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Landscape matrix and species traits mediate responses of Neotropical resident birds to forest fragmentation in Jamaica

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Abstract. Land cover and land use surrounding fragmented habitat can greatly impact species persistence by altering resource availability, edge effects, or the movement of individuals throughout a landscape. Despite the potential importance of the landscape matrix, ecologists still have limited understanding of the relative effects of different types of land cover and land uses on species patterns and processes in natural systems. Here we investigated whether Neotropical resident bird communities in limestone forest patches differed if they were embedded in three different human-dominated matrix types (agriculture, peri-urban development, and bauxite mining) relative to sites in continuous forest in central Jamaica. We found that species richness, community composition, and abundances were matrix-dependent, with agricultural landscapes supporting greater avian diversity and more intact community assemblages than either peri-urban or bauxite landscapes. Abundance of almost 70% of species differed in forest embedded in the different landscape matrix types. Traits related to resource use best predicted species responses, including diet guild, nest height, habitat association, and foraging strata. Insectivores, frugivores, canopy nesters, understory and canopy foragers, and forest-restricted species rarely observed in matrix habitats had lower abundances in forest fragments embedded in human-dominated matrix types than in continuous forest. In contrast, nectarivores, omnivores, granivores, ground and multi-strata nesters, ground foragers, and species regularly in matrix habitats were least sensitive to forest fragmentation. Results suggest that structure, composition, and land use disturbance regimes in matrix areas impact overall habitat quality in landscapes by potentially mediating resource availability inside as well as outside forest habitat. This study reinforces the importance of differentiating among land cover and land uses in fragmentation research and lends support to the hypothesis that resource availability may be a primary factor driving Neotropical bird responses to fragmentation.

Key words: birds; Caribbean; community ecology; habitat fragmentation; life history traits; matrix effects; Neotropics; tropical conservation.

Introduction

In early assessments of forest fragmentation effects, landscapes were often simply dichotomized between forest (i.e., habitat) or non-forest (or non-habitat). This binary view was due in part to strong influences from island biogeography (MacArthur and Wilson 1967) and later to metapopulation theories (Hanski 1998). The drastic contrast in structure and species composition between natural forest remnants and modified non-forest habitats made this simplification seem reasonable, and many insights regarding the effects of habitat loss and isolation were gained under this landscape model (Fahrig 2003). In reality though, landscapes are complex mosaics of heterogeneous land cover types and species are affected not only by the size, shape, and spatial location of primary habitat, but also by the structure and the composition of the land cover surrounding isolated patches (termed "the matrix") (Haila 2002, Kupfer et al. 2006).

Despite the potential importance of the matrix, its effects are only beginning to be understood (Kupfer et al. 2006), and empirical data remain limited in terms of the range of matrix types, species responses, and potential mechanisms that have been examined. Most studies to date have compared species patterns (i.e., richness, community composition, or occupancy) in forest patches surrounded by intensely human-modified matrix (typically agriculture) to those found in patches surrounded by matrix types that are more similar in structure to once-contiguous forest. Specifically for bird communities, researchers have compared forest patches embedded in pasture to patches embedded in secondary forest (Laurance et al. 2002), exotic tree plantations

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(Estades and Temple 1999, Hobson and Bayne 2000, Renjifo 2001, Lindenmayer et al. 2002, Wethered and Lawes 2003), or managed forests (i.e., undergoing silviculture; Andren 1992, Aberg et al. 1995, Bayne and Hobson 1997, Norton et al. 2000). Results based on comparisons of agricultural vs. forested landscapes indicate that matrix effects on species are strongest when structural contrast to remnant habitat is high (i.e., when vegetation structure differs in physiognomy or cover). Matrix types with high structural contrast are thus predicted to be less permeable to movement and more hostile to species than those with low-contrast boundaries (e.g., Stamps et al. 1987, Forman 1995, Strayer et al. 2003). Therefore, in forested landscapes, land uses that create "open" deforested habitats, such as for agriculture or residential development, may be considered equally hostile to forest-dwelling species. This prediction, however, remains largely untested given the paucity of studies that examine the relative impacts of different types of human-modified land cover on species patterns and processes.

The most commonly studied mechanism by which matrix type affects species is its effect on inter-patch movement (i.e., dispersal hypothesis) (e.g., Ricketts 2001, Gobeil and Villard 2002, Revilla et al. 2004, Bender and Fahrig 2005). The landscape matrix, however, can mediate processes that influence species–area and isolation relationships other than dispersal (Ewers and Didham 2006, Kupfer et al. 2006). First, different matrix types may provide alternative or supplemental resources (e.g., food or nest sites) that support greater species abundances than would be expected based on amounts or quality of primary habitat alone (i.e., habitat compensation hypothesis) (e.g., Gascon et al. 1999, Norton et al. 2000, Brotons et al. 2003, Luck and Daily 2003, Cook et al. 2004). Second, the type and extent of contrast between matrix habitats and forest remnants can also mediate the magnitude of edge effects, such as nest predation and parasitism (Donovan et al. 1997, Chalfoun et al. 2002, Driscoll and Donovan 2004), or the alteration of within-patch conditions (e.g., vegetation structure, microclimate) (Saunders et al. 1991, Ries et al. 2004) (i.e., edge effects hypothesis). Third, anthropogenic land use disturbance, such as hunting, logging, noise, and burning in remaining habitat patches, may vary as a function of matrix type (i.e., disturbance hypothesis) (Hobbs 2001, Laurance and Cochrane 2001, Peres 2001). Collectively, these hypotheses outline mechanisms by which "matrix effects" may drive colonization–extinction dynamics in fragmented landscapes (e.g., Vandermeer and Carvajal 2001), with greater research attention having been focused on the former (dispersal and edge effects) rather than the latter (disturbance) hypotheses.

With few notable exceptions (e.g., Renjifo 2001, Rodewald and Yahner 2001, Rodewald and Bakermans 2006), previous empirical research has failed to identify unique impacts of the matrix in part because forest amount and spatial configuration are commonly confounded with one another and because the amount of forest is further confounded with matrix composition and associated human land uses (Rodewald 2003, Laurance 2008). Avoiding such conflation of factors is essential, because the influence due to habitat elements likely outweighs the influence of matrix elements (Goodwin and Fahrig 2002); thus, matrix effects can easily go undetected. Moreover, multiple human-modified land cover types with similar structural "edge contrast" (Strayer et al. 2003) are rarely examined in a single setting; thus, few empirical data exist to evaluate the relative impact of different human activities on fauna within forest remnants.

Here, we investigate how forest-dependent Neotropical resident birds in Jamaica respond to habitat patches in landscapes that are similar in structural habitat fragmentation but that are surrounded by different human-modified land cover types. Specifically, we examined whether species richness, community composition, or abundances of birds differed in forest fragments embedded in three dominant land use types in the Caribbean: agriculture (i.e., pasture), residential (peri-urban) development, or mining for bauxite (i.e., human-dominated matrices) relative to sites in continuous forest (i.e., natural "matrix"). We sampled forest patches in replicate human-dominated landscapes that were similar in the major components of fragmentation (i.e., forest amount and configuration) to isolate the influence of the surrounding matrix. Throughout the Caribbean (Lugo 2002, Evelyn and Camirand 2003) and in many other parts of the world (DeFries et al. 2004), land cover is increasingly being converted from agriculture to more intensive urban and extractive land uses. Despite their pervasiveness, these intensively developed matrix types have rarely been assessed to understand whether they differentially impact species existing in fragmented forest remnants.

When different landscape matrices have been examined, species responses to habitat fragmentation often appear idiosyncratic (e.g., Mac Nally 2007). Even though researchers have addressed associations between species traits and species responses to fragmentation for over 20 years (e.g., Laurance 1991, Hansen and Urban 1992, Pereira et al. 2004, Lampila et al. 2005, Sigel et al. 2006), a clear consensus has yet to emerge on which traits govern species-specific responses and why (Henle et al. 2004). Moreover, patterns detected are often contingent upon which landscape matrix types are examined (Bender et al. 1998, Debinski and Holt 2000, Ewers and Didham 2006), a factor that is not often explicitly addressed. To elucidate potential mechanistic explanations underlying species responses to forest conversion, we selected a suite of traits proposed to influence species persistence in fragmented systems (Ewers and Didham 2006). We considered phylogenetic relatedness, body size, rarity, geographic and altitudinal ranges, clutch size, nest type, nest height, diet guild, foraging strata, and habitat association. Each of these traits can affect dispersal ability, resource acquisition, and/or population growth potential (Henle et al. 2004); thus, we predicted these traits would relate to species responses to human-altered forested landscapes.

METHODS

Study area

We conducted research 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 in the premontane moist forest climatic zone (Holdridge 1967), with mean annual temperature of 26°C. Rainfall is bimodal, peaking in May/June and September/October, with 1000 mm/yr average (Jamaican Meteorological Service, *unpublished data*). The karst substrate that underlies the region yields a topographically complex landscape with numerous white limestone hills and plateaus, ranging between ~400 and 800 m elevation (Porter 1990) and separated from one another by small to moderate-sized valleys.

