Differential matrix use by Neotropical birds based on species traits and landscape condition

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Abstract. There is considerable uncertainty about the role of human-modified habitats in supporting species in fragmented landscapes. This is because few studies sample outside of native habitats in the “matrix.” Those that do, often fail to sample landscapes in a way that accounts for the confounding effects of native habitat pattern and species detection biases that can obscure species responses. We employed multi-species hierarchical occupancy models to determine the use of human-modified habitats by Neotropical birds in landscapes that were similar in forest amount and configuration but surrounded by a matrix of agriculture (predominantly pasture), bauxite mining (surface mining for aluminum), or suburban development in central Jamaica. We found that the vast majority of bird species used the matrix; with the highest mean occurrences for open-associated, followed by generalist, and last forest-associated species. Migrant species had higher mean occurrences in all matrix types relative to resident species. Contrary to our expectation, mean occurrence for the entire species community, and for forest-associated and migrant species, were highest in bauxite, intermediate in suburban, and lowest in agriculture. Open-associated species had higher occurrences in both bauxite and agricultural matrices, whereas generalist species had higher occurrences in suburban matrices. Additional behavioral observations indicated that Neotropical birds used matrix areas, particularly scattered trees, to acquire food, and secondarily, as movement conduits. Matrix use patterns reflected the differential availability of potential resources and structural connectivity across the three landscape types, but only for those species adapted to open/edge environments and with generalized habitat requirements. Patterns of matrix use by forest specialists reflected the differential levels of degradation of the native forest; thus, we propose that higher matrix use for forest-dependent species may be induced by diminished within-forest resources. These results underscore that effective management of human-modified matrices requires in-depth understanding of the trade-offs between the benefits available in the matrix and the impacts on the disturbance of native habitats.

Key words: avifauna; Caribbean; countryside biogeography; ecological trap; habitat fragmentation; hierarchical model; landscape matrix; occupancy dynamics.

Introduction

The protection of large tracts of native habitats is essential for maintaining the world’s biodiversity (Gray et al. 2016). At the same time, the degree to which such reserves are successful is inextricably linked to their surrounding landscapes (Laurance et al. 2012, Gray et al. 2016); and the fate of many species hinge upon their ability to use human-modified areas (Ewers and Didham 2006). Despite this recognition, global ecological research remains disproportionately focused on protected areas: with an estimated >60% of field sites in natural protected areas vs. only 12.5% in agricultural areas and 3.9% in human settlements (Martin et al. 2012). Even when ecologists conduct fieldwork in human-modified landscapes, sampling largely takes place within natural fragments (Prevedello and Vieira 2010, Martin et al. 2012). Nevertheless, these studies reveal that species persistence in native habitats is contingent upon the intervening land cover (commonly referred to as the “matrix”; Prevedello and Vieira 2010, Driscoll et al. 2013).

Despite the importance of the matrix, we lack an empirical foundation to ascertain the role of human-modified habitats in supporting species (Chazdon et al. 2009, Gardner et al. 2009). One main reason is that few studies sample outside of native habitats, thus, constraining our understanding of matrix use and tolerance (Prevedello and Vieira 2010). Of those that have, the vast majority are concentrated in the developed world or in a few well-studied tropical systems and focus on avifauna in agricultural landscapes dominated by agroforestry or other low-intensity land uses (e.g., Daily et al. 2001, Hughes et al. 2002, Fischer et al. 2005, Sekercioglu et al. 2007, Haslem and Bennett 2008, Mendoza et al. 2014).
The patterns of matrix use for a wide range of species across varying landscape contexts is unknown given the scarcity of studies that have sampled different, intensely human-modified, matrices in a single setting. Moreover, the effects attributed to the matrix may be obscured given that studies (1) do not always untangle matrix features from native habitats by failing to account for habitat amount and configuration that often have overriding influence on species patterns (Fahrig 2003, Ewers and Didham 2006); (2) are commonly site-based rather than landscape-level assessments, and as such, might not discern broad-scale patterns that characterize fragmented systems (Fahrig 2003, Gardner et al. 2009); and (3) rarely account for species detection biases, which may cause misleading inferences (Kellner and Swihart 2014).

To fill this knowledge gap, we employed multi-species hierarchical occupancy models that account for species detection probabilities and determined the differential use of matrix habitats by Neotropical birds in three types of human-modified landscapes in central Jamaica. Specifically, we examined bird richness and occurrence patterns outside of native forest remnants in replicate landscapes that were similar in forest extent but dominated by one of three matrix types: agriculture (predominately pasture), bauxite mining (surface mining for aluminum), and suburban development (Fig. 1). We also observed the behavior of birds in matrix areas across the same landscapes to inform the nature of resource use underlying differences in occurrence. For brevity, we collectively refer to the sampled agriculture, bauxite, and suburban lands as “matrix” areas. However, we acknowledge that the definition of “habitat” vs. “matrix” is species-specific and falls along a continuum that is often not known.

