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BIODIVERSITY RESEARCH

Occupancy dynamics in human-modified landscapes in a tropical island: implications for conservation design

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ABSTRACT

Aim Avian communities in human-modified landscapes exhibit varying patterns of local colonization and extinction rates, determinants of species occurrence. Our objective was to model these processes to identify habitat features that might enable movements and account for occupancy patterns in habitat matrices between the Guanica and Susua forest reserves. This knowledge is central to conservation design, particularly in ever changing insular landscapes.

Location South-western Puerto Rico.

Methods We used a multiseason occupancy modelling approach to quantify seasonal estimates of occupancy, and colonization and extinction rates of seven resident avian species surveyed over five seasons from January 2010 to June 2011. We modelled parameters by matrix type, expressions of survey station isolation, quality, amount of forest cover and context (embedded in forest patch).

Results Seasonal occupancy remained stable throughout the study for all species, consistent with seasonally constant colonization and extinction probabilities. Occupancy was mediated by matrix type, higher in reserves and forested matrix than in the urban and agricultural matrices. This pattern is in accord with the forest affinities of all but an open-habitat specialist. Puerto Rican Spindalis (*Spindalis portoricensis*) exhibited high occupancy in the urban matrix, highlighting the adaptability of some insular species to novel environments. Highest colonization rates occurred when perching structures were at $\leq$ 500 m. Survey stations with at least three fruiting tree species and 61% forest cover exhibited lowest seasonal extinction rates.

Main conclusions Our work identified habitat features that influenced seasonal probabilities of colonization and extinction in a human-modified landscape. Conservation design decisions are better informed with increased knowledge about interpatch distances to improve matrix permeability, and habitat features that increase persistence or continued use of habitat stepping stones. A focus on dynamic processes is valuable because conservation actions directly influence colonization and extinction rates, and thus, a quantitative means to gauge their benefit.

Keywords
colonization, conservation design, extinction, habitat matrices, occupancy, Puerto Rico, resident birds, tropics.

INTRODUCTION

Human activities transform landscapes into a patchwork of habitats of differing quality for fauna (Gascon *et al.*, 1999; Grau *et al.*, 2003; Lambin *et al.*, 2003; Hobbs *et al.*, 2006). This patchwork, often referred to as habitat matrices, represents portions of the landscape that have, at some point in time, undergone intense anthropogenic perturbation

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(Antongiovanni & Metzger, 2005). Species are confronted with a modified environment of reduced area, increased isolation and novel ecological boundaries (Ewers & Didham, 2006). These conditions may trigger reorganization of species assemblages (Gustafson & Gardner, 1996; Szacki, 1999; Brown *et al.*, 2001) due, in part, because species lack the biological repertoire (e.g. exploit novel resources) or habitat features to bridge gaps of inhospitable matrices or survive in remnant patches (Saunders *et al.*, 1991; Croci *et al.*, 2008). The manner in which landscape changes influence faunal behaviour and demographic processes have a determinant influence on distribution, and ultimately, persistence (Hanski, 1998; Brotons *et al.*, 2003; Watling *et al.*, 2011; Yackulic *et al.*, 2015).

Landscapes in the Caribbean have undergone dramatic changes and are under continued pressure for multiple anthropogenic uses (Evelyn & Camirand, 2003; Aide & Grau, 2004; Lugo *et al.*, 2012a). Puerto Rico represents a unique case because up to 90% of the island was in some form of agriculture by the late 1930s (Dietz, 1986; Birdsey & Weaver, 1987), but a shift towards an industrial-based economy in the 1950s prompted a transition in land cover, and by 1991, 42% of the island's land cover was forested (Helmer *et al.*, 2002; Lugo & Helmer, 2004). Despite this gain, the island exhibits a high level of habitat fragmentation, with few areas of continuous forest surrounded by urban or other land covers (Lugo & Helmer, 2004). The implications of these changes for resident avifauna have been assessed only recently. Brash (1987) posited that shade coffee plantations helped ameliorate extinction rates of avian species, a role that may have been mediated by foraging and breeding habitat provided by the shade layer (Carlo *et al.*, 2004; Gleffe *et al.*, 2006). More recently, Acevedo & Restrepo (2008) reported that endemics were closely associated with plant communities in higher elevations (e.g. cloud forests), whereas exotic species were associated with open habitats in lowlands. Similarly, Vázquez-Plass and Wunderle (2012) reported that endemic species were sensitive to urbanization (nearly absent) as compared to exotic species.

While these studies have advanced our understanding of how species may cope with land cover changes or are currently distributed in human-modified landscapes, there is continued interest in investigating the processes that underlie patterns of distribution and persistence (Lugo *et al.*, 2012b). Arguably, this understanding could also inform decisions on conservation design (Diamond, 1975; Hanski, 1998), suggesting where, why and how resources could be directed to enhance habitat for conservation. These research needs were the impetus for this work, and were addressed in the context of emerging interests to implement strategies to facilitate seasonal movements between two forest reserves in south-western Puerto Rico, Guanica and Susua State Forests. The potential for seasonal movements between reserves, for example, could be driven by the breeding chronology of resident birds (Collazo & Groom, 2000; Gleffe *et al.*, 2006; Wiewel *et al.*, 2013), such that birds, as needed, seek suitable breeding habitat, followed by post-breeding adult and juvenile dispersal. The Guanica and Susua forest reserves, however, are separated by modified landscapes characterized by agriculture, urban sprawl and low-density human habitation embedded in a forested landscape. Studies have shown that avian forest specialists, including tropical species, take longer to complete movements between patches if traversing human-modified landscapes (Gobeil & Villard, 2002; Awade & Metzger, 2008; Boscolo *et al.*, 2008; Hadley & Betts, 2009; Kennedy & Marra, 2010; Irizarry, 2012).