In pre-Columbian times, this region was covered in wet limestone forest (Asprey and Robbins 1953) composed of evergreen and semi-deciduous trees, referred to as Evergreen Season Forest formation (Beard 1944, 1955). Dominant canopy species included broadleaf (*Terminalia latifolia*), Jamaican cedar (*Cedrela odorata*), sweetwoods (*Nectandra* spp.), and bulletwoods (*Daphnopsis* spp.) (Asprey and Robbins 1953). Today, <30% of native forest remains (Evelyn and Camirand 2003), which is within the range at which the effects of fragmentation are postulated to occur (Fahrig 2003). Forest is now restricted to small hilltop remnants on limestone outcrops, surrounded by valleys cleared for three dominant land uses: agriculture (i.e., primarily cattle pasture), residential development, and mining for bauxite. The vast majority of forest fragments in this region are ≤100 ha, with only a few large forest tracts remaining along hilltop ridges. Large-scale deforestation occurred by the 18th century, largely for agricultural development (Eyre 1987*a*, *b*). Since the 1950s, land cover change in Jamaica has resulted largely from conversion of agriculture to residential development and mining for bauxite. The exact rate of ongoing deforestation in the region is unknown but is estimated to be as low as 0.1% annually for the country, with current land use change largely occurring among human-modified matrices (Evelyn and Camirand 2003). We are thus investigating the role of the matrix in a region that has undergone historic rather than contemporary forest loss and fragmentation. Locations and extent of forest fragments in this region have remained fairly stationary in recent time but are embedded within a changing matrix. This setting provided a unique opportunity to investigate the influence of matrix land cover on Neotropical birds in fragmented forests.

Site selection

We surveyed 20 1-km^2 landscapes that were typical of land cover patterns in central Jamaica: six landscapes comprising continuous forest and 14 landscapes in which forest has been fragmented by agriculture ($N = 5$), by residential (peri-urban) development ($N = 4$), or by bauxite mining ($N = 5$; Fig. 1). The 1-km^2 scale is biologically relevant given known territory sizes of forest songbirds (Robbins et al. 1989, Terborgh et al. 1990) and movement patterns for Jamaican birds (Cruz 1981, Kennedy 2009). To increase the probability that birds were independently sampled, replicate landscapes were separated by >1–26 km, with the exception of peri-urban landscapes due to logistical constraints. This distance range should be sufficient to prevent overlap in territories or daily movement of the majority of Jamaican forest birds within our sampling periods (A. M. Haynes-Sutton, *personal communication*; S. E. Koenig, *unpublished data*). We identified landscapes based on 2001–2002 IKONOS imagery, land cover maps (Forestry Department 1999), and field verification. To assess the spatial characteristics of forest habitat, we digitized forest cover from IKONOS multispectral pan-sharpened imagery (1-m resolution; Space Imaging 2002) and ground-truthing surveys using ArcGIS 9.3 (ESRI 2008). Forest habitat was categorized by a closed canopy and visual dominance of native broadleaf trees; producer's and user's accuracy for this cover type were estimated at 92% and 84%, respectively (Kennedy 2009). We selected fragmented landscapes that contained a similar proportion and spatial configuration of remnant forest, but that were dominated by only one of the three target matrix types. Human-dominated landscapes contained ~36% of forest cover and ~20 fragments that were an average of 4–6 ha. Shape complexity of forest fragments (1.3–1.4 perimeter-area fractal dimension), inter-patch distances (20–30 m), and patch connectivity (~34% of patches interconnected) were also similar among the different landscape matrix types. (Comparisons of patch- and landscape-level patterns of forest fragmentation in agricultural, peri-urban, and bauxite landscapes are detailed in Appendix A.) To serve as reference sites, we selected landscapes in the largest intact forested areas in the region (Fig. 1).

Matrix land cover composition and vegetation structure differed substantially among the three types of human-dominated landscapes. We conducted >700 vegetation surveys documenting both land cover composition and foliage structure in matrix areas (see Appendix B for full details). Agricultural landscapes were dominated by introduced pasture and herbaceous gardens (~60%), followed by tree-lined fencerows (18%), paddock trees (9%), and secondary growth of *Acacia* stands (10%) that were interspersed in valleys between forested hilltops. Peri-urban landscapes consisted mainly of low-density residential housing and roads that were surrounded by lawns (~10%), herbaceous gardens (9%), fruiting tree gardens (26%),

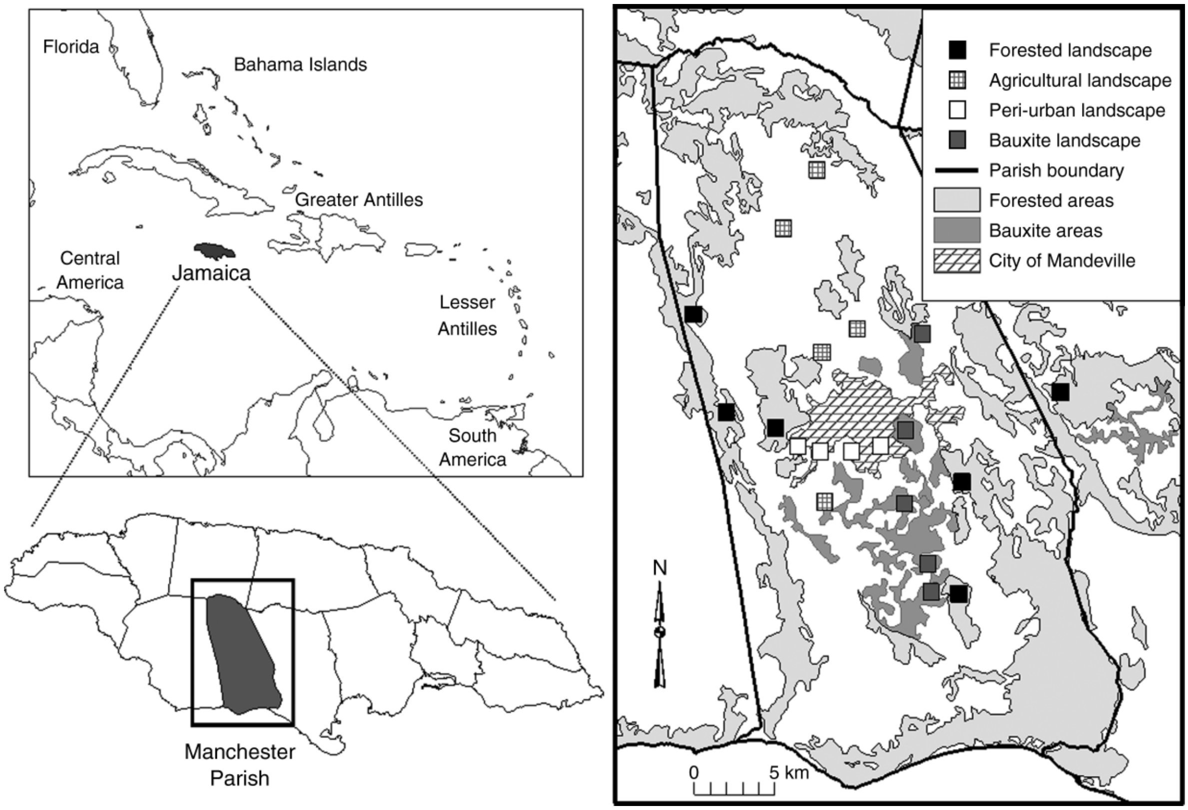


FIG. 1. Locations of the 20 1-km^2 landscapes surveyed in Manchester and Clarendon Parishes on the island of Jamaica as shown in the context of the West Indies.

ornamental shrubbery (19%), ornamental trees (12%), and mixed woodlands (11%). Bauxite landscapes were former agricultural lands that had been converted to mining within the past 10 years; relictual forests were surrounded by exposed bauxitic soils with vegetation cover dominated by planted grassland or ferns (~78%) and recent growth of *Acacia* trees (19%). Peri-urban and agricultural matrices had greater foliage cover and vertical complexity than bauxite lands, largely due to the presence of scattered trees in peri-urban areas (i.e., ornamental tree gardens, vacant woodlots) and in agricultural pasture (i.e., paddock trees, live fences, fencerows; Appendix B).

We surveyed an average of five forest fragments per replicate landscape using stratified random sampling to represent the patch size distribution. Twenty-two of these fragments were sampled in an agricultural matrix, 19 in a peri-urban matrix, and 27 in a bauxite-mining matrix. Qualitative assessment based on aerial photographs taken in 1968 indicated that sampled fragments have been in existence for at least 40 years (Evelyn 1997), although the nature of matrices may have changed within this time period. Within forested landscapes, we selected 31 "pseudo-patches" by randomly accumulating consecutive samples along transects that were located in continuous forest, such that sampled areas were approximately equal in size to patches in fragmented landscapes. We refer to both pseudo-patches sampled in a natural "matrix" and forest fragments sampled in human-modified matrices as "patches." In total, 99 forest patches were sampled across 20 landscapes.

Sampled patches also had similar forest area (3.89 ± 0.45 ha; mean ± SE) and isolation (33.58 ± 3.48 m, 160.80 ± 19.79 m, and 2381.75 ± 147.07 m to the nearest fragment >0.5 ha, 5 ha, and 100 ha, respectively; Appendix A). All patches across all landscapes were located between 400 and 800 m elevation. Even though surveyed landscapes had similar environmental conditions (e.g., elevation, climate, soil substrate), vegetation structure in forest patches differed among the four matrix types based on vegetation surveys conducted at point count stations (Appendix C). Patches in agricultural landscapes, and to a lesser extent in continuous forest, had greater stand basal area, leaf area index, tree diameter, tree canopy height, and tree cover than patches in peri-urban and bauxite landscapes. Forest fragments embedded in bauxite and peri-urban matrices had lower and relatively more open canopies and a greater proportion of herbaceous cover and low shrubs (Appendix C). We did not exclude patches where selective logging or moderate human use has occurred, because (1) all forest in the region is unprotected secondary forest that is subject to ongoing human encroachment and (2) we wanted to document bird richness and abundance patterns in landscapes undergoing disturbance that was representative of each matrix type.

