiguously partition the effects of area, width, and edge amount of forest patches, and therefore recommend that an IOC forest patch be no narrower than the average width (73.0 m) and contain no more than the average edge density (514.5 m/m^2) as patches within the size range on our IOC farms (1.4–2.6 ha). In addition to area, width and edge, richness of forest birds was also influenced by internal characteristics, such as increased basal area and vine growth. Increased richness with these variables is expected because they represent conditions associated with stand maturity (Clark 1996; Guariguata and Ostertag 2001; Nadkarni et al. 2004; Bakermans et al. 2012).

In the case of basal area, the conservation of even young forest is valuable, as demonstrated by the findings of Chandler et al. (2013), who found that the number of forest-dependent species shared with primary forest was 75.3% higher in 10–30 year-old forest patches on IOC farms than in shade coffee. Furthermore, forests develop rapidly in the tropics and soon provide at least some of the ecosystem function of mature forests (Letcher and Chazdon 2009). Thus, it might be advantageous to allow farmers with young forest to claim them as part of their IOC farms, and because the value of the carbon is a direct function of basal area, farmers conserving more biologically desirable mature forest as IOC will receive more benefit. An alternative would be to permit farmers who own forest with basal area values of at least 5.51 m^2/ha (corresponding to a forest approximately 15–20 years old at our site) to participate in carbon sales, which would strike a balance between making IOC applicable to farms even with little or highly degraded forests and ensuring that it in fact conserves the desired forest values. Vine tangles could be more problematic, since it is not really feasible to mandate that farmers

Table 1 Bird species classified as forest-dependent according to Stiles (1985) detected on point count surveys in forest patches in the Tilarán range, Costa Rica, during 2012

Common name	Species	Frequency	N
Lesser Greenlet	*Pachysylvia decurtata*	0.88	58
Long-tailed Manakin	*Chiroxiphia linearis*	0.80	81
Slate-throated Redstart	*Myioborus miniatus*	0.72	54
Keel-billed Toucan	*Ramphastos sulfuratus*	0.52	25
White-fronted Parrot	*Amazona albifrons*	0.48	33
Green Hermit	*Phaethornis guy*	0.44	21
Golden-browed Chlorophonia	*Chlorophonia callophrys*	0.40	27
Golden-crowned Warbler	*Basileuterus culicivorus*	0.40	52
Gray-breasted Wood-Wren	*Henicorhina leucophrys*	0.40	14
Paltry Tyrannulet	*Zimmerius vilissimus*	0.36	13
Rufous-and-white Wren	*Thryophilus rufalbus*	0.32	10
Bright-rumped Attila	*Attila spadiceus*	0.28	11
Golden-olive Woodpecker	*Colaptes rubiginosus*	0.28	13
Common Chlorospingus	*Chlorospingus flavopectus*	0.24	29
Plain Antvireo	*Dysithamnus mentalis*	0.24	8
Scale-crested Pygmy-Tyrant	*Lophotriccus pileatus*	0.24	12
Immaculate Antbird	*Myrmeciza immaculata*	0.20	9
Rufous-capped Warbler	*Basileuterus rufifrons*	0.20	21
Black-throated Green Warbler	*Setophaga virens*	0.16	4
Chestnut-capped Brush-Finch	*Arremon brunneinucha*	0.16	6
Tropical Parula	*Setophaga pitiayumi*	0.16	6
Orange-breasted Trogon	*Trogon collaris aurantiiventris*	0.12	3
Purple-throated Mountain-gem	*Lampornis calolaemus*	0.12	6
Rufous-tailed Jacamar	*Galbula ruficauda*	0.12	3
Spotted Woodcreeper	*Xiphorhynchus erythropygius*	0.12	3
Violet Sabrewing	*Campylopterus hemileucurus*	0.12	4
Black Guan[a]	*Chamaepetes unicolor*	0.08	4
Black-and-white Warbler	*Mniotilta varia*	0.08	2
Bay-headed Tanager	*Tangara gyrola*	0.08	5
Northern Emerald Toucanet	*Aulacorhynchus prasinus*	0.08	2
Scarlet-thighed Dacnis	*Dacnis venusta*	0.08	5
Spotted Barbtail	*Premnoplex brunnescens*	0.08	2
Swainson's Thrush	*Catharus ustulatus*	0.08	5
Three-wattled Bellbird[b]	*Procnias tricarunculatus*	0.08	3
Chestnut-headed Oropendola	*Psarocolius wagleri*	0.04	1
Coppery-headed Emerald	*Elvira cupreiceps*	0.04	1
Highland Tinamou	*Nothocercus bonapartei*	0.04	1
Long-billed Gnatwren	*Ramphocaenus melanurus*	0.04	1
Olivaceous Woodcreeper	*Sittasomus griseicapillus*	0.04	1
Pale-billed Woodpecker	*Campephilus guatemalensis*	0.04	1
Silver-throated Tanager	*Tangara icterocephala*	0.04	2
Slaty-backed Nightingale-Thrush	*Catharus fuscater*	0.04	1
Stripe-tailed Hummingbird	*Eupherusa eximia*	0.04	1
White-breasted wood wren	*Henicorhina leucosticta*	0.04	2