Decisions to improve connectivity between reserves would benefit from modelling processes such as colonization and extinction rates, that provide a means to identify habitat features that facilitate movements and foster occurrence over time (persistence = 1-extinction probability), respectively. The theoretical foundation for these incidence functions and potential application to conservation design have been advanced in the literature (e.g. Diamond, 1975; Gilpin & Diamond, 1981; Hanski, 1994 & 1998; Yackulic *et al.*, 2015). This body of work underscores that changes in occurrence are mediated by the degree of isolation, size and quality of patches or points of interest on the landscape.

In this work, we obtained estimates of occupancy and colonization and extinction probabilities using a multiseason occupancy framework (MacKenzie *et al.*, 2003, 2006), and encounter histories (presence/non-presence) derived from surveys of six forest-dependent species and an open-habitat specialist over five seasons from January 2010 to June 2011, two pre-breeding seasons, two breeding seasons and a post-breeding season. We hypothesized that the state of survey stations (occupied or not) would be a function of the habitat matrix where species occurred at the onset of the study (initial occupancy), given their primary habitat associations (Andrén, 1994; Table 1). We also posited that subsequent variation in occurrence would be a function of the spatial arrangement, amount, size and quality of habitat features at survey stations (*sensu* Tews *et al.*, 2004; Table 1). In concert with Hanski (1998) and Kennedy *et al.* (2011), we modelled colonization rates as a function of isolation of survey stations, and extinction rates as a function of the size of the forest patch in which the survey station was imbedded, and the amount of forest/herbaceous cover and a proxy of habitat quality (fruit availability) within survey stations. Given the dominance of forest-dependent species in our surveys, we expected occupancy to be higher in forest reserves and forested matrix, followed by urban and agricultural matrices (Table 1). We also expected that survey stations in urban and agricultural matrices would exhibit lower colonization and higher extinction rates because survey stations would be more isolated, nested in smaller forested patches and of lesser quality than in the forested matrix and reserves.

We derived inferences from randomly established survey stations across each matrix. We adopted this approach for two reasons. First, Lugo *et al.* (2012b) posited that island avifauna are better adept at using human-modified landscapes. A broader understanding about species responses is

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Table 1 Hypotheses and *a priori* predictions about the influence (direction of slope) of covariates on local initial occupancy (ψ_{init}), colonization (γ) and extinction (ε) probabilities of resident avian species surveyed in three habitat matrices, namely agriculture (A), urban (U), forest (F) in south-western Puerto Rico, 2010–2011. Matrices were located between Guánica and Susúa State Forest reserves (R). Detailed description of covariates is available in Tables S1, S2.

Hypothesis	Covariate (abbreviation)	Predicted direction of slope (β) parameter(s)
Structure and composition of habitat in protected and human modified landscapes influence occurrence of avian species from the onset of the study (Andrén, 1994; Tews *et al.*, 2004)	Forest (F) Forest Reserves (R) Urban (U) Agriculture (A)	ψ_{init}: initial occupancy F (+) R (+) U (−) A (−)
Isolation will influence local (survey station) colonization probability (Hanski, 1998; Kennedy *et al.*, 2011)	Distance (m) to the nearest perch (DP); and distance to nearest patch with average forest cover percentage of the matrix [≥ 61% (7.5 ha); DF]	γ: patch colonization DP (−) DF (−)
Patch size will influence extinction probability (Hanski, 1994, 1998; Kennedy *et al.*, 2011)	Area (ha) of forest within which the survey station is embedded (PS_i); 'i' for imbedded	ε: patch extinction PSi(−)
Amount of habitat within survey stations will influence local extinction (Hanski, 1998; Tews *et al.*, 2004; Kennedy *et al.*, 2011).	Percentage forest (SSFC) herbaceous cover (SSHC) 'SS' stands for survey station	ε: patch extinction SSFC (−) SSHC (−)
Patch quality (forage) will influence local patch extinction probability (Hanski, 1998; Tews *et al.*, 2004; Kennedy *et al.*, 2011)	Average number of fruit tree species per survey station (FAI).	ε: patch extinction SSFC (−) SSHC (−) FAI (−)

gained by a scheme that does not restrict itself to large patches of vegetation, but instead samples the range of conditions across such landscapes. Second, matrix permeability can be achieved through the use of habitat 'stepping stones', such as small clumps of vegetation (Hanski, 1998; Baum *et al.*, 2004; Boscolo *et al.*, 2008), not just larger patches or linear strips of vegetation. In this sense, we expand on the work conducted by Kennedy *et al.* (2011), which emphasized the latter. We discuss the implications of this work for avian conservation in Puerto Rico and elsewhere in the Caribbean.

METHODS

Study area

The study area consisted of the municipalities of Guánica, Yauco, as well as parts of Lajas and Sábana Grande in south-western Puerto Rico (Fig. 1). The landscape that separates the Guánica and Susúa forest reserves was divided into three identifiable matrices using ArcGIS (Gould *et al.*, 2007; ESRI, 2010). The extent of each matrix was 7066 ha (agricultural), 6116 ha (urbanized) and 5536 ha (forested). Boundaries were set to highlight the dominant cover class within each matrix: agriculture (53%), urban (23%) and forested (40%). We note that the agricultural matrix was historically used for growing sugar cane, and since the 1950s, converted to pasture lands with hedgerows and clumps of trees bisecting or nested within parcels of lands (Dietz, 1986). The eastern and western boundaries were aligned up with the Luchetti (east) and Rio Loco (west) watersheds, focal features in the potential creation of corridors between Guanica and Susua forest reserves (Greene *et al.*, 2001).