Sampling of resident bird communities

We conducted point counts at 286 locations on two or three separate occasions from early February to mid-June during the height of breeding activity (Raffaele et al. 1998) each year for three consecutive breeding seasons (2005–2007). Point counts were conducted along a centrally placed transect in each of the 68 forest patches in human-dominated landscapes and along 1–3 randomly placed transects (averaging 1500 m in length) in each forested landscape. We surveyed an average of 12–15 stations per replicate landscape per occasion. We conducted sampling proportional to forest area to ensure representative coverage, typically adding one station for each additional hectare (conditional on the terrain). 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. Surveying intensity was uniform among landscapes and sufficient in representing resident bird diversity in the region based on species accumulation curves that reached definitive asymptotes in all four landscape types during the survey period (Appendix D; Gotelli and Colwell 2001).

At each point count station, we recorded the number of individuals per species seen or heard during a 10-min count (recorded in three sequential intervals: 2 min, 3 min, and 5 min) and in a 25-m fixed-radius area (Hutto et al. 1986). We selected a 25-m radius because it was found to provide the most reliable detection across sites based on field tests in our system and in the Caribbean (Wunderle and Waide 1993). We conducted surveys between 06:00 and 10:00 on clear days without rain. Each site was visited by one of three trained observers that were rotated for repeat counts within a season, and the order of site visitation was rotated throughout each field season to diminish detection bias due to observer and time-of-day effects. To investigate potential differences in species detectability among matrix types due to potential variation in noise, vegetation structure, or bird abundances in different landscape contexts (e.g., Simons et al. 2007), we modeled species detection probabilities with and without detection heterogeneity among the four matrix types based on removal method analyses (after Farnsworth et al. 2002). We found no evidence that species detection varied by matrix type as determined by model comparisons (Appendix E). Based on this finding, we had no a priori reason to suspect systematic biases in species detectability in our study; thus, we used count data as indices of bird abundance in our analyses. Detected trends based on observed point counts are expected to reflect those based on true abundances, because we implemented standardized survey protocols to control for confounding detection biases due to landscape matrix effects and those due to observer, time, or sampling effort (Johnson 2008, Etterson et al. 2009).

To determine species occurrence in and potential use of matrix habitats, we conducted 241 point counts in 2005 in matrix land cover surrounding forest patches in fragmented landscapes. Two to four point count stations were located midway between adjacent forest fragments and >100 m from a matrix–forest boundary in at least two cardinal directions. We conducted matrix point counts using similar protocol as forest point counts (i.e., 10-min count, 25-m fixed radius) during a similar time span (early March to mid-June). Matrix surveys were used to determine categorical bird–habitat associations for trait analyses.

Species traits

We considered the influence of 11 traits on bird responses to landscape matrix type. Trait values for each species were determined from published information in field guides and primary literature, consultation with ornithological experts, and personal field observations (Appendix F). We recorded species taxonomic order and derived body mass and clutch size based on averaged, published estimates. Species were classified into diet guilds based on dominant food sources consumed (i.e., frugivore, nectarivore, insectivore, omnivore, granivore, and carnivore). We categorized species foraging and nesting locations into four height zones: ground (<0.5 m), understory (shrub layer to midstory canopy, up to 5 m), canopy (upper forest layer, >5 m), or multiple strata (commonly using more than one height zone). Nest type was classified as open or closed, with the former containing large openings (i.e., cup, saucer, and platform nests) and the latter being partially enclosed (i.e., cavity, burrow, sphere, and pendant nests). Geographic range was based on whether species distributions were restricted to Jamaica, the Caribbean, the New World Tropics, or spanned both Nearctic and Neotropical regions. Altitudinal range was based on presences or absences of species distributions in three elevation classes in Jamaica: lowland, mid-elevation, and montane.

We determined species habitat associations and rarity based on our own field data. We classified species as forest-restricted, generalist, or open-associated by comparing their average densities in continuous forest to their average densities in matrix habitats. Species were classified as restricted to forest habitat if their average densities were at least three times greater in forest than in matrix areas. In contrast, species were classified as associated with open habitats if their average densities were at least three times greater in matrix areas than in continuous forest. Species with densities within a factor of three between forest and matrix habitats were classified as generalists. We chose this cutoff to ensure that species categorized as forest- and open-associated exhibited a strong affinity for their respective cover types. This admittedly arbitrary cut-off was necessary, because no standard exists in the literature to delineate habitat specificity. Our resulting classifications, however, closely matched habitat associations published in field guides (e.g., Downer and Sutton 1995, Raffaele et al. 1998) and with the opinion of ornithologists with expertise in Jamaican avifauna (P. P. Marra, A. M. Haynes-Sutton, and H. A. Davis, *personal communications*). Based on those convergences, we are confident our habitat classifications reflect potential differential forest vs. matrix usage. Rarity was based on the average density of each species in its primary habitat over the three-year sampling period (e.g., open-associated relied on average densities in matrix habitats and forest-restricted and generalist species relied on average densities in forest patches).

Statistical analyses

Community composition.—Resident native birds detected in our study region are included in analyses, with the exception of nocturnal and aquatic birds, vultures, swifts, and swallows. We used nonmetric multidimensional scaling (NMDS) to describe variation in the composition of resident bird communities in forest patches embedded in the four matrix types. Nonmetric multidimensional scaling is a nonparametric ordination technique effective for graphically depicting multivariate relationships in ecological data, via maximizing the rank correlation between calculated distances in an original matrix and distances in reduced ordination space (Clarke 1993). The NMDS was performed using a Bray-Curtis dissimilarity matrix derived from species relative abundances at the patch level, where patches were standardized by dividing species abundances by the total number of point counts conducted within each patch across all years. To avoid spurious effects of rare species, we excluded species that occurred in $<5\%$ of patches and standardized community matrices by species maximum. Overall statistical significance of the ordination was determined based on a Monte Carlo unrestricted permutation test with 100 randomizations. Standardized avian species composition was compared among matrix types using multiresponse permutation procedure (MRPP; based on Bray-Curtis distance matrix), which compares distances among samples within a priori groups from those derived from a randomization procedure (Mielke and Berry 2001, McCune and Grace 2002). To determine the importance of spatial dependence among sampled patches, we tested for the overall correlation between the standardized species community matrix with a corresponding matrix of geographic distance between patches using a Mantel test (Bray-Curtis distance matrix, $N = 9999$ randomizations; Legendre and Legendre 1998).

Species richness and individual species abundances.—The influence of the landscape matrix on species richness and individual abundances was analyzed using linear and generalized linear mixed models, respectively. Both richness and abundances were based on total point counts in each forest patch for each sampling occasion. Species richness was estimated using Chao1; this estimator adjusts for bias due to missed species as determined by the number of rare species observed within samples based on abundance data (Colwell and Coddington 1994) and has been found to be more robust than other richness estimators (Walther and Moore 2005). Based on model diagnostics (e.g., histograms and plots of residuals vs. fitted values) and dispersion scores, we modeled richness via a normal distribution and abundances via a Poisson probability distribution using a log link function.

Because sampling was conducted hierarchically (i.e., patches sampled within landscapes) and over multiple time intervals (i.e., within and across three years), we examined eight models that captured three distinct error structures that were logical based on our sample design: (1) correlations among repeat observations of a patch (temporal correlation); (2) correlations among patches within a landscape (spatial correlation); and (3) correlations among patches within a landscape across different sampling occasions (temporal and spatial correlations; Pinheiro and Bates 2002). Based on the lowest Akaike information criterion, corrected for small sample sizes ($\mathrm{AIC_c}$), and using maximum likelihood estimation (Burnham and Anderson 2002), the most supported model for species richness and for $\sim 60\%$ of the bird species accounted for within-patch correlation due to repeated measures but lacked explicit correlation among years and due to patch location. Our final models therefore included landscape matrix type as the fixed effect and patch identity as a random effect, using a Laplace likelihood approximation, which is considered more accurate for count data with small means (Bolker et al. 2009).

Significance of differences in species richness and relative bird abundances among forest patches embedded in the four matrix types was determined based on ANOVA F tests and Wald χ^2 tests, respectively. Post hoc pairwise comparisons were conducted using Tukey's multiple comparison procedure to separate treatment means (Westfall and Young 1993). We used a family-wise $\alpha = 0.10$ to indicate a biologically relevant response. Failing to detect an effect when species were in fact differing in abundance by landscape matrix type (making a Type II error) had as severe a consequence as falsely detecting an effect (making a Type I error). Therefore, using a family-wise $\alpha < 0.10$ would have led us to substantially under-predict species that were responding to forest fragmentation given stronger evidence to the contrary, which would have impeded our subsequent analyses.

Matrix response and species traits.—We categorized species into one of four response classes based on differences in relative abundance in forest patches among the human-dominated matrix types relative to a continuous forest matrix, as detected by mixed models and post hoc tests: (1) lower abundance(s) in patches embedded in one or more of the human-dominated matrix types (type L); (2) higher abundance(s) in patches embedded in one or more of the human-dominated matrix types (type H); (3) mixed-matrix response, with higher abundance in patches in at least one human-dominated matrix type and lower abundance in patches in a different human-dominated matrix type (type M); and (4) no significant difference in abundance in patches among any of the three human-dominated matrix types relative to intact forest (type N).

