

Habitat selection in transformed landscapes and the role of forest remnants and shade coffee in the conservation of resident birds

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Abstract

1. Biodiversity conservation in transformed landscapes is becoming increasingly important. However, most assessments of the value of modified habitats rely heavily on species presence and/or abundance, masking ecological processes such as habitat selection and phenomena like ecological traps, which may render species persistence uncertain. High species richness has been documented in tropical agroforestry systems, but comparisons with native habitat remnants generally lack detailed information on species demography and habitat use.
2. We generated a multi-species, multi-measure framework to evaluate the role of habitat selection in the adaptation of species to transformed landscapes, and demonstrate that its use could affect how we value the contribution different land uses make to biodiversity conservation.
3. We analysed 7 years of capture–mark–recapture and observation data for twelve species of resident birds present in native forest remnants and shade coffee plantations in a mega-diverse region. We assessed whether species behaved adaptively by evaluating the correlation between measures of habitat preference (occurrence, abundance, fidelity, inter-seasonal variance and age) and performance (body condition, muscle, primary moult, breeding and juveniles) in forest and coffee, and generated hypotheses about their role in species persistence.
4. We documented adaptive habitat selection for seven species, non-ideal selection for four and maladaptive selection for one. While many species showed equal preference and/or equal performance in many traits, in general we found more evidence for birds preferring and/or performing better in forest than coffee, although relationships between our indicators and population adaptation need to be studied further before our proposed framework can be applied to more species and landscapes.
5. While shade coffee can act as a biodiversity-friendly matrix providing complementary or supplementary habitat to a wide range of resident bird species, protecting remnants of native vegetation is still of paramount importance for biodiversity conservation in agricultural landscapes.

KEYWORDS

agroforestry systems, ecological traps, habitat performance, habitat preference, habitat selection, novel ecosystems, source and sink, undervalued resources

1 | INTRODUCTION

Presently, the majority of the world's species inhabit heterogeneous landscapes combining native habitat remnants with novel ecosystems varying in their degree of intervention (Hobbs et al., 2006; Johnson, Wiens, Milne, & Crist, 1992). As human population and resource consumption continue to grow, conservation focus has expanded from the protection of native remnants to include land uses with intermediate levels of transformation (Daily, Ehrlich, & Sanchez-Azofeifa, 2001; Norris, 2008). Shade coffee plantations have been promoted as a biodiversity-friendly production system that can harbour communities intermediate between those of sun coffee monocultures and remnants of native forest (Jha et al., 2014; Perfecto, Rice, Greenberg, & VanderVoort, 1996; Philpott et al., 2008), so financial tools and social incentives have arisen to prevent their replacement by homogeneous land uses (Perfecto, Vandermeer, Mas, & Pinto, 2005; Philpott, Bichier, Rice, & Greenberg, 2007). However, most assessments of the conservation value of tropical agroforestry systems rely heavily on community-level measures (Hughes, Daily, & Ehrlich, 2002; Petit & Petit, 2003), and while there is recent evidence on differences for migrant birds (Bakermans, Vitz, Rodewald, & Rengifo, 2009; Bayly, Gómez, Hobson, & Rosenberg, 2016), information on demography and persistence of resident species is still scarce (Gleffe, Collazo, Groom, & Miranda-Castro, 2006; Irizarry, Collazo, Pacifici, Reich, & Battle, 2018; Komar, 2006; Sánchez-Clavijo, Arbeláez-Alvarado, & Renjifo, 2008).

When species presence is used to compare the relative conservation value of habitats, the implicit assumption is that species show neither preference for any of the habitats occupied, nor differences in performance once they occupy them (Figure 1e); subsequently, the availability of one habitat could theoretically compensate for the absence of another. While this may sometimes be the case, assuming this pattern as a rule may lead to inaccurate assessments of population persistence that cannot be corrected by including abundance (Johnson, 2007; Jones, 2001; Van Horne, 1983), for example where novel habitats are used in complementary or supplementary ways by populations that still depend on native remnants for critical resources (Dunning, Danielson, & Pulliam, 1992). In contrast, including habitat-specific demography in comparisons allows for the explicit recognition that species performance varies between habitats and that given adaptive selection behaviours (Pulliam, 1988), individuals prefer to settle in higher-quality habitats (sources—Figure 1c) and avoid settling in lower-quality habitats (sinks—Figure 1g). Under source–sink dynamics, the best strategy to ensure species persistence in a landscape is to prioritize the conservation of sources within networks of well-connected sinks (Furrer & Pasinelli, 2016; Gilroy & Edwards, 2017; Pulliam & Danielson, 1991).