Table 1 continued

Common name	Species	Frequency	N
White-throated Spadebill	*Platyrinchus mystaceus*	0.04	1
White-throated Thrush	*Turdus assimilis*	0.04	1
Wood Thrush[a]	*Hylocichla mustelina*	0.04	1
Yellowish Flycatcher	*Empidonax flavescens*	0.04	1

[a] IUCN “near threatened

[b] IUCN “vulnerable”

Species listed as “vulnerable” or “near-threatened” by the IUCN are identified with numerical superscipts

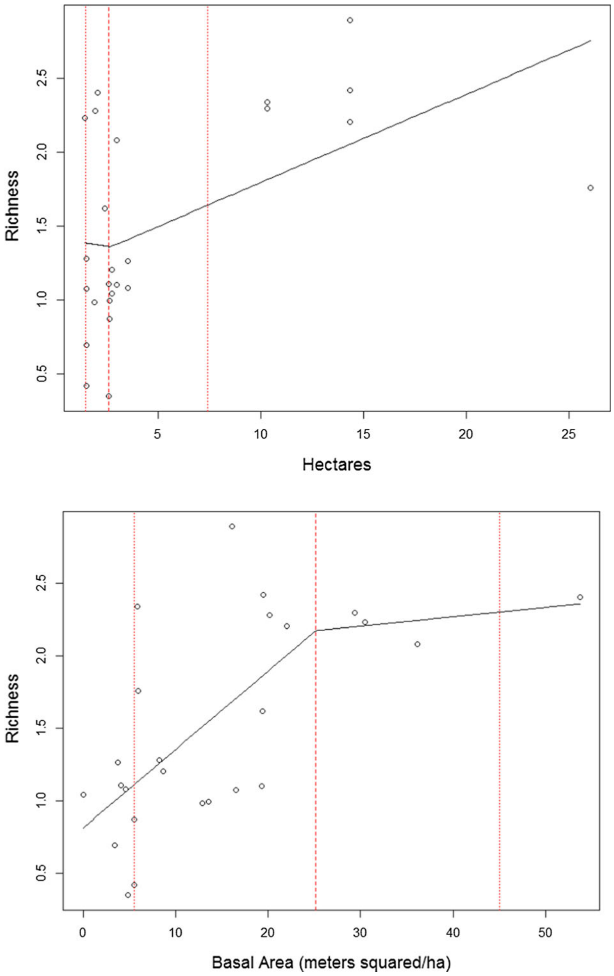

Fig. 2 Estimated richness of forest dependent species as a function of patch area (top) and basal area of trees (bottom). The estimated breakpoint for area = approximately 2.6 ha (center line) with a 95% confidence interval of 1.44–7.41 (outside lines). The estimated breakpoint for basal area corresponds to 25.2 m^2/ha (95% CI 5.51–45.0 m^2/ha)

manipulate vine levels, or even clear whether it would be possible to do so.