We used a classification decision tree analysis to assess whether species responses shared biological traits. This nonparametric method determines membership in predefined groups based on a suite of characteristics using recursive data partitioning. It is well suited for non-normal, intercorrelated, multivariate data characteristic of life history traits (De'ath and Fabricius 2000). We selected the final model based on a series of 1000 10-fold cross-validations, using the 1-SE rule and Gini index of impurity and prior probabilities proportional to sample sizes. Overall statistical significance of the final tree was determined based on Monte Carlo resampling ($N = 1000$ randomizations; Breiman et al. 1993).

We tested the relative importance of each trait with regard to species sensitivity to forest fragmentation and landscape matrix type in two ways. First, we calculated the ability of each trait to distinguish among matrix response types as determined by the decrease in impurity attributable to the best surrogate split for each variable on the final classification tree (Breiman et al. 1993). We also conducted goodness-of-fit tests to determine the statistical significance of each trait in relation to matrix response. These univariate tests complement the tree-based approach by detecting important variable(s) that may be masked in a tree-based framework (McCune and Grace 2002, Maindonald and Braun 2003). For both the classification decision tree analysis and the goodness-of-fit tests, we excluded the one species with a mixed-matrix response, because this unique response was insufficient to analyze independently. To increase the reliability of the contingency table analyses, we increased cell counts by combining the seven species with higher abundances in patches in fragmented landscapes with species that lacked an abundance response. This contrast provided a distinct comparison between birds likely to be negatively affected by forest fragmentation (i.e., exhibit lower abundances, type L) vs. those that may not (i.e., exhibit higher or constant abundances in human-dominated landscapes relative to continuous forest, types H and N). Due to multicollinearity among traits, separate tests were conducted on each trait and based on randomized χ^2 tests using Monte Carlo simulations ($N = 1\,000\,000$ randomizations), which are more accurate for sparse cell counts (Sokal and Rohlf 1995). We examined adjusted residuals from χ^2 tests to determine classes that were driving significant overall differences (Everitt 1992).

Statistical packages.—Statistical analyses were performed using the R statistical system (version 2.8.1; R Development Core Team 2008) and SAS (version 9.2; SAS Institute, Cary, North Carolina, USA). Richness (Chao1) estimation, NMDS, MRPP, and Mantel tests were performed using the R "vegan" package (version 1.13.1; Oksanen et al. 2008). Model selection for linear and generalized linear mixed models was conducted using the "nlme" (Pinheiro et al. 2008) and "lme4" (Bates et al. 2008) packages, respectively. The final linear mixed model was implemented using "nlme" and multiple comparisons performed via "multcomp" package (Hothorn et al. 2008) in R; final generalized linear mixed models were implemented using PROC GLIMMIX in SAS. The χ^2 tests were performed using "stats" package and classification regression trees using the "rpart" package in R (Therneau and Atkinson 2009).

RESULTS

Species richness and community composition

In total we detected 16 996 resident birds in forest patches among all landscapes and observed 44 resident species, of which 23 were endemic to Jamaica. Estimated richness of resident birds significantly differed in patches embedded in the four different matrix types (mixed-model ANOVA, $F_{3,95} = 6.29$ $P = 0.0006$). Based on pairwise comparisons, forest patches in an agricultural matrix had greater richness than did patches in peri-urban and bauxite matrices ($P = 0.0225$ and $P = 0.0027$, respectively). Patches embedded in a continuous-forest matrix exhibited richness greater than patches in a bauxite matrix ($P = 0.0075$) and marginally greater than patches in a peri-urban matrix ($P = 0.0595$). Avian richness did not differ in patches embedded in forest vs. agricultural matrices ($P = 0.9341$), nor did it differ between patches in peri-urban and bauxite matrices ($P = 0.9665$; Table 1).

We retained 41 of the 44 resident species detected in the community analyses based on the >5% detection rule. The NMDS ordination resulted in a three-axis solution, with a final stress of 17.702, which is within the range reliable for community data and unlikely to have been obtained by chance (Monte Carlo test, $P < 0.001$; McCune and Grace 2002). The three axes together represented 96.9% of the variance in resident bird communities, using a fit-based R^2 measure (Oksanen et al. 2008). Patches within the same matrix type tended to group together in ordination space, indicating a similarity in bird community composition (Fig. 2). Substantial overlap in patches in forest and agricultural matrices in ordination space indicated shared species assemblages. Despite these similarities, the MRPP analyses confirmed that forest bird communities differed significantly among all matrix types ($A = 0.0587$, $P < 0.0001$; Fig. 2). Differences in community assemblage among matrix types cannot be attributed to mere spatial correlation among patches (Mantel test, $r = 0.0869$, $P = 0.102$).

TABLE 1. Estimated means (and SE) of linear and generalized linear mixed models for richness and abundances of native resident birds in forest patches in agricultural ($N = 22$), peri-urban development ($N = 19$), or bauxite mining ($N = 25$) landscapes, or sites in intact forest ($N = 31$) in central Jamaica during the study period (2005–2007).

Species and response type	Forest		Agriculture		Peri-urban		Bauxite	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Species richness	26.25^{a}	1.76	27.30^{a}	1.35	21.79^{b}	1.92	20.94^{b}	1.81
Lower abundance in peri-urban and bauxite landscapes								
Arrow-headed Warbler (*Dendroica pharetra*) (e)	0.48^{a}	0.10	0.76^{a}	0.18	0.06^{b}	0.02	0.14^{b}	0.04
Jamaican Becard (*Pachyramphus niger*) (e)	0.23^{a}	0.06	0.29^{a}	0.09	0.02^{b}	0.01	0.01^{b}	0.01
Jamaican Elaenia (*Myiopagis cotta*) (e)	0.28^{a}	0.07	0.39^{a}	0.11	0.02^{b}	0.01	0.11^{c}	0.04
Jamaican Pewee (*Contopus pallidus*) (e)	0.36^{a}	0.10	0.25^{a}	0.09	0.00^{b}	0.00	0.01^{b}	0.01
Jamaican Woodpecker (*Melanerpes radiolatus*) (e)	0.67^{a}	0.11	0.68^{a}	0.14	0.31^{b}	0.07	0.22^{b}	0.05
Rufous-tailed Flycatcher (*Myiarchus validus*) (e)	0.28^{a}	0.07	0.36^{a}	0.10	0.05^{b}	0.02	0.04^{b}	0.02
Lower abundance in peri-urban landscapes								
Greater Antillean Bullfinch (*Loxigilla violacea*)	1.04^{a}	0.15	1.12^{a}	0.19	0.61^{b}	0.12	0.95^{ab}	0.15
Jamaican Lizard-Cuckoo (*Saurothera vetula*) (e)	0.06^{a}	0.03	0.04^{ab}	0.02	0.00^{b}	0.00	0.03^{ab}	0.02
Jamaican Vireo (*Vireo modestus*) (e)	1.41^{a}	0.22	1.49^{a}	0.28	0.45^{b}	0.10	0.84^{ab}	0.16
Olive-throated Parakeet (*Aratinga nana*)	0.15^{a}	0.05	0.13^{a}	0.06	0.02^{b}	0.01	0.14^{a}	0.06
White-crowned Pigeon (*Columba leucocephala*)	0.68^{a}	0.12	0.83^{a}	0.17	0.28^{b}	0.07	0.60^{a}	0.12
Yellow-shouldered Grassquit (*Loxipasser anoxanthus*) (e)	0.34^{a}	0.06	0.26^{a}	0.06	0.09^{b}	0.03	0.42^{a}	0.09
Lower abundance in bauxite landscapes								
Black-faced Grassquit (*Tiaris bicolor*)	0.13^{ab}	0.04	0.06^{bc}	0.02	0.25^{a}	0.06	0.019^{c}	0.01
Higher abundance in agricultural and bauxite landscapes								
Loggerhead Kingbird (*Tyrannus caudifasciatus*)	0.19^{b}	0.04	0.46^{a}	0.10	0.30^{ab}	0.07	0.44^{a}	0.09
Higher abundance in peri-urban and bauxite landscapes								
Smooth-billed Ani (*Crotophaga ani*)	0.00^{b}	0.00	0.03^{ab}	0.02	0.05^{a}	0.03	0.05^{a}	0.03
Higher abundance in agricultural landscapes								
Jamaican Spindalis (*Spindalis nigricephala*)† (e)	0.68^{b}	0.13	1.33^{a}	0.27	0.64^{b}	0.14	0.54^{b}	0.11
Jamaican Oriole (*Icterus leucopteryx*)	0.57^{b}	0.08	0.99^{a}	0.14	0.55^{b}	0.09	0.75^{ab}	0.11
White-bellied Dove (*Leptotila jamaicensis*)	0.13^{b}	0.03	0.36^{a}	0.08	0.14^{b}	0.04	0.26^{ab}	0.06
White-winged Dove (*Zenaida asiatica*)	0.03^{b}	0.01	0.22^{a}	0.07	0.04^{b}	0.02	0.06^{b}	0.03
Higher abundance in peri-urban landscapes								
Vervain Hummingbird (*Mellisuga minima*)	0.15^{b}	0.04	0.21^{ab}	0.06	0.37^{a}	0.10	0.15^{b}	0.04
Higher abundance in agricultural and lower abundance in bauxite landscapes								
White-eyed Thrush (*Turdus jamaicensis*) (e)	0.29^{b}	0.07	0.72^{a}	0.19	0.12^{bc}	0.04	0.06^{c}	0.03
No difference in abundance in human-dominated landscapes than intact forest								
Bananaquit (*Coereba flaveola*)	2.28	0.28	2.39	0.35	2.19	0.34	2.12	0.29
Chestnut-bellied Cuckoo (*Hyetornis pluvialis*) (e)	0.12	0.03	0.09	0.03	0.13	0.04	0.06	0.02
Common Ground-Dove (*Columbina passerina*)	0.08	0.03	0.06	0.03	0.06	0.03	0.05	0.02
Jamaican Euphonia (*Euphonia jamaica*) (e)	0.54	0.10	0.75	0.16	0.47	0.11	0.52	0.11
Jamaican Mango (*Anthracothorax mango*) (e)	0.02	0.01	0.06	0.03	0.01	0.01	0.04	0.02
Jamaican Tody (*Todus todus*) (e)	0.92	0.13	1.25	0.21	1.08	0.19	0.84	0.14
Mangrove Cuckoo (*Coccyzus minor*)	0.04^{ab}	0.02	0.03^{ab}	0.02	0.00^{b}	0.00	0.07^{a}	0.03
Northern Mockingbird (*Mimus polyglottos*)	0.01	0.01	0.03	0.02	0.06	0.03	0.05	0.02
Orangequit (*Euneornis campestris*) (e)	2.63^{ab}	0.31	3.33^{a}	0.46	2.27^{ab}	0.34	2.08^{b}	0.28
Red-billed Streamertail (*Trochilus polytmus*) (e)	1.65	0.23	2.18	0.35	1.82	0.31	1.74	0.26
Ruddy Quail Dove (*Geotrygon montana*)	0.15^{ab}	0.05	0.32^{a}	0.10	0.07^{b}	0.03	0.12^{ab}	0.04
Sad Flycatcher (*Myiarchus barbirostris*) (e)	0.26^{ab}	0.05	0.48^{a}	0.10	0.17^{b}	0.04	0.14^{b}	0.04
White-chinned Thrush (*Turdus aurantius*) (e)	0.99	0.12	1.26	0.18	1.34	0.19	1.41	0.18
Yellow-faced Grassquit (*Tiaris olivacea*)	0.11	0.03	0.08	0.03	0.09	0.03	0.15	0.05
Zenaida Dove (*Zenaida aurita*)	0.08	0.02	0.19	0.06	0.12	0.04	0.17	0.05