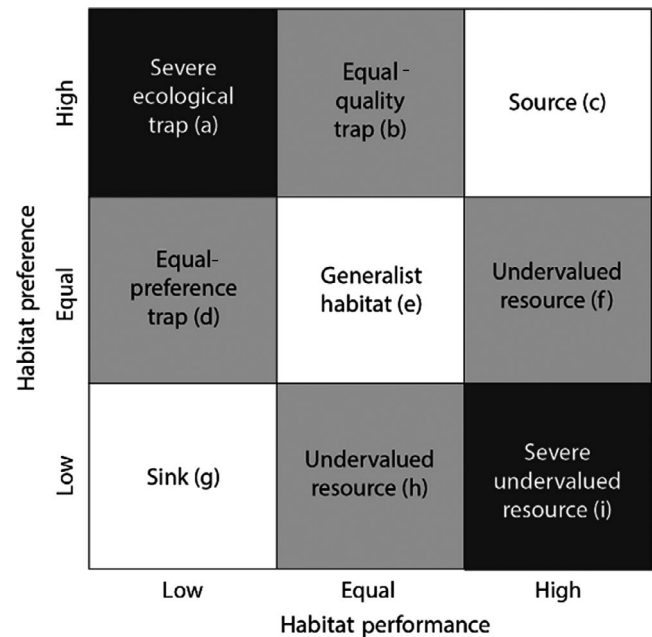


FIGURE 1 Outcomes when comparing preference and performance for a species using two habitats (white: adaptive, grey: non-ideal, black: maladaptive habitat selection)

Measuring habitat preference and performance in a multi-species framework is not straightforward, especially for species with poorly known natural history (Garshelis, 2000; Part, Arlt, & Villard, 2007). To further complicate the understanding of species–habitat relationships and their application to decision-making in conservation, rapid and widespread landscape change may lead to the uncoupling of cues used for habitat selection from habitat quality, resulting in maladaptive choices where individuals prefer lower-quality habitats (ecological traps sensu Schlaepfer, Runge, & Sherman, 2002—Figure 1a) and avoid higher-quality options (undervalued resources sensu Gilroy & Sutherland, 2007—Figure 1i). Novel ecosystems may share selection cues with the habitats they replaced, while offering a different set of resources and hazards that reduce overall fitness (Fletcher, Orrock, & Robertson, 2012; Robertson, Rehage, & Sih, 2013; Schlaepfer et al., 2002). As a result, species presence in novel habitats may mask maladaptive processes, making populations more vulnerable to further landscape change.

Source–sink and ecological trap–undervalued resource dichotomies are extreme cases in a continuum of possible outcomes from the interaction between habitat availability, selection and quality (Battin, 2004), and ideally, we would evaluate mismatches between preference and performance as continuous variables (Kristan, 2003). A compromise is to include outcomes resulting from equal preference and equal performance. Robertson and Hutto (2006) distinguished severe ecological traps from equal-preference traps

(Figure 1d), which, while still a result of non-ideal selection, are expected to have less severe consequences at the population level. Filling in the gaps from these outcomes allows for the recognition of three additional cases of mild, non-ideal selection (Figure 1b,f,h) that lead to consequences intermediate between those of adaptive (Figure 1c,e,g) and maladaptive (Figure 1a,i) behaviours.

We used this extended framework (Figure 1) to evaluate the correlation between measures of habitat preference (occurrence, abundance, site fidelity, temporal variance in population size and distribution of dominant individuals) and performance (body condition, muscle scores, primary plumage moults, breeding evidence and frequency of juveniles) for twelve relatively common resident birds, inhabiting pre-montane forest remnants and shade coffee plantations at mid-elevations in the Sierra Nevada de Santa Marta, Colombia. Because our focal species are associated with habitats representing a gradient of tree cover, we expected marked variation in the outcomes resulting from the interaction of their habitat preference and performance. Our use of field data to generate hypotheses about the role that native forest and shade coffee play in the conservation of resident birds serves as a demonstration of a multi-species approach to compare the contribution of different land uses to biodiversity conservation in a mega-diverse region.

2 | MATERIALS AND METHODS

2.1 | Data collection

2.1.1 | Study area

Data were collected in Hacienda La Victoria (Magdalena, Colombia, 11°7'19.84"N, 74°5'34.14"W), chosen for this study because: (a) coffee production in the region started in the late 1800s and has always taken place under shade trees as commercial polycultures (Moguel & Toledo, 1999)—creating a novel habitat with intermediate levels of transformation that species have had time to adapt to; (b) the watershed where the farm is situated retains 47% native forest cover between 600 and 1,700 m above sea level (Bayly, Páez, Gómez, & Mora, 2012)—meaning there is still substantial native habitat available; and (c) it is located in a global hot spot for biodiversity and endemism (Cracraft, 1985; Myers, Mittermeier, Mittermeier, Fonseca, & Kent, 2000), experiencing exponential growth in nature-related tourism (Lara, Rojas, & Velásquez-Tibatá, 2017; Ocampo-Peñuela & Winton, 2017)—consequently, assessing the conservation potential of this productive system is of environmental and economic importance (see Supporting Information for further details on study area).

2.1.2 | Sampling scheme

Between 2009 and 2015, we set up 17 banding stations, eight in pre-montane forest remnants and nine within shade coffee plots, at altitudes ranging from 900 to 1,300 m (Figure S1). Banding stations consisted of five to ten 12-m mist-nets, installed at each site for 5–30 days and operated daily for approximately 6 hr starting at

sunrise, following guidelines for the safe and ethical treatment of animals (Fair et al., 2010). Sampling occurred between mid-March and mid-November, which corresponds to a gradient of increasing precipitation and coincides with the onset of breeding for the majority of resident birds, while avoiding sampling during annual coffee harvests. Effort was concentrated in capturing, marking and recapturing individuals, but complementary observations were carried out around banding stations. We used standardized protocols (Ralph, Geupel, Pyle, Martin, & DeSante, 1993; Wolfe, Ryder, & Pyle, 2010) to measure wing chord and body mass, and assess age class, muscle score, breeding and moulting activity of captured individuals. Variation in sampling effort among sites and seasons was taken into account during data analysis.

