

Landscape matrix mediates occupancy dynamics of Neotropical avian insectivores

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Abstract. In addition to patch-level attributes (i.e., area and isolation), the nature of land cover between habitat patches (the matrix) may drive colonization and extinction dynamics in fragmented landscapes. Despite a long-standing recognition of matrix effects in fragmented systems, an understanding of the relative impacts of different types of land cover on patterns and dynamics of species occurrence remains limited. We employed multi-season occupancy models to determine the relative influence of patch area, patch isolation, within-patch vegetation structure, and landscape matrix on occupancy dynamics of nine Neotropical insectivorous birds in 99 forest patches embedded in four matrix types (agriculture, suburban development, bauxite mining, and forest) in central Jamaica. We found that within-patch vegetation structure and the matrix type between patches were more important than patch area and patch isolation in determining local colonization and local extinction probabilities, and that the effects of patch area, isolation, and vegetation structure on occupancy dynamics tended to be matrix and species dependent. Across the avian community, the landscape matrix influenced local extinction more than local colonization, indicating that extinction processes, rather than movement, likely drive interspecific differences in occupancy dynamics. These findings lend crucial empirical support to the hypothesis that species occupancy dynamics in fragmented systems may depend greatly upon the landscape context.

Key words: *avian insectivores; Caribbean; colonization; extinction; Jamaica; matrix effects; metapopulation; Neotropical birds; occupancy; tropical conservation.*

INTRODUCTION

Island biogeography theory (MacArthur and Wilson 1967) and metapopulation models (Hanski 1998) predict that the processes of extinction and colonization, as influenced by island/habitat area and isolation, determine species distributions and persistence patterns. These conceptual models have frequently been applied to explain species patterns and processes in fragmented landscapes (e.g., Laurance 2008). Decreasing patch size and increasing patch isolation, associated with the fragmentation process, are predicted to alter natural extinction and colonization rates (e.g., Fahrig 2003). Smaller fragments are expected to exhibit increased species extinction, and more isolated fragments are expected to have reduced colonization. The occupancy and richness patterns expected based on these theoretical predictions, however, are not always observed in natural systems. Empirical relationships of species responses to

patch size and isolation have been found to be weak or absent in fragmented systems (Bender et al. 1998, Debinski and Holt 2000, Prugh et al. 2008), a discrepancy that may be attributed to simplification of habitat fragments as islands separated by homogeneously inhospitable habitat (Haila 2002).

Habitat in fragmented landscapes is often embedded in complex mosaics of different land cover types, termed the “matrix.” Species may be affected not only by the size and spatial location of primary habitat, but also by the structure and composition of this matrix (Ewers and Didham 2006, Kupfer et al. 2006). The matrix can affect interpatch movement of animals (e.g., Revilla et al. 2004, Bender and Fahrig 2005), can alter the resource base within a landscape by providing alternative or supplemental resources (e.g., Perfecto and Vandermeer 2002, Brotons et al. 2003), and can impact the type and magnitude of edge effects (e.g., habitat quality, microclimate, predation rates) (e.g., Chalfoun et al. 2002, Ries et al. 2004). Expected species isolation relationships may be altered if species interpatch movements differ based on varying composition and configuration of matrix land cover (e.g., Ricketts 2001, Bender and Fahrig 2005). The type of matrix could directly influence local

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extinction within primary habitat if patch resident species commonly obtain resources from matrix areas; this behavior has been observed in birds (e.g., Graham et al. 2002, Luck and Daily 2003). This phenomenon could result in lower extinction rates in smaller patches embedded in a hospitable matrix than in larger patches embedded in an inhospitable matrix (Sisk et al. 1997, Estades 2001). Species–area relationships may also be obscured if habitat quality is differentially altered due to land use practices in the matrix (Donovan et al. 1997, Rodewald and Yahner 2001, Rodewald and Bakermans 2006). For example, hunting pressures, selective logging, or spread of fire or invasives may disproportionately increase in landscapes with greater human access (Hobbs 2001, Peres 2001). The matrix may thus obscure commonly assumed relationships among species occupancy and patch size and isolation, and may ultimately mediate colonization–extinction dynamics in fragmented systems (e.g., Vandermeer and Carvajal 2001).

Although the potential importance of the landscape matrix has been recognized for almost two decades (e.g., Saunders et al. 1991, Bierregaard et al. 1992), its effects on patterns and dynamics of species occurrence remain poorly understood. The relative importance of multiple human-modified land cover types is rarely examined in a single setting, and different matrix types are often combined in one category or are assumed to be of subordinate importance to habitat components (i.e., patch area and isolation). Moreover, few empirical studies have untangled effects of the matrix from those of patch area or isolation because the amount and spatial configuration of habitat are commonly confounded with one another and then further confounded with matrix composition (Rodewald 2003, Laurance 2008). Most inferences about fragmentation and matrix effects are also based solely on species diversity, abundance, or occurrence patterns, rather than directly addressing the underlying processes of extinction or colonization (Fahrig 2003, Lampila et al. 2005); and studies rarely account for detection biases that may lead to false inference (Moilanen 2002, MacKenzie et al. 2006).

In this paper, we seek to understand the relative effects of patch area, patch isolation, within-patch habitat structure, and matrix type on occupancy dynamics in fragmented landscapes. We examine avian insectivores to determine (1) how patch area and within-patch habitat (vegetation) structure affect the probabilities of local extinction, (2) how patch isolation affects the probabilities of local colonization, and (3) whether and how matrix conditions may mediate isolation, area, and habitat relationships. We chose to investigate resident (nonmigratory) Neotropical, forest-dependent, insectivorous birds because this guild is disproportionately declining in fragmented tropical forests worldwide (Sodhi et al. 2004, Sigel et al. 2006, Stouffer et al. 2009). To reduce bias, we applied recently developed dynamic patch-occupancy models to account for the fact that

species are often imperfectly and/or differentially detected (MacKenzie et al. 2006). Models were based on repeat surveys conducted over a three-year period (2005–2007) in forest patches embedded in three common human-modified matrix types in the Caribbean (agricultural, suburban, and bauxite mining development) and in sites in a natural matrix (i.e., continuous forest). We applied estimation methods that explicitly incorporate detection bias to test whether occupancy dynamics differ across landscapes that are similar in structural habitat fragmentation (i.e., forest patch area and isolation) but that vary in surrounding human-modified land cover.

METHODS

Study area and site selection

Our study sites were located in Manchester and Clarendon Parishes in central Jamaica (17°56'24"–18°11'6" N, 77°23'13"–77°37'5" W). This region lies within the premontane moist forest climatic zone (Holdridge 1967) and was once covered in predominantly wet limestone forest (Asprey and Robbins 1953). Less than 30% of native forest currently remains, and most of the human land conversion occurred by the 18th century (Eyre 1987). Forest is now largely restricted to small hilltop remnants on limestone outcrops, with surrounding valleys cleared for agriculture (primarily cattle pasture), residential development, and mining for bauxite (Evelyn and Camirand 2003).

We sampled a total of 20 landscapes (delineated as 1-km² areas): six comprising continuous forest cover and 14 in which forest has been fragmented by agriculture ($N = 5$), by suburban development ($N = 4$), or by bauxite mining ($N = 5$) (Fig. 1). Forest remnants were surrounded by introduced pasture, tree-lined fencerows, paddock trees, and herbaceous gardens in agricultural landscapes and by low-density residential housing, ornamental gardens, abandoned woodlots, and roadside secondary growth in suburban landscapes (see Plate 1). Suburban landscapes adhered to the land cover definition proposed by Robinson et al. (2005). Bauxite landscapes were former agricultural lands that had been converted to mining within the past 10 years, where relictual forests were surrounded by exposed bauxitic soils, with some recent growth of ferns, *Acacia* trees, or planted grassland. Suburban and agricultural matrices contained greater foliage cover and vertical complexity than bauxite lands, and thus were expected to provide greater potential resources (e.g., food or nesting sites) (Kennedy et al. 2010) and to enhance structural connectivity to aid movement outside forest remnants relative to bauxite landscapes (Kennedy and Marra 2010). Beyond direct effects on movement among patches, matrix land cover composition and structure can affect species extinction processes within remnant forest patches through human land use practices associated with particular matrix types (Hobbs 2001, Peres 2001). For example, suburban and bauxite

