Influence of landscape structure and forest age on the richness and abundance of different bird feeding guilds and forest-dependent birds in a seasonal dry tropical forest of Yucatan, Mexico

WALDEMAR SANTAMARÍA-RIVERO, EURÍDICE LEYEQUIÉN[*], JOSÉ LUIS HERNÁNDEZ-STEFANONI & PAUL WOOD

Centro de Investigación Científica de Yucatán, Unidad de Recursos Naturales, Calle 43 #130 Chuburná de Hidalgo, C.P. 97200, Merida, Yucatan, Mexico

Abstract: Tropical dry forests (TDF) are subject to intense human intervention leading to an increase of secondary forests and changes in habitat suitability for birds. Despite the increasing research on secondary forests, we have little understanding of how such changes in tropical dry forests have affected animal communities. The main goal of this research was to investigate the influence of successional age, vegetation structure, and landscape characteristics on tropical bird species or functional groups (i.e. feeding guilds, forest-dependent birds, and individual species of conservation interest) in a TDF. Specifically, we addressed the following questions for both the breeding season and for the non-breeding season: (1) do different successional stages (age) support different levels of total bird species richness and of species richness of different feeding guilds and the group of forest-dependent bird species; (2) does the relative abundance of individual bird species of conservation interest differ across successional stages, and, (3) what is the relative contribution of succession age, vegetation physical structure, and configuration of landscape elements on the species richness of various feeding guilds and the group of forest-dependent birds, and on the relative abundance of individual species of conservation interest? We used a stratified sampling design based on 274 sites that varied according to successional stages over an area of 352 km² in Yucatan, Mexico to assess bird numbers during 2008 and 2009 using the double-observer method. We used a SPOT5 imagery (2005) to produce a land cover map in which the vegetation classes represented different stages of forest succession as well as topographic position. From the land cover map several landscape metrics were calculated and used to relate bird species richness in the different feeding guilds, as well as the relative abundance of the individual species of conservation interest, with landscape structure. We detected 103 species of birds, which were assigned to one of nine feeding guilds and forest-dependent group. Bird species richness was often similar across the successional gradient with guilds changing across the gradient. Specifically, forest age was associated with an increase in species richness of guilds vulnerable to habitat modification and forest-dependent species. Our findings indicate that large, preferably interconnected, patches of older successional forest could aid bird conservation in TDF.

Key words: Ecological succession, landscape structure, neo-tropical avifauna, secondary forests, tropical dry forests.

Handling Editor: Christopher A. Lepczyk

Corresponding Author; e-mail: leyequien@cicy.mx

Introduction

Tropical dry forests (TDF) account for 42 % of tropical forest cover worldwide (Murphy & Lugo 1986). TDF are subject to intense pressure from human intervention in the form of deforestation, fragmentation, and changes in land use (Chazdon *et al.* 2005) leading to an intricate landscape mosaic in which secondary forests represent an important element. Globally, secondary tropical forests together with degraded forestland that has been severely damaged by the excessive harvesting of wood and/or non-wood forest products comprise nearly half of the remaining tropical forest (ITTO 2002), and are increasing in area (FAO 2007). The increase in secondary forests has led to changes in the quantity and quality of available habitat to forest birds (Warkentin *et al.* 1995). Secondary forests influence changes in species numbers in bird communities and also in different bird feeding guilds (Pineda-Diaz de Bonilla *et al.* 2012). Despite the potential importance of tropical secondary forests for maintaining comparable bird abundance, species richness and diversity with older forest stages, the potential for them to sustain tropical bird communities is still poorly understood (Smith *et al.* 2001). Some tropical bird species may be resilient to changes in habitat area, quality, and the surrounding matrix (Laurance & Bierregard 1997), however, other species such as forest-dependent birds have a greater vulnerability to loss and fragmentation of habitat (Arriaga-Weiss *et al.* 2008; Leyequien *et al.* 2010). Specifically, feeding guilds vary in their resilience to habitat disturbance (Dunn 2004; Gray *et al.* 2007; Pearman 2002; Pineda-Diez *et al.* 2012), and bird diversity and guild specialization increase with forest age in the tropics (Brady & Noske 2009).

The degree of fragmentation that characterizes a given landscape can be described as a function of the size, shape, similarity, and contrast of forest patches and other metrics of the geometry and structure of landscape patterns (Gustafson 1998; MacGarigal *et al.* 2002). Landscape structure influences bird communities due to changes in vegetation, food resources, predation, brood parasitism, and competition, which in turn influence species richness and abundance of different birds (MacGarigal & McComb 1995). Some functional groups (e.g., feeding guilds) and forest-dependent bird species have been found to be more sensitive to changes in habitat structure since they require trees with larger diameters and heights for foraging and nesting (e.g., Dendrocolaptidae and Picidae). On the other hand, open-habitat species (e.g., certain species of Columbidae or Icteridae) may be favoured by landscape fragmentation since the resulting habitats resemble their natural habitat or provide abundant food resources (Gray *et al.* 2007; Stouffer *et al.* 2006). Feeding guilds, therefore, represent ecologically significant units that can help identify key resources for bird communities and provide information about changes that take place in animal community structure and functioning after a disturbance (Gray *et al.* 2007).

The main goal of this research was to investigate the influence of successional age, vegetation structure, and landscape characteristics on tropical bird species and functional groups (i.e. feeding guilds, forest-dependent birds, and individual species of conservation interest) (Chazdon *et al.* 2009) in a TDF. In other words, to what extent tropical bird species in a TDF can use the secondary forests and how configuration of landscape elements within the surrounding mosaic affects bird use. Specifically, we addressed the following questions for both the breeding season (northern summer) and for the non-breeding season (northern winter): (1) do different successional stages (age) support different levels of total bird species richness and of species richness of different feeding guilds and the group of forest-dependent bird species; (2) does the relative abundance of individual bird species of conservation interest differ across successional stages; and, (3) what is the relative contribution of succession age, vegetation physical structure, and configuration of landscape elements on the species richness of various feeding guilds and the group of forest-dependent birds, and on the relative abundance of individual species of conservation interest?