2.1.3 | Focal species

A total of 214 resident bird species have been recorded in La Victoria (Bayly & Gómez, 2013), but to guarantee adequate sample sizes to assess preference/performance, we required species that: were frequently detected in both habitats, were regularly captured in mist-nets and represented a gradient of sensitivity to forest loss. Based on these criteria, we selected *Mionectes olivaceus* (Olive-striped Flycatcher), *Mionectes oleagineus* (Ochre-bellied Flycatcher), *Turdus flavipes* (Yellow-legged Thrush), *Turdus albicollis* (White-necked Thrush), *Ramphocelus dimidiatus* (Crimson-backed Tanager), *Tangara gyrola* (Bay-headed Tanager; endemic subspecies), *Saltator maximus* (Buff-throated Saltator), *Saltator striatipectus* (Streaked Saltator), *Myiothlypis conspicillata* (White-lored Warbler; endemic species), *Basileuterus rufifrons* (Rufous-capped Warbler), *Myioborus miniatus* (Slate-throated Redstart) and *Euphonia laniirostris* (Thick-billed Euphonia) (Table S1).

While these species are not representative of the original mountain forest avifauna of the Sierra Nevada de Santa Marta, they are representative of bird communities in Colombian coffee-growing regions (Sánchez-Clavijo, Botero, & Espinosa, 2009). Consequently, conclusions from this study do not extend to highly sensitive species known to be forest-dependent for their conservation, or open-area species that exist only in deforested areas, but rather the ones in between that potentially use shade coffee plantations as suitable habitat.

2.2 | Data processing

We screened the banding database (4,108 captures of 3,214 individuals) to ensure data were consistent within species and individual capture histories (e.g. that individuals followed logical age and plumage sequences, or sex and breeding classifications). Inconsistencies were either resolved based on information from captures of the same individual or changed to unknowns (see Supporting Information for further details on data processing).

2.3 | Data analysis

We carried out analyses in three levels: using statistical tests to generate separate indicators of habitat preference and performance;

weighting the evidence from level 1 to generate composite indexes of habitat preference and performance; and contrasting the indexes from level 2 to evaluate whether habitat selection was acting adaptively in our study system (see Supporting Information for further details on data analysis).

2.3.1 | Level 1: separate indicators of habitat preference and performance

We used multiple measures of preference and performance, under the assumption that more indicators pointing in the same direction would give us greater confidence in our assessments, but that contradictory patterns were a warning that more evidence was necessary. We designed five statistical tests to evaluate which habitat was preferred by each species (hereafter occurrence, abundance, fidelity, inter-seasonal variance and age) and five to evaluate in which habitat individuals experienced higher average performance (body condition, muscle, primary moult, breeding and juveniles—Table 1).

Occurrence

The most commonly used indicator for preference is how often a species is detected in a habitat, but because higher frequencies can result from either more individuals in a habitat or a higher tenacity of individuals towards the sites they occupy (Garshelis, 2000), occurrence represents an emergent attribute of different demographic properties that can have contradictory preference interpretations. Occupancy models take into account differences in detection

probabilities to yield corrected occurrence probabilities in a cost-effective manner (Kéry & Schaub, 2012; Ruiz-Gutiérrez, Zipkin, & Dhondt, 2010). We used observation data to implement a Bayesian occupancy model with the effect of habitat (forest/coffee) on the probability of detection (p), and effects of habitat and altitude on the probability of occurrence (ψ).

Abundance

In the absence of strong dominance hierarchies and differences in habitat availability, we would expect more individuals to settle in their preferred habitat over other available habitats (Pulliam & Danielson, 1991), rendering true abundance a good proxy for preferential choice. Calculating precise estimates of abundance is a field-intensive and data-hungry procedure, especially for highly mobile animals with low probabilities of detection (Ruiz-Gutiérrez et al., 2012). Unlike observation data, capture–mark–recapture data allow for the recognition of individuals within a species, and are therefore well suited to calculate abundance in relatively small, intensively sampled areas. To estimate the total number of individuals present in our study area across the entire sampling period, we used mist-net data to run capture–recapture analyses, using closed population models for species with low recapture rates and Jolly–Seber models for species with higher recapture rates (Kéry & Schaub, 2012; Royle & Dorazio, 2008). We ran separate analyses for each species–habitat combination, which included the effect of sampling effort (standardized net hours) on detection probability (p) and random variation in apparent survival (ϕ) by occasion.

TABLE 1 Analyses used to generate indicators of habitat preference (rows 1–5) and performance (rows 6–10) for twelve resident birds in native forest and shade coffee