Recognizing that species traits influence matrix responses (Ewers and Didham 2006, Kennedy et al. 2010, Prevedello and Vieira 2010), we estimated differences in mean richness and occurrences based on a priori categorizations of habitat association (forest-associated, generalist, or open-associated) and migratory status (resident or migrant). We predicted that the most common species in matrix areas would be those that are considered adapted to edge and open habitats (i.e., open-associated species), followed by generalist species, given their increased likelihood of utilizing resources outside forest remnants (Ewers and Didham 2006). In contrast, forest specialists or species affiliated with forest remnants, would only rarely use matrix areas given they are suboptimal landscape features. Further, we predicted that matrix use would be higher for migrants than for residents due to their expected greater mobility (e.g., Mettke-Hofmann and Gwinner 2004), reduced aversion to open habitats (e.g., Greenberg 1983), and more generalized diets during the non-breeding season on wintering grounds (e.g., Confer and Holmes 1995).

![Figure 1](image.png)

**Fig. 1.** Locations of the 13 1-km² landscapes surveyed in Manchester Parish on the island of Jamaica (latitude 17°56′44″–18°05′36″ N; longitude 77°23′19″–77°34′18″ W).
Land-cover change in Jamaica (Evelyn and Camirand 2003) and other Caribbean islands (Lugo 2002) has resulted from the conversion of agriculture to residential development and mining for bauxite. These cover types could be construed as equal in their conservation value in that they are all medium to high-intensity land uses and comprise novel habitats that dramatically differ from native forests. However, we predicted that species use would vary because these matrix types are heterogeneous in composition and structure. Due to the presence of scattered trees in suburban areas (ornamental tree gardens, mixed woodlots), and to a lesser extent in agricultural pasture (paddock trees, live fences), foliage cover and vertical complexity were higher in suburban, intermediate in agricultural, and lowest in bauxite matrices (see Methods). Therefore, we expected that suburban and to lesser extent agricultural landscapes would provide greater potential resources (food, cover, or nesting sites) for generalist and forest-affiliated species (Kennedy et al. 2010) and structural connectivity to aid movement relative to bauxite landscapes (Kennedy and Marra 2010). Correspondingly, we predicted that the use of matrix habitats overall by birds, reflected in both richness and occurrence estimates, would be highest in suburban, followed by agricultural, and lowest in bauxite landscapes.

**METHODS**

**Study area**

Our study sites were located in Manchester Parish in central Jamaica. This region was once dominated by wet limestone forest; by the 18th century, large-scale deforestation occurred and currently less than 30% of native forest remains. Forests are now restricted to small hilltop remnants on limestone outcrops, with low-lying areas originally converted for agriculture (historically for cultivation of cash crops and later for cattle pasture) and more recently (since the 1950s) for residential (suburban) development and mining for bauxite (raw material for aluminum and alumina production; Evelyn and Camirand 2003). For further details on the study region, see Kennedy et al. (2010).

We sampled a total of 13 human-modified landscapes (delineated as 1-km² areas): five landscapes in which forest has been fragmented by agriculture (cattle pasture), four by bauxite mining, and four by suburban development (Fig. 1). The area of our landscapes (100 ha) is expected to be a biologically relevant scale because it exceeds known territory sizes of birds in this region. Based on information available for over one-half of the species in this region, 72% of species have reported territory sizes ≤5 ha and all but two raptor species have territory sizes ≤15 ha (Kennedy et al. 2010, and Birds of North America online database). Climate, geology, elevation, and forest type were similar among these landscapes as well the forest fragmentation pattern (i.e., amount, shape, and inter-patch connectivity of forest remnants). Sampled landscapes contained ~36% forest cover, ~20 fragments of 4–6 ha in size, and forested hilltops averaging 100–200 m apart (for further details on patch and landscape metrics; see Kennedy et al. [2010]).

Although the spatial pattern of forest was similar across the landscapes, matrix composition and structure differed significantly among the three human-modified matrices (Fig. 2; Appendix S1: Table S1). 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* shrubs (10%) that were interspersed in valleys between forested hilltops. Bauxite landscapes were former agricultural lands that had been converted to mining within the past 10 years; forest fragments were surrounded by exposed bauxitic soils with vegetation cover dominated by planted grassland or ferns (~78%) and early growth of *Acacia* shrubs (19%) but few trees. Suburban landscapes consisted mainly of remnant forest surrounded by roads and low-density residential housing with lawns (~10%), herbaceous gardens (9%), fruiting tree gardens (26%), ornamental shrubbery (19%), ornamental trees (12%), and small mixed woodlots (11%). Based on extensive vegetation sampling, foliage cover and vertical complexity was greatest in suburban matrices, intermediate in agricultural matrices, and lowest in bauxite matrices (see Appendix S1 in detail).