Notes: P values are based on ANOVA F tests and Wald χ^2 tests (values in boldface are significant at $P < 0.05$). Superscripted lowercase letters indicate results of pairwise comparisons among matrix types based on post hoc Tukey's honestly significant difference (hsd) tests. Species are categorized based on abundance differences among human-dominated matrix types relative to intact forest. Species included in community analyses but with insufficient detections for Poisson mixed models were: American Kestrel (*Falco sparverius*), Jamaican Crow (*Corvus jamaicensis*) (e), Red-tailed Hawk (*Buteo jamaicensis*), Rufous-throated Solitaire (*Myadestes genibarbis*), and Stolid Flycatcher (*Myiarchus stolidus*). Species detected in the study region, but with insufficient detections to include in any analyses were: Crested Quail Dove (*Geotrygon versicolor*) (e); Yellow-billed Parrot (*Amazona collaria*) (e); and Greater Antillean Grackle (*Quiscalus niger*). "(e)" Indicates species endemic to Jamaica. Primary diet guild abbreviations are: C, carnivore; F, frugivore; G, granivore; I, insectivore; N, nectarivore; O, omnivore. Primary habitat association abbreviations are: FR, forest-restricted; G, generalist; OA, open-associated. Primary nesting height or foraging strata abbreviations are: G, ground; U, understory; C, canopy; M, multiple strata.

† Previously named Jamaican Stripe-headed Tanager (*Spindalis nigricephalus*) (Banks et al. 2000).

Table 1. Extended.

P	Diet	Habitat association	Nest height	Foraging strata
0.0006				
<0.0001	I	FR	U	M
<0.0001	I	FR	C	C
<0.0001	I	FR	C	C
0.0001	I	FR	C	U
0.0001	I	G	C	M
<0.0001	I	FR	C	C
0.0834	F	FR	M	U
0.0482	C	FR	U	U
0.0001	I	FR	U	U
0.0294	F	G	C	M
0.0074	F	FR	M	C
0.0008	F	G	U	U
0.0001	G	OA	U	G
0.0100	O	OA	M	M
0.0455	O	OA	M	G
0.0125	F	G	U	C
0.0188	I	G	U	M
0.0093	G	G	G	G
0.0004	G	OA	U	G
0.0616	N	G	U	U
<0.0001	O	FR	M	M
0.9382	N	G	M	M
0.2974	C	G	M	M
0.7754	G	G	U	G
0.4265	F	G	M	C
0.1648	N	OA	C	U
0.3179	I	FR	G	M
0.0408	C	FR	U	U
0.2325	O	OA	M	G
0.0857	N	FR	NA	M
0.6130	N	G	U	M
0.0275	G	FR	G	G
0.0007	I	G	U	U
0.1974	O	G	M	G
0.5329	G	OA	G	G
0.1446	G	OA	M	G

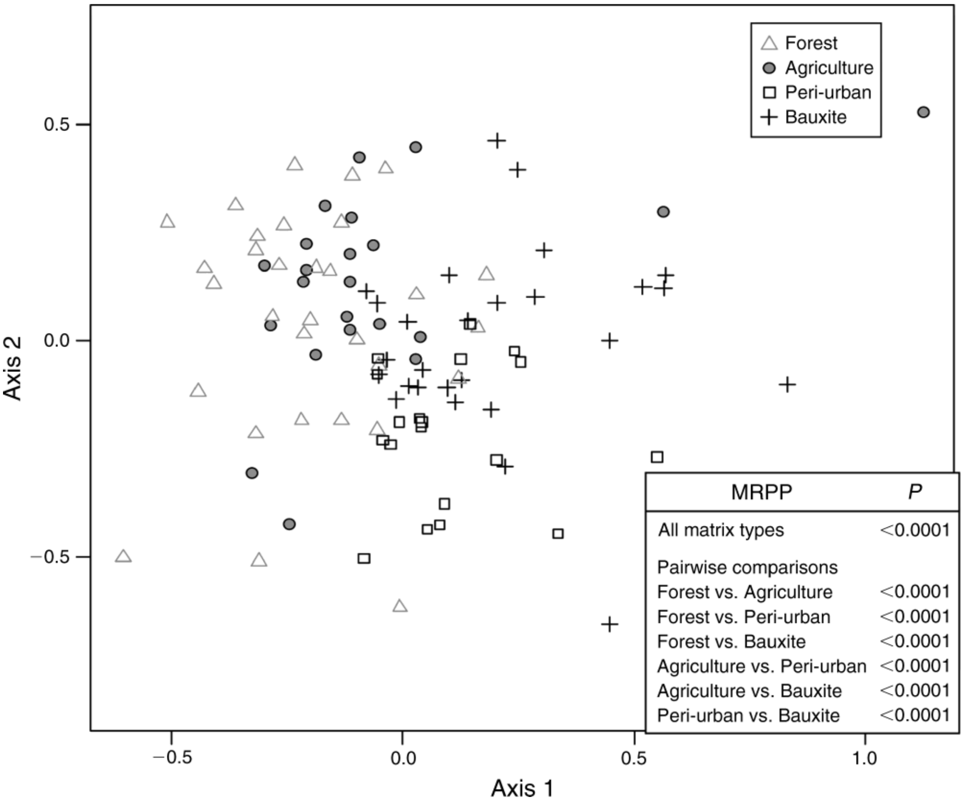
Individual species responses

Thirty-six species that were detected in >15% of patches had sufficient occurrences to model via Poisson regressions (i.e., likelihood functions converged with reliable model fit and parameter estimates). Relative abundances of 69.4% of these species differed significantly in forest patches among the four matrix types, which is greater than would be expected by chance (binomial test, $P = 0.014$). Thirteen species had lower abundances in one or two of the human-dominated matrix types (agriculture, peri-urban, and/or bauxite; Table 1). Six of these species had abundances that were lower in forest fragments in peri-urban and bauxite matrices relative to a forest matrix, but their abundances in fragments in an agricultural matrix were similar to that in an intact forest. Seven species had reduced abundances in only one human-dominated matrix type; for all but one of these species, abundances were lowest in peri-urban forest fragments. The Black-faced Grassquit was the exception, being least abundant in fragments in a bauxite matrix, but equally as abundant in fragments embedded in a peri-urban matrix as in a forest matrix (Table 1). No species was consistently lower in abundance in fragments in all three human-dominated matrix types. Two species, however, showed patterns suggesting this response, but were too scarce for statistical analyses: 87% of 15 Stolid Flycatcher detections were in continuous forest and all eight Rufous-throated Solitaire detections were in continuous forest.

No species exhibited abundances that were consistently higher in forest fragments in all three human-dominated matrix types, but seven species were higher in abundance in one or two of the human-dominated matrix types relative to continuous forest. Of these species, five were higher in abundance in fragments in an agricultural matrix but lower in abundance in fragments in peri-urban and bauxite matrices. Two species were more abundant in two types of human-dominated landscapes relative to continuous forest: the Loggerhead Kingbird was higher in abundance in forest embedded in both agriculture and bauxite and the Smooth-billed Ani was higher in abundance in forest embedded in both bauxite and peri-urban development. Only one species, the Vervain Hummingbird, was more abundant in forest patches in a peri-urban matrix than in all other matrix types.