Avian survey stations

One hundred and twenty-eight survey stations (SS) were randomly established across the study area. Selection excluded urbanized/impervious surfaces and water. We allocated 30 stations in each of the agricultural, urban and forested matrices, for a total of 90 stations. An additional 38 stations were established in the Guánica and Susúa Forest Reserves within a strip of forest at least 300 m away from the edge of the reserves, but not more than 1500 m inward. Eighteen (18) of these stations were established in the Guánica Forest and the remaining twenty (20) in the Susúa forest (Fig. 1). Stations occurred at 50–240 m elevation, all within tropical dry tropical forest (Gould *et al.*, 2007).

Presence–non-presence surveys

We surveyed six forest-dependent species (three insectivores, three frugivores) and an open-habitat specialist. Emphasis on forest-dependent species was justified because most native avian species evolved and are associated with forest land cover (Raffaele *et al.*, 1998; Gould *et al.*, 2007; Acevedo & Restrepo, 2008; Lugo *et al.*, 2012b). Insectivores were the Puerto Rican Vireo (*Vireo latimeri*), Puerto Rican Woodpecker (*Melanerpes portoricensis*) and Caribbean Eleania

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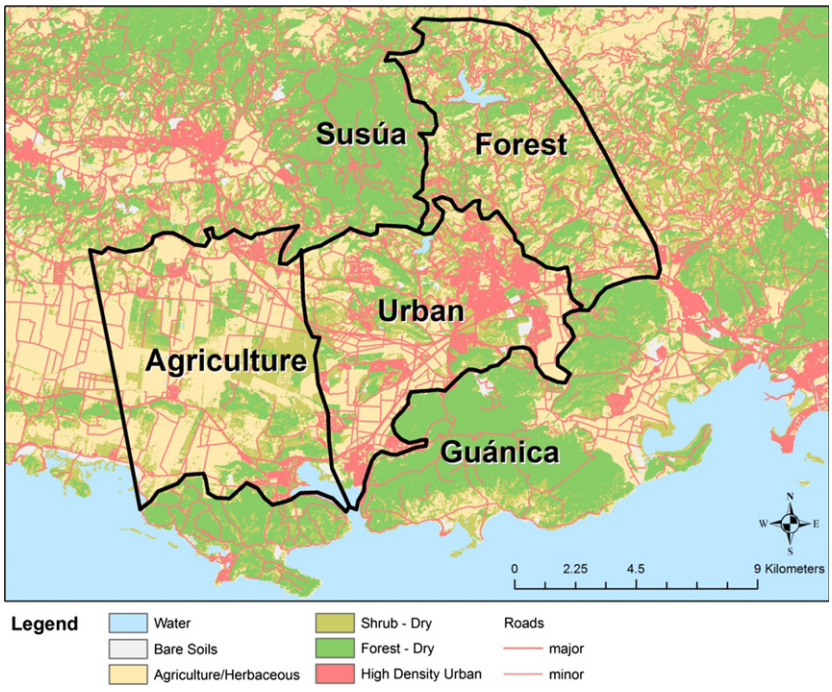

Figure 1 Map of the study area showing three habitat matrices (agriculture, urban, forest) and the Guánica and Susúa State Forests in south-western Puerto Rico. The map also depicts major land cover classes and roads.

(*Elaenia martinica*). Frugivores were the Puerto Rican Bullfinch (*Loxigilla portoricensis*), Puerto Rican Spindalis (*S. portoricensis*) and Antillean Euphonia (*Euphonia musica*). The open-habitat species was the Black-Faced Grassquit (*Tiaris bicolor;* Raffaele *et al.*, 1998).

Avian surveys were designed following a multiseason occupancy framework with five seasons as the primary sampling periods, and three surveys per season as the secondary sampling occasions (MacKenzie *et al.*, 2003, 2006). In this design, survey stations are closed to changes in occupancy within seasons, but open to changes between seasons through the processes of local colonization and extinction. Surveys were conducted during two pre-breeding seasons (January–February 2010 & 2011), two breeding seasons (April–May 2010 & 2011) and a post-breeding season (July–August 2010). Primary sampling periods were defined on the basis of breeding chronology. The breeding season occurs between mid-March and early June, with presumed periods of movements or dispersal before and after the breeding season (Collazo & Groom, 2000; Gleffe *et al.*, 2006; Wiewel *et al.*, 2013). Surveys were conducted from sunrise until 1000 h. Avian species seen or heard during a 10-min period were recorded within a 100 m radius. We used this radius to facilitate detecting birds in open habitat (e.g. agriculture), and individuals with different home range sizes and densities (Efford & Dawson, 2012). Home ranges of Puerto Rican Bullfinch, Bananquits (*Coereba flaveola*) and Adelaide's Warbler (*Dendroica adelaidae*) range from 9 to 17.4 ha (Kornegay, 2011).

Habitat covariates

We measured canopy height (CAHT, m), canopy cover (CACOV) and understorey cover (UC) at each survey station (Table S1). Understorey and canopy cover were coded as: 1 = 0–20%, 2 = 21–40%, 3 = 41–60%, 4 = 61–80%, 5 = 81–100%. We also assessed fruiting tree availability within a 10 m radius from the centre of each survey station (FAI). On every survey, we coded the number of fruiting tree species with available fruit as: 0 = none, 1 = 1–2 species, 2 = 3–4 species, 3 = 4–5 species, 4 = 6 or more species (Carlo *et al.*, 2003). We expressed data as an average per season. Data per sampling occasion (i.e. sampling covariate) overparameterized models.