Indicator	Input	Analysis	Output	Interpretation
Occurrence	Detection/non-detection matrix (9 sites \times 16 occasions)	Hierarchical occupancy model; probability of occurrence (ψ)	Habitat coefficient (95% credibility intervals)	95% CI did not contain 0
Abundance	Capture–non-capture matrix (individuals \times 12 occasions)	Capture–recapture model; total number of individuals (N_{super})	Posterior distribution for total number of individuals (per habitat)	No overlap in 50% CI
Fidelity	Capture–non-capture matrix (individuals \times 12 occasions)	Capture–recapture model; mean apparent survival (ϕ)	Mean and standard deviation of iterations (per habitat)	No overlap in mean \pm SD
Inter-seasonal variance	Estimated number of individuals per occasion (N_{occ})	Coefficient of variation for (N_{occ})	Mean and standard deviation of iterations (per habitat)	No overlap in mean \pm SD
Age	Number of adults versus immatures	GLM (binomial/logit), AICc model averaging	Habitat coefficient (95% confidence intervals)	95% CI did not contain 0
Body condition	Vector of body condition index for all captures	GLM (normal/identity), AICc model averaging	Habitat coefficient (95% confidence intervals)	95% CI did not contain 0
Muscle	Number of records with muscle score 3 versus muscle score 2	GLM (binomial/logit), AICc model averaging	Habitat coefficient (95% confidence intervals)	95% CI did not contain 0
Primary Moulting	Number of records with active versus inactive primary moulting	GLM (binomial/logit), AICc model averaging	Habitat coefficient (95% confidence intervals)	95% CI did not contain 0
Breeding	Number of records with active versus inactive breeding	GLM (binomial/logit), AICc model averaging	Habitat coefficient (95% confidence intervals)	95% CI did not contain 0
Juveniles	Number of juveniles versus immatures and adults	GLM (binomial/logit), AICc model averaging	Habitat coefficient (95% confidence intervals)	95% CI did not contain 0

Abbreviations: AIC, Akaike's information criterion; GLM, Generalized Linear Model.

Fidelity

Individuals of territorial species are expected to show higher site fidelity when occupying their preferred habitat relative to less-preferred ones (Robertson & Hutto, 2006). Capture–recapture models allow for the estimation of apparent survival (ϕ), which is a compound measure of site fidelity and true survival (Kéry & Schaub, 2012). We used this parameter as a surrogate for fidelity because the contribution of mortality to the parameter was expected to be minimal given the short time between sampling occasions (1–6 months) and the known longevities of tropical birds (Ruiz-Gutiérrez et al., 2012). For species with high recapture rates, ϕ per occasion was jointly estimated in Jolly–Seber models, and for species with low recapture rates, we used Cormack–Jolly–Seber models with a similar parameterization (Kéry & Schaub, 2012; Royle & Dorazio, 2008). Resulting parameters were then used to calculate mean site fidelity for each iteration of the model.

Inter-seasonal variance

Because species may use different habitats according to life stage or seasonal variation in resources, measuring abundance during different times of year may yield different interpretations about habitat preference in places with high seasonality (Skagen & Yackel Adams, 2010; van Horne, 1983). We assumed a habitat with less inter-seasonal variation in abundance is experiencing lower individual turnover, which can be interpreted as a sign of preference (Robertson & Hutto, 2006). Since Jolly–Seber models allow for the estimation of the number of individuals present per occasion, we used this output to calculate the coefficient of variance for each iteration of the model for available species.

Age

Abundance may not be a true indicator of habitat preference when individuals follow a despotic distribution where dominant individuals settle in preferred habitats and displace a larger number of submissive individuals to less-preferred ones (Fretwell & Lucas, 1970). Although dominance hierarchies are not well described in Neotropical passerines, we assumed that adult birds would displace immature individuals from their preferred habitat (as shown for migratory birds in Marra, Sherry, & Holmes, 1993 & Stutchbury, 1994). Therefore, a habitat with a significantly higher proportion of adults could be considered as preferred. To test for segregation according to age, we calculated the model-averaged coefficient for the effect of habitat on the probability of capturing an adult over an immature individual, in a model set that included a null model, model with a nonlinear effect of day of the year, model with effect of habitat and model with the additive effects of day and habitat.

Body condition

Body mass in birds is expected to reflect overall condition under most circumstances, after being corrected by body size (Schamber, Esler, & Flint, 2009; Schulte-Hostedde, Zinner, Millr, & Hickling, 2005). We used the residuals of a standard major axis regression

between wing chord length and body mass to calculate a scaled index of body condition (Peig & Green, 2009) and assumed that higher condition meant better performance in a given habitat. We calculated the model-averaged coefficient for the effect of habitat on the index with the same model set we used for age (changing error structure and link as shown in Table 1). The same statistical procedure using GLMs and model averaging was used for all habitat performance variables.

Muscle

Breast muscle condition is important to species performance, as lower scores indicate reduced flight capacities from competing energy needs (Lindstrom, Kvist, Piersma, Deking, & Dietz, 2000). Although this variable is typically used to assess condition in migratory birds, variation in residents could be related to the amount and/or quality of resources in a habitat. We interpreted higher probabilities of capturing individuals with a muscle score of 3 (the highest in our classification) as an indication of better performance in a habitat (healthy immature and adult tropical residents rarely have scores below 2).

Primary moult

Birds undergoing primary feather moults typically associated with annual complete moults have high energy demands and are compromised in their ability to fly; consequently, this activity is usually undertaken when and where resources are high (Echeverry-Galvis & Córdoba-Córdoba, 2008; Echeverry-Galvis & Hau, 2013). We interpret higher probabilities of capturing individuals undergoing active primary moults as an indication of better performance in a habitat.

Breeding

Since breeding-related activities such as incubation and food provisioning are energy demanding, their timing and location are typically constrained by resource availability (Echeverry-Galvis & Córdoba-Córdoba, 2008; Echeverry-Galvis & Hau, 2013). We interpret a higher probability of capturing individuals with evidence of active breeding as an indication of better performance in a habitat.