The White-eyed Thrush was the only species that exhibited a mixed matrix response, with abundances higher in agricultural patches but lower in bauxite patches. The remaining 15 species did not differ in abundance in forest patches in human-dominated matrices relative to a forest matrix. Four of these species, however, had abundances that varied among the three types of human-dominated landscapes.

Overall, peri-urban and bauxite landscapes had the highest frequency of resident species with reduced abundances relative to continuous forest: eight species were lower in abundance in bauxite patches and 12 species were lower in abundance in peri-urban patches (Fig. 3). No species was less abundant in patches in agricultural landscapes relative to forested landscapes. Six species were more abundant in forest patches in an agricultural matrix whereas only three species were more abundant in patches in bauxite and/or peri-urban matrices relative to a forest matrix.



MRPP	*P*
All matrix types	<0.0001
Pairwise comparisons	
Forest vs. Agriculture	<0.0001
Forest vs. Peri-urban	<0.0001
Forest vs. Bauxite	<0.0001
Agriculture vs. Peri-urban	<0.0001
Agriculture vs. Bauxite	<0.0001
Peri-urban vs. Bauxite	<0.0001

FIG. 2. Nonmetric multidimensional scaling (NMDS) ordination (stress = 17.0170) of resident bird communities in 99 forest patches in four landscape matrix types over the study period (2005–2007). For illustration purposes NMDS axis 1 and axis 2 (of a three-dimensional solution) are presented, which capture most of the variation in community structure and depict the overall pattern. Dimensions represent the relative position among sampled patches based on species assemblages, with patches with similar avian composition containing similar scores in multidimensional space. Community composition among the four matrix types significantly differed (based on familywise $\alpha = 0.05$) based on overall and pairwise comparisons based on multiresponse permutation procedure (MRPP) results (inset).

Role of species traits

The most parsimonious classification tree model (with the greatest prediction accuracy) included only 1 of 11 traits (diet guild) and predicted two matrix response types. Of observed bird responses to landscape matrix, 66% were correctly classified based on diet guild alone, which is greater than expected by chance (Monte Carlo simulation, $P = 0.0079$; Fig. 4). The model correctly classified 84.6% of species with observed lower abundances (type L), and 80.0% with observed similar abundances in patches in human-dominated matrices compared to a forest matrix (type N). Misclassifications largely stemmed from the erroneous categorization of the seven species with higher abundances in fragmented landscapes (type H). Five of these species were incorrectly predicted to have no difference in abundance (i.e., misclassified as type N) and two of these species were incorrectly predicted to have lower abundances in fragmented forest relative to continuous forest (i.e., misclassified as type L).

Based on both variable importance from the decision tree analysis and statistical significance from χ^2 tests, diet guild, nest height, habitat association, and, to a lesser extent, foraging strata were strongly associated with bird responses to landscape matrix (Table 2). Taxonomic order, geographic and altitudinal range, body size, rarity, clutch size, and nest type had weak prediction power and lacked any statistical association.

Diet guild.—A total of 70% of insectivores and 67% of frugivores had lower abundances in patches in human-dominated matrices than a forest matrix. In contrast, 100% of nectarivores and omnivores and 86% of granivores had higher or similar abundances in fragments (Figs. 4 and 5a). Carnivores lacked a consistent response, with the Jamaican Lizard-Cuckoo exhibiting lower abundances and the Chestnut-bellied Cuckoo and the Mangrove Cuckoo exhibiting similar abundances between human-dominated and forested landscapes.

Habitat association.—The extent to which a species was known to be a forest specialist rather than to use matrix habitats impacted its response to fragmentation. Forest-restricted species exhibited the greatest reductions in abundance, with 70% lower, 30% similar, and none higher in abundance in forest patches in human-dominated matrices than in a forest matrix (Fig. 5b). In

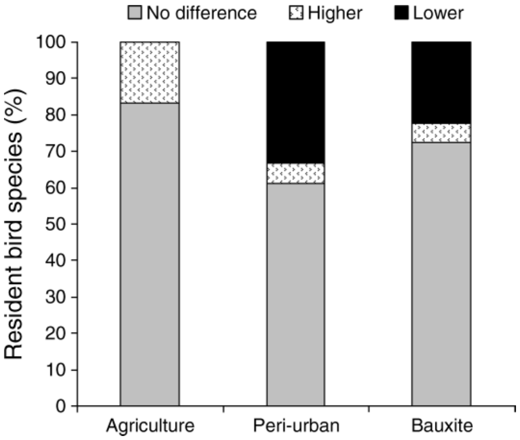


FIG. 3. Percentages of resident bird species in agricultural, peri-urban, or bauxite mining landscapes that exhibited significantly lower abundance, higher abundance, or no abundance difference relative to forested landscapes over the study period ($N = 36$ species).

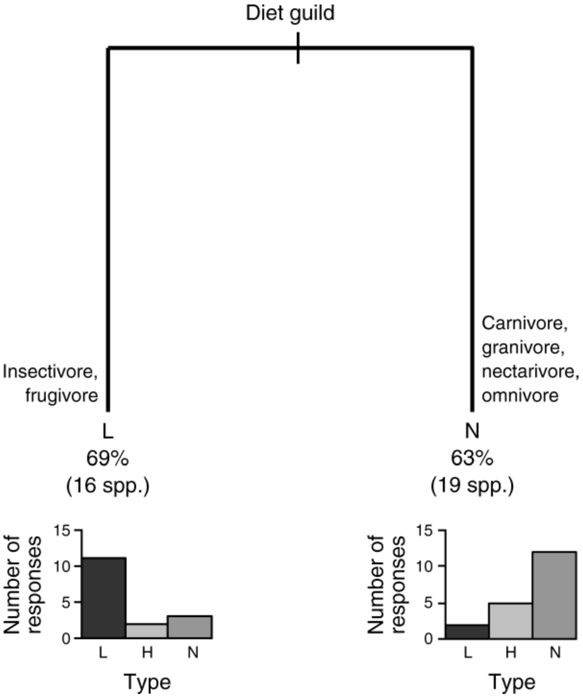


FIG. 4. Predicted response type, percentage of observations correctly classified per response type, the number of species (in parentheses), and the distribution of the observed bird responses per group based on classification tree analysis of bird responses to the landscape matrix in relation to 11 traits. Species responses were categorized as: (1) type L, lower in abundance in any of the human-dominated matrix type(s) relative to intact forest; (2) type H, higher in abundance in any of the human-dominated matrix type(s) relative to intact forest; and (3) type N, no difference in abundance in fragmented landscapes relative to intact forest. Diet guild was the only trait retained in the final model, with two matrix types predicted (type L and type N) (with 34% misclassification rate).

TABLE 2. The strength of association among the 11 traits with landscape matrix responses by resident birds in central Jamaica.

Trait	Variable importance	*P*
Diet guild	100.00	**0.0105**
Nest height	72.93	**0.0113**
Habitat association	67.57	**0.0092**
Foraging strata	45.12	
Taxonomic order	30.45	0.2135
Geographic range	28.93	0.3944
Rarity†	25.54	0.4888
Nest type‡	19.29	0.1566
Clutch size§	18.26	0.1621
Altitudinal range	8.46	0.2639
Body mass¶	2.61	0.7461

Notes: Variable importance was determined by calculating the change in impurity (i.e., Gini index) when a trait was substituted for the original variable on the final decision tree (i.e., diet) and is expressed as the relative magnitude of the total decrease in impurity (based on normalized quantiles). The variable with the greatest prediction accuracy is attributed the highest value (100), and the variable with the lowest prediction accuracy is attributed the lowest value (0). *P* values from randomized χ^2 tests are provided; values in boldface are significant at $P < 0.05$.

† Variable importance was based on continuous distribution; χ^2 test was based on classified groups (<0.25 and >0.25 density).

‡ One bird with unknown nest height was excluded from the χ^2 test.

§ Variable importance was based on continuous distribution; χ^2 test was based on classified groups (<3 and >3 eggs).

¶ Variable importance was based on continuous distribution; χ^2 test was based on classified groups (<15, 15–50, and >50 g).

contrast, ~90% of birds associated with open habitats and ~80% of generalist birds had greater (38% and 29%, respectively) or equal abundances (50% each) in fragments as compared to continuous forest.

Nest height.—The dominant height at which a species nested also impacted its fragmentation response. Eighty-six percent of canopy-nesting species were less abundant and 14% were equally abundant in forest patches in human-dominated matrices relative to a forest matrix (Fig. 5c). In contrast, 100% of ground-nesting species either had similar abundances (75%) or had higher abundances (25%) and 80% of multi-strata nesters had similar or higher abundances in patches in human-dominated matrices (60% and 20%, respectively) than in a forest matrix. Understory nesters failed to exhibit a consistent response, with roughly one-third of species with higher (31%), lower (38%), or equal abundances (31%) in patches in human-dominated landscapes relative to intact forest.