**Bird surveys**

*Point-count surveys.*—We conducted 246 point-count surveys from early March to mid June 2005 during the height of migration and breeding activity for birds (Raffaele et al. 1998). During this sampling period, average temperature (27.93° ± 1.15°C [mean ± 1 SD]) and precipitation (0.34 ± 0.87 cm) were similar to those between 2000 and 2015 (27.13° ± 1.29°C, and 0.36 ± 1.18 cm; Appendix S2: Table S1), and fell within a consistent annual trend (Appendix S2: Fig. S1). We sampled 120 different locations in the matrix outside of forest remnants that were dominated exclusively by agriculture, bauxite mining, or suburban development (40 sampling locations per matrix type and an average of nine locations per landscape). We visited each site on one (22%), two (50%), or three (23%) separate occasions (on different days), with the same frequency of repeated visits per matrix type. We sampled the three broad matrix vegetation types (i.e., herbaceous cover, shrubs, or scattered trees) in proportion to their occurrence. Specifically, 56%, 24%, and 20% of locations in agricultural matrices; 57%, 33%, and 10% of locations in bauxite matrices; and 9%, 19%, and 72% of locations in suburban matrices resided within or near herbaceous cover, shrubs, or scattered trees, respectively. We captured these habitat features with similar frequencies in our point-count surveys across the different landscapes per matrix type. We established point-count stations in two different cardinal directions outside of forest remnants and
Fig. 2. Three landscape types where birds were sampled in matrix areas. In each panel, the left frame shows example landscapes from aerial view based on IKONOS imagery and the right frame shows the ground view based on photographs taken near sampled sites (by C. M. Kennedy). Native forest fragments were (a) largely surrounded by pasture, tree-lined fencerows, and paddock trees in agricultural landscapes; (b) exposed bauxitic soil, fallow fields, early growth of ferns and young Acacia stands in bauxite landscapes; and (c) ornamental lawns, gardens, roadside vegetation, roads, and houses in suburban landscapes. See Appendix S1 for further details. [Color figure can be viewed at wileyonlinelibrary.com]
located them midway between adjacent forest remnants whenever logistically feasible. Euclidean nearest neighbor distances between each sampled matrix location and the nearest forest edge in four cardinal quadrats revealed that the matrix-forest distances were similar across landscape treatments. On average, matrix points were 104 ± 34 m, 115 ± 33 m, and 103 ± 41 m from forest edges in agricultural, bauxite mining, and suburban landscapes, respectively. To minimize double counting, stations were separated by forested hilltops and were on average 680 ± 335 m apart within a landscape and 9075 ± 6288 m apart among all landscapes, which well exceeds known daily movement patterns documented for species in this region (Cruz 1981, Kennedy 2009).

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 09:00 on clear days without rain) and whether detected within or beyond a 25-m fixed-radius area (Hutto 2016). We included individuals detected only within the 25-m radius in our analyses because it provided the most reliable detection across sites in our system (Kennedy et al. 2011), as found by other avian studies in the Caribbean (Wunderle and Waide 1993). We mapped site locations of all birds seen or heard. In our analyses, we included only individuals detected within matrix habitats by sight or sound and excluded flyovers and those detected on the edge of forest remnants. Each site was visited by one of three trained observers that were rotated for repeat counts within a season, and all observers sampled a similar number of sites per landscape and matrix type. The order of visitation was rotated throughout the field season to diminish detection bias due to observer and time-of-day effects.

**Resource use observations.** To inform the nature of bird use of matrix microhabitats underlying occurrence patterns, we conducted supplemental surveys on resource use across the same landscapes using a protocol modified from Hughes et al. (2002). We conducted 46+ person-hours of observation in matrix areas (averaging three person-hours per landscape, 16 person-hours per matrix type) between 06:00 and 10:00 from early February through late March 2007. Starting from a randomly selected matrix point-count location, one of two observers walked in a random direction at a slow pace, stopped every 100-m for 5 min to record any new individuals encountered, and then moved to new areas to minimize double counting. We visited each landscape on one occasion (day), with per-observer effort equal across the three matrix types. We recorded individual birds detected only by sight and those encountered within a 25 m fixed-radius area to be consistent with our point-counts and to maximize detectability of bird-habitat relationships (Hutto 2016). Similar to our point-count surveys, we mapped site locations of all birds seen, noted only individuals observed using matrix areas, and excluded flyovers and detections on native forest edges. For each individual bird, we recorded its activity (foraging, nesting, moving only, or perching only) and its associated microhabitat type. We classified microhabitats to match our matrix vegetation surveys: herbaceous cover (including bauxite regrowth, pasture, herbaceous garden, ornamental lawn), shrubland (including natural shrubs, in particular Acacia stands, and ornamental shrubs), linear vegetation (including hedgerows and fencerows of trees and roadside vegetation), and scattered trees (including tree stands, tree gardens, and mixed woodlots; see Appendix S1 for details). We examined potential differences in the frequencies of activities (foraging, moving, perching) and the potential disproportionate use of microhabitats (by comparing detected use vs. availability) using χ² tests with R 3.2.5 (R Core Team 2016). Due to the similarity of landscape replicates per matrix type, we aggregated detections per matrix type. Given that we did not conduct repeated per-site behavioral surveys in each landscape, we could not statistically model detection probabilities. Thus, our counts are naïve estimates of resource use, which we interpret as frequencies of detections and use to indicate general patterns of resource use across (not between) matrix types.