Methods

Study area

The study area is located in the south of Yucatan State (20º 01' 21" - 20º 09' 50" N, and 89º 23' 06"- 89º 36' 32" W) and occupies 352 km² within a mosaic of seasonally dry tropical forest (medium stature sub-deciduous forest) in different successional stages, agricultural areas (both mechanized and traditional slash-and-burn shifting cultivation), and human settlements. According to the classification system of Köppen, modified by García (1973), the climate type is Aw and is characterized as being warm and sub-humid, with

a wet season from June and October and a marked dry season from March to May. The average annual temperature is 26 ºC with annual rainfall fluctuating between 800 - 1440 mm. The study area consists of Cenozoic limestone hills with moderate slope (10 - 25°) alternating with flat areas, and the elevation ranges from 62 to 196 m.

Land cover mapping

We used imagery acquired in 2005, which was selected because it was the most current free-cloud imagery for the studied area. Using bands 2 (red), 3 (near infrared), and 4 (mid infrared) of Spot 5 satellite imagery (10 m spatial resolution), a false colour composite image was created. Every band was previously geo-referenced and radiometrically corrected to diminish the effect of atmospheric scattering. This composite image was used as a spatial reference framework for selecting suitable training sites for the different land cover types to be identified on the ground. At least ten training sites were selected for each land cover type (see Appendix 1). Using a Global Positioning System (GPS) unit, the selected training sites were located in the field, for each of the following land cover types: (a) 3-8 y-old secondary forest (vegetation class 1); (b) 9-15 y-old secondary forest (vegetation class 2); (c) >15 y-old secondary forest on flat areas (vegetation class 3); (d) >15 y-old secondary forest on hills (vegetation class 4); (e) agricultural fields; and, (f) urban areas and roads. The vegetation classes represented different stages of forest succession as well as topographic position (hills vs. flat areas), for which hills only occur in the >15 y-old secondary forest classes. Both attributes have an influence on vegetation structure and composition (Dupuy *et al.* 2012). After removing some redundant training sites, a total of 26 training areas were used for performing a supervised classification with the Maximum Likelihood Algorithm to produce a land cover raster map. To remove the speckle in the classified image a 3 × 3 median filter was applied, which replaces the central pixel of the filter array with the median of the total array as it passes over the image thereby smoothing out the image for continuity (Bahadur 2009; Martínez-Beltran & Calera-Belmonte 2001; Zhu 2013). A total of 276 field-sampling plots were used for assessing the accuracy of the classified land cover map. These samples had a dual function, not only were they used to compute vegetation structure at sampling locations, but also to test the accuracy of the classes generated from the satellite image classification. Two procedures were used for accuracy assessment, namely, overall accuracy and the Cohen's Kappa statistic (see Hernández-Stefanoni *et al.* 2011 for details).

Vegetation data and sampling design

Vegetation data were recorded from a hierarchical plant survey conducted during the rainy season of 2008 and 2009. First, 23 landscapes of 1 km² were selected for sampling that differed in degree of forest fragmentation, from those units dominated by agricultural areas to those dominated by the oldest stage of forest succession. Within each landscape 12 plots of 200 m² were located following a stratified random design considering each of the four vegetation classes (276 sampling sites in total) (Fig. 1). Each circular plot of ~200 m², was located using a GPS unit, where diameter and height were recorded for all woody plants > 1 cm in DBH (diameter at breast height, 1.3 m). Stand age (i.e. succession vegetation age) of sampling plots and training sites was determined by interviewing local ≥ 40-year-old residents, who owned or worked the land (for details see Dupuy *et al.* 2012).

Calculation and selection of landscape metrics

To calculate the landscape metrics we considered the landscape mosaic model, in which the fragments are bounded by patches of other patch types that may be more or less similar to the focal patch type (MacGarigal & Cushman 2002). Landscape metrics were calculated across the 23 landscapes for the four vegetation classes and a class named as background, which represented areas with no vegetation. The individual patches were defined on the basis on cover type, grouping contiguous pixels of the same class (i.e. all clusters of vertical, horizontal, or diagonal pixels), while a patch type considers all the individual patches of the same vegetation class. Most of the metrics applied to vegetation classes can be interpreted as fragmentation indices, because they measure the configuration of a particular patch type (McGarigal *et al.* 2002). We used patch-type metrics and selected *a priori* indices of perimeter, shape, proximity, similarity, and contrast that were ecologically relevant.