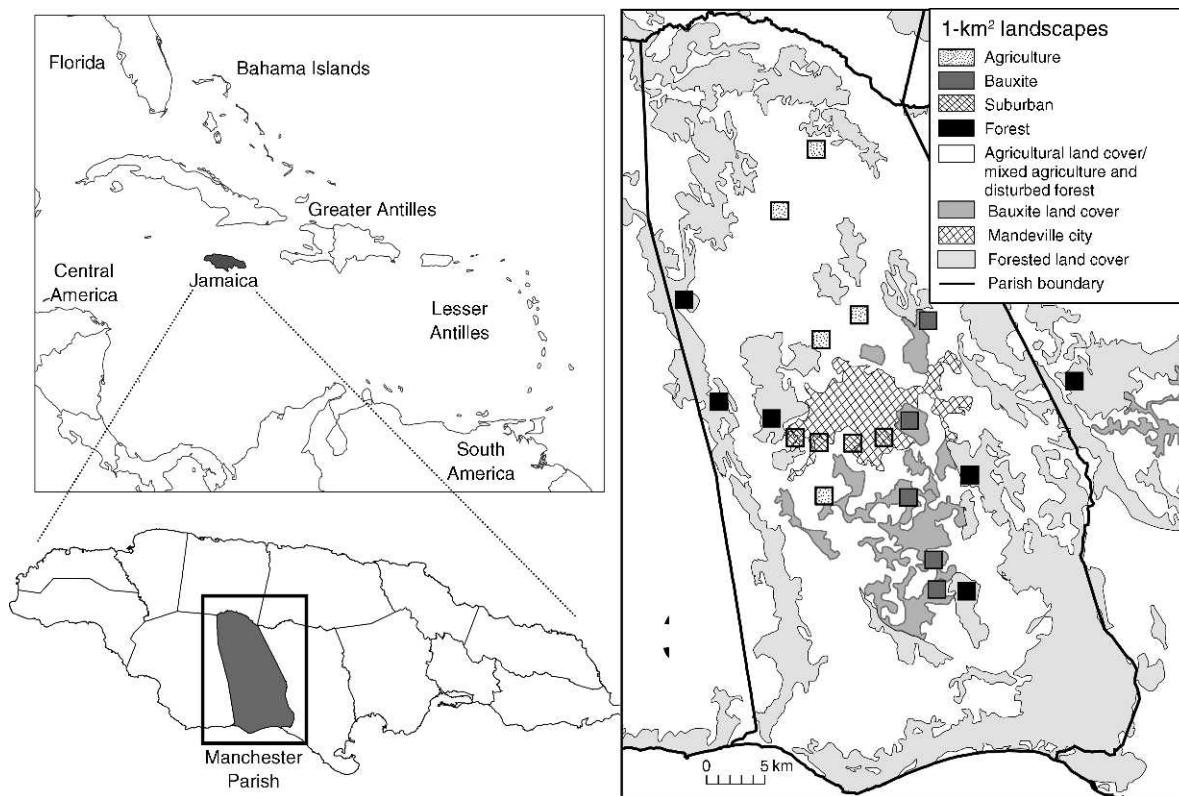


FIG. 1. Locations of the 20 1-km² landscapes surveyed on the island of Jamaica as shown in the context of the West Indies.

landscapes are exposed to more ongoing human disturbance, including hunting, selective logging, noise, road and surface-mining impacts, fire ignition sources, and domestic animals than are agricultural landscapes that tend to be large, private landholdings (C. M. Kennedy, *unpublished data*). Thus we predicted that agricultural and suburban landscapes would have colonization rates most similar to intact forest relative to bauxite landscapes, and that agricultural landscapes would have extinction rates most similar to intact forest relative to both suburban and bauxite landscapes.

We surveyed an average of five forest patches per replicate landscape using stratified random sampling of patches to represent the size distribution. Twenty-two of these patches were sampled in an agricultural matrix, 19 in a suburban matrix, and 27 in a bauxite mining matrix. Because forested landscapes comprise continuous forest cover, we sampled 31 “pseudo-patches,” which were transects whose length (i.e., number of point-count locations) were proportional to patch sizes in fragmented landscapes. We refer to both pseudo-patches sampled in forested landscapes and forest remnants sampled in anthropogenic landscapes as “patches.” To increase the probability that birds were independently sampled, replicate patches within landscapes were 10.31 ± 5.85 km (mean \pm SD) apart and replicate landscapes were separated by $\sim 1\text{--}28$ km, which is believed to well exceed territory size for target species (Cruz 1981, Kennedy and

Marra 2010; A. M. Haynes-Sutton, *personal communication*; C. M. Kennedy, *unpublished data*). Previous analyses of related field data from this system revealed no significant spatial correlation between resident bird community composition and abundances and the spatial distance of sampled patches (Kennedy et al. 2010).

To isolate the potential influence of matrix type, agricultural, suburban, and bauxite landscapes were selected such that they were similar in the major components of fragmentation. Sampled patches had similar forest area (3.89 ± 3.77 ha) and isolation (33.58 ± 28.72 m, 160.80 ± 163.15 m, and 2381.75 ± 1212.81 m [mean \pm SD] to the nearest fragment >0.5 ha, 5 ha, and 100 ha, respectively). Patches were also embedded in landscapes with a similar proportion (35.84 ± 5.95) and spatial configuration (i.e., shape complexity, interpatch connectivity) of forest cover (Kennedy et al. 2010).

Target species

We modeled occupancy dynamics for nine of the 11 native resident insectivorous bird species in our region (Table 1). These species are ideal for investigation of multipatch dynamics because they are specialized in Jamaica’s limestone forests, thus allowing for spatial delineation of primary habitat. They are also sensitive to forest fragmentation (Kennedy et al. 2010). Although these species are in the same broad diet guild, they are taxonomically and ecologically diverse in that they

TABLE 1. Life history and ecological traits of the nine resident insectivorous bird species included in analyses.

Order, family and species	Body mass (g) [†]	Altitudinal range [‡]	Foraging strata [§]	Foraging mode [¶]	Nest height [#]	Nest type
Coraciiformes: Todidae						
Jamaican Tody (<i>Todus todus</i>)	6.8	low to mid-montane	multiple	sally, glean	ground	closed
Passeriformes: Cotingidae						
Jamaican Becard (<i>Pachyramphus niger</i>)	38.6	mid-montane	canopy	sally, glean	canopy	closed
Passeriformes: Parulidae						
Arrow-headed Warbler (<i>Dendroica pharetra</i>)	10.3	mid-montane	multiple	glean	understory	open
Passeriformes: Tyrannidae						
Jamaican Elaenia (<i>Myiopagis cotta</i>)	12.8	low to mid-montane	canopy	sally	canopy	open
Jamaican Pewee (<i>Contopus pallidus</i>)	9.9	mid-montane	understory	sally	canopy	open
Rufous-tailed Flycatcher (<i>Myiarchus validus</i>)	41.4	mid-montane	canopy	sally	canopy	closed
Sad Flycatcher (<i>Myiarchus barbirostris</i>)	13.4	low to mid-montane	understory	sally	understory	closed
Passeriformes: Vireonidae						
Jamaican Vireo (<i>Vireo modestus</i>)	10.5	low to mid-montane	understory	glean	understory	open
Piciformes: Picidae						
Jamaican Woodpecker (<i>Melanerpes radiolatus</i>)	99.8	low to mid-montane	multiple	peck	canopy	closed

Note: All species were endemic to the island of Jamaica and known to breed in mid-elevation limestone forests within the study region.

[†] Estimated body mass, averaged across male, female, and unknown sexes (Lack 1976, Windsor Research Centre 2009).

[‡] Altitudinal distribution on the island of Jamaica: found in lowland, mid-elevation, and montane forest (0–2000 m); found in mid-elevation (300–1200 m) up to montane forests (600–2000 m) (Lack 1976).

[§] Foraging height most commonly observed: understory in lower to mid-forest or shrub layer (0.5 to <5 m); upper canopy (>5 m); among multiple heights (i.e., undergrowth up to canopy) (Cruz 1974, Cruz 1980, Raffaele et al. 1998; P. P. Marra, A. M. Haynes-Sutton, and H. A. Davis, *personal communication*).

[¶] Foraging behavior most commonly observed: pecking/excavating in bark; gleaning from nearby substrate (e.g., leaves, twigs); sallying from perch to perch to attack prey (Lack 1976, Downer and Sutton 1995, Raffaele et al. 1998; definitions from Remsen and Robinson 1990).

[#] Nesting height most commonly observed: ground level (<0.5 m); understory (0.5 to <5 m); upper canopy (>5 m) (Bond 1993, Downer and Sutton 1995, Raffaele et al. 1998; P. P. Marra, A. M. Haynes-Sutton, and H. A. Davis, *personal communication*).

^{||} Typical nest construction: partially closed, including cavity, burrow, sphere, and pendant nests; nests with large openings, including cup, saucer, and platform nests (Downer and Sutton 1995, Raffaele et al. 1998; definitions from Ehrlich et al. [1998]).

represent six families and a range of body masses (~7 to 100 g), and different (but overlapping) altitudinal ranges (Table 1). Species represented both foraging and nesting specialists and generalists and exhibited a variety of foraging behaviors. The two species we did not include in the study were either too common (Jamaican Oriole, *Icterus leucopteryx*) or too rare (Stolid Flycatcher, *Myiarchus stolidus*) to model.