A principal advantage of IOC from the standpoint of the farmer is that it increases yields by allowing farmers to grow coffee in the cultivated portion in whatever conditions they choose to maximize harvests (Arce et al. 2009). Nevertheless, farmers could further increase their income by converting forested portions of farms to coffee as well. Recent investigations suggest, however, that the value foregone by not converting forest to coffee is offset to some degree by the ecosystem services provided by forest to farmers.

Table 2 Best multiple linear regression models for richness of forest-dependent bird species detected on point count surveys in forest patches in the Tilaran range, Costa Rica, as a function of log10 area, log10 width, and edge

Shape variable	Parameter	Estimate	SE	t	*p*
Log10 area	Constant	− 3.33	1.08	− 3.09	0.006
	Log_{10} Area	0.92	0.21	4.48	< 0.001
	Vine	0.20	0.09	2.34	0.030
	Basal	0.38	0.006	6.50	< 0.001
	Canopy Height	− 0.035	0.017	− 2.00	0.059
Log10 width	Constant	− 2.97	0.60	− 4.93	< 0.001
	Log_{10} Width	1.68	0.27	6.30	< 0.001
	Vine	0.23	0.084	2.78	0.011
	Basal	0.028	0.006	4.98	< 0.001
Edge	Constant	1.49	0.32	4.64	< 0.001
	Edge	− 0.003	0.0004	− 5.75	< 0.001
	Vine	0.22	0.089	2.50	0.021
	Basal	0.027	0.006	4.51	< 0.001

For example, depredation of the larva of the coffee-borer beetle (*Hypothenemus hampei*), considered the most devastating insect of coffee (Vega et al. 2009) and causing losses of over $500 million dollars annually worldwide (Infante 2018), has been quantified through exclosure experiments in Jamaica (Kellermann et al. 2008) and Costa Rica (Karp et al. 2013). These investigations found that the economic value of birds on farms ranges from $75 to $437 ha/yr, and that the abundance of bird species that depredate coffee-borer beetle is strongly associated with strips or patches of natural vegetation within coffee-growing landscapes (Kellermann et al. 2008; Perfecto et al. 2003; Mendenhall et al. 2011; Karp et al. 2013).

In addition, pollination by native bees is another valuable ecosystem service provided to coffee farmers by forest. Studies have shown that although coffee can self pollinate or wind pollinate, insect pollination greatly increases fruit set and yield. Ricketts et al. (2004) performed an exclosure study in Costa Rican coffee farms and estimated the value of bees on farms averaged $129 ha/yr, and the abundance of native bees increased with greater proximity to forest (Ricketts et al. 2004). Using average coffee yields and carbon values from sites where IOC coffee cultivation is being implemented in Honduras (King et al. 2016), the midpoint values for pest control, and Rickett's value for bees, we calculate farmers would receive approximately 61% of the value from forest patches they would gain from converting the forest to coffee. Although this is still a considerable gap, coffee prices are highly volatile and yields variable depending on weather conditions, thus income from carbon sales and ecosystem services could serve as insurance, guaranteeing farmers at least some income in years of market collapse or crop failure. Although carbon prices are also volatile, carbon income is a fixed value guaranteed for the term of a carbon contract, and in this way, they may provide income even in years when coffee prices collapse.

IOC is practiced on farms with small areas under cultivation, resulting in small patches of forest which, although they conserve forest species that would otherwise be absent, may fail to support forest-dependent species that are highly sensitive to area. Nevertheless, IOC could potentially contribute to the conservation of more area-sensitive or wider ranging species by facilitating movement among larger reserves, perhaps even facilitating the persistence of metapopulations (Falcy and Estades 2007). This of course will vary by species due to different area requirements, perception of scale, dispersal abilities, and tolerance to the surrounding landscape matrix (Phalan et al. 2011). Though the needs of more sensitive birds like large frugivorous and insectivorous species (Şekercioğlu 2012) may not be met within IOC farms themselves, the permanent protection of even small forest patches could make these landscapes more permeable to these species (Castellón and Sieving 2006).