Since many landscape metrics are redundant or represent an alternative formulation of the same information (see Appendix 2 for all metrics), we used Pearson correlation coefficients between each pair of the *a priori* selected metrics to choose
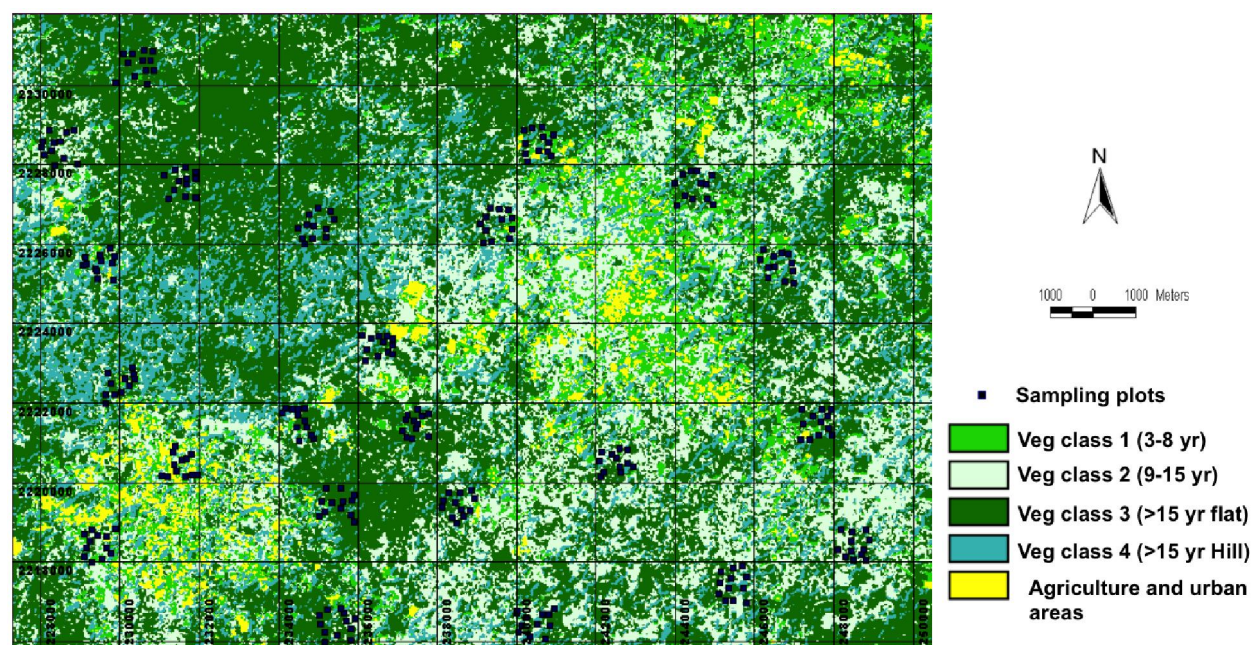
Fig. 1. Land cover map of the study area obtained from a supervised classification and field sample units' location. Vegetation class 1 = 3-8 y-old secondary forest, vegetation class 2 = 9-15 y-old secondary forest, vegetation class 3 > 15 y-old secondary forest on flat areas, and vegetation class 4 > 15 y-old secondary forest on hills.

those metrics with the minimum correlations (Hargis *et al.* 1998). Metric selection was done by considering variables that quantify different aspects of landscape configuration, and the potential explanatory power of a given metric for bird species richness and abundance (e.g., Fahrig 2003; Leyequien *et al.* 2007, 2010). For example, both patch area and landscape isolation variables affect species presence, abundance, or richness (Mazerolle & Villard 1999). We also considered how such measurements are used successfully in the landscape ecology literature (Thornton *et al.* 2011). On the basis of these points we selected: (1) the proportional abundance of each patch type (PLAND), (2) edge density (ED), (3) patch density (PD), (4) patch shape complexity (SHAPE), (5) the proximity of similar patch types (PROXI), (6) the similarity of neighboring patches (SIMI), and (7) edge contrast (TECI), where higher values indicate greater contrast along the patch perimeter (MacGarigal & McComb 1995) (see Appendix 3 for details and description). To calculate the proximity index, a search radius of 30 pixels (300 m) was selected, which coincides with empirically derived evidence about the average size of a patch in the area. The weighted edge contrast between vegetation cover classes, required to compute the total edge contrast index, was calculated as the

inverse of the Morisita-Horn similarity index between each pair of vegetation cover classes (Hernández-Stefanoni *et al.* 2011).

Bird data

Bird data were recorded following the same sampling design as the plant surveys, however, two plots located in slash-and-burn shifting cultivation were excluded from bird surveys because there were no more plots under this land use category and statistical analysis could not be done using only two plots. In total, 274 points were included in the analysis, with 47 in vegetation class 1, 76 in class 2, 87 in class 3, and 64 in class 4. We used a modified double-observer method (Nichols *et al.* 2000) to conduct each point count in order to minimize the bias of birds present but not detected. The double-observer sampling has been reported as suited to estimate detectability, which is a function of the conspicuousness of cues (e.g., vocalizations, conspicuous movements) and the abundance of cues (McCallum 2005). In our study we had two couples of observers, for each couple a primary observer was designated who indicated to the secondary observer all birds detected. The secondary observer recorded all detections of the primary observer as well as any birds not detected

by the primary observer. We also conducted standardisation exercises testing for differences in distance calculation between couples (see Kepler & Scott 1981). All dubious detections were eliminated from the database to avoid commission errors. We carried out a screening to find dubious detections using the following criteria: (a) the main region of the species distribution reported in Mexico; (b) difficulty to identify the species only by aural register; and, (c) difficulty to identify the species without capture techniques. We also excluded carnivores (e.g., hawks and eagles) and highly aerial birds (e.g., swifts) because of their low number of records. We used the same four observers (two pairs) during all sampling periods. Point counts had a fixed radius of 40 m and were a minimum of 200 m apart. To reduce estimation error, we recorded the distance and position for each individual heard or seen within the fixed radius over a 12-minute period (Hutto *et al.* 1986; Ralph *et al.* 1996; Volpato *et al.* 2009). Counts were initiated 10 min after dawn, and continue until ≈ 10:00 hrs. On arrival at each point, observers waited 5 min before starting the count in order to minimize the effects of disturbance. Counts were not conducted in rain, fog, or strong winds (Arriaga-Weiss *et al.* 2008; Vergara & Armesto 2009). At each point, counts were conducted once during the breeding season and once during the non-breeding period for migrants. A total of 166 point counts (14 landscapes) were conducted during 2008 and 108 point counts (9 landscapes) during 2009, all points were sampled in both the breeding and non-breeding season.