We further characterized the landscape using data layers from Puerto Rico Gap Analysis and program ArcGIS (Gould *et al.*, 2007; ESRI, 2010), as well as aerial imagery obtained through Google Earth (Google Inc., 2011). We estimated distance to perch(es) (DP), a measure of survey station isolation, defined as the straight line (m) between the centre of the station and the nearest discernible trees (clumps), hedgerows or forest irrespective of its patch size using aerial imagery. This covariate represented the nearest potential stepping-stone birds could use while travelling or seeking shelter (Baum *et al.*, 2004; Awade & Metzger, 2008; Boscolo *et al.*, 2008). We also considered a standardized forest patch size (DF) as another measure of isolation. This covariate was defined as the distance from the survey station to the nearest forested patch that matched the average forest patch cover containing survey stations in reserves and forested matrix (61% forest cover or 7.5 ha). We used a 200 m radius from the centre of each station to estimate this value because it was easier to capture the thematic context of each station with remotely sensed data (Gould *et al.*, 2007). We assumed that reserves and the forested matrix contained best habitat conditions for forest-depended species (except grassquits). Moreover, the average patch cover (61%) was similar to the

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patch cover (70–80%) used by Puerto Rican Bullfinches to return to site-of-capture during translocation experiments (Irizarry, 2012), conferring the metric a biological functional value. We used the same approach (200 m radius/survey station) to estimate two metrics across all matrices and reserves. These were survey-station per cent forest (SSFC) and herbaceous (SSHC) cover. We used the latter as a proxy of habitat openness for the Black-faced Grassquit, and the former as a measure of the amount of forest cover within a count station. Lastly, we estimated the size of forest patch within which each survey station was imbedded (PS_i). The subscript is meant to underscore that some survey stations (e.g. agriculture) will not be nested in a forested context, by definition, but might still contain forest cover (SSFC). This metric was calculated using the four cardinal direction patch rule (ESRI 2010). In this rule, pixels (30 × 30 m) in a raster dataset were grouped provided a full side, not a corner, touched the adjacent pixel of the same cover class type (i.e. forest). The initial point of this process was the survey station location. Patch size (ha) was the sum of the area of all the pixels that met the criterion for the cardinal rule. A summary of covariate definitions, the parameters modelled by each covariate, median, minimum and maximum values for each covariate are presented in Tables S1–S2.

Modelling approach

We constructed multiseason occupancy models to estimate initial occupancy (ψ_1), local seasonal colonization (γ) and local seasonal extinction (ε) (MacKenzie *et al.*, 2006). Initial local occupancy was defined as the probability that a surveyed station was occupied by a species in the initial season of the study ($\psi_{\text{pre-breeding 2010}}$). Local extinction probability (ε_s) is the probability that a survey station occupied by that species at season S is no longer occupied by the species in season $S + 1$. Local colonization probability (γ_s) is the probability that a survey station unoccupied by a species at season S becomes occupied at season $S + 1$. In this modelling framework, parameters are adjusted by detection probability, or the probability that at least one individual of a species is detected in season S, provided the individuals are available to be detected. Count data for every surveyed station were converted into an encounter history of presence (1), non-presence (0), or missed (−).

We developed a candidate model set to test *a priori* hypotheses and predictions listed in Table 1. The candidate set was created in two steps. First, we modelled the detection process to determine whether detections were constant (.) or season-specific (S) and whether detection was affected by three habitat covariates (Table 1). We also determined whether colonization and extinction probabilities were constant or season-specific. We adopted the model with lowest AIC obtained in this process to finalize the process (Anthony *et al.*, 2006). We determined whether support in the data favoured a model whose initial occupancy probability was influenced by matrix type. For some species, only two matrix types were modelled because the model would be overparameterized. We concluded by modelling colonization rates by measures of survey station isolation (DP or DF), and extinction rates by measures of habitat quality (FAI), and the amount of forest/herbaceous cover within stations (SSFC, SSHC), and size of the forest patch containing survey stations (PS_i). We modelled all covariates as additive factors. We did not model extinction rates by PS_i and SSFC because covariates were highly correlated. As in Kennedy *et al.* (2011), design and data constraints did not support modelling interaction terms. Before running models, all continuous covariates were normalized. Data were analysed using program PRESENCE (Hines, 2006).

Careful consideration of model assumptions is important for interpreting results. Multiseason occupancy models assume that: (1) occupancy state at each survey site does not change over surveys within a season; (2) the species was not falsely detected; and (3) species detections and detection histories at each survey site were independent. The first two assumptions were likely met given that surveys were conducted in a short period of time (< 2 months), at 2-week intervals by qualified bird observers. Also, sampling did not occur during transition periods between seasons. We addressed the third assumption by establishing survey sites at ≥ 500 m within matrices, many exceeding 1 km apart. Between matrices, the two closest survey stations were at 1.1 km (urban-forest) and 2.9 km (agriculture – urban).

We used Akaike's information criterion (AIC) to select the most parsimonious model (Burnham & Anderson, 2002). Models were ranked by AIC, and the model with the lowest AIC value had the most support in the data. The difference in AIC values (ΔAIC) between the best-supported model and other models was used to calculate model weights (AIC wgt), which indicate the relative likelihood of the model given the data and the model set (Burnham & Anderson, 2002). Models with ΔAIC ≤ 2 were considered models with highest support (Burnham & Anderson, 2002). Parameter estimates were model-averaged per species to account for parameter variability in competing models (ΔAIC ≤ 2). We considered an effect (i.e. covariate beta coefficient) to be strongly supported if the 95% confidence intervals did not overlap zero (otherwise the support was weak).