Foraging strata.—Canopy foragers and, to a lesser extent, understory foragers had lower abundances in fragmented landscapes than did ground foragers (Fig. 5d). Two-thirds of canopy foragers were lower in abundance in fragments, whereas 17% were higher and another 17% were equal in abundance in fragments as in intact forest. Abundances were lower for 56% of understory foragers, equal for 33%, and higher for only 11% (one species) in patches in human-dominated

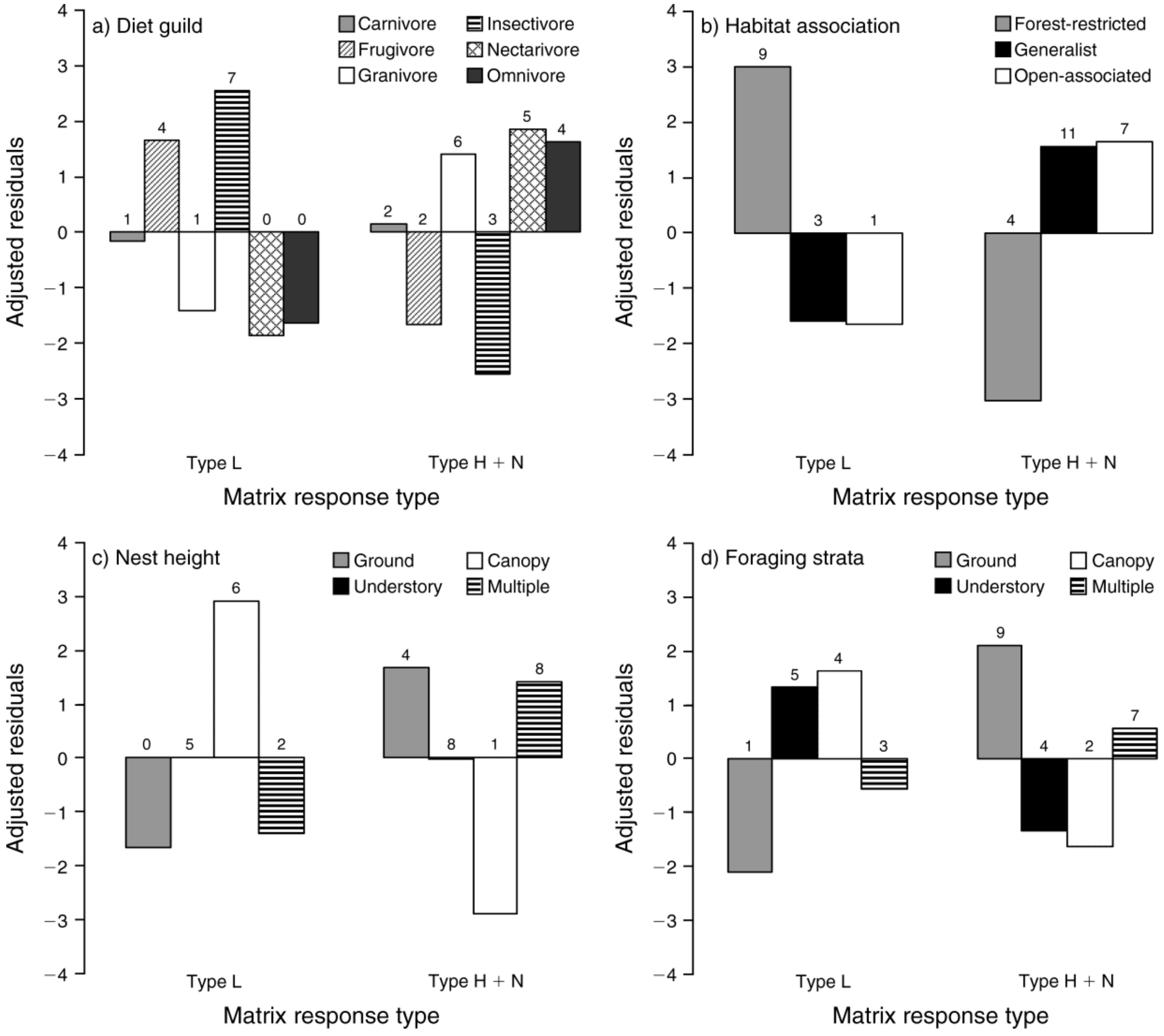


FIG. 5. Adjusted residuals of the χ^2 analyses relating the number of resident bird species exhibiting two matrix responses types to (a) diet guild, (b) habitat association, (c) nest height, and (d) foraging strata. The two response types were classified as (1) type L, lower in abundance in any of the human-dominated matrix type(s) relative to intact forest, and (2) type H + N, higher in abundance or similar in abundance among human-dominated landscapes relative to intact forest. The number above each bar represents the number of species observed to exhibit the respective response type and trait class combination. Adjusted residuals with the largest absolute values indicate the class driving overall significant differences among matrix responses and the trait in question.

matrices than in a forest matrix. In contrast, all but one ground-foraging species had greater (30%) or similar (60%) abundances in human-dominated landscapes as compared to forested landscapes. Species that foraged among multiple strata failed to exhibit a strong response, with 20% higher, 30% lower, and 50% exhibiting no change in abundance among fragmented vs. forested landscapes.

DISCUSSION

Ostensibly, landscapes in Jamaica would seem to adhere to the classic binary habitat vs. non-habitat model in that historically forested areas have been converted to similar matrix types comprising novel habitats with relatively little or no forest cover. This study demonstrates, however, that simplistic models of habitat fragmentation do not adequately reflect responses of Neotropical bird communities in this region. Suites of species were profoundly affected by whether once-continuous forest was converted to agricultural, peri-urban, or bauxite mining development. Almost 70% of bird species differed in abundance in patches among the four landscape matrix types. More than 36% of species had lower abundances in forest fragments embedded in peri-urban and bauxite mining matrices relative to a forested matrix. Another 20% had higher abundances in fragments embedded in an agricultural matrix than in a forest matrix. Overall, no species was consistently more or less abundant in all human-dominated landscape types. Species richness and community composition behaved similarly to species abundances, with an agricultural matrix having little effect on richness (Table 1) and community composition (Fig. 2) relative to a forest matrix; but peri-urban and bauxite matrix types had substantial impacts on both multispecies response metrics. The agricultural matrix had seemingly little effect even on forest-restricted species and some generalist species, and species associated with open habitats actually increased in this landscape type. In contrast, peri-urban and mined landscapes had lower native resident bird diversity and had communities that were strikingly different from those in forested landscapes, in that many insectivores and frugivores were absent or less abundant. Different measures of species responses (i.e., richness, community composition, and abundances) thus provided convergent results, which strengthens the reliability of these patterns. Moreover, matrix-specific responses were detected despite similar climate, geology, elevation, and forest type and despite controlling for the amount and configuration of forest cover among anthropogenically fragmented landscapes.

Role of species traits and possible mechanisms mediating responses to forest fragmentation

Four proximate mechanisms have been proposed to explain divergent species responses to forest fragmentation as a function of the composition and the configuration of matrix land cover: (1) differential impedance or facilitation of inter-patch movement (e.g., Renjifo 2001, Ricketts 2001, Gobeil and Villard 2002, Revilla et al. 2004, Bender and Fahrig 2005); (2) differential alteration of interspecific interactions, in particular predation (Rodewald and Yahner 2001, Chalfoun et al. 2002); and differential mediation of resources either (3) by habitat compensation via the addition of alternative or supplemental resources (e.g., food or nesting sites) in certain matrix areas (e.g., Gascon et al. 1999, Norton et al. 2000, Brotons et al. 2003, Cook et al. 2004) or (4) by the disparate reduction of within-patch habitat quality (i.e., microclimate and vegetation structure) due to dissimilar edge effects (Saunders et al. 1991, Ries et al. 2004) or different human disturbances (Friesen et al. 1995, Rodewald and Bakermans 2006).

Collectively, our results are consistent with the hypothesis that resource availability may be the important driver of bird community changes in Jamaica's fragmented landscapes. Although we cannot tie any single trait to a particular mechanistic explanation, in part because of the correlational nature of our data, several traits emerged as significant and in combination support resource availability as an important mechanism. Diet guild, habitat association, nest height, and foraging stratum best predicted the variation in bird responses to forest fragmentation across matrix types. These four traits relate to a species ability to acquire and use resources, including food and nest sites, in human-dominated landscapes. In particular, Jamaica's insectivorous birds had lower abundances in fragmented landscapes relative to other guilds, which is consistent with growing evidence that insectivores are declining disproportionately in tropical forest remnants (e.g., Castelletta et al. 2000, Ribon et al. 2003, Sodhi et al. 2004, Sigel et al. 2006, Stouffer et al. 2009). Such declines are thought to be potentially due to the interdependent effects of the loss of microhabitats and the decline of prey availability (e.g., Burke and Nol 1998, Zanette et al. 2000). Agricultural landscapes supported a greater number of insectivores, which could be a consequence of forest fragments in these landscapes providing greater foraging substrates due to their greater leaf area indices (Appendix C). Frugivores were also less abundant in human-dominated landscapes in the region. As with insectivores, survival of frugivorous birds has been found to be lower in other fragmented tropical forests (Kattan et al. 1994, Ribon et al. 2003, Ruiz-Gutierrez et al. 2008), potentially due to lack of year-round fruit in deforested tropical areas (Sodhi et al. 2004). Understory and canopy foragers and canopy nesters also had lower abundances, which may be due to the reduction in the vertical complexity of forest structure and the loss of canopy and emergent trees in peri-urban and bauxite mining landscapes (Appendix C), an effect that has also been shown to accompany tropical forest fragmentation (Tabarelli et al. 2004). In contrast, Jamaican nectarivores, omnivores, and granivores were insensitive to fragmentation, particularly in agricultural matrices. Edge- and matrix-foraging birds are increasingly shown to persist and even thrive in fragmented tropical systems (e.g., Stouffer and Bierregaard 1995, Renjifo 1999, Sigel et al. 2006) due to potential cross-boundary subsidies (Fagan et al. 1999, Cantrell et al. 2001). A species tolerance of forest conversion is increasingly linked to its ability to utilize resources in matrix habitats (e.g., Laurance 1991, Gascon et al. 1999, Henle et al. 2004).