Classification of feeding guilds

We used the following criteria to group bird species into feeding guilds based upon literature (Arriaga-Weis *et al.* 2008; Milesi *et al.* 2002) and *in situ* field observations as well as consulting ornithologists with > 20 years of experience in the region (MacKinnon & Wood *unpublished observations* 2009): (1) primary food source (insectivores, frugivores, granivores, and omnivores), and (2) foraging stratum or substrate (bark, arboreal, shrub, understorey, terrestrial or ground) (Arriaga-Weiss *et al.* 2008; Gray *et al.* 2007; MacKinnon & Wood *unpublished observations* 2009; Milesi *et al.* 2002). Using these two criteria, we selected the following feeding guilds: (1) bark-gleaning insectivores (BGI), (2) arboreal insectivores (AI), (3) shrub insectivores (SI), (4) understory insectivores (UI), (5) ground-foraging insectivores (GFI), (6) arboreal frugivore (AF), (7) understory frugivore (UF), (8) terrestrial granivore (TG), and (9) arboreal omnivore (AO). Otherfeeding guilds were excluded from analysis since they were represented by few species with few records. Also, we grouped forest-dependent birds (FD) into a category and classified these species based on: (a) food source, (b) reproductive needs, (c) relative abundance in the study area, and (d) susceptibility to habitat modification and/or associated with old-growth forest (see Appendix 5 for the list of species). Finally, we selected 15 individual species of conservation interest to investigate species level responses based on one or more of the following criteria: (a) higher abundance, (b) vulnerability to habitat disturbance, and (c) endemic to the Yucatan Peninsula (see Appendix 5).

Statistical analyses

We carried out separate analyses for each sampling period (breeding and non-breeding). We used analysis of variance (ANOVA) to test for differences in bird species richness and abundance among the four vegetation classes. The response variables (species richness or abundance) were coded by adding one to each observation, in order to avoid observations with zero values, and then they were square-root transformed before applying the ANOVA analysis, in order to meet the assumptions of normality. We confirmed that all analyses met homogeneity of variance. In those cases where we found significant differences, we used Tukey's posthoc test ($P < 0.05$) to determine which vegetation class differed from each other.

We used multiple regression analysis to relate bird species richness in the different feeding guilds, as well as the relative abundance of the individual species of conservation interest, with landscape structure, successional age, and vegetation physical attributes. The dependent variables were species richness for each of the six feeding guilds, and the relative abundance of the 15 individual species of conservation interest. These variables were formally tested for normality and homogeneity of variances in the residuals (Zar 1999).The explanatory variables were successional stage (AGE), average canopy height of each vegetation class (CANOPY HEIGHT), and a group of seven patch-type metrics (PLAND, ED, PD, SHAPE, PROXI, SIMI, and TECI).

We considered a set of 15 plausible models (Table 1) predicting species richness of bird feeding

Table 1. Candidate models considered for predicting species richness of various bird feeding guilds and abundance of species from stand age, vegetation physical structure and landscape metrics. AGE: age after abandonment following slash-and-burn shifting cultivation; HEIGHT: Mean canopy height (m) per plot; PROXI: Distinguishes sparse distributions of small patches from complex cluster of large patches; PD: patch density; SIMI: % of the landscape occupied by the same patch type.

Model Identification	Model Description
1	$DV^* = B_0 + B_1 (AGE) + B_2 (HEIGHT)$
2	$DV^* = B_0 + B_1 (SHAPE) + B_2 (TECI)$
3	$DV^* = B_0 + B_1 (PROXI) + B_2 (SIMI)$
4	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD)$
5	$DV^* = B_0 + B_1 (SHAPE) + B_2 (TECI) + B_3 (AGE) + B_4 (HEIGHT)$
6	$DV^* = B_0 + B_1 (PROXI) + B_2 (SIMI) + B_3 (AGE) + B_4 (HEIGHT)$
7	$DV^* = B_0 + B_1 (PROXI) + B_2 (SIMI) + B_3 (SHAPE) + B_4 (TECI)$
8	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD) + B_4 (AGE) + B_5 (HEIGHT)$
9	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD) + B_4 (SHAPE) + B_5 (TECI)$
10	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD) + B_4 (PROXI) + B_5 (SIMI)$
11	$DV^* = B_0 + B_1 (PROXI) + B_2 (SIMI) + B_3 (SHAPE) + B_4 (TECI) + B_5 (AGE) + B_6 (HEIGHT)$
12	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD) + B_4 (SHAPE) + B_5 (TECI) + B_6 (AGE) + B_7 (HEIGHT)$
13	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD) + B_4 (PROXI) + B_5 (SIMI) + B_6 (AGE) + B_7 (HEIGHT)$
14	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD) + B_4 (PROXI) + B_5 (SIMI) + B_6 (SHAPE) + B_7 (TECI)$
15	$DV^* = B_0 + B_1 (PLAND) + B_2 (ED) + B_3 (PD) + B_4 (PROXI) + B_5 (SIMI) + B_6 (SHAPE) + B_7 (TECI) + B_8 (AGE) + B_9 (HEIGHT)$

* Dependent variable is species richness of abundance of species.