RESULTS

Survey stations in the agriculture and urban matrices were more isolated, had lower forest cover, and except for urban matrix stations, were not imbedded in forest patches. Fruit availability was highest in the urban matrix owing to the mix of natural and ornamental/consumptive trees, and was lowest in the agriculture matrix (Table S2). Below, we focus the discussion on models with strong support (ΔAIC > 2). The full set of competing models for each species is presented in supplemental information (S3-9). In all cases, initial occupancy was influenced by matrix type (Table 2). Parameter estimates were adjusted by detection probabilities which varied season-

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Table 2 Occupancy models whose support was $\Delta AIC \leq 2$ for seven species of native avian species in south-western Puerto Rico. Model parameters were estimated using multiseason occupancy models and avian surveys conducted in three habitat matrices, namely agriculture (A), urban (U), forest (F) (January 2010–June 2011). Matrices were located between Guánica and Susúa State Forest reserves (R). Model parameters were as follows: ψ is the probability of a survey station being occupied, given that the species was available for detection. γ is the probability of a species being present at season S + 1, given that it was absent at S. ε is the probability of a species being absent at season S + 1, given that it was present at S. *P* is the probability of a species being detected at a survey station. Model parameters that are strongly influenced by a covariate (95% CIs for beta estimates did not overlap zero) are identified with an asterisk (*). Model covariates, definitions and predictions are listed in Table 1 and Tables S1 and S2, and model selection tables presented in Tables S3–S9.

Model	AIC	AIC wgt	Parameters	−2*LogLike
Puerto Rican Spindalis				
ψ (F + R), γ (DP), ε (FAI*), *P* (S + CAHT)	1148.72	0.43	13	1122.72
ψ (F + R), γ (DP), ε (FAI*+SSFC), *P* (S + CAHT)	1148.72	0.31	14	1121.41
Puerto Rican Woodpecker				
ψ (A + U), γ (DP), ε (F + A + U + SSFC + FAI*), *P* (S + CACOV)	1283.70	0.45	17	1249.70
ψ (F + A + U), γ (DP), ε (SSFC + FAI*), *P* (S + CACOV)	1284.20	0.35	15	1254.20
Antillean Euphonia				
ψ (F + A + U), γ (F + A* + U*), ε (F* + R), *P* (S + CACOV)	955.39	0.32	17	921.39
ψ (F + A + U), γ (F + A* + U*), ε (F* + R + PS), *P* (S + CACOV)	957.22	0.13	18	921.22
Black-faced Grassquit				
ψ (F + A + U), γ (F* + A* + U), ε (SSFC*), *P* (S + CACOV)	2194.88	0.38	16	2162.88
ψ (F + A + U), γ (F* + A* + U + DP), ε (SSFC*), *P* (S + CACOV)	2196.17	0.20	17	2162.17
ψ (F + A + U), γ (F* + A* + U + DP), ε (SSHC*), *P* (S + CACOV)	2196.52	0.17	16	2164.52
Puerto Rican Bullfinch				
ψ (F + R), γ (F + R + DF*), ε (F* + R*), *P* (S + UC)	1248.16	0.35	16	1216.16
ψ (F + R), γ (F + R + DF*), ε (F* + R* + FAI), *P* (S + UC)	1249.1	0.22	17	1215.1
ψ (F + R), γ (F + R + DF*), ε (F* + R* + PS_i), *P* (S + UC)	1250.05	0.14	17	1216.05
ψ (F + R), γ (F + R + DF*), ε (F* + R* + SSFC), *P* (S + UC)	1250.07	0.13	17	1216.07
Puerto Rican Vireo				
ψ (F + A + U), γ (.), ε (SSFC*), *P* (S + UC)	822.78	0.35	13	796.78
ψ (F + A + U), γ (DP), ε (SSFC*), *P* (S + UC)	823.35	0.26	14	795.35
ψ (F + A + U), γ (.), ε (SSFC* + PS_i), *P* (S+UC)	824.78	0.13	14	796.78
Caribbean Elaenia				
ψ (F + A + U), γ (DP), ε (.), *P* (UC)	681.75	0.22	9	663.75
ψ (F + A + U), γ (.), ε (.), *P* (UC)	681.88	0.20	8	665.88
ψ (F + A + U), γ (DP), ε (PS_i), *P* (UC)	683.21	0.10	10	663.21
ψ (F + A + U), γ (DF), ε (.), *P* (UC)	683.37	0.09	9	665.37
ψ (F + A + U), γ (.), ε (PS_i), *P* (UC)	683.43	0.09	9	665.43
ψ (F + A + U), γ (DP), ε (SSFC), *P* (UC)	683.66	0.08	10	663.66
ψ (F + A + U), γ (.), ε (SSFC), *P* (UC)	683.66	0.08	9	665.66

ally, and in all cases, influenced strongly by one of three habitat covariates that could affect the ability of an observer to detect birds (Table 2).

Local colonization rates were constant across seasons, but influenced by distance to perches for the Puerto Rican Spindalis and woodpecker (Table 2). Spindalis extinction rates were also constant across seasons, and competing models featured a strong and negative influence of fruit availability (Table 3, Fig. 2). Extinction rates for woodpeckers were also constant across seasons, but moulded by matrix type (positive and strong in forest matrix). Competing models featured forest cover and fruit availability, which had a negative, and strong influence on extinction rates (Table 3, Fig. 2). Colonization rates for the Antillean Euphonia were constant over seasons, but influenced strongly and negatively influenced at the agriculture and urban matrices (Table 3). Extinction rates were also constant over seasons, influenced by matrix type, negatively and strongly in the forest matrix (Table 3).