Juveniles

Higher reproductive performance by a species in a habitat will result in higher proportions of recently fledged juvenile birds, assuming that their dispersal is limited by dependence on adults and reduced movement capacities (Cox, Thompson, Cox, & Faaborg, 2014). We interpret higher probabilities of capturing juveniles as an indication of better performance in a habitat.

2.3.2 | Level 2: composite indexes of habitat preference and performance

Because our five tests of performance used the same statistical method and model set, we generated a quantitative estimate of differences between habitats for each species by weighting mean

effect sizes by their standard deviation, using a fixed-effects model in a meta-analysis. Species were classified as having higher performance in forest when the 90% confidence intervals of this estimate were above zero, as having higher performance in coffee when below zero, and as having equal performance when they included zero.

The same method was not available for calculating a composite index of habitat preference because for two of our indicators the output was a habitat coefficient, while the remaining three relied on comparisons of habitat-specific parameters. Additionally, we were unable to identify a clear method for estimating the standard error around measures coming from iterative procedures. We calculated a preference score by subtracting the number of times evidence showed coffee was preferred from the number of times forest was preferred (response range -5 to $+5$). Birds with positive scores were classified as preferring forest, negative scores as preferring coffee, and zero as having equal preference.

2.3.3 | Level 3: Is habitat selection acting adaptively?

Our different approaches to create composite indexes of habitat preference and performance were not quantitatively comparable. Therefore, we qualitatively compared each species assigned habitat preference and performance, and used the framework in Figure 1 to generate hypotheses about the role of shade coffee and native forests.

3 | RESULTS

We were able to perform 88% of the planned comparisons (52/60 for preference and 54/60 for performance), omitting those without an adequate sample size for certain species/habitat/response combinations (which appear as NAs). Outcomes gave us multiple lines of evidence to classify the twelve species according to preference and performance, and therefore to assess the adaptiveness of habitat choices (see Supporting Information for further details on sample sizes and data outputs).

3.1 | Level 1: Separate indicators of habitat preference and performance

Of the tests performed for preference, 33 showed statistically unclear (Dushoff, Kain, & Bolker, 2019) differences between habitats, 12 favoured forest, and seven favoured coffee. Abundance was the most informative indicator (eight clear differences), followed by fidelity (6), inter-seasonal variance (2), age (2) and occurrence (1) (Table 2).

Of the tests for performance, 41 showed no statistically clear differences between habitats, five favoured forest, and eight favoured coffee. Breeding was the most informative indicator (five clear differences), followed by body condition (4), muscle (3), primary moult (1) and juveniles (0) (Table 3).

TABLE 2 Indicators of habitat preference for twelve resident birds in native forest and shade coffee

Species	Occurrence		Abundance		Fidelity			Inter-seasonal variance				Age	
	HC	Int.	C	F	Int.	C	F	Int.	C	F	Int.	HC	Int.
<i>Mionectes olivaceus</i>	4.72 (8.01)	Equal	1,257 (571)	1,173 (91)	Equal	0.49 (0.08)	0.66 (0.03)	Forest	NA	NA	-	NA	-
<i>Mionectes olegineus</i>	-5.88 (6.89)	Equal	253 (65)	674 (83)	Forest	0.68 (0.05)	0.71 (0.03)	Equal	0.51 (0.10)	0.41 (0.06)	Equal	NA	-
<i>Turdus flavipes</i>	4.70 (7.97)	Equal	766 (149)	1,239 (153)	Forest	0.63 (0.06)	0.70 (0.04)	Equal	NA	NA	-	-0.40 (0.20)	Coffee
<i>Turdus albicollis</i>	1.44 (8.48)	Equal	NA	482 (41)	Forest	0.50 (0.09)	0.71 (0.03)	Forest	NA	NA	-	1.29 (0.50)	Forest
<i>Ramphocelus dimidiatus</i>	4.55 (8.03)	Equal	613 (165)	329 (64)	Coffee	0.65 (0.04)	0.74 (0.04)	Forest	0.68 (0.12)	0.62 (0.09)	Equal	-0.07 (0.29)	Equal
<i>Tangara gyrola</i>	4.80 (7.93)	Equal	558 (105)	591 (48)	Equal	0.64 (0.04)	0.73 (0.02)	Forest	1.01 (0.13)	0.46 (0.04)	Forest	0.29 (0.20)	Equal
<i>Saltator maximus</i>	4.74 (7.83)	Equal	208 (48)	165 (31)	Equal	0.62 (0.06)	0.68 (0.05)	Equal	NA	NA	-	0.00 (0.31)	Equal
<i>Saltator striaticeps</i>	4.66 (7.96)	Equal	235 (82)	NA	Coffee	0.68 (0.06)	0.54 (0.08)	Coffee	NA	NA	-	-0.87 (0.51)	Equal
<i>Myiothlypis conspicillata</i>	4.64 (7.71)	Equal	317 (97)	604 (100)	Forest	0.65 (0.05)	0.68 (0.04)	Equal	0.70 (0.13)	0.71 (0.08)	Equal	-0.39 (0.26)	Equal
<i>Basileuterus rufifrons</i>	4.71 (7.69)	Equal	481 (94)	319 (115)	Coffee	0.67 (0.04)	0.64 (0.05)	Equal	0.79 (0.10)	0.53 (0.14)	Forest	-0.26 (0.26)	Equal
<i>Myioborus miniatus</i>	14.42 (6.02)	Coffee	231 (72)	273 (187)	Equal	0.64 (0.04)	0.63 (0.06)	Equal	0.80 (0.17)	0.64 (0.16)	Equal	0.07 (0.35)	Equal
<i>Euphonia lamirostris</i>	-2.63 (6.30)	Equal	249 (58)	606 (224)	Forest	0.68 (0.06)	0.53 (0.07)	Coffee	NA	NA	-	-0.27 (0.32)	Equal

Note: Coffee was the reference for occurrence, while forest was the reference for age.