guilds and abundance of individual species from all possible combinations of the four main groups of explanatory variables: Area/Age (PLAND, ED, PD), Isolation/Proximity (PROXI, SIMI), Shape/Contrast (SHAPE, TECI) and Vegetation (AGE, CANOPY HEIGHT). We used the Akaike's Information Criterion (AIC; Anderson *et al*. 2000; Anderson & Burnham 2002) for the selection of the best models in the set of 15 models. The resulting models were ranked based on both the delta AIC values (differences of AIC or Δ_i) and the Akaike weights (a measure of the weight of evidence of being the best model or w_i) (Anderson *et al*. 2000; Johnson & Omland 2004). Subsequently, and because no single model is clearly superior to the others in the resulting set, we thus computed a weighted estimate of the predicted value, weighting the prediction by the Akaike weights, i.e., the model-averaged parameters and unconditional standard errors based on the Akaike weights (Burnham & Anderson 1998; Johnson & Omland 2004). Estimates obtained in this way typically have better precision and less bias than when based on a single model (Anderson *et al*. 2000). For

the calculation of the weighted estimate we used only the set of top candidate models with delta AIC values < 4, and an Akaike weight > 0.1 (Burnham & Anderson 1998). In our study we used delta AIC values < 4 based on Shibata (1989) that argues that underfitted models are a more serious issue in data analysis and inference than overfitted models.

Results

Land cover map

The study area covered 37,242 ha, of which 94.3 % was forest and the remaining 5.7 % being comprised of agriculture, urban areas and roads (Fig. 1). Among the forest cover, vegetation class 4 (> 15 y-old secondary forest on hills) was the largest land cover type spanning > 31 % of the total area (11,545 ha), followed by vegetation class 3 (> 15 y-old secondary forest on flat areas) with 27.3 % of the total area (10,158 ha), vegetation class 1 (3-8 y-old forest) with 18.5 % of the total area (6,900 ha), and vegetation class 2 (9 - 15 y-old forest) with 17.5 % of the total area (6,525 ha). The
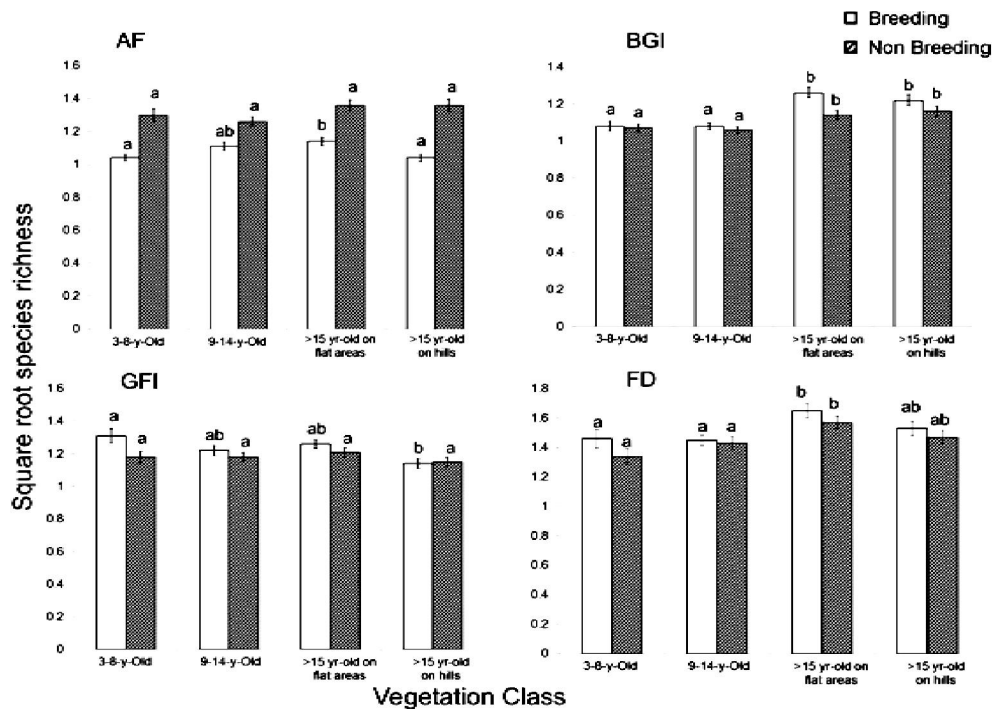
Fig. 2. Total species richness of various bird feeding guilds among vegetation classes, during breeding and non-breeding seasons. Different letters (a-d) indicate significant differences according to Tukey's post hoc test ($P < 0.05$). Only bird-feeding guilds with significant differences in one of both seasons are shown: AF (Arboreal frugivore), BGI (Bark-gleaning insectivores), GFI (Ground-foraging insectivores) and FD (Forest-dependent birds). Number of species data was root transformed.
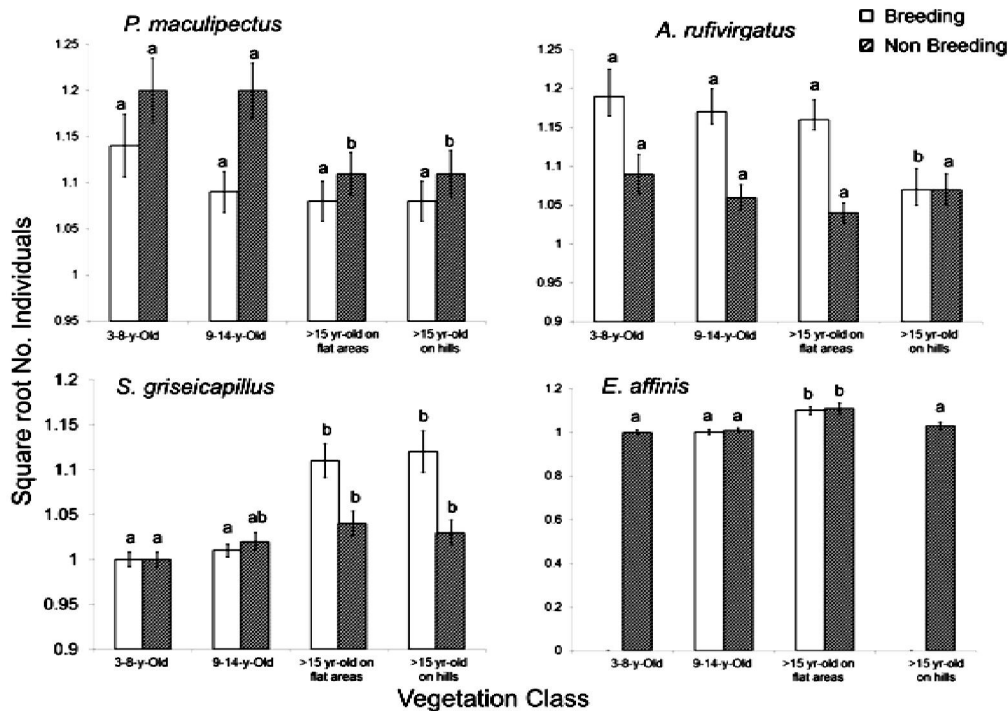
Fig. 3. Abundance of some species representative of various feeding guilds among vegetation classes; during breeding and non-breeding seasons. Different letters (a-d) indicate significant differences according to Tukey's post hoc test ($P < 0.05$). Only bird species with significant differences in one of both seasons are shown: *P. maculipectus*, *A. rufivirgatus*, *S. griseicapillus* and *E. affinis*. Abundance data were root transformed.