Colonization rates for the Black-faced Grassquit were seasonally constant, and strongly and negatively influenced within the forest and agriculture matrices (Tables 2 and 3). Two of the competing models featured distance to perches. Extinction rates were strongly and positively influenced by station-survey forest cover (Table 3). Colonization rates for the Puerto Rican Bullfinch were negatively and strongly influenced by distance to forest patches (Fig. 3), and extinction rates negatively and strongly by forest matrix and reserves (Table 3, Fig 4). Colonization rates for the Puerto Rico Vireo were seasonally constant, with a competing model featuring a weak influence by distance to perches. Conversely, extinction rates were strongly and negatively

Table 3 Beta (± SE) estimates for factors affecting local colonization (γ) and extinction (ε) probability from the top multiseason occupancy model of each species based on avian surveys conducted in three habitat matrices, namely agriculture (A), urban (U), forest (F) in south-western Puerto Rico (January 2010–June 2011). Matrices were located between Guánica and Susúa State Forest reserves (R). Strong influence means that 95% CIs for beta estimates did not overlap zero; weak is the opposite. Model covariates, definitions and predictions are listed in Table 1 and Tables S1 and S2, and model selection tables presented in Tables S3–S9.

Species	Colonization (γ)	Extinction (ε)	Beta Estimate	SE	Influence
Puerto Rican Spindalis	DP	–	−1.93	1.26	Weak
	–	FAI	−1.01	0.46	Strong
Puerto Rican Woodpecker	–	F	4.79	2.21	Strong
	–	A	0.17	1.64	Weak
	–	U	0.21	2.03	Weak
	DP	–	−1.93	1.26	Weak
	–	FAI	−3.17	1.33	Strong
		SSFC	−1.87	1.06	Weak
Antillean Euphonia	F	–	−1.02	1.14	Weak
	A	–	−1.20	0.52	Strong
	U	–	−2.75	0.91	Strong
		F	−5.28	2.17	Strong
		R	−2.04	1.21	Weak
Black-Faced Grassquit	F	–	−2.48	0.83	Strong
	A	–	−1.86	0.88	Strong
	U	–	−1.51	1.02	Weak
	–	SSFC	0.51	0.16	Strong
Puerto Rican Bullfinch	F	–	−1.07	1.01	Weak
	R	–	−0.81	1.8	Weak
	DF	–	−1.19	0.53	Strong
	–	F	−1.56	0.66	Strong
	–	R	−3.58	0.9	Strong
Puerto Rican Vireo	–	SSFC	−1.25	0.40	Strong
Caribbean Elaenia	DP	–	−1.84	2.47	Weak

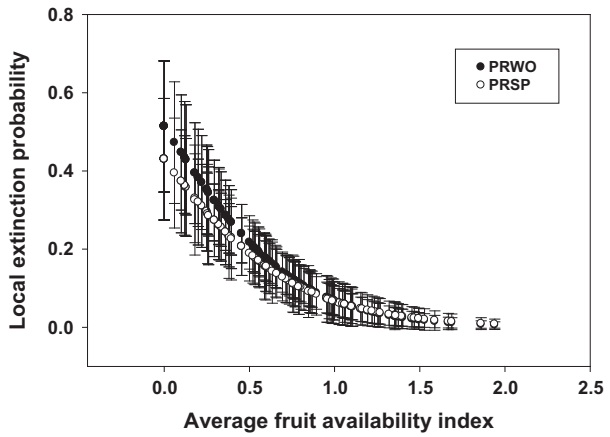

Figure 2 Local extinction probability (± SE) for Puerto Rican Spindalis (PRSP) and Woodpecker (PRWO) as a function of the average fruit availability index at survey stations in three habitat matrices, namely agriculture (A), urban (U), forest (F) and forest reserves (R). Matrices were located between Guánica and Susúa State Forest reserves in south-western Puerto Rico.

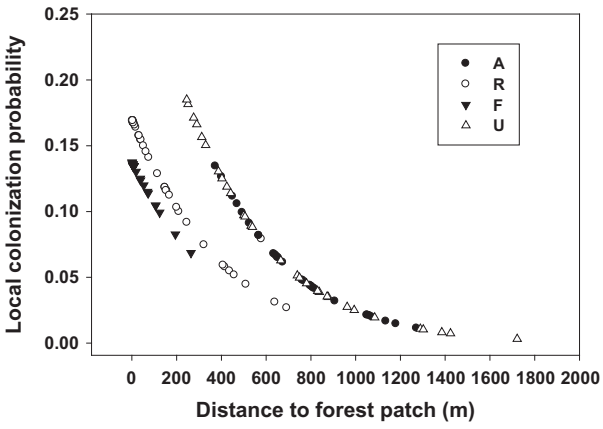

Figure 3 Local colonization probability for Puerto Rican Bullfinches at survey stations as a function of distance to forest patches in three habitat matrices, namely agriculture (A), urban (U), forest (F). Matrices were located between Guánica and Susúa State Forest reserves (R) in south-western Puerto Rico. This metric was defined as the distance from the survey station to the nearest forested patch that matched the average forest patch cover in survey stations in reserves and forested matrix (mean = 61%, range: 24–88%). Estimates of colonization probability were model-averaged. SE were not plotted to avoid obscuring estimate grouping by matrix type.

influenced by forest cover (Table 3). Model selection for Caribbean Elaenia exhibited the highest degree of uncertainty. Six models were considered plausible alternatives

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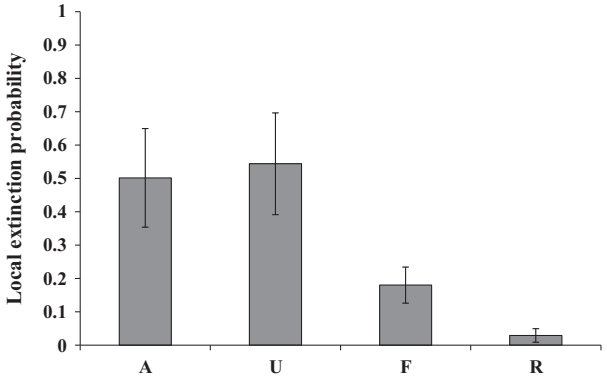

Figure 4 Local extinction probability (± SE) for the Puerto Rican Bullfinch at survey stations as a function of matrix type, namely agriculture (A), urban (U), forest (F) and forest reserves (R). Matrices were located between Guánica and Susúa State Forests in south-western Puerto Rico. Estimates were model-averaged.