Abbreviations: C, parameter estimate for coffee (standard deviation); F, parameter estimate for forest (standard deviation); HC, habitat coefficient (standard error); Int., interpretation, that is preferred habitat according to that indicator.

TABLE 3 Indicators of habitat performance for twelve resident birds in native forest and shade coffee

Species	Body condition	Muscle	Primary moult	Breeding	Juveniles
<i>Mionectes olivaceus</i>	0.25 (0.09)	Forest -0.01 (0.22)	Equal -0.09 (0.54)	Equal 0.20 (0.45)	Equal NA
<i>Mionectes oleagineus</i>	0.18 (0.11)	Equal -0.44 (0.24)	Equal NA	Equal -0.50 (0.42)	Equal NA
<i>Turdus flavipes</i>	0.02 (0.08)	Equal -0.04 (0.17)	Equal 0.41 (0.48)	Equal -0.92 (0.19)	Coffee 0.80 (0.50)
<i>Turdus albicollis</i>	-0.30 (0.23)	Equal 0.45 (0.51)	Equal -1.24 (1.50)	Equal 0.07 (0.64)	Equal NA
<i>Ramphocelus dimidiatus</i>	-0.27 (0.12)	Coffee 0.73 (0.26)	Forest -0.19 (0.55)	Equal -0.31 (0.33)	Equal 0.02 (0.83)
<i>Tangara gyrola</i>	0.11 (0.08)	Equal -0.40 (0.19)	Coffee 0.07 (0.22)	Equal -0.41 (0.18)	Coffee 0.99 (0.58)
<i>Salpator maximus</i>	0.19 (0.14)	Equal 0.35 (0.34)	Equal 0.94 (0.58)	Equal 0.29 (0.34)	Equal 1.05 (1.44)
<i>Salpator striatipectus</i>	-0.35 (0.22)	Equal 0.23 (0.44)	Equal -0.44 (0.86)	Equal -1.47 (0.64)	Coffee 0.78 (0.88)
<i>Myiothlypis conspicillata</i>	0.40 (0.12)	Forest 0.14 (0.25)	Equal 1.16 (0.88)	Equal -0.30 (0.27)	Equal -0.34 (0.85)
<i>Basileuterus rufifrons</i>	0.04 (0.12)	Equal 0.28 (0.26)	Equal -1.15 (0.57)	Coffee -0.97 (0.34)	Coffee 0.80 (0.61)
<i>Myioborus miniatus</i>	0.31 (0.16)	Equal 1.31 (0.49)	Forest -1.10 (1.20)	Equal 0.33 (0.40)	Equal NA
<i>Euphonia lanirostris</i>	-0.29 (0.14)	Coffee -0.19 (0.30)	Equal NA	Forest 0.71 (0.33)	Forest 0.20 (1.46)

Note: Values in the first column correspond to model-averaged habitat coefficients (standard errors), and second column shows interpretation, i.e. in which habitat the species performed better according to that indicator; forest was the reference habitat in all analyses.

3.2 | Level 2: composite indexes of habitat preference and performance

We classified five species as preferring forest (*M. olivaceus*, *M. oleagineus*, *T. albicollis*, *T. gyrola* and *M. conspicillata*), two as preferring coffee (*S. striatipectus* and *M. miniatus*) and five as having equal preference (*T. flavipes*, *R. dimidiatus*, *S. maximus*, *B. rufifrons* and *E. lanirostris*). There were varying degrees of evidence available to make these assignments, with preference scores ranging from -2 to 3 (Table 4).

We classified four species as experiencing higher performance in forest (*M. olivaceus*, *S. maximus*, *M. conspicillata* and *M. miniatus*), one as experiencing higher performance in coffee (*S. striatipectus*) and the remaining seven as experiencing no difference in performance between habitats (*M. oleagineus*, *T. flavipes*, *T. albicollis*, *R. dimidiatus*, *T. gyrola*, *B. rufifrons* and *E. lanirostris*). There were varying degrees of evidence available to make these assignments, with coefficients of the meta-analysis for the effect of habitat ranging from -0.30 to 0.38 (Table 4).

3.3 | Level 3: is habitat selection acting adaptively?

We documented the following: (a) three species preferring their higher-performance habitat (*M. olivaceus*, *M. conspicillata* for forest, and *S. striatipectus* for coffee); (b) three species preferring forest but without consistent evidence for differences in performance (*M. oleagineus*, *T. albicollis* and *T. gyrola*); (c) four species without consistent differences in either trait (*T. flavipes*, *R. dimidiatus*, *B. rufifrons* and *E. lanirostris*); (d) *S. maximus* potentially being caught in an equal-preference trap (preferring neither habitat despite forest showing higher performance); and (e) *M. miniatus* potentially being caught in a severe ecological trap (higher preference for coffee despite higher performance in forest) (Table 4).