We can't say for certain why we did not detect the relationship between species richness of forest birds and distance from the Monteverde Reserve Complex reported by Chandler et al. (2013), however one reason may be the relatively low number of forest dependent bird species that were common to both studies (15%). It is known that bird species differ with respect to their sensitivity to landscape-scale variation in habitat conditions (Luck and Daily 2003), so it is possible that the species pool in our study included birds that were on average less sensitive to landscape characteristics than that sampled by Chandler et al. (2013). The difference between these two studies in species composition is likely due to the fact that the detectability of bird species is known to differ between the mistnet surveys employed by Chandler et al. (2013) and the point count surveys we employed (Blake and Loiselle 2001).

Although our findings suggest the forest patches within our study area are occupied by forest-associated bird species, birds in highly altered landscapes such as ours may select habitat maladaptively, preferring habitats in which local reproductive success fails to keep pace with local mortality (Pulliam 1988). For example, Bailey and King (2019) found that habitats selected by wood thrush in Honduras did not correspond with those habitats associated with high survival and site persistence. Similarly, Sánchez-Clavijo et al. (2020) reported several bird species at their sites in Colombia were more abundant in habitats in which fitness measures were relatively low. Thus, in the absence of measures of survival, reproduction, or related measures, our results should be viewed as a first-order indication of the value of these forest patches to forest-dependent birds. Nevertheless, the relationship between habitat selection and fitness is more likely to be decoupled in human-altered habitats (Bock and Jones 2004), whereas the forest patches in our study area still resemble native forest in terms of structure and species composition. This is consistent with the findings of Bailey and King (2019), who found survival and persistence was decoupled in shade coffee, but not native forest, and the findings of Sánchez-Clavijo et al. (2020), who reported that in general more species preferred and/or performed better in forest than coffee.

We acknowledge our study was conducted on a limited number of farms in a single year over a two-month period, which limits the generality of our findings. Nevertheless, we were able to sample more farms than Chandler et al. (2013), and the general pattern we report, that species richness increases with patch area, is consistent with other studies in the tropics (e.g. Graham and Blake 2001; Ferraz et al. 2007). Furthermore, recent studies from Honduras have shown some forest-dependent species are present on IOC farms and absent from shade coffee farms (Murillo et al. unpublished). We hope future studies will replicate our approach to determine whether the area thresholds we identify are similar to those in other regions. In addition, Costa Rican birds are known to shift their habitat use among seasons (Şekercioğlu et al. 2007), and thus the forest patches present on IOC farms may not accommodate the habitat needs of forest birds throughout the annual cycle. For this reason, we urge that the application of IOC coffee be combined with the retention of other habitats used by forest birds in the landscape, such as shade coffee (Leyequién et al. 2010, Mendenhall et al. 2011). Fortunately, there currently exists a framework for conserving these non-forest habitats (e.g. Philpott et al. 2007).

The threshold values we calculated for IOC forest patches represent an important step in implementing this land-sparing agricultural practice within a market-based framework to support the conservation of habitat for forest-dependent species. IOC is currently being implemented on 20 farms in Honduras, and farmers are receiving carbon payments for sequestered carbon facilitated by the Mesoamerican Development Institute. Work is currently underway to quantify the contribution of IOC forest patches to pollination and pest control services, and preliminary findings on the value of IOC to other taxa suggest it supports forest-associated bats as well (España, unpublished data). Finally, modeling exercises to gauge the contribution of IOC forest patches to landscape-level conservation of forest-dependent bird species is planned to further specify the value of this approach and guide its implementation.

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