**Classification of birds: habitat association, migratory status, and diet guild**

We a priori classified species as forest-associated (FR), generalist (G), or open-associated (OA) based on their habitat associations published in field guides, Birds of North America online database, and expert judgment by ornithologists with expertise in Jamaican avifauna (Kennedy et al. 2010). Forest-associated species were considered specialized on or predominately associated with native forest habitats. Generalist species were those that exhibited moderate degrees of forest dependency and relied on native forests but were also found to use non-forest habitats. Open-associated species were those that exhibited low dependency on forests and were associated with open habitats. We classified species as resident (RES; Raffaele et al. 1998) or migrant (MIG; including both Intratropical and Neotropical migrants; Rodewald 2015) and categorized them into six exclusive diet guilds based on dominant food sources consumed (frugivore, nectarivore, insectivore, omnivore, granivore, and carnivore; Cruz 1974, 1981, Raffaele et al. 1998, Rodewald 2015). For model development (described below), we included the a priori habitat classifications directly into our analysis and examined differences in migrant vs. resident species post-hoc. We used diet guild simply to further characterize the community composition of each bird group descriptively.

**Occupancy modeling framework**

Based on our point-count surveys, we estimated species occurrences in matrix habitats using a multi-species hierarchical community model with survey-specific detection/non-detection data (for similar approach, see Zipkin et al. 2010). We specified occurrence (z) of each species (i) in each
matrix site \((j)\) as a Bernoulli random variable, \(z_{i,j} \sim \text{Bern}(\psi_{i,j})\), where \(\psi_{i,j}\) is the probability that species \(i\) occurs at site \(j\). Given that true occurrence is imperfectly observed, we distinguished between species absence and non-detection by estimating species detection probabilities from the pattern of detections/non-detections from repeat surveys \((k)\) at each site \(j\) (MacKenzie et al. 2006). We defined our detection model for species \(i\) at site \(j\) during replicate \(k\) as \(x_{i,j,k} \sim \text{Bern}(p_{i,j,k} \times z_{i,j})\), where \(p_{i,j,k}\) is the detection probability of species \(i\) for replicate \(k\) at site \(j\), given that species \(i\) was present \((z_{i,j} = 1)\). An assumption of the detection model is that the community remains closed to changes in species occurrences for the duration of the surveys. This assumption of closure is likely violated for those species in which the sampled matrix features do not constitute primary habitats but rather are being used as temporary feeding grounds or movement conduits. For these birds, we expected that movement in and out of sampled areas was random. As such, our occupancy estimator remains unbiased, but “occurrence,” in this case, is best interpreted as “use” or the proportion of sites in matrix areas that are used by birds (MacKenzie et al. 2006).

We allowed individual species occurrence probabilities \((\psi_{i,j})\) to vary by matrix type (agriculture, bauxite, suburban; sensu Ruiz-Gutierrez et al. 2010). We did not model different occurrence probabilities for specific matrix microhabitat features (e.g., herbaceous cover, shrubs, or scattered trees; Appendix S1), because our interest was to discern overall species use patterns per matrix type. Because landscape replicates per matrix type were selected to be consistent (i.e., had similar environmental conditions, forest type, fragmentation pattern, and proportions of matrix microhabitat features), we did not include sampling locations within landscapes as random effects and expected the fixed effect of matrix type to capture the substantial variability. Species-specific occurrence probabilities were linked together in the model through group-level distributions, governed by hyper-parameters (Royle and Dorazio 2008). Specifically, we assumed that species within the same habitat association group (e.g., forest-associated, generalist, or open-associated) had individual occurrence probabilities in each matrix type that were drawn from a common, group-level normal distribution (Ruiz-Gutierrez et al. 2010). For example, all species classified as forest-associated were linked together by assuming that their parameter values for occupancy were drawn from a common distribution dependent on matrix type. The advantage of this type of community-level hierarchical modeling is that it increases the precision of species-specific parameter estimates by drawing on multiple species occurrence responses that are expected to be ecologically similar (Zipkin et al. 2009) and allows for specific hypothesis testing (Pacifici et al. 2014).

We modeled detection probabilities individually by species and allowed those to vary across matrix habitat type. We modeled species detection probabilities in agriculture using a single community-level hyper-prior across all species (no group effects), which was then allowed to shift in bauxite and suburban matrices. Due to issues of model convergence, the effect of bauxite and suburban habitats on detection was not species-specific but rather the same (on the logit scale) across species. This assumption is based on the observation that the main factors affecting detection across the different landscapes (e.g., variation in noise, disturbance, vegetation structure) are likely to influence species detections in a similar manner within a single matrix type (Kennedy et al. 2010). Because we implemented standardized sampling protocols to diminish detection biases due to observer, time, date, or sampling effort, we did not include those factors in our detection model.

We analyzed the model with a Bayesian approach using independent, non-informative prior distributions for hyperparameters and running three chains of 20000 length after a burn-in of 5000 and thinned priors by 15 (see Appendix S3 for R and WinBUGS code). We assessed model convergence through plots of the Markov chain Monte Carlo (MCMC) chains and with the R-hat statistic (Gelman and Hill 2007). We estimated posterior distributions for each species and group (forest-associated, generalist, or open-associated) occupancy and detection parameters by summarizing 3000 random samples of the MCMC chain. We then calculated mean, SD, and 95% Bayesian credible intervals (BCIs) for species- and group-level parameters for both occurrence and detection probabilities. We determined differences in matrix use by each species habitat association group by comparing the posterior distributions of the group-level hyper-parameters for each matrix type. We summarized the results by migratory status (migratory vs. resident) by assessing individual species’ occupancy estimates (using the full posterior distribution) and calculating group means post hoc. Following Ruiz-Gutierrez et al. (2010), we computed the proportions of MCMC iterations in which occurrence is estimated to be higher or lower among the different matrix types, which can be interpreted as a probability (and denoted as PR); i.e., a value of 0.95 can be interpreted as a 95% probability that one parameter is greater (or less) than the other whereas a value of \(0.05\) suggests there is no difference in parameter estimates. We calculated site-specific species richness by summing the estimated number of species (e.g., the latent occurrences, \(z\) values) for each of the three matrix habitat types across all species and by habitat association and migratory status.