4 | DISCUSSION

We evaluated the role of native forest and shade coffee in the conservation of resident birds by assessing the correlation between measures of habitat preference and performance in a three-level analytical approach designed to gauge whether habitat selection was acting adaptively in an intermediately modified landscape.

At the first level of analysis, where we calculated separate indicators of habitat preference and performance, 70% of statistical tests showed no statistically clear differences between habitats, partly possibly due to unaccounted variation such as temporal effects, but also reflecting high levels of use of both habitats by our focal species. Indicators pointed more commonly towards higher preference in forest (12 vs. 7) and higher performance in coffee (8 vs. 5). Evidence provided by these indicators was rarely consistent within a species, so no single indicator could accurately assess either process for all of them. While using a suite of indicators gave us more confidence in our assessments and is recommended when little is

TABLE 4 Composite indexes of habitat preference and performance, and hypotheses about the role that shade coffee, native forest and habitat selection play at the landscape level for populations of twelve resident birds

Species	Preference		Performance		Interpretation		
	Index	Int.	Index	Int.	Coffee	Forest	Selection
<i>Mionectes olivaceus</i>	1	Forest	0.21 (0.08)	Forest	Sink	Source	Adaptive
<i>Mionectes oleagineus</i>	1	Forest	0.04 (0.10)	Equal	Undervalued resource	Equal-quality trap	Non-ideal
<i>Turdus flavipes</i>	0	Equal	-0.08 (0.07)	Equal	Generalist habitat	Generalist habitat	Adaptive
<i>Turdus albicollis</i>	3	Forest	-0.17 (0.20)	Equal	Undervalued resource	Equal-quality trap	Non-ideal
<i>Ramphocelus dimidiatus</i>	0	Equal	-0.12 (0.10)	Equal	Generalist habitat	Generalist habitat	Adaptive
<i>Tangara gyrola</i>	2	Forest	-0.01 (0.06)	Equal	Undervalued resource	Equal-quality trap	Non-ideal
<i>Saltator maximus</i>	0	Equal	0.26 (0.12)	Forest	Equal-preference trap	Undervalued resource	Non-ideal
<i>Saltator striatipectus</i>	-2	Coffee	-0.30 (0.18)	Coffee	Source	Sink	Adaptive
<i>Myiothlypis conspicillata</i>	1	Forest	0.26 (0.10)	Forest	Sink	Source	Adaptive
<i>Basileuterus rufifrons</i>	0	Equal	-0.03 (0.10)	Equal	Generalist habitat	Generalist habitat	Adaptive
<i>Myioborus miniatus</i>	-1	Coffee	0.38 (0.14)	Forest	Severe ecological trap	Severe undervalued resource	Maladaptive
<i>Euphonia laniirostris</i>	0	Equal	-0.14 (0.12)	Equal	Generalist habitat	Generalist habitat	Adaptive

known about the behaviour of the species of interest, further work is needed to validate our chosen variables (see Supporting Information for further discussion of these issues). Preference assessment could be improved by measuring settlement patterns (Hollander, Dyck, San Martin, & Titeux, 2011), which in resident species would imply being able to follow young during post-natal dispersal (Cox et al., 2014) or conducting choice experiments involving the manipulation of selection cues (Robertson & Hutto, 2006). Performance assessment could be improved by including parameters more directly related to survival and reproduction (Johnson, 2007), as the relationship between fitness and parameters such as body condition, muscle and plumage has not been evaluated directly for the focal species (Labocha & Hayes, 2012).

At the second level of analysis, the composite index for habitat preference had the disadvantage of not taking into account uncertainty in estimates or the strength of evidence supporting preference for each habitat; however, it allowed us to deal with contradictory evidence and gauge whether unclear differences were pointing to equal preference or insufficient information. Although effect sizes of habitat at the first level of analysis were generally small, the index of habitat performance allowed us to weight the strength of evidence when combining the five indicators (further work could develop an index that allows for non-equal weighting of variables in relationship to how strongly they correlate with fitness). Half of the resulting assignments pointed to patterns expected for generalist species (equal preference and equal quality), while in the remaining comparisons, evidence favoured forest over coffee as the preferred (5 vs. 2) and better-performance (4 vs. 1) habitat.

At the third level of analysis, we found evidence of source-sink dynamics for three species, although these patterns need to be corroborated with detailed demographic information (Furrer & Pasinelli, 2016; Gilroy & Edwards, 2017). Four species showed a pattern consistent with the equal-preference and equal-quality assumption

underlying community-level analyses. Of the four species displaying evidence of mild non-ideal selection, three appeared to undervalue coffee as a suitable habitat. If this trend is explored further and proves to be relatively common, detailed studies into the cues used for selection may provide straightforward management actions to raise the conservation value of coffee and similar novel ecosystems (Gilroy & Sutherland, 2007).

We only found evidence of one species being caught in a severe ecological trap, but the strength of evidence behind preference and performance was weak (statistically clear differences were only found for occupancy and muscle score). If this pattern were to hold with additional evidence, actions could be designed to reduce the attractiveness of shade coffee for the species (Gilroy & Sutherland, 2007). Indeed, abundance (Chandler et al., 2013) and demographic (Mumme, 2015) data from Central America suggest a high sensitivity of *M. miniatus* to landscape structure, making it an interesting species for further study.