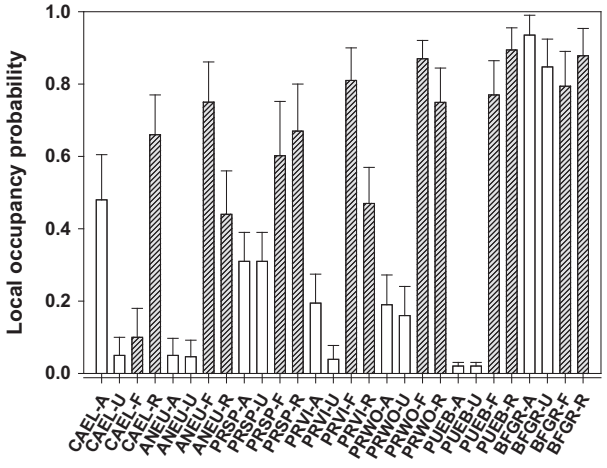

Figure 5 Local initial occupancy probability (± SE) for the Caribbean Elenia (CAEL), Antillean Euphonia (ANEU), Puerto Rican Spindalis (PRSP), Puerto Rican Vireo (PRVI), Puerto Rican Woodpecker (PRWO), Puerto Rican Bullfinch (PRBU) and Black-faced Grassquit (BFGR) at survey stations highlighting the contrast between agriculture (A) and urban (U) matrices (clear bars), and forest (F) matrix and forest reserves (R) (hatched bars). Matrices were located between Guánica and Susúa State Forest reserves in south-western Puerto Rico. Initial occupancy was defined as the probability that a surveyed station was occupied by a species in the initial season of the study ($\psi_{\text{pre-breeding 2010}}$). Occupancy estimates were model-averaged.

(ΔAIC < 2; Table 2). Colonization rates featured weak influence of distance to perches or forest patches (Table 2 & 3). There was also weak support for the influence of forest patch size (PS_i) and forest cover on extinction rates.

All species but the Black-faced Grassquit and Caribbean Elaenia had markedly higher occupancy probabilities in forested habitats (Fig. 5). The Elaenia exhibited high occupancy in the agricultural matrix, and grassquits were pervasive in all habitats. Seasonal occupancy probabilities followed the same pattern, that is, higher in forested habitats during all seasons as compared to the remaining matrices as illustrated by the euphonia (Fig. 6). For all species, occupancy rates varied seasonally, but the 95% CI of the initial and last occupancy estimates overlapped, suggesting that there was no support for a statistical trend.

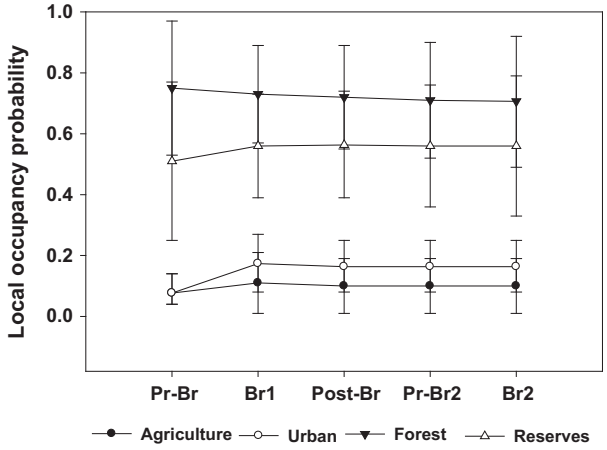

Figure 6 Local seasonal occupancy probability for the Antillean Euphonia at survey stations in three habitat matrices, namely agriculture, urban, forest. Matrices were located between Guánica and Susúa State Forest reserves in south-western Puerto Rico. Estimates were model-averaged. The 95% confidence intervals for each seasonal estimate are depicted.

DISCUSSION

We quantified seasonal occupancy of seven resident avian species in south-western Puerto Rico to gain insights about the processes that influence species occurrence in human-modified landscapes. As predicted, species occupancy was mediated by matrix type. Occupancy was higher in forest reserves and forested matrix than in the urban and agricultural matrices, a finding in accord with the strong forest affinities of the forest-dependent species (Gould *et al.*, 2007; Acevedo & Restrepo, 2008; Vázquez-Plass & Wunderle, 2012). Contrary to expectation, we found no evidence for season-specific local colonization and extinction rates. This finding is in concert with the lack of statistical change in occupancy among five seasons. Seasonal changes would be associated with changes of habitat conditions in and around survey stations, and we did not witness any appreciable change during the study. Another possibility is that seasonal movements do occur, but survey stations never become unoccupied (i.e. always at least one bird present). In this scenario, the presence of transients is not measurable because the influx of birds is better measured as changes in numbers per station. It is also possible that transients move through the landscape, but our biweekly sampling schedule was too coarse to detect changes in station state (occupied or not). Our findings, however, paralleled those of Kennedy *et al.*

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(2011) in that habitat matrices exerted a strong influence on the processes governing distribution of avian species, but their occupancy rates remained stable over a multiyear study in Jamaica.