overall accuracy calculated for the map was 75.6 %, while the kappa index was 0.7. The greatest misclassifications among the vegetation-mapped classes occurred in the vegetation class 3 (relative accuracy of this vegetation type in the map was 66.0%). This misclassification can be explained by the fact that class 3 is not well differentiated in terms of structure of vegetation and species composition from vegetation class 4 (see Appendix 4).

Bird total species richness

A total of 103 bird species representing 22 families were recorded. Of these, 83 species were residents and 20 species were non-breeding (Appendix 5). Out of a total 4,377 records, 81.6 % were auditory and 18.6 % were visual. The most species-rich families were Tyrannidae (18 species), Parulidae (13 species), and Icteridae (9 species).

Species richness of feeding guilds amongst different vegetation classes

Overall bird species richness was higher in vegetation class 3 than that in classes 1, 2, and 4 during the breeding season ($F_{3, 271}$ = 4.95, $P <$ 0.002). However, bird species richness was similar during the non-breeding period ($F_{3, 271}$ = 1.62, $P <$ 0.19). Species richness differed among vegetation classes for the arboreal frugivores and ground-foraging insectivores during the breeding season ($F_{3,271}$ = 4.79, $P <$ 0.001 and $F_{3,271}$ = 4.55, $P <$ 0.001, respectively). These two guilds presented an opposite pattern, with arboreal frugivores richness increasing in the later successional stages (vegetation classes 3 and 4) and ground-foraging insectivores decreasing in the older forest (Fig. 2). However, species richness of both arboreal frugivores and ground-foraging insectivores was similar among vegetation classes during non-breeding season ($F_{3,271}$ = 2.02, $P <$ 0.11 and $F_{3,271}$ = 0.79, $P <$ 0.49, respectively). Bark-gleaning insectivores and forest-dependent birds were significantly different in species richness among vegetation classes during both breeding ($F_{3,271}$ = 10.99, $P <$ 0.001 and $F_{3,271}$ = 4.73, $P <$ 0.001, respectively) and non-breeding ($F_{3,271}$ = 3.81, $P <$ 0.01 and $F_{3,271}$ = 4.23, $P <$ 0.001, respectively) seasons. Species richness in bark-gleaning insectivores and forest-dependent birds was significantly higher in the older forests (Fig. 2). For arboreal insectivores, shrub insectivores, understory insectivores, understory frugivores, terrestrial granivores, and arboreal omnivores species richness was similar across the vegetation classes.

Abundance of individual species amongst different vegetation classes

Of the 15 individual species of conservation interest evaluated only four exhibited changes in abundance with vegetation class. Specifically, the abundance of *Pheugopedius maculipectus* differed among vegetation classes in the non-breeding season ($F_{3,271}$ = 2.84, $P <$ 0.003), with a greater abundance being detected in younger vegetation classes (Fig. 3). However, *P. maculipectus* abundance was similar among vegetation classes during the breeding season ($F_{3,271}$ = 0.876, $P <$ 0.45). On the other hand, *Arremonops rufivirgatus* and *Sittasomus griseicapillus*, differed in abundance among vegetation classes during the breeding season ($F_{3,271}$ = 3.47, $P <$ 0.01 and $F_{3,271}$ = 12.33, $P <$ 0.001, respectively). *A. rufivirgatus* was less abundant in vegetation class 4 than in all other classes, whereas *S. griseicapillus* was less abundant in the youngest forest (Fig. 3). Neither species abundances differed among vegetation classes during the non-breeding season ($F_{3,271}$ = 3.34, $P <$ 0.25 and $F_{3,271}$ = 1.54, $P <$ 0.20, respectively). Finally, the abundance of *Euphonia affinis* differed among vegetation classes during both breeding and non-breeding seasons ($F_{3,271}$ = 4.52, $P <$ 0.004 and $F_{3,271}$ = 6.49, $P <$ 0.001, respectively), with the species being more abundant in vegetation class 3 than in all other classes in both seasons.