Even though the expansion of coffee plantations in the Sierra Nevada de Santa Marta was rapid and widespread, it occurred in the late 19th century (Carriker, 2001), raising the question as to why species subject to maladaptive selection should persist. Methodologically, trade-offs between different aspects of preference and performance may compensate for what appears to be maladaptive selection (Battin, 2004; Chalfoun & Martin, 2007), and both density dependence and the mixing of territorial and floater individuals may interfere with our ability to detect phenomena that lead to ecological traps (Sherry & Holmes, 1996; Watkinson & Sutherland, 1995), especially if population-level phenomena such as source-sink dynamics compensate for differences in individual-level performance. Ecologically, traps originating from novel components in a landscape seem less likely to facilitate extinction than those arising from habitat degradation (Fletcher et al., 2012). We know from simulations of our study system that

even if the effect of an ecological trap is not strong enough to lead to population extinction under current conditions, this may change rapidly with further landscape change (Sánchez-Clavijo, Hearn, & Quintana-Ascencio, 2016), so that under further forest loss, the landscape could lose more species than predicted by models assuming adaptive habitat selection.

Our preference/performance results showed no clear pattern of association with individual species characteristics such as habitat guild, family, size and connectedness of the subspecies distributions, diet, participation in mixed flocks, body size or previous classifications of sensitivity to human activity (Table S1). Most of the characteristics hypothesized to make species vulnerable to traps (speed of evolution, rate of learning, behavioural plasticity, etc.—Battin, 2004) are unknown for the majority of tropical species, and even though we assume residents have better knowledge of their environments than their migrant counterparts, our ability to prove this is hindered by the lack of studies that go beyond community-level measures for resident birds.

4.1 | Research and conservation implications

For future applications of this framework in the assessment of the value of different land uses for biodiversity conservation, we strongly advise using multiple lines of evidence to simultaneously assess habitat preference and performance, as indicator choice may lead to different interpretations about the adaptiveness of habitat selection (Chalfoun & Martin, 2007; Robertson & Hutto, 2006). The value of this approach will increase as our understanding of the relationship between the variables of interest and the chosen indicators improves (Noss, 1990). A further refinement will be to extend our framework into a continuous approach to evaluate the adaptiveness of habitat selection, by evaluating preference and performance in a way that makes them directly comparable. A quantitative approach would help reduce the subjectivity of interpretations and is more realistic for cases in which the habitats being compared do not hold independent populations of the species of interest (Kristan, 2003; Part et al., 2007).

While the ideal way to measure the value of a habitat would be to estimate survival and reproduction parameters based on long-term demographic and/or movement studies of species showing a representative range of ecological and behavioural traits (Milder et al., 2014; Sekercioglu, Loarie, Brenes, Ehrlich, & Daily, 2007), these are rarely feasible in tropical ecosystems. Our results show that occupancy and abundance models generated from the wide-scale application of simple sampling methodologies (Irizarry et al., 2018; Ruiz-Gutiérrez, Hooten, & Campbell Grant, 2016) may neglect important differences in habitat preference and performance. Capture data allow for the exploration of habitat-species relationships at a resolution intermediate between these two extremes (Ruiz-Gutiérrez et al., 2012; Sekercioglu, 2012), but to increase the reliability of our inference, we need further research into the relationships between individual-level data and consequences at the population level. An ideal approach would be to combine these three scales of analysis.

For example, studies comparing 'spare' (leaving remnant habitats as intact as possible and intensifying the use of surrounding lands to provide goods and services) and 'share' (promoting land uses where farming and biodiversity conservation occur simultaneously) approaches to rural management still assess land use contributions to biodiversity conservation based solely on species abundance (Fischer et al., 2008; Gilroy & Edwards, 2017; Phalan, Onial, Balmford, & Green, 2011; von Wehrden et al., 2014). Monitoring approaches using a multi-species, multi-indicator and multi-scale approach to quantify preference and performance in landscapes of different compositions could advance our understanding of biodiversity responses to landscape heterogeneity and support better decision-making for conservation and sustainable use.

Even though our site has an unusual combination of large remnants of native forest and shade coffee plantations with 60% average canopy cover (Guhl, 2004; Sánchez-Clavijo et al., 2009), our findings are similar to those from comparable studies carried out in tropical agricultural landscapes (Chandler et al., 2013; Kremen, 2015; Perfecto & Vandermeer, 2002). The mostly adaptive or neutral selection behaviours found for our focal species suggest that shade coffee can be a biodiversity-friendly matrix that provides complementary or supplementary habitat to a wide range of resident birds, even becoming a favourable breeding habitat for some generalist species. However, higher preference and performance in forest for species with varied life histories reinforce the importance of protecting remnants of native vegetation in agricultural landscapes.

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AUTHORS' CONTRIBUTIONS

L.M.S.-C. and P.F.Q.-A. conceived the ideas, designed methodology and analysed the data; N.J.B. guided data collection and provided additional data; L.M.S.-C. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.


DATA AVAILABILITY STATEMENT

Raw data used in this paper are available from SiB Colombia (Asociación SELVA, 2016—<https://doi.org/10.15472/2kwarh>), while curated datasets for all analyses presented are available from the Dryad Digital Repository (Sánchez-Clavijo, Bayly, & Quintana-Ascencio, 2019—<https://doi.org/10.5061/dryad.mp5rn5b>).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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