Sampling methods

For three consecutive years (2005–2007) we conducted 286 point counts on two to three separate occasions from early February to mid-June during the height of breeding activity (Raffaele et al. 1998). Point counts were conducted along a centrally placed transect within each of the 68 forest patches in anthropogenic landscapes and along randomly placed transects in forested landscapes. We sampled 1–13 stations per patch (3.30 ± 2.14, mean ± SD), proportional to patch area, and 12–15 stations on average per replicate landscape per occasion. To minimize double-counting, stations were located 100 m apart and >25 m from a matrix–forest boundary, and during each census, we mapped locations and flight paths of all birds seen or heard. We considered

the patch as our sampling unit, and temporal replication was achieved by visiting each point-count station two to three times per year over the three breeding seasons.

At each sampling station, we recorded the number of individuals per species seen or heard within a 10-minute period (conducted between 06:00 and 10:00 hours on clear days without rain) and in a 25 m fixed-radius area (Hutto et al. 1986). We selected a 25 m radius because it provided reliable detection across sites based on field tests in our system and in the Caribbean (Wunderle and Waide 1993). Each patch was visited by one of three trained observers for repeat counts within a season, and the order of site visitation was rotated throughout each field season.

Patch-level covariates

We considered four patch-level covariates: matrix type, patch area, patch isolation, and local vegetation structure. Matrix type was determined categorically from 2001–2002 IKONOS imagery (1-m resolution; Space Imaging 2002) and field verification. Patch area was the size of a forest patch in hectares. Patch isolation was calculated as the Euclidean nearest-neighbor (ENN) distance from each sampled patch to a forest patch >100

ha (variable ENN_100ha), reflecting the distance a bird may travel to reach a potential source population given directed movement. Within-patch vegetation structure was determined by axis 1 scores of a principal components analysis (PC1) based on 12 vegetation variables measured at each point-count station (tree diameter, basal area, canopy height, leaf area index, leaf litter depth, abundance of woody and herbaceous vines, and percent herbaceous cover [0–0.5 m height class], low shrub [0.5–2 m], tall shrub [2–6 m], trees [>6 m], and open canopy). Appendix A details how patch area, isolation, and vegetation structure were quantified. A major difficulty in discerning the relative influence of components of fragmentation (e.g., habitat amount, configuration, and quality) and the role of the matrix is that effects are often highly intercorrelated (Fahrig 2003, Rodewald 2003, Laurance 2008). Thus we examined whether the continuous covariates of patch area, isolation, and vegetation structure were intercorrelated and whether they differed by matrix type based on Spearman's rank correlation (ρ) and one-way ANOVA, respectively. Statistical analyses were performed using the "stats" package in the *R* statistical system (R Development Core Team 2008). All variables were tested for normality and homogeneity of variances, and transformations were performed where necessary. Untransformed means \pm SE are reported.

Occupancy analyses

We used dynamic occupancy models to estimate initial occupancy (ψ_{2005}), local colonization (γ), and local extinction (ϵ) probabilities from 2005 to 2007 for each bird species separately (MacKenzie et al. 2006). Initial occupancy (ψ_t) is defined as the probability that a sampled patch is occupied by a species in the initial year (i.e., $t = 2005$). Local extinction probability (ϵ_t) is the probability that a patch occupied by that species at year t is no longer occupied by the species at year $t + 1$. Local colonization probability (γ_t) is the probability that a patch unoccupied by a species at year t becomes occupied at year $t + 1$. In contrast with other occupancy models (Moilanen 2002), this modeling framework explicitly incorporates detection probability (i.e., the probability that at least one individual of a species is detected in year t) into the estimation of initial occupancy and rate parameters (i.e., colonization and extinction probabilities), which reduces bias in parameter estimation (MacKenzie et al. 2006). A detection history was constructed for each species and forest patch; a presence indicated detection of at least one individual of a species during any point-count survey event, and absence indicated failure to detect a species. To separate true absence (i.e., species not occupying a site) from false absence (i.e., failure to detect a species that is truly present during a survey event), we used multiple surveys conducted over a short enough period to adequately meet the assumption of population closure (i.e., the occupancy state of a patch at the

species level does not change). Local colonizations and local extinctions are allowed between seasons and are adjusted for false absences by using repeat surveys within a season where closure is assumed. Colonization and extinction probabilities were determined based on between-year detection histories and estimated via likelihood maximization (MacKenzie et al. 2006).

We developed a candidate model set to test the main effects of patch isolation, patch area, vegetation structure, and matrix type; we predicted that these factors would influence local colonization and local extinction processes of birds in our region (28 models; Appendix B: Table B1). Initial occupancy was always modeled without any covariates to focus our investigation on rate parameters (after Ferraz et al. 2007). We evaluated potential bias in this approach via simulation using the GENPRES program (outlined in Bailey et al. 2007), and found a small positive bias in some of the colonization probabilities. The bias was negligible compared to the estimated differences among matrix types and does not significantly change our inference. Following classic island biogeography and metapopulation models (MacArthur and Wilson 1967, Hanski 1998), we predicted that the process of colonization depended upon the spatial isolation of forest habitat (i.e., patch isolation), and extinction processes depended upon patch size. To expand upon these traditional models, we tested whether local vegetation structure covaried with local extinction, given that this environmental feature is known to influence habitat quality for birds due to its effects on availability of food resources, perching/nesting sites, predation, and shelter against abiotic conditions (e.g., Wiens 1989).

To test how species colonization and extinction dynamics were influenced by the landscape matrix, we modeled both extinction and colonization as a function of matrix type. One might hypothesize that the matrix may interact with patch area, isolation, and habitat structure. However, we only considered additive relationships for all covariates, because we standardized patch area and patch isolation among all fragmented landscapes, which allowed us to compare the effects of matrix habitat alone. Thus complex models with several interaction parameters could not be reasonably supported by our study design and data set.

Prior to modeling occupancy and associated rate parameters, we determined the best covariance structure on detection probability (p) using the most general structure for the other parameters. We predicted that survey month and number of point counts were the two most important factors influencing potential variability in bird detection (Appendix B). Other covariates, such as observer and time of day, might influence species detection (Ralph and Scott 1981), but their effects were diminished by rotating observers and the temporal order of sampling. We also considered the effect of matrix type on detection probability given potential variation in noise, vegetation structure, and bird abundances among

different landscape contexts. Initial modeling of matrix type on p for over half of the species gave systematic model convergence and parameter identifiability problems; for those models that did converge, matrix type had low model weight, suggesting a lack of relationship between matrix type and detection. Thus we were confident that survey order and sampling effort captured the essential components of detection variability in our study.

We modeled p without a covariate relationship (i.e., constant) and as a function of survey month, sampling effort, or the additive effect of both (Appendix B: Table B2). Using the most general model structure for occupancy dynamics (i.e., global model), we selected the covariance structure on p with the lowest Akaike's Information Criterion (AIC), and then fit the 28 occupancy models separately for each bird species, including the global model with all patch-level covariates on γ and ϵ , as well as reduced model forms. We standardized all covariates to their z scores, and fit models in the program PRESENCE (Hines and MacKenzie 2008). Models that failed to converge or that contained nonsensical parameter estimates were eliminated from the model set for the appropriate species and were not used for inference. We ranked models based on AIC, identified top models (i.e., $\Delta\text{AIC} < 2.0$) for each species, and calculated the associated model weights (w) (Burnham and Anderson 2002). To determine the most supported model structure for the avian insectivore community, we averaged the weight of each model across all species. To assess the relative effects of patch area, isolation, vegetation structure, and matrix type, we calculated model-averaged estimates of the coefficients for each of these covariates based on the 95% confidence set per species (Burnham and Anderson 2002). Model averaging combines parameter estimates from each model using their associated AIC weights to provide an estimate that incorporates both within- and across-model uncertainty. This approach reduces model bias and allows for more robust inferences than those based on a single selected best model (Burnham and Anderson 2002). We calculated model-averaged colonization ($\hat{\gamma}$) and extinction ($\hat{\epsilon}$) for each species by matrix type, holding all other covariates constant using their mean values. Because we were most interested in interpreting estimates of colonization and extinction as a function of landscape matrix, we graphed model-averaged covariates against $\hat{\gamma}$ and $\hat{\epsilon}$ to assess the direction and strength of relationships.

RESULTS

Patch isolation, area, and vegetation structure

Isolation and area of our sampled patches were similar across matrix types. Forest patches in agricultural, suburban, and bauxite landscapes were, on average, 2381 m (± 147 m) from another fragment ≥ 100 ha; and isolation distances did not differ among matrix types ($F_{2,65} = 1.43$, $P = 0.25$). Sampled pseudo-

patches in continuous forest ranged from 1.2 to 25 ha, and patches in fragmented landscapes ranged from 0.6 to 19.6 ha in agricultural landscapes, 1.0 to 8.3 ha in suburban landscapes, and 0.6 to 13.3 ha in bauxite landscapes. Overall, patch area did not differ among matrix types (ANOVA, $F_{3,95} = 0.39$, $P = 0.76$; Appendix A: Table A1).