In contrast to many studies that indicate matrix effects are best explained by dispersal or movement limitation in temperate (e.g., Ricketts 2001, Bélisle and Clair 2002, Gobeil and Villard 2002) and tropical regions (e.g., Robinson 1999, Renjifo 2001, Laurance et al. 2002, Sekercioglu et al. 2002, Stratford and Robinson 2005), we found that traits linked to dispersal abilities were not associated with species–matrix responses. Body size and taxonomic order, which tend to correlate significantly with potential dispersal power of birds (Sutherland et al. 2000), did not emerge as important predictors. Geographic and altitudinal range sizes, which relate in part to species dispersal and establishment abilities (Gaston 1996), also failed to predict landscape matrix responses. Moreover, frugivores had disproportionately lower abundances in forest remnants than in intact forest; but we would not predict that these species would be dispersal limited due to their adaptations to search for resources that are patchily distributed in both space and time (Bowler and Benton

2005). The karst countryside in central Jamaica is characterized by small forested hilltops, often <10 ha in size, which are separated by other land uses but remain in close proximity (e.g., hundreds of meters apart) relative to potential bird dispersal. Such small distances between forest patches may not prohibit frequent movement of many bird species. Moreover, the evolutionary history of Caribbean avifauna has likely promoted selection of species with stronger dispersal abilities and fewer physiological or morphological limitations than mainland counterparts; these characteristics have allowed them to (re)colonize and (re)establish in island habitats and to withstand large-scale natural disturbance events such as hurricanes (Lack 1976, Ricklefs and Bermingham 2008).

Other frequently 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, Chalfoun et al. 2002, Driscoll and Donovan 2004). Traits such as nest type and nest height may affect a species susceptibility to nest predation, with open- and ground-nesting species found to be at greater risk (Ford et al. 2001, Chalfoun et al. 2002, Lampila et al. 2005, but see Martin 1993). In Jamaica, however, abundance differences between fragmented and intact forest were not related to nest type. Moreover, species predicted to be most sensitive to nest predation (ground nesters) were least likely to exhibit lower abundances and species predicted to be least sensitive to nest predation (canopy nesters) were more likely to exhibit lower abundances in human-dominated landscapes. Traits related to reproductive potential (i.e., rarity and clutch size) also failed to predict bird abundance patterns. Thus, differential functional connectivity (i.e., via altering species dispersal and recolonization events) and differential population growth potential (i.e., via population sinks due to higher predation) do not appear to be dominant mechanisms underlying bird responses to forest fragmentation in Jamaica.

Impacts of matrix land cover and land use interact with forest fragmentation effects

We propose that birds in Jamaica may be influenced more by the extent to which the landscape matrix mediates the availability of critical resources, either via resource supplementation in matrix habitats or differential reduction of within-patch forest resources or some combination of both. In many cases, matrix habitats may be hospitable for native species and may provide supplemental or additional resources that allow for population maintenance or growth in fragmented systems (Norton et al. 2000, Brotons et al. 2003, Cook et al. 2004). In comparison to bauxite lands, peri-urban and agricultural matrices contained greater vegetation cover and complexity (Appendix B). Vegetation in agricultural matrices (e.g., pasture, paddock trees, and live fences) may have provided additional resources for omnivores and granivores, which were more abundant in these landscapes than in other matrix types. Similarly, nectarivores may have benefited from residential gardens, given these birds were equally or more abundant in peri-urban landscapes than in the other human-modified landscapes.

Beyond these obvious modifications to external matrix habitats, landscape matrix type can also impact internal forest conditions. For example, surface-mining activities in bauxite areas involve large-scale removal of vegetation and topsoil and the creation of open pits of exposed earth, all of 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 impact within-forest microclimate and structure and can alter the composition of fauna, but the degree and direction of these changes are largely unknown (Simmons et al. 2008). Even after post-mining restoration, ecological communities may not fully recover to their original state (Parrotta and Knowles 1999, 2001). Bird species in peri-urban landscapes may be disproportionately affected by forest disturbance from human activities (e.g., hunting, selective logging, noise, spread of fire or invasives; e.g., Theobald et al. 1997, Marzluff et al. 2001, Miller et al. 2003, Rodewald and Bakermans 2006). Forest remnants in bauxite and peri-urban matrices have low stature and more open canopies, less structural complexity, and greater percentage of shrub layer (Appendix C); these factors indicate that these forests may have undergone greater disturbance and/or be in earlier successional stages than forests in agricultural matrices (Asprey and Robbins 1953). Agricultural areas tend to be in large private land holdings, which afford a greater level of forest protection than commonly found in bauxite and peri-urban areas.

Even though the landscapes we surveyed had similar environmental conditions, vegetation structure differed in remnant forests as a function of matrix land cover, potentially due to associated land use practices in matrix areas. Rarely will alterations to the surrounding landscape proceed without associated changes to the internal habitat (Laurance et al. 2002, Laurance 2008). Thus, effects on forest conditions must be considered part of the collective matrix effects in Jamaica. Avian community structure could be driven as much by the degree of disturbance to the internal properties of remnant forest as by the external properties of the matrix.

Data limitations, research needs, and other caveats

Several factors must be considered when interpreting our results. First, several species were detected in low abundance and with low probability (Appendix E), which increases uncertainty about whether species patterns are robust or will remain consistent over the long term. Second, we may have failed to detect relationships between species traits and their responses to matrix type due to the limited ways in which we were able to categorize their life history attributes. There is a general lack of biological data for many Jamaican bird species; additional research on foraging, nesting, and movement patterns must be completed before more refined considerations of species traits are possible. We relied in part on information provided in field guides (Appendix F), because this level of detail is often all that is available to researchers when determining trait specificities. Even under the best circumstances, traits are surrogates for actual mechanistic responses that are best tested experimentally. Measures of reproductive output, survival, and movement for species in a range of habitats in different landscape contexts are ideally needed to isolate mechanistic explanations. Such detailed investigations, however, are rarely possible for even the best-studied species, much less entire communities. Thus, examining surrogates such as traits that help inform mechanistic explanations behind why groups of species respond similarly to landscape change can be informative first steps (Ewers and Didham 2006), particularly in poorly studied regions such as the tropics.

Historic declines and temporal differences among land uses must also be considered. Examination of current-day abundance patterns may underestimate the effects of forest fragmentation on species persistence in regions such as the West Indies, where flora and fauna have been altered by a long history of habitat conversion, human disturbance, and introductions of novel predators (e.g., rats, mongoose; Ricklefs and Bermingham 2008). Abundance patterns detected in Jamaica's fragmented landscapes may be underestimates, given that the reference baseline is itself unprotected secondary forest that has been altered by decades of selective logging, fuelwood collection, and human-caused fire (Forestry Department 2001, Tole 2001). Moreover, the full extent of species responses may not have been captured uniformly among landscapes due to the temporal differences among land use practices. Bauxite matrices were more recently converted (<10 years); therefore, their full impacts may not be fully manifested. Future research in this system, and elsewhere, should specifically address the temporal effects of land use practices and the relative importance of extinction vs. colonization processes on species long-term persistence.

Conservation implications

Treating all anthropogenically modified lands as a single cover type (i.e., non-habitat) in fragmentation research and/or conservation planning has consequences for biodiversity. All matrix types examined in our study could be classified as having similar "edge contrast" (Strayer et al. 2003) in that they differed dramatically in structure, composition, and microclimate from once-contiguous native forest. Consequently, matrix areas could be considered equally hostile to native species. Bird communities, however, responded differently to the three human-modified matrix types. Patches surrounded by an agricultural matrix maintained greater native bird diversity and more intact community assemblages than did patches embedded in a peri-urban or a bauxite mining matrix. Treating all modified lands equally and categorizing Jamaica's landscapes into "matrix" vs. "forest" components would have hidden these important patterns. The trajectory of land conversion in many regions of the world is from subsistence agriculture to increasing urbanization (DeFries et al. 2004). Since the 1950s, land cover change in Jamaica (Evelyn and Camirand 2003) and on other Caribbean islands (Lugo 2002) results largely from conversion of agriculture to residential development and mining for bauxite. Our study strongly suggests that such land conversion would cause the loss of a large proportion of the Neotropical bird community, even without additional forest loss or isolation. Although we have not experimentally confirmed the mechanism, evidence suggests that human land use practices in the matrix may be driving differential abundance patterns via mediating resource availability both within the forest and in external matrix habitats.

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APPENDIX A

Forest fragmentation pattern among human-dominated landscape types (*Ecological Archives* M080-023-A1).

APPENDIX B

Habitat structure within human-dominated matrices (*Ecological Archives* M080-023-A2).

APPENDIX C

Vegetation structure within forest patches by matrix type (*Ecological Archives* M080-023-A3).

APPENDIX D

Sampling effort across landscapes in 2005–2007 (*Ecological Archives* M080-023-A4).

APPENDIX E

Estimating species detection probabilities by matrix type (*Ecological Archives* M080-023-A5).

APPENDIX F

Traits of native resident Jamaican birds (*Ecological Archives* M080-023-A6).