Results

We detected 58 species in matrix habitats \((N = 48\) species in agricultural and suburban and 47 species in bauxite). Of these species, 29% were forest associated and predominately insectivores (53%) or frugivores (18%); 34% were generalist insectivores (30%), frugivores (25%) or nectarivores (15%); and 36% were open-associated insectivores (38%), granivores (33%), or omnivores (19%). Forty-four species (76%) were residents that were equally composed of different habitat associations (32–34%) and spanned all diet guilds (11% carnivores, 11% nectarivores,
16% frugivores, 16% omnivores, 18% graminivores, and 27% insectivores). The remaining migratory species (24%) were largely insectivores (79%) and open-associated (50%), generalist (36%) and forest-associated (14%) species (Appendix S3: Table S1).

In matrix areas, we detected 86% of all endemic, 96% of all resident, and 58% of all migrant species reported within native forest in this region (both forest fragments in the same landscapes and in the largest intact forested areas) and four novel species (Appendix S3: Tables S1 and S4). Of the one resident and three migrant species detected only in matrix areas (but not in forest), three were classified a priori as open-associated and one as a generalist (Appendix S3: Table S1). Of those species not found in matrix areas, the three Jamaican endemic species and the one resident species were all classified a priori as forest-associated and the 10 migrant species were forest-associated (N = 6) and generalist (N = 4) species (Appendix S3: Table S4).

Species detection
Crossing all 58 species, we made 1478 detections in point-count surveys, with individual detections ranging from 1 to 126 (25.48 ± 28.37 [mean ± 1 SD]). The number of detections and observed individual birds was lowest in bauxite (N = 413 and 581, respectively), intermediate in agriculture (N = 467 and 718, respectively), and highest in suburban (N = 598 and 841, respectively; Appendix S3: Table S2). Mean detection probabilities (P) were variable across species (ranging from 0.01 ± 0.01 to 0.79 ± 0.11), but were estimated to be lowest in bauxite (0.12 ± 0.01), intermediate in agriculture (0.17 ± 0.02; probability PR(Baux < PrAg) = 1.00), and highest in suburban matrices (0.20 ± 0.01; PR(urban > PAg) = 0.92).

Species and group-level richness by matrix type
We estimated that the 58 observed species occurred across each matrix type, with mean point-level richness of 57.55 ± 0.83 in agricultural, 57.43 ± 1.07 in bauxite, and 55.14 ± 1.91 in suburban matrices. The richness distributions across all species and species groups had wide overlap, indicating no richness difference by matrix type (Appendix S3: Fig. S1). Of the total 17 forest-associated species detected, we estimated mean richness to be 16.59 ± 0.80 in agricultural, 16.52 ± 1.02 in bauxite, and 14.45 ± 1.82 in suburban matrices. Of the total 20 generalist and 21 open-associated species detected, we estimated mean richness to be 20.00 ± 0.03 and 20.97 ± 0.20 in agricultural, 19.99 (±0.10) and 20.92 (±0.35) in bauxite, and 19.89 (±0.31) and 20.81 (±0.45) in suburban matrices, respectively. Finally, of the total 44 resident and 14 migrant species detected, we estimated mean richness to be 43.57 ± 0.81 and 13.98 ± 0.12 in agricultural, 43.46 ± 1.05 and 13.97 ± 0.17 in bauxite, and 41.25 ± 1.87 and 13.90 ± 0.30 in suburban matrices, respectively.

Species and group-level occurrence by matrix type
We estimated mean occurrence to be high across all matrix types for the entire species community (0.71 ± 0.07). In line with our prediction, open-associated species had higher group-level mean occurrence probabilities across all matrix types (0.80 ± 0.14) relative to generalist species (0.64 ± 0.19; PR(ψAllMatrix_G > ψAllMatrix_MIG) = 0.71) and forest-associated species (0.43 ± 0.24; PR(ψAllMatrix.FR > ψAllMatrix.FR) = 0.94). In addition, generalist species had higher group-level mean occurrences relative to forest-associated species (PR(ψAllMatrix_G > ψAllMatrix_MIG) = 0.77). Migrant species also had slightly higher mean occurrences (0.76 ± 0.13) relative to resident species (0.66 ± 0.14) across matrix types (PR(ψAllMatrix.FR > ψAllMatrix.FR) = 0.74). We note, however, that BCIs often overlapped between species across the habitat association and migratory status groups (Fig. 3; Appendix S3: Table S3).