Vegetation structure in patches (as determined by principal components analysis axis 1 [PC1]) differed significantly by matrix type ($F_{3,95} = 4.62$, $P = 0.01$; Appendix A: Tables A1, A2). Forest and agricultural patches tended to have greater forest cover and vertical structure, larger and more abundant trees, and more leaf litter (i.e., lower, negative PC1 values) than patches in bauxite, and to a lesser extent, in suburban landscapes. Forest in bauxite and suburban landscapes tended to have greater low shrub and herbaceous cover and more vines (i.e., higher, positive PC1 values). Only patches within bauxite landscapes, however, significantly differed from those in other landscape types ($P < 0.05$). None of the continuous covariates were significantly intercorrelated (patch area with PC1, $\rho = 0.04$, $P = 0.67$; patch area with ENN_100ha, $\rho = -0.10$, $P = 0.32$; PC1 with ENN_100ha, $\rho = 0.03$, $P = 0.76$).

Estimated species occupancy and detection

Initial occupancy estimates ($\hat{\psi}_{2005}$) ranged from 0.39 to 1.00, and estimated species detection was always < 1 across species based on top models (Appendix C: Tables C1, C2). For all species, detection probability was best modeled with sampling effort, with detection increasing with the number of point counts surveyed. For five species the most supported model structure on detection included both survey month and sampling effort, with the greatest detection earlier in the breeding season rather than later for all species except one (Jamaican Tody) (Appendix C: Table C2). We used the best covariate structures on detection probability for each species to investigate covariate relationships with the rate parameters, which were of primary interest in our study.

Relative importance of patch isolation, area, and vegetation structure, and matrix type for colonization and extinction

Patch isolation was an important covariate on local colonization probabilities for five of the nine species, and matrix type was important for six of them (Table 2). Matrix type was included as a covariate in top-ranking models with higher AIC weights ($w > 0.20$), indicating that it is a better predictor for colonization than is patch isolation. Patch area was an important covariate on local extinction probabilities for about half of the species but was included in models with lower weights. Extinction was most consistently related to both vegetation structure and matrix type; these patch-level covariates were included in high-ranking models with higher weights for almost all species. The most

TABLE 2. Contribution of patch-level covariates to top models (i.e., $\Delta AIC < 2$) of local colonization and extinction dynamics of nine resident insectivorous birds in Jamaica.

Species	Colonization, γ		Extinction, ϵ		
	Isolation	Matrix type	Area	Vegetation	Matrix type
Arrow-headed Warbler	X	X	X	X	
Jamaican Becard		X		X	X
Jamaican Elaenia		X		X	X
Jamaican Pewee		X		X	X
Jamaican Tody			(X)	(X)	X
Jamaican Vireo	(X)		(X)	X	X
Jamaican Woodpecker	(X)	(X)	(X)	(X)	(X)
Rufous-tailed Flycatcher	X	X		X	X
Sad Flycatcher	(X)		(X)	(X)	X

Notes: The symbol “X” indicates a covariate included in a top model with associated model weight $w > 0.20$; “(X)” indicates a covariate included in a top model with $w < 0.20$. Results were qualitatively similar with other breakpoints (i.e., $w < 0.10$ or $w < 0.30$) (see Appendix C for individual model results). Isolation is the nearest-neighbor distance from each sampled patch to a forest fragment ≥ 100 ha. Area is the size of a forest patch. Vegetation is the principal components analysis score that is a composite index of 12 variables measuring forest vegetation structure (Appendix A: Table A2). Matrix type identifies whether a patch was in an agricultural, suburban development, bauxite mining, or forested matrix.

commonly supported model structures were ones in which colonization was either a function of matrix type or modeled as constant, and covariates on extinction probability included an additive function of matrix type and vegetation structure (Appendix C: Table C1).

When weights for each model were averaged across all species, the best model we considered was one in which local colonization was a function of matrix type only, and local extinction was a function of both vegetation structure and matrix type. This model had an average weight of 34%, which was three times higher than that of any other model. Thus matrix type and vegetation structure were the two most important covariates influencing occupancy dynamics of the insectivorous bird community in our study system.

Effects of patch isolation, area, and vegetation structure on colonization and extinction

Patch isolation had no effect on colonization probabilities for three species: Jamaican Becard, Jamaican Elaenia, and Jamaican Pewee (Appendix C: Table C1). For the other six species, when models included patch isolation on colonization probability, increasing isolation had a negative effect as predicted by theory (except for the Jamaican Woodpecker), but the effect was often estimated near zero (based on approximated 95% CIs) (Appendix C: Table C3). The magnitude and slope of the relationship between colonization and isolation was similar across the different matrix types for the majority of species with a detected effect (Appendix C: Fig C1). However, increasing patch isolation negatively affected colonization only in suburban and bauxite mining landscapes for the Jamaican Tody, and only in bauxite landscapes for the Rufous-tailed Flycatcher (Fig. 2a; see Appendix C for all species graphs).

As expected, local extinction probabilities generally declined with increasing patch area (Appendix C: Table C3, Fig. C2), but we found no effect of area for four

species (Jamaican Becard, Jamaican Elaenia, Jamaican Pewee, and Rufous-tailed Flycatcher). Patch area had a strong influence on local extinction for only two species: the Arrow-headed Warbler, for which patch area had a uniformly negative effect across all matrix types; and the Jamaican Woodpecker, for which patch area had a negative effect only in bauxite and suburban landscapes (Fig. 2b).

The effect of vegetation structure on extinction probabilities was greater than the effect of patch area. For all species, except the Jamaican Vireo, probability of extinction increased with greater percent herbaceous cover and low shrubs and abundance of vines, and decreasing canopy cover and height, tree diameter and basal area, and leaf area index (i.e., increasing PC1 value) (Appendix C: Table C3). For five species, the slope of this relationship was consistent among matrix types, but the rate of increase in extinction probability was matrix dependent (Appendix C: Fig. C3). For example, extinction probability reached 100% for the Jamaican Becard at negative PC values in both bauxite and suburban landscapes but at positive PC values in forested and agricultural landscapes. For the remaining species, the relationship between vegetation structure and local extinction was matrix dependent, demonstrating a sharper increase in extinction probabilities for some matrix types than others. For example, vegetation structure affected extinction probabilities for the Jamaican Pewee only in agricultural and forested landscapes because extinction was inevitable in patches in bauxite and suburban landscapes (regardless of vegetation structure). Conversely, vegetation structure affected extinction probabilities for the Jamaican Woodpecker largely in bauxite and suburban landscapes, while occupied patches in agricultural and forested landscapes remained occupied except for the most extreme positive PC values (Fig. 2c). Large standard errors for many of the estimated coefficients