Relationships between species richness of feeding guilds, stand age and landscape structure

One to five models predicted species richness, depending on the group of feeding guilds (Table 2). Based on model average using the top models, we predicted the species richness of various feeding guilds and the group of forest-dependent species, and the abundance of individual species from stand age, vegetation physical structure and landscape metrics (Table 3). During the non-breeding season species richness of arboreal frugivores was related to stand age and proximity of patches, indicating that species richness increased in old forest and with a landscape configuration composed by larger patches connected. Similarly, species richness of bark-gleaning insectivores and forest-dependent birds were positively associated with stand age or some of its concomitant structural features (canopy height) during both the breeding and non-breeding seasons (Table 3).

Table 2. Best models and model selection statistics for the analyses of effects of landscape patterns and structure of vegetation of individual patches on predicting species richness of various bird feeding guilds and abundance of species. Models were selected with Akaike weights greater than 0.1 and with delta AIC lower than 4.

Response Variable / Season	Feeding guilds or Species	Best models	Number of parameters	AIC	Delta AIC	Akaike weights
Species richness						
Non-Breeding	Arboreal frugivore	6	5	236.4	0.00	0.36
		1	3	237.2	0.83	0.24
	Bark-gleaning insectivores	1	3	216.3	0.00	0.44
		6	5	217.4	1.04	0.26
	Forest-dependant birds	1	3	357.7	0.00	0.78
Breeding	Bark-gleaning insectivores	1	3	245.5	0.00	0.72
		6	5	249.4	3.90	0.11
	Forest-dependant birds	15	3	400.1	0.00	0.21
		6	5	400.6	0.48	0.17
		4	4	401.2	1.13	0.12
		5	5	401.3	1.24	0.12
		3	3	401.4	1.25	0.11
Abundance of species						
Non-Breeding	*Arremonops chloronotus*	2	3	-193.9	0.00	0.24
		6	5	-193.3	0.63	0.18
		3	3	-192.6	1.36	0.12
		5	5	-192.3	1.62	0.11
		1	3	-192.1	1.79	0.11
Breeding	*Piranga roseougularis*	3	3	-118.1	0.00	0.60
		10	6	-115.2	2.88	0.14
		7	5	-115.1	3.06	0.13
	Sittasomus griseicapillus	5	5	-111.5	0.00	0.53
		1	3	-110.4	1.10	0.30

Relationship between species abundance, stand age, and landscape structure

In the case of species abundances, only three species showed relationships after the selection of the best models in the set of 15 models (Table 2). *Arremonops chloronotus*, a ground-foraging insectivore, was more abundant during the non-breeding period in landscapes dominated by patches of more regular shape (SHAPE) and with greater proximity to neighbouring patches of the same type (PROXI), according to model-averaged results (Table 3). On the other hand, during the breeding season the abundance of *Piranga roseogularis* (arboreal insectivore) showed a strong positive relationship with greater proximity to patches of the same vegetation type and *Sittasomus griseicapillus* (bark-gleaning insectivore) was posi-

tively related to vegetation height and negatively related to edge contrast (Table 3).

Discussion

Overall, our results indicate that different successional stages in tropical dry forests support distinct levels of bird species richness during the non-breeding season where older secondary forests support higher species richness, though there were no significant differences during the non-breeding season. In the case of feeding guilds, only two guilds differ in species richness among successional stages, bark-gleaning insectivores and arboreal frugivores, which had higher species richness in older secondary forests and were associated to greater vegetation structural complexity or continuity of forest. In contrast, ground-

Table 3. Model-averaged parameter estimates and (unconditional standard error) for predicting species richness of various bird feeding guilds and abundance of species from stand age, vegetation physical structure and landscape metrics. AGE: age after abandonment following slash-and-burn shifting cultivation; HEIGHT: Mean canopy height (m) per plot; PROXI: Distinguishes sparse distributions of small patches from complex cluster of large patches; PD: patch density; SIMI: % of the landscape occupied by the same patch type. Parameter estimates in bold indicate that 95 % confidence interval excludes 0.

Response Variable/ Season	Feeding guilds or Species	Model terms								
		Plan D	ED	PD	Proxi	Simi	Shape	Teci	Age	Height
Species richness										
Non-Breeding	Arboreal frugivore				**0.04** (0.01)	0.00 (0.00)			**0.03** (0.01)	0.02 (0.08)
	Bark-gleaning insectivores				0.00 (0.00)	0.00 (0.00)			**0.03** (0.01)	0.01 (0.07)
	Fores-dependant birds								**0.03** (0.01)	0.01 (0.08)
Breeding	Bark-gleaning insectivores				0.00 (0.00)	0.00 (0.00)			**0.05** (0.01)	0.01 (0.09)
	Fores-dependant birds	0.05 (0.06)	0.01 (0.01)	0.00 (0.02)	0.00 (0.00)	0.00 (0.00)	0.34 (0.31)	-0.03 (0.04)	0.04 (0.03)	**0.15** (0.05)
Abundance of species										
Non-Breeding	*Arremonops chloronotus*				**0.03** (0.01)	0.00 (0.00)	**0.04** (0.01)	0.00 (0.00)	0.00 (0.00)	0.02 (0.08)
Breeding	*Piranga roseougularis*	0.00 (0.00)	**0.01** (0.00)	0.00 (0.00)	**0.03** (0.01)	0.00 (0.00)	-0.01 (0.02)	0.00 (0.00)		
	Sittasomus griseicapillus						-0.03 (0.03)	**-0.01** (0.00)	0.00 (0.00)	**0.06** (0.02)

foraging insectivores showed the opposite pattern presenting lower species richness in older secondary forests in comparison to bark-gleaning insectivores and arboreal frugivores.The forest-dependent species had higher species richness in older succession and were associated to some of its concomitant structural characteristics.

At the species level, only three species' abundances varied with succession age and/or in association with certain landscape metrics.