Black-faced Grassquits, an open-habitat specialist, were prevalent in all habitat matrices and forest reserves, but not surprisingly, attaining highest levels of occupancy in the agriculture matrix. High occupancy rates in forested habitats suggested that some stations contained herbaceous habitat, and indeed that was the fact (13% cover, on average). The Caribbean Elaenia also exhibited high occurrence in the agriculture matrix, facilitated by the presence of perching structures (DP is featured in 4/7 competing models). The flycatcher probably takes advantage of hedgerows and similar structural features during foraging. Of the forest-dependent species we studied, Puerto Rican Spindalis exhibited the highest occupancy rates in urban matrix (0.31 ± 0.08). Vázquez-Plass & Wunderle (2012) and Suarez-Rubio & Thomlinson (2009) reported greater abundance of Puerto Rican Spindalis in urbanized landscapes as compared to another forest specialist, the Puerto Rican Bullfinch. Our results affirm this pattern, lending support to the possibility that some forest-dependent species might be adept at exploiting urban landscapes. This trait may allow insular, forest-dependent species to exploit novel habitats as they have evolved in an environment that undergoes frequent disturbances (Lugo *et al.*, 2012b).

Local extinction rates were mediated by matrix type for euphonia, bullfinch, and woodpecker. Regardless of species, rates were predominantly and strongly influenced by amount of forest within stations (SSFC) and a proxy of habitat quality, fruiting trees. Patch size was featured in competing models for 4/7 species, all forest dependent, but its influence was weak (beta 95% CIs overlapped zero). We note that survey stations, at least in the forest matrix and reserves, occurred in patches ranging from 0.25 to 5420 ha. Kennedy *et al.* (2011) reported that patch size was strongly associated with patch extinction, but only for 2/9 species. Our findings were similar to Kennedy *et al.* (2011) in that within-patch quality and context (matrix type) were stronger determinants of extinction rates. Patch size does have a strong influence on avian occupancy (Ferraz *et al.*, 2007); however, it appears that its influence may not hold in all habitat contexts, particularly those strongly modified by humans (Tews *et al.*, 2004). This array of context-dependent results, while valuable, also suggests that further research is warranted to better understand the demographic implications of human-modified landscapes. We suggest that approaches such as multistate occupancy models could be useful in such endeavours as it provides the analytical framework to estimate, for example, the probability of detecting reproductive activities given that a patch or point of interest on the landscape is occupied (Nichols *et al.*, 2007; MacKenzie *et al.*, 2009; Rogers *et al.*, 2013).

Our findings provide a quantitative basis to guide conservation design in south-western Puerto Rico. Occupancy rates in the forested matrix were similar to those estimated for the forest reserves despite the presence of low-density human habitation in the former (Gould *et al.*, 2007). Similarities highlight the value of such matrices for conservation (Watling *et al.*, 2011). Our work highlights the value of different habitat features on the landscape to facilitate colonization and persistence (1 – extinction) (e.g. small clump of trees, fruiting trees). Local colonization probabilities occurred at higher rates when habitat stepping stones (DP) were ≤ 0.5 km from the survey station. In the case of the Puerto Rican Bullfinch, distance to habitat patches (61%) strongly influenced colonization rates. This finding is consistent with independent work that showed that bullfinches moved through the urban matrix using similar forest patches (70–80% cover) to return to the place of capture during translocation experiments (Irizarry, 2012). It follows that permeability, the ease with which birds move through a matrix (Gobeil & Villard, 2002), could be enhanced by integrating knowledge about interpatch distance (Hanski, 1998 Haddad, 1999, 2000; Leider & Haddad, 2010; Irizarry, 2012). This implies that improvements in permeability across the eastern portion of our study area (i.e. Rio Loco watershed) could focus on minimizing interpatch distance as this was the matrix containing the longest distances to perches. We also highlight the value of proxies of habitat quality, particularly for the agricultural matrix. We found that stations that averaged ≥ 3 trees bearing fruits per season exhibited the lowest patch extinction rates. Moreover, the value of habitat patches or habitat stepping stones could be enhanced by planting trees species known to be part of the diet of resident species (e.g. Carlo *et al.*, 2003; Beltrán & Wunderle, 2013). Increasing forest cover (SSFC) is also worth considering as it contributed to lower extinction rates for species like the Puerto Rican Vireo. Increasing cover might provide greater foraging resources (e.g. arthropods) and potential nesting substrates (Woodworth, 1997).

Islands in the Caribbean have undergone dramatic changes in land cover, with marked impacts on their flora and fauna (Lugo *et al.*, 2012b). The scale of these changes highlights the importance of investigating the underlying processes governing distribution shifts and persistence. Our work expands the incipient body of work in the tropics (e.g. Kennedy *et al.*, 2011; Watling *et al.*, 2011) by drawing inferences from sampling units across the range of conditions in matrices, measured at a temporal scale that tracked important demographic cycles (e.g. seasonal reproduction). A focus on local extinction and colonization probabilities is of interest because they are directly influenced by management actions, and thus, a means to gauge their benefit (Nichols & Williams, 2006). Inferences about dynamic processes, however, require multiyear or multiseason databases (Guisan & Thuiller, 2005). Because building such databases involves costs, they should be nested in clearly defined conservation objectives (Nichols & Williams, 2006; Conroy *et al.*, 2011).

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Table S1. List of covariates, definitions, codes and modelled parameters to estimate local occupancy [psi, (ψ)], colonization [gamma, (γ)], extinction [epsilon (ε)], and detection (ρ) probabilities in three habitat matrices and Guánica and Susúa State Forests in south-western Puerto Rico.

Table S2. Summary of covariates used to model local colonization (γ) and extinction (ε) probabilities of resident avian species in three habitat matrices and the Guánica and Susúa State Forest reserves in south-western Puerto Rico.

Tables S3–S9. Model selection tables for Puerto Rican Spindalis, Puerto Rican Woodpecker, Antillean Euphonia, Black-faced Grassquit, Puerto Rican Bullfinch, Puerto Rican Vireo, and Caribbean Elaenia.

BIOSKETCH

The authors are interested in avian ecology and conservation. This endeavour values understanding the underlying processes that influence distribution patterns in human-modified landscapes to inform conservation design in the United States and the Caribbean.

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