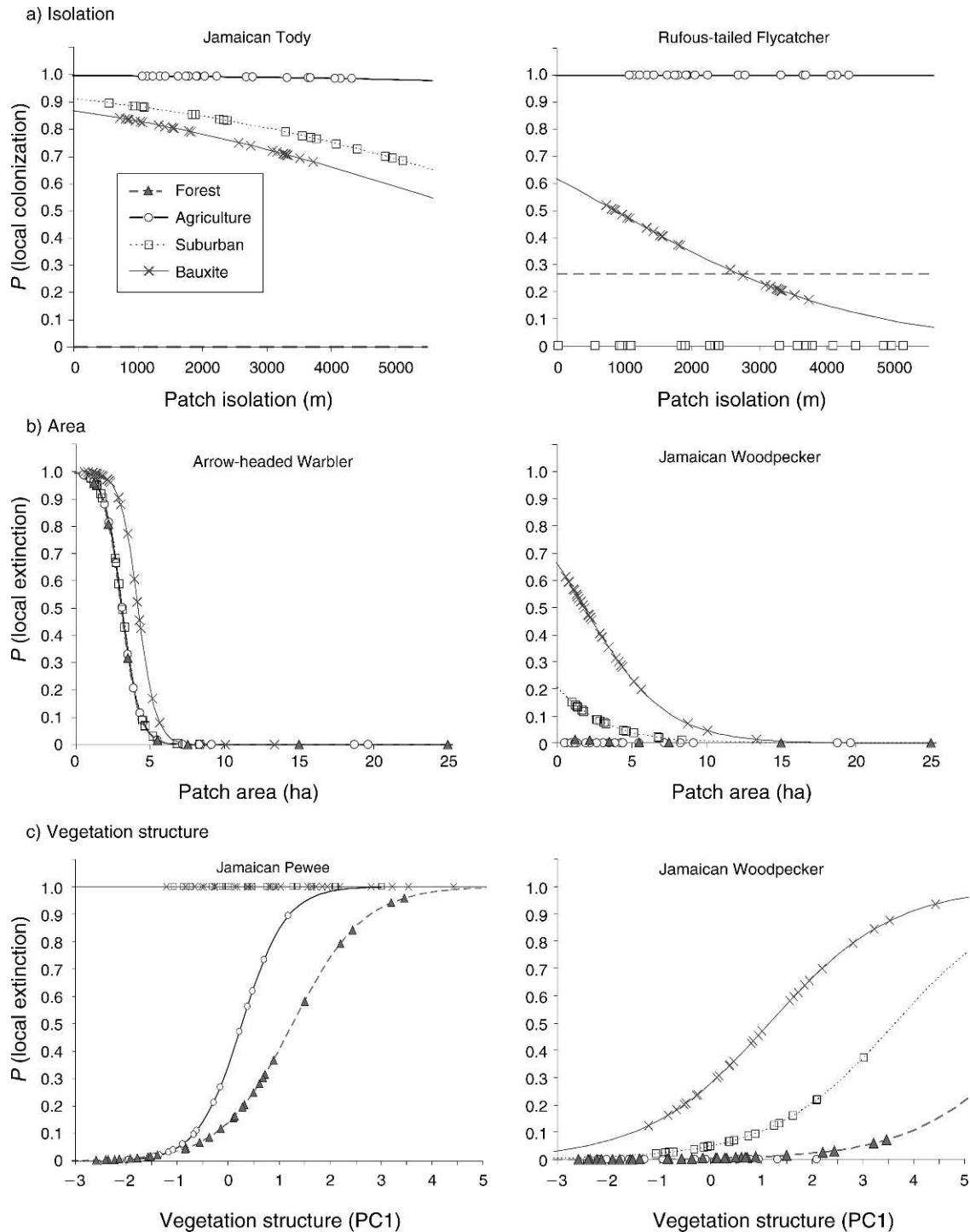


FIG. 2. Model-averaged point estimates (probabilities, P) of occupancy parameters for representative bird species in relation to (a) local colonization probabilities as a function of patch isolation by matrix type; (b) local extinction probabilities as a function of patch area by matrix type; and (c) local extinction probabilities as a function of within-patch vegetation structure by matrix type. To distill the variation in the 12 patch-level vegetation variables into fewer noncorrelated components, we conducted a principal components (PC) analysis. The averaged PC axis 1 score was used as proxy for patch-level vegetation structure in models. All patch-level covariates were modeled via additive relationships. Species presented exhibited rate parameters strongly influenced by patch-level covariates (see Table 3 and Appendix C: Table C3 for unconditional standard errors; see Appendix C for additional species graphs).

TABLE 3. Model-averaged estimates for local colonization and local extinction probabilities (\pm SE) by landscape matrix type for each species. Estimates were determined when all other patch-level covariates (i.e., area, isolation, and vegetation structure) were held constant at mean value.

Species	Colonization, $\hat{\gamma}^\dagger$				Extinction, $\hat{\epsilon}^\ddagger$			
	Forest	Agriculture	Suburban	Bauxite	Forest	Agriculture	Suburban	Bauxite
Arrow-headed Warbler	0.41 (0.37)	0.24 (0.27)	0.13 (0.27)	0.29 (0.26)	0.16 (0.46)	0.1 (0.49)	0.18 (0.50)	0.57 (0.85)
Jamaican Becard	0.00 (...)	1.00 (...)	0.00 (...)	0.00 (...)	0.00 (...)	0.00 (...)	1.00 (...)	1.00 (...)
Jamaican Elaenia	1.00 (...)	0.44 (...)	0.00 (...)	0.00 (...)	0.00 (...)	0.00 (...)	1.00 (...)	0.00 (...)
Jamaican Pewee	0.18 (0.12)	0.30 (0.28)	0.00 (...)	0.00 (0.05)	0.17 (0.11)	0.35 (0.35)	1.00 (...)	1.00 (...)
Jamaican Tody	0.00 (...)	0.99 (0.03)	0.86 (0.44)	0.80 (0.58)	0.10 (0.06)	0.00 (...)	0.00 (...)	0.28 (0.21)
Jamaican Vireo	0.78 (0.30)	0.81 (0.24)	0.66 (0.36)	0.65 (0.36)	0.00 (...)	0.00 (...)	0.23 (0.34)	0.08 (0.16)
Jamaican Woodpecker	0.69 (1.65)	0.64 (1.49)	0.00 (...)	0.00 (...)	0.01 (0.03)	0.00 (...)	0.05 (0.25)	0.31 (0.92)
Rufous-tailed Flycatcher	0.26 (1.95)	1.00 (...)	0.00 (...)	0.39 (1.79)	0.10 (19.12)	0.00 (...)	0.00 (...)	1.00 (...)
Sad Flycatcher	0.00 (...)	0.00 (...)	0.00 (...)	0.00 (...)	0.27 (0.34)	0.10 (0.23)	0.42 (0.39)	0.51 (0.34)

Notes: Ellipses indicate variances that could not be estimated due to estimation of Beta at boundary (i.e., 0 or 1) and/or due to variance-covariance errors. Standard errors were calculated based on model-averaged Betas, using delta method (Williams et al. 2002), when covariances are assumed to be 0 and only including models with estimable variance-covariance matrices.

† Local colonization probabilities estimated at mean value of isolation for all fragmented landscapes and at 0 isolation for forested landscapes.

‡ Local extinction probabilities estimated at mean value of patch area and mean value of vegetation structure (PC1) for all landscapes.

for patch isolation and area, and to a lesser extent vegetation structure, may suggest these relationships are not significant or that our sample size was too small (Table C3); but model selection results clearly support the influence of within-patch vegetation structure and matrix type on occupancy dynamics across the avian insectivore community (Appendix C: Table C1).

Estimated colonization and extinction by matrix type at mean patch area, isolation, and vegetation structure values

Landscape effects on colonization differed among the species. The Jamaican Elaenia, Jamaican Pewee, and Jamaican Woodpecker were most likely to colonize forested and agricultural landscapes; the Jamaican Becard and Rufous-tailed Flycatcher had higher estimated colonization in agricultural landscapes; and the Jamaican Tody colonized all fragmented landscape types equally (Table 3). The remaining species (Arrow-headed Warbler, Jamaican Vireo, and Sad Flycatcher) exhibited weak relationships between colonization and matrix types. On average, point estimates of model-averaged colonization probabilities were highest in agricultural landscapes (0.60 ± 0.12), followed by forested (0.37 ± 0.12), bauxite (0.24 ± 0.10), and suburban landscapes (0.18 ± 0.11). Lower colonization probabilities in forested landscapes were due to consistent occupancy of patches for several species (e.g., Jamaican Becard, Jamaican Pewee, Jamaican Tody). Point estimates revealed that colonization probabilities were higher in only the agricultural relative to both suburban and bauxite landscapes.

In contrast, model-averaged extinction probabilities differed more strongly among matrix types, with the insectivore community as a whole having higher extinction in both suburban (0.43 ± 0.15) and bauxite (0.53 ± 0.13) landscapes than in either forested ($0.09 \pm$

0.03) or agricultural (0.07 ± 0.04) landscapes based on point estimates (Table 3). All species consistently had higher model-averaged point estimates of extinction in suburban and/or bauxite landscapes: two species with higher extinction in suburban (Jamaican Elaenia, Jamaican Vireo), four higher in bauxite (Arrow-headed Warbler, Jamaican Tody, Jamaican Woodpecker, and Rufous-tailed Flycatcher), and three higher in both suburban and bauxite landscapes (Jamaican Becard, Jamaican Pewee, and Sad Flycatcher).