In contrast to our prediction, we estimated that overall species occurrence was highest in bauxite (0.81 ± 0.09), intermediate in suburban (0.68 ± 0.10; PR(ψBaux.AllSpp > ψUrban.AllSpp) = 0.84), and lowest in agricultural matrices (0.58 ± 0.09; PR(ψBaux.AllSpp > ψAg.AllSpp) = 0.96; PR(ψUrban.AllSpp > ψAg.AllSpp) = 0.78; Fig. 3; Appendix S3: Table S3). This trend held for both resident and migrant communities, for which we estimated higher mean occurrences in bauxite (RES, 0.79 ± 0.10; MIG, 0.86 ± 0.08), intermediate in suburban (RES, 0.64 ± 0.11, PR(ψBaux.RES > ψUrban.RES) = 0.85; MIG, 0.76 ± 0.11, PR(ψBaux.MIG > ψUrban.MIG) = 0.76), and lowest in agricultural matrices (RES, 0.55 ± 0.09, PR(ψBaux.RES > ψAg.RES) = 0.97, PR(ψUrban.RES > ψAg.RES) = 0.76; MIG, 0.65 ± 0.11, PR(ψBaux.RES > ψAg.RES) = 0.92, PR(ψUrban.RES > ψAg.RES) = 0.73).

The occurrence patterns in different matrix types varied by habitat association (Fig. 3). Open-associated species had slightly higher group-level mean occurrences in bauxite (0.90 ± 0.09) relative to agricultural (0.85 ± 0.09; PR(ψBaux.OA > ψAg.OA) = 0.70), but with greater probabilities of higher mean occurrences in both of these matrices relative to a suburban matrix (0.67 ± 0.12; PR(ψBaux.OA > ψUrban.OA) = 0.95; PR(ψAg.OA > ψUrban.OA) = 0.88). On the other hand, generalist species had highest mean occurrences in suburban (0.83 ± 0.11; PR(ψUrban.G > ψAg.G) = 1.00; PR(ψUrban.G > ψBaux.G) = 0.91), intermediate in bauxite (0.65 ± 0.10), and lowest in agricultural matrices (0.44 ± 0.07; PR(ψBaux.G > ψAg.G) = 0.98). Last, forest-associated species had higher mean occurrences in bauxite (0.68 ± 0.17) relative to both suburban (0.33 ± 0.18; PR(ψBaux.FR > ψUrban.FR) = 0.93) and agricultural matrices (0.27 ± 0.10; PR(ψBaux.FR > ψAg.FR) = 0.99), but with similar (lower) mean occurrences in the latter two matrix types (PR(ψUrban.FR > ψAg.FR) = 0.59).
**Resource use within matrices**

We recorded the behavior of 57 species during 1185 resource-use detections in the matrix. We detected a similar number of species and percentage of individuals across the three matrix types: 48, 48, and 41 species and 29%, 32%, and 39% of individuals in agricultural, bauxite, and suburban areas, respectively. Across all species and matrix types, the frequency of the three main activities (foraging, moving, and perching) differed ($\chi^2 = 36.44, df = 4, P < 0.0001$; Appendix S4: Fig. S1a). We observed resident and migrant birds most commonly foraging (46% by all species, 53% by forest-associated, 57% by generalist, and 35% by open-associated species), secondarily moving (25% by all species, 32% by forest-associated, 27% by generalists, and 29% by open-associated species), and perching (26% by all species, 12% by forest-associated, 16% by generalists, and 35% by open-associated species). We rarely observed nesting behavior (<1% of 883 observations; Appendix S4: Fig. S1).

Activity patterns differed by habitat association ($\chi^2 = 56.96, df = 4, P < 0.0001$) and migratory status ($\chi^2 = 78.50, df = 2, P < 0.0001$). Across all matrix types, we most frequently observed generalist and forest-associated species foraging (57% and 53%, respectively), or moving (27% and 32%), and less often observed perching (16% and 12%; Appendix S4: Fig. S1b, c). In contrast, we observed open-associated species to more equally exhibit different behaviors: 36% perching, 35% foraging, and 29% moving (Appendix S4: Fig. S1d). We observed migrant species to be most frequently foraging in matrix microhabitats (79% in agriculture, 78% in bauxite, and 72% in suburban) relative to resident species (47% in agriculture, 41% in bauxite, and 33% in suburban). Resident species were more frequently observed moving in matrix areas (30% for residents, 19% for migrants) and perching (30% for residents vs. 4% for migrants) (Appendix S4: Fig. S1e, f).

Across the whole community, birds used microhabitats in different proportions than available in each matrix.
Differential use by species across matrix types

The likelihood of matrix use differed by species traits and landscape types. Open-associated species had higher estimated occurrences in both bauxite and agricultural matrices, which we suspect are largely granivores, insectivores, and omnivores that can use open habitats and pasture fields that dominated these landscapes. In support of this finding, we previously found omnivores and granivores to be more abundant in agricultural than in intact forested landscapes in this region (Kennedy et al. 2010). In contrast, generalist species had highest estimated occurrences in suburban landscapes; and this group includes high numbers of frugivores and nectarivores observed to use residential gardens. In concordance, generalist species, and in particular nectarivores, were found to be most abundant in suburban landscapes (Kennedy et al. 2010). These results, along with our observations that foraging was the dominant activity by birds in matrix areas, suggest that microhabitats in agricultural and suburban areas likely provide additional foraging resources that benefit open-associated and generalist species.