DISCUSSION

Occupancy dynamics mediated by landscape matrix

This study reveals that species occupancy dynamics, and ultimately species persistence in fragmented landscapes, may depend in large part on the quality of land cover surrounding primary habitat. The nature and strength of matrix effects on species extinction and colonization processes may also be influenced by the type of human-modified land cover; in Jamaica, species were differentially impacted by whether once-continuous forest was converted to agricultural, suburban, or bauxite mining development. This finding underscores the importance of delineating among different types of anthropogenically modified lands, rather than treating them as a single cover type (i.e., nonhabitat), in fragmentation research and/or conservation planning, because they may impact meta-population dynamics differently. Our results further indicate that the landscape matrix, regardless of patch isolation, best explains local colonization; and the additive effect of within-patch vegetation structure and matrix type, regardless of patch area, best explains local extinction of Neotropical avian insectivores (Table 2; Appendix C). The effects of patch area, isolation, and vegetation structure on occupancy dynamics also tended to be contingent upon matrix context (Fig. 2). Thus occupancy dynamics in

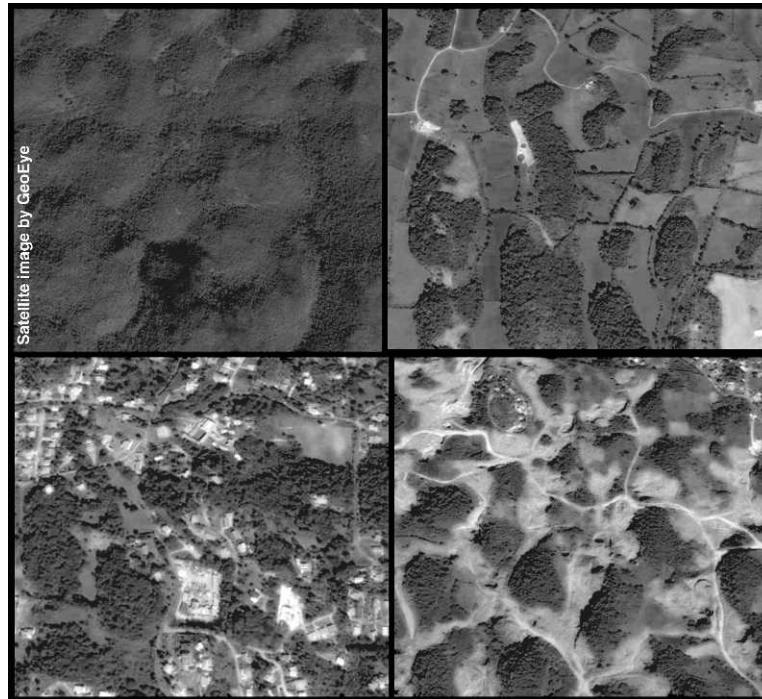


PLATE 1. Aerial view of representative landscapes in Jamaica: (upper left) landscape composed of continuous forest cover, (upper right) landscape fragmented by agriculture, (lower left) landscape fragmented by suburban development, and (lower right) landscape fragmented by bauxite mining. Forest cover appears as dark areas and is surrounded by pasture, tree-lined fencerows, and paddock trees in agricultural landscapes; by houses, roads, ornamental lawns and gardens, and roadside vegetation in suburban landscapes; and by exposed bauxitic (terra rossas) soil and early growth of ferns and *Acacia* stands in bauxite mining landscapes. Photo credit: GeoEye.

Jamaica are driven more by matrix conditions than by the commonly assumed patch area and isolation, and local extinction rates are driven more by within-patch habitat structure than by patch area.

These relationships were detected even though patch area, isolation, and vegetation structure were uncorrelated, and despite similar climate, geology, forest type, and forest cover across fragmented landscapes. The strong contribution of the matrix on occupancy dynamics of birds in this region may be attributed to the fact that the karst countryside in central Jamaica is characterized by small forested hilltops, often <10 ha in size (Appendix A: Table A1), which are expected to be greatly impacted by surrounding human-modified land uses (Kennedy et al. 2010). To confirm how the landscape matrix mediates bird dynamics over the long term and the impacts of patch-level characteristics, we recommend further examination with longer-term data and a model set that explicitly tests for these interactive effects.

Landscape matrix effects on colonization and extinction

Although individual species responded differently, a general communitywide pattern emerged. Local extinction of resident avian insectivores was substantially higher and local colonization marginally lower in forest embedded in suburban and bauxite mining landscapes relative to agricultural and forested landscapes (Table

3). As predicted, species colonization was higher in agricultural relative to bauxite landscapes, but not in suburban landscapes, perhaps due to higher mortality during movement (e.g., predation). Colonization patterns, however, were variable across species (Table 3). In many cases, colonization did not clearly differ across matrix types, and constant colonization rates among patches were supported for some species (Appendix C: Table C1). In contrast, there was unequivocal support that extinction probabilities across the community were influenced by both within-patch vegetation structure and matrix type. All species exhibited extinction estimates that were consistently higher in bauxite mining and/or suburban landscapes in accordance with our predictions. Similarly, Kennedy et al. (2001) found lower abundances of resident avian insectivores in forest remnants in suburban and bauxite mining landscapes than in agricultural or forested landscapes in the region. Thus we suggest that differential abundance and occupancy patterns among fragmented landscape types are being driven more by extinction than colonization dynamics.

Potential mechanisms underlying differential occupancy patterns among matrix types

Three broad mechanisms have been proposed to explain the decline of avian insectivores in fragmented forests: (1) impedance of interpatch movement, which

reduces functional landscape connectivity (e.g., Stratford and Stouffer 1999, Sekercioglu et al. 2002); (2) increased nest parasitism and predation of birds (e.g., Chalfoun et al. 2002, Lampila et al. 2005); and (3) reduction of habitat quality, including the interdependent effects of the loss of microhabitats and the decline of prey availability (e.g., Burke and Nol 1998, Zanette et al. 2000).

Interpatch movement.—Previous research, based on both observational (mark–recapture) (Robinson 1999, Sekercioglu et al. 2002, Laurance et al. 2004) and movement data (Moore et al. 2008, Lees and Peres 2009), has argued that dispersal limitation is the dominant factor underlying the decline of insectivorous birds in fragmented tropical forests. Such studies support the hypothesis that insectivores (particularly understory specialists) have low mobility and/or are reluctant to move through nonforested habitats (i.e., matrix) due to potential behavioral inhibition (e.g., Greenberg 1983) or physiological or morphological limitations (Laurance et al. 2002, Stratford and Robinson 2005), which could explain their extinction vulnerability. However, the reverse pattern has also been found. Based on long-term data at the Biological Dynamics of Forest Fragments Project in Brazil, bird species previously assumed to be dispersal limited have been found to disperse more widely postfragmentation than previously thought (Van Houtan et al. 2007). Thus isolation has been found not to influence occupancy dynamics of many tropical birds (Ferraz et al. 2007), suggesting that habitat connectivity may not be the limiting factor determining long-term population dynamics in fragmented landscapes.

Our findings are consistent with the hypothesis that dispersal limitation is not the primary mechanism explaining bird distributions among forest fragments. Interpatch distances of forest patches in central Jamaica are small relative to potential bird dispersal (i.e., with forested hilltops hundreds of meters apart) (Appendix A: Table A1), leading to high probabilities of local colonization (Table 3). Further, the evolutionary history of Caribbean avifauna may have led to species with stronger dispersal abilities and with fewer physiological or morphological limitations relative to mainland counterparts, characteristics that have allowed them to (re)colonize and (re)establish in island habitats and to withstand large-scale disturbance events like hurricanes (Ricklefs and Bermingham 2008).

Nest parasitism and predation.—Other commonly cited causes of forest bird declines are increased nest parasitism and predation (e.g., Robinson et al. 1995, Lampila et al. 2005), the impact of which can vary by landscape context (Donovan et al. 1997, Rodewald and Yahner 2001). In other parts of the world, open- and ground-nesting species suffer greater predation than those with nests of other types or heights off the ground (Chalfoun et al. 2002, Lampila et al. 2005). In contrast, for Jamaican birds, Kennedy et al. (2001) found no detectable association between nest type and differential

bird abundances between intact and fragmented forest, and species predicted to be most sensitive to nest predation (ground nesters) were least likely to exhibit lower abundances in fragmented landscapes. Moreover, insectivores in this study showed no differences in local extinction patterns in relation to either nest type or nesting height (Table 1). Brood parasitism, particularly by cowbirds (*Molothrus* spp.), has been shown to increase in disturbed landscapes in North America (Robinson et al. 1995), but this threat is currently considered minimal in Neotropical systems (Stratford and Robinson 2005); and the generalist brood parasite, the Shiny Cowbird (*M. bonariensis*), was detected on only six of 1681 occasions in our study. Lastly, predation of juvenile or adult birds by raptors may be a source of mortality for certain insectivores (e.g., obligate mixed-species foragers; Canaday 1996), but raptors were detected infrequently and in equal numbers across landscapes (Kennedy 2009).

Reduction of habitat quality.—Our evidence suggests that occupancy dynamics in Jamaica are driven by local extinctions, likely as a function of differential habitat quality (e.g., food and cover) among landscapes. We emphasize that area and isolation of forest patches did not vary among fragmented landscapes, but within-patch vegetation structure did. Forest remnants in bauxite and suburban matrices had low stature and more open canopies, less structural complexity, reduced leaf litter, and more shrubs (Appendix A: Table A1), indicating that they may be in earlier successional stages and/or have been subjected to greater disturbance than forests in agricultural matrices (Asprey and Robbins 1953). Birds in suburban landscapes may be disproportionately affected by human-induced forest disturbance, including selective harvesting, road impacts, or spread of fire or invasive species (Marzluff et al. 2001). Surface mining activities in bauxite areas involve large-scale removal of vegetation and topsoil, which could alter soil water retention, create dust pollution, and lead to biogeochemical and hydrologic changes (Bell and Donnelly 2006). All of these factors likely alter within-forest vegetation structure and microclimate and may have led to a reduction in invertebrate biomass, thereby affecting insectivorous birds (e.g., Burke and Nol 1998, Zanette et al. 2000).