The overall community trend, and the trend for both forest-associated species and migrant species, were highest estimated occurrences in bauxite, intermediate in suburban, and lowest in agricultural matrices. Despite less available and suboptimal habitats in bauxite relative to agricultural or suburban matrices, the resident and migrant bird communities had higher potential use. We suspect that this finding relates to the fact that forest remnants embedded in bauxite mining, and to lesser extent in suburban development, were more degraded or disturbed than in agriculture, i.e., had low stature and more open canopies, reduced vertical structure, fewer and smaller trees, more shrubs, and less leaf litter that altered the microclimate, within the forest vegetation structure, and likely lowered food resources (for details, see Kennedy et al. 2010). Thus, forest-affiliated birds may be required to move more frequently between forest remnants or to expand their territories to acquire sufficient resources for their survival or to supplement resources by foraging in matrix areas.

Thus, we posit that higher frequency use of matrix areas, as detected in this study, could be induced by diminished within-forest resources for forest specialists. To confirm this hypothesis, however, experimental investigation is needed to tease apart the effects of the external matrix habitats from those that impact the internal forest conditions. We note that this hypothesis is in contrast to other studies that have detected higher matrix use in landscapes with greater forest cover because they provide critical resources (e.g., foraging and roosting sites; e.g., Haslem and Bennett 2008, Mendoza et al. 2014). These additional foraging resources that benefit open-associated and generalist species.
studies, however, tend to focus on a single matrix type (i.e., agriculture) and do not evaluate matrix use across different human-modified landscapes with similar forest pattern. Such uncertainties underscore the need for further study on the potential mechanisms underlying matrix use by species across different fragmented systems.

Accounting for species detectability across matrices

Our findings are based on occurrence patterns that included detection probabilities that differed by matrix type. Had we not corrected for differential detectability, our comparisons of richness and occurrences between matrix types would have been biased and potentially produced spurious patterns (as also found by Ruiz-Gutiérrez and Zipkin 2011). One caveat is that, unlike for agricultural matrices, we modeled the effects of bauxite and suburban areas on detection to be uniform across all species in each of these two matrices. This led our model to produce estimates in which detections were consistently lowest in bauxite, intermediate in agriculture, and highest in suburban matrices for all modeled species. Although the lower detections in bauxite mining landscapes are in line with observed noise and abundance patterns, we recognize that, in reality, detection is likely to vary across species. Our raw data, however, support these results because nearly the same number of species was observed in each matrix type, but the number of detections was lower in bauxite relative to agriculture and suburban. This suggests that species detection was in fact lower in bauxite relative to the other landscapes.

Caveats and research needs

Several factors should be considered when interpreting our results. First, our occurrence patterns are based on species detectability being lower in bauxite areas. The lower detection in bauxite may be attributed to these landscapes being subject to greater noise from surface-mining impacts and construction (C. M. Kennedy, personal observation) or due to lower abundances of birds. We suspect that lower detections in bauxite areas were not simply due to more zero-count visits; there were only five instances of site visits where no species were detected of which all occurred in agricultural landscapes. Other contributing factors could have been quicker movements by birds that are likely to spend less time in stressful environments or temporary immigrations. We observed a higher percentage of movement and a lower percentage of perching by birds in bauxite (35% and 16%) relative to suburban (27% and 34%) or agricultural (23% and 22%, respectively) matrices, but these estimates fail to account for any differences in detectability. Thus, additional data on bird movements would be needed to isolate any mechanism. Second, our species-specific occurrence estimates had low precision and many species were detected with low probabilities. Our detection probabilities fall within the range reported by other empirical studies (Kellner and Swihart 2014), and we captured the uncertainty in our occupancy estimates in our analyses (Guillera-Arroita et al. 2014). One exception is that we did not account for imperfect detection in our resource use surveys, although we carefully designed our data collection scheme to minimize biases. Regardless, we acknowledge that additional sampling of site locations, greater per-site replication, and full accounting of detection biases would help confirm matrix use patterns.

We modeled species occurrences because they were more reliably estimated than abundances based on our data that included rare and infrequently observed species, which is typical of community-level data (DeWan and Zipkin 2010). Although occupancy and abundance are expected to be positively correlated and abundance or density are often correlated with recruitment for birds (Bock and Jones 2004), we caution that such static metrics may not be honest indicators of the drivers (vital rates) of population dynamics: especially in human-modified landscapes that are fragmented, comprise novel habitats, and often undergo rapid land use change that could lead them to be population sinks or ecological traps (Bock and Jones 2004). Thus, we emphasize that high species occurrence or use, such as that detected in our bauxite areas, does not necessarily indicate high habitat quality (Johnson 2007). In addition, single-season occurrence patterns do not reveal underlying mechanisms or potential long-run implications. To confirm how matrix use may support (or jeopardize) species persistence and to gauge their true conservation value, we recommend multi-season sampling to estimate local extinction and colonization (source–sink) dynamics (e.g., Kennedy et al. 2011), population-level data on movement, reproductive, and survival rates (e.g., Sekercioglu et al. 2007, Evans et al. 2014), or an evaluation of body condition of individuals across matrix types (e.g., Mazerolle and Hobson 2002). Although demographic data are ultimately needed to discern habitat quality for species (Johnson 2007), such detailed investigations are often intractable for entire communities across different landscape contexts. Thus, occupancy-based studies, such as this one, serve as an important first step towards characterizing community-level patterns of matrix use.