Even though surveyed landscapes had similar environmental conditions (e.g., elevation, climate, soil substrate), the effects of habitat structure cannot be disentangled from landscape type, because land use practices in the matrix are driving internal forest changes. The nature of within-patch vegetation structure, however, does not fully capture matrix effects on habitat quality, because matrix type provided additional predictive ability for bird occupancy dynamics and affected the influence of local vegetation (Fig. 2; Appendix C). Thus we argue that the matrix is mediating resource availability, both within the primary habitat and in the surrounding land cover. In many cases, matrix habitats may be hospitable for native

species and may provide resources that allow for population maintenance or growth in fragmented habitats (Norton et al. 2000, Brotons et al. 2003). In fact, the ability to utilize matrix areas has been identified as a key determinant of species tolerance to forest conversion (e.g., Gascon et al. 1999, Henle et al. 2004). Resource supplementation may have played a role in buffering against local extinction. Based on sampling conducted outside forest remnants (Kennedy 2009), the disproportionate use of matrix habitats coincides with reduced local extinction probabilities for certain species in Jamaica. For example, the Sad Flycatcher and the Jamaican Becard were disproportionately detected in agricultural matrix habitats (e.g., foraging in grasslands and using hedgerows/paddock trees as perching and nesting habitat) relative to other matrix types, which may have reduced their local extinction in agricultural landscapes (Table 3). Similarly, the Jamaican Tody and the Jamaican Woodpecker were rarely detected in bauxite relative to suburban or agricultural matrices and exhibited comparatively higher estimates of extinction in forests embedded in bauxite (Kennedy 2009). Compared to most avian foraging guilds, insectivores exhibit enhanced specialization; thus we suspect that resource supplementation in matrix areas is not driving differential occupancy dynamics as much as is the reduction in internal forest habitat quality.

Conservation implications

In this system, occupancy patterns of insectivorous birds differed not only between human-dominated vs. natural matrix types as is more typically found (e.g., Prugh et al. 2008), but also among the different human land use types. Treating all modified lands equally and categorizing Jamaica's landscapes into matrix vs. forest components would have masked these important patterns. Land conversion in Jamaica (Evelyn and Camirand 2003) and worldwide (DeFries et al. 2004) is from agriculture to increasing urbanization and development. This study strongly suggests that conversion of agricultural lands to more intensive development will result in further losses of avian insectivores even without increased forest loss or fragmentation. Although we have not experimentally confirmed the mechanism, our evidence suggests that local extinction, rather than local colonization, is causing differential occupancy dynamics of insectivores among fragmented landscapes in Jamaica. Thus we recommend greater attention be given to the role of resource provisioning in different landscape contexts as a potential selective mechanism driving the decline of insectivores in fragmented landscapes.

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LITERATURE CITED

- Asprey, G. F., and R. G. Robbins. 1953. The vegetation of Jamaica. *Ecological Monographs* 23:359–412.
- Bailey, L. L., J. E. Hines, J. D. Nichols, and D. I. MacKenzie. 2007. Sampling design trade-offs in occupancy studies with imperfect detection: examples and software. *Ecological Applications* 17:281–290.
- Bell, F. G., and L. J. Donnelly. 2006. Mining and its impact on the environment. Taylor and Francis Group, New York, New York, USA.
- Bender, D. J., T. A. Contreras, and L. Fahrig. 1998. Habitat loss and population decline: a meta-analysis of the patch size effect. *Ecology* 79:517–533.
- Bender, D. J., and L. Fahrig. 2005. Matrix structure obscures the relationship between interpatch movement and patch size and isolation. *Ecology* 86:1023–1033.
- Bierregaard, R. O., T. E. Lovejoy, V. Kapos, A. A. Dossantos, and R. W. Hutchings. 1992. The biological dynamics of tropical rainforest fragments. A prospective comparison of fragments and continuous forest. *BioScience* 42:859–866.
- Bond, J. 1993. A field guide to birds of the West Indies. Fifth edition. Houghton Mifflin, New York, New York, USA.
- Brotons, L., M. Monkkonen, and J. L. Martin. 2003. Are fragments islands? Landscape context and density-area relationships in boreal forest birds. *American Naturalist* 162:343–357.
- Burke, D. M., and E. Nol. 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding Ovenbirds. *Auk* 115:96–104.
- Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. Second edition. Springer Science+Business Media, Fort Collins, Colorado, USA.
- Canaday, C. 1996. Loss of insectivorous birds along a gradient of human impact in Amazonia. *Biological Conservation* 77:63–77.
- Chalfoun, A. D., F. R. Thompson, and M. J. Ratnaswamy. 2002. Nest predators and fragmentation: a review and meta-analysis. *Conservation Biology* 16:306–318.
- Cruz, A. 1974. Feeding assemblages of Jamaican birds. *Condor* 76:103–107.
- Cruz, A. 1980. Feeding ecology of the Black-whiskered Vireo and associated gleaning birds in Jamaica. *Wilson Bulletin* 92:40–52.
- Cruz, A. 1981. Bird activity and seed dispersal of a montane forest tree (*Dunalia arborescens*) in Jamaica. *Biotropica* 13:34–44.
- Debinski, D. M., and R. D. Holt. 2000. A survey and overview of habitat fragmentation experiments. *Conservation Biology* 14:342–355.
- DeFries, R. S., J. A. Foley, and G. P. Asner. 2004. Land-use choices: balancing human needs and ecosystem function. *Frontiers in Ecology and the Environment* 2:249–257.