Conservation implications

Studies that have sampled in human-modified matrices reveal that a large fraction of species exist outside of native forests, particularly when these matrices contain high tree cover, structural complexity, and habitat heterogeneity (e.g., Daily et al. 2001, Hughes et al. 2002, Fischer et al. 2005, Sekercioglu et al. 2007, Haslem and Bennett 2008, Perfecto and Vandermeer 2008). Such studies (as corroborated by our observations) find that species use matrix features, including secondary growth, scattered trees, plantations, live fences, hedgerows, and roadside and riparian vegetation. These features are therefore often assumed to provide stepping stones, refugia, and resources that enhance landscape permeability and habitat quality, and have led to the proposal that matrix quality may
mitigate the impacts of habitat loss and fragmentation (Ewers and Didham 2006, Perfecto and Vandermeer 2008). Although such novel habitats have also been shown to act as movement barriers for some species (Villard and Haché 2012) or to promote the reproduction of nest predators (Poulin and Villard 2011).

We predicted that the use of human-modified areas by birds would be highest in suburban, followed by agricultural, and lowest in bauxite landscapes. These expectations were based on the amount of tree cover and structural complexity in matrix areas that followed the same pattern (i.e., highest in suburban, intermediate in agriculture, and lowest in bauxite), because these features have been shown to influence potential resources (food and cover; Kennedy et al. 2010) and structural connectivity (Kennedy and Marra 2010). Accordingly, we detected higher bird occurrences in suburban and agricultural matrices, but only for those species adapted to and tolerant of open/edge environments and with generalized habitat requirements. These species were also found to be most abundant and less sensitive to forest fragmentation in agricultural and suburban landscapes (Kennedy et al. 2010). Our findings suggest that matrix habitats can provide additional food resources and movement conduits, which may mitigate the effects of habitat loss and fragmentation for more common species. Although open-associated and generalist species groups are often not of conservation concern, maintaining a more hospitable matrix to support their persistence is likely to promote forest regeneration and ecosystem services, such as pest control, pollination, and seed dispersal (Sekercioğlu 2006).

In contrast to our predictions, species classified as forest-dependent had highest occurrence probabilities in bauxite, followed by suburban, and finally in agricultural matrices. Thus, their patterns of use did not reflect the differential availability of potential resources and structural connectivity found externally in matrix areas, as commonly assumed. Rather, they reflected the aggregate levels of degradation internally within native forest remnants, which was greatest in bauxite mining, intermediate in suburban development, and lowest in agricultural landscapes (Kennedy et al. 2010).

Alongside provision of resources and facilitation of movement, matrix areas can impact the internal conditions of native habitats via changes in the abiotic environment (e.g., microclimate, disturbance regimes; Prevedello and Vieira 2010, Driscoll et al. 2013). Surface-mining activities in bauxite areas involve large-scale removal of vegetation and topsoil, which can alter soil water retention, create dust pollution, and lead to biogeochemical or hydrologic changes (Bell and Donnelly 2006). Birds in suburban landscapes are likely affected by human-induced forest disturbance, including selective harvesting, road impacts, spread of fire or invasive species (Marzluff et al. 2001). All of these factors alter within-forest vegetation structure and microclimate. Insectivores, which make up the majority of forest-associated species within this community, were found to have higher local extinction probabilities (Kennedy et al. 2011) and lower abundances (Kennedy et al. 2010) within native forest embedded in bauxite, and secondarily, in suburban development (but not in agriculture); and these declines are likely a function of differential within-forest habitat quality. Previous evidence therefore suggests that increased matrix use by forest-dependent species, as detected in this study, does not appear to buffer against their declines and may even cause detrimental effects on population persistence if matrix habitats lead to elevated stress levels or increased mortality risk (e.g., predation), as has been detected for birds in other human-modified areas (Evans et al. 2014). Thus, managing novel matrix habitats should not be considered a substitute for reducing the loss and degradation of native forests from intensive human uses (Perfecto and Vandermeer 2008, Chazdon et al. 2009, Gardner et al. 2009), especially for habitat specialists, such as insectivorous birds that are declining in fragmented forests worldwide (Sodhi et al. 2004).

While matrix habitats can and should play a fundamental role in conserving species (Ewers and Didham 2006, Perfecto and Vandermeer 2008), especially in working landscapes as found in Jamaica and elsewhere, we urge that more empirical evidence is needed on how to manage the matrix in a way that can help support specialized species and diverse functional groups. We also suggest that more research attention is warranted to discern the influence of matrix types as potential demographic sinks (Driscoll et al. 2013). This requires understanding how species dynamically use native habitats together with different matrix types; differentiating among species along low- to high-intensity land uses; and discerning the trade-offs between the benefits in provision of resources or facilitation of movement from external matrix conditions from the costs due to their internal impacts on native habitats. Doing so will enable a fuller understanding of how human-modified areas are affecting species persistence in fragmented landscapes.

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**Supporting Information**

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