- Donovan, T. M., P. W. Jones, E. M. Annand, and F. R. Thompson. 1997. Variation in local-scale edge effects: mechanisms and landscape context. *Ecology* 78:2064–2075.
- Downer, A., and D. Sutton. 1995. *Birds of Jamaica: a photographic field guide*. Cambridge University Press, New York, New York, USA.
- Ehrlich, P. R., D. S. Dobkin, and D. Wheye. 1988. *The birder's handbook: a field guide to the natural history of North American birds*. Simon and Schuster, New York, New York, USA.
- Estades, C. F. 2001. The effect of breeding-habitat patch size on bird population density. *Landscape Ecology* 16:161–173.
- Evelyn, O. B., and R. Camirand. 2003. Forest cover and deforestation in Jamaica: an analysis of forest cover estimates over time. *International Forestry Review* 5:354–363.
- Ewers, R. M., and R. K. Didham. 2006. Confounding factors in the detection of species responses to habitat fragmentation. *Biological Reviews* 81:117–142.
- Eyre, L. A. 1987. Jamaica: test case for tropical deforestation? *Ambio* 16:338–343.
- Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution, and Systematics* 34:487–515.
- Ferraz, G., J. D. Nichols, J. E. Hines, P. C. Stouffer, R. O. Bierregaard, and T. E. Lovejoy. 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science* 315:238–241.
- Gascon, C., T. E. Lovejoy, R. O. Bierregaard, J. R. Malcolm, P. C. Stouffer, H. L. Vasconcelos, W. F. Laurance, B. Zimmerman, M. Tocher, and S. Borges. 1999. Matrix habitat and species richness in tropical forest remnants. *Biological Conservation* 91:223–229.
- Graham, C., J. E. Martinez-Leyva, and L. Cruz-Paredes. 2002. Use of fruiting trees by birds in continuous forest and riparian forest remnants in Los Tuxtlas, Veracruz, Mexico. *Biotropica* 34:589–597.
- Greenberg, R. 1983. The role of neophobia in determining the degree of foraging specialization in some migrant warblers. *American Naturalist* 122:444–453.
- Haila, Y. 2002. A conceptual genealogy of fragmentation research: from island biogeography to landscape ecology. *Ecological Applications* 12:321–334.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.
- Henle, K., K. F. Davies, M. Kleyer, C. Margules, and J. Settele. 2004. Predictors of species sensitivity to fragmentation. *Biodiversity and Conservation* 13:207–251.
- Hines, J. E., and D. I. MacKenzie. 2008. PRESENCE. Version 2.3. (<http://www.mbr-pwrc.usgs.gov/software/presence.html>)
- Hobbs, R. J. 2001. Synergisms among habitat fragmentation, livestock grazing, and biotic invasions in southwestern Australia. *Conservation Biology* 15:1522–1528.
- Holdridge, L. R. 1967. Life zone ecology. Tropical Science Center, San Jose, Costa Rica.
- Hutto, R. L., S. M. Pletschet, and P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. *Auk* 103:593–602.
- Kennedy, C. M. 2009. Matrix effects on individual and community-level responses of birds to forest fragmentation in Jamaica. Dissertation. University of Maryland, College Park, Maryland, USA.
- Kennedy, C. M., and P. P. Marra. 2010. Matrix mediates avian movements in tropical forested landscapes: inference from experimental translocations. *Biological Conservation* 143:2136–2145.
- Kennedy, C. M., P. P. Marra, W. F. Fagan, and M. C. Neel. 2010. Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica. *Ecological Monographs* 80:651–669.
- Kupfer, J. A., G. P. Malanson, and S. B. Franklin. 2006. Not seeing the ocean for the islands: the mediating influence of matrix-based processes on forest fragmentation effects. *Global Ecology and Biogeography* 15:8–20.
- Lack, D. 1976. *Island biogeography illustrated by the land birds of Jamaica*. University of California Press, Berkeley, California, USA.
- Lampila, P., M. Monkkonen, and A. Desrochers. 2005. Demographic responses by birds to forest fragmentation. *Conservation Biology* 19:1537–1546.
- Laurance, S. G. W., P. C. Stouffer, and W. F. Laurance. 2004. Effects of road clearings on movement patterns of understory rainforest birds in central Amazonia. *Conservation Biology* 18:1099–1109.
- Laurance, W. F. 2008. Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. *Biological Conservation* 141:1731–1744.
- Laurance, W. F., T. E. Lovejoy, H. L. Vasconcelos, E. M. Bruna, R. K. Didham, P. C. Stouffer, C. Gascon, R. O. Bierregaard, S. G. Laurance, and E. Sampaio. 2002. Ecosystem decay of Amazonian forest fragments: a 22-year investigation. *Conservation Biology* 16:605–618.
- Lees, A. C., and C. A. Peres. 2009. Gap-crossing movements predict species occupancy in Amazonian forest fragments. *Oikos* 118:280–290.
- Luck, G. W., and G. C. Daily. 2003. Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. *Ecological Applications* 13:235–247.
- MacArthur, R. H., and E. O. Wilson. 1967. *The theory of island biogeography*. Princeton University Press, Princeton, New Jersey, USA.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier Academic Press, Burlington, Massachusetts, USA.
- Marzluff, J. M., R. Bowman, and R. Donnelly. 2001. *Avian ecology and conservation in an urbanizing world*. Kluwer Academic Publishers, Boston, Massachusetts, USA.
- Moilanen, A. 2002. Implications of empirical data quality to metapopulation model parameter estimation and application. *Oikos* 96:516–530.
- Moore, R. P., W. D. Robinson, I. J. Lovette, and T. R. Robinson. 2008. Experimental evidence for extreme dispersal limitation in tropical forest birds. *Ecology Letters* 11:960–968.
- Norton, M. R., S. J. Hannon, and F. K. A. Schmiegelow. 2000. Fragments are not islands: patch vs landscape perspectives on songbird presence and abundance in a harvested boreal forest. *Ecography* 23:209–223.
- Peres, C. A. 2001. Synergistic effects of subsistence hunting and habitat fragmentation on Amazonian forest vertebrates. *Conservation Biology* 15:1490–1505.
- Perfecto, I., and J. Vandermeer. 2002. Quality of agroecological matrix in a tropical montane landscape: ants in coffee plantations in southern Mexico. *Conservation Biology* 16:174–182.
- Prugh, L. R., K. E. Hodges, A. R. E. Sinclair, and J. S. Brashares. 2008. Effect of habitat area and isolation on fragmented animal populations. *Proceedings of the National Academy of Sciences USA* 105:20770–20775.
- R Development Core Team. 2008. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Austria.
- Raffaele, H., J. Wiley, O. Garrido, A. Keith, and J. Raffaele. 1998. *A guide to the birds of West Indies*. Princeton University Press, Princeton, New Jersey, USA.
- Ralph, C. J., and J. M. Scott, editors. 1981. *Estimating numbers of terrestrial birds*. Studies in Avian Biology No. 6. Allen Press, Lawrence, Kansas, USA.
- Remsen, J. V., Jr., and S. K. Robinson, editors. 1990. *A classification scheme for foraging behavior of birds in*

- terrestrial habitats. *Studies in Avian Biology* No. 13. Allen Press, Lawrence, Kansas, USA.
- Revilla, E., T. Wiegand, F. Palomares, P. Ferreras, and M. Delibes. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. *American Naturalist* 164:E130–E153.
- Ricketts, T. H. 2001. The matrix matters: effective isolation in fragmented landscapes. *American Naturalist* 158:87–99.
- Ricklefs, R., and E. Bermingham. 2008. The West Indies as a laboratory of biogeography and evolution. *Philosophical Transactions of the Royal Society B* 363:2393–2413.
- Ries, L., R. J. Fletcher, J. Battin, and T. D. Sisk. 2004. Ecological responses to habitat edges: mechanisms, models, and variability explained. *Annual Review of Ecology, Evolution, and Systematics* 35:491–522.
- Robinson, L., J. P. Newell, and J. A. Marzluff. 2005. Twenty-five years of sprawl in the Seattle region: growth management responses and implications for conservation. *Landscape and Urban Planning* 71:51–72.
- Robinson, S. K., F. R. Thompson, T. M. Donovan, D. R. Whitehead, and J. Faaborg. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- Robinson, W. D. 1999. Long-term changes in the avifauna of Barro Colorado Island, Panama, a tropical forest isolate. *Conservation Biology* 13:85–97.
- Rodewald, A. D. 2003. The importance of land uses within the landscape matrix. *Wildlife Society Bulletin* 31:586–592.
- Rodewald, A. D., and M. H. Bakermans. 2006. What is the appropriate paradigm for riparian forest conservation? *Biological Conservation* 128:193–200.
- Rodewald, A. D., and R. H. Yahner. 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82:3493–3504.
- Saunders, D. A., R. J. Hobbs, and C. R. Margules. 1991. Biological consequences of ecosystem fragmentation: a review. *Conservation Biology* 5:18–32.
- Sekercioglu, C. H., P. R. Ehrlich, G. C. Daily, D. Aygen, D. Goehring, and R. F. Sandi. 2002. Disappearance of insectivorous birds from tropical forest fragments. *Proceedings of the National Academy of Sciences USA* 99:263–267.
- Sigel, B. J., T. W. Sherry, and B. E. Young. 2006. Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. *Conservation Biology* 20:111–121.
- Sisk, T. D., N. M. Haddad, and P. R. Ehrlich. 1997. Bird assemblages in patchy woodlands: modeling the effects of edge and matrix habitats. *Ecological Applications* 7:1170–1180.
- Sodhi, N. S., L. H. Liow, and F. A. Bazzaz. 2004. Avian extinctions from tropical and subtropical forests. *Annual Review of Ecology, Evolution, and Systematics* 35:323–345.
- Space Imaging. 2002. IKONOS imagery products and product guide. Space Imaging, Thornton, Colorado, USA.
- Stouffer, P. C., C. Strong, and L. N. Naka. 2009. Twenty years of understory bird extinctions from Amazonian rain forest fragments: consistent trends and landscape-mediated dynamics. *Diversity and Distributions* 15:88–97.
- Stratford, J. A., and W. D. Robinson. 2005. Gulliver travels to the fragmented tropics: geographic variation in mechanisms of avian extinction. *Frontiers in Ecology and the Environment* 3:91–98.
- Stratford, J. A., and P. C. Stouffer. 1999. Local extinctions of terrestrial insectivorous birds in a fragmented landscape near Manaus, Brazil. *Conservation Biology* 13:1416–1423.
- Vandermeer, J., and R. Carvajal. 2001. Metapopulation dynamics and the quality of the matrix. *American Naturalist* 158:211–220.
- Van Houtan, K. S., S. L. Pimm, J. M. Halley, R. O. Bierregaard, and T. E. Lovejoy. 2007. Dispersal of Amazonian birds in continuous and fragmented forest. *Ecology Letters* 10:219–229.
- Wiens, J. A. 1989. *The ecology of bird communities*. Cambridge University Press, New York, New York, USA.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. *Analysis and management of animal populations*. Academic Press, San Diego, California, USA.
- Windsor Research Centre. 2009. Windsor Research Centre online bird banding database. (<http://www.cockpitcountry.com/Birds.php>)
- Wunderle, J. M., and R. B. Waide. 1993. Distribution of overwintering Nearctic migrants in the Bahamas and Greater Antilles. *Condor* 95:904–933.
- Zanette, L., P. Doyle, and S. M. Tremont. 2000. Food shortage in small fragments: evidence from an area-sensitive passerine. *Ecology* 81:1654–1666.

APPENDIX A

Characterization of patch-level covariates for avian landscapes in central Jamaica (*Ecological Archives* A021-083-A1).

APPENDIX B

Candidate model set (*Ecological Archives* A021-083-A2).

APPENDIX C

Model selection results (*Ecological Archives* A021-083-A3).