Patterns of total species richness

During the non-breeding period total species richness among the different vegetation classes was similar. Our results match those of other studies that found bird species richness can be similar between early and late successional stages (Petit *et al.* 1995; Smith *et al.* 2001), since many migrant species, which can account for up to 50 % of the individuals at this time, can occur across the successional gradient (Greenberg 1992; Lynch 1992;

Salgado-Ortiz 2000; Wood 2005). On the other hand, during the breeding period, species richness was greater in older forest on level terrain. Resident Neotropical birds thus appear to be more dependent on mature vegetation during the breeding season than during the non-breeding period. During the breeding season, many resident species are restricted by their specialized nesting requirements, while they are free to roam across a greater variety of habitats at other times of year (Volpato *et al.* 2009). Older forest provides greater structural complexity than young successional stages (Bu *et al.* 2014), and thus may offer a greater availability of nest sites for placement and construction (Thompson *et al.* 1995), as well as offering greater protection from predators, solar radiation, wind, and rain (Laurance & Bierregard 1997). Outside the breeding season, however, resident species may be more widespread as a result of the post-breeding dispersal of juveniles, seasonal changes in the abundance and availability of food resources, and the breakdown

of territorial behaviour in species that do not defend territories year round.

Species richness of feeding guilds and association with succession age, vegetation, and landscape structure

At the guild level, bark-gleaning insectivores showed differences in species richness between the older and younger successional stages in both the breeding and non-breeding periods. Higher species richness of bark-gleaning insectivores was found in older successional stages where there is greater structural complexity. A plant successional study conducted in the same area showed that height and basal area increased logarithmically with stand age (i.e. succession age), mainly due to the contribution of woody plants > 5 cm dbh (Dupuy *et al.* 2012), which may provide a greater surface area for foraging (Lentijo & Kattan 2005; Raman *et al.* 1998), as well as more potential nest sites (Blake 1983). Hence, vegetation structure may explain in part the BGI species richness differences between older and younger successional stages.

Arboreal frugivores only showed differences in species richness between flat terrain (vegetation class 3) and vegetation class 1 and 4 during the breeding season but not during the non-breeding period. Also, arboreal frugivores showed a positive relationship with stand age, and with a more continuous mosaic of larger habitat patches, which suggests that higher species richness of arboreal frugivores depended on older successional stages, specifically on flat terrain, and relied on more continuous forest. Dupuy *et al.* (2012) found higher canopy height (a concomitant structural characteristic of older successional forests) in older secondary forest on flat terrain in comparison to hills in the same study area. The latter suggests that old succession on flat terrain may provide some structural characteristics, such as bigger trees, suitable to a wide range of arboreal frugivores (e.g., *Amazona albifrons*, *Aratinga nana*) that depend on tree cavities for nesting (Forshaw & Cooper 1977) and that are more vulnerable to fragmentation (Arriaga-Weiss *et al.* 2008) than similar habitat on hills.

Ground-foraging insectivores include species that forage in dense vegetation, mostly on the ground by gleaning insects from the litter. All ground-foraging insectivores use insects as their primary food source, with *Arremonops rufivirgatus* and *Arremonops chloronotus* complementing their

diet with seeds. However, these latter two species have been reported as primarily insectivorous (Arriaga-Weiss *et al.* 2008), and specifically in our study area our field observations confirmed this diet. We did not find differences in ground-foraging insectivores species richness among successional stages, with the exception of the older successional stage on hills during the breeding season that presented lower species richness. In general, species in the ground-foraging insectivores guild can tolerate a wide range of microclimatic conditions and have been associated with different ages of successional forests (Arriaga-Weiss *et al.* 2008). Moreover, our results suggest higher species richness in early succession compared to old succession. The stem density in our study area showed a decrease with succession age, where early succession had the densest undergrowth (Dupuy *et al.* 2012). Dense undergrowth may reduce the risk of predation for species in the ground-foraging insectivores guild, whereas in older forests the shade cast by continuous canopy cover may inhibit the development of a dense understory (e.g., Whittingham & Evans 2004). The forest-dependent species showed an increase in species richness with older succession and some of its concomitant structural characteristics (e.g., canopy height), highlighting the importance of older successional forests to avoid the loss of these species.

Among the remaining feeding guilds (i.e. arboreal insectivores, shrub insectivores, understory insectivores, understory frugivores, terrestrial granivores and arboreal omnivores), we found no relationships between species richness and vegetation age and structure, or landscape structure. For some of these guilds it is possible that point count surveys may exclude or underestimate small and secretive species (Wang & Finch 2002), for example, understory insectivores, or large frugivores that forage on the ground. A recent study in successional forests found that point counts frequently overlook secretive or non-vocalizing species, and suggest that point counts are less effective than mist netting when used in second growth in comparison to mature forests (Blake & Loiselle 2001), which concur with Rappole *et al.* (1998).

Patterns in the abundance of representative species in relation to succession age, and vegetation and landscape structure

The abundance of three species varied with succession age and/or in association with certain

landscape metrics. Specifically, *Arremonops chloronotus* is generally found in forest edge or clearings within the forest (Howell & Webb 1995). Thus our finding that *A. chloronotus* increased with greater patch shape complexity support the description of the species being found in greater numbers in edge habitat. Also, *A. chloronotus* showed a positive association with the proximity to similar patch types (that is a surrogate for landscape connectivity). Landscape connectivity may thus partially explain the increase in abundance of *A. chloronotus* as previous studies have found that corridors have a positive effect on bird movement in fragmented landscapes, including for *A. chloronotus* (Ibarra-Macias *et al.* 2011).

The bark-gleaning insectivore *Sittasomus griseicapillus* depended on older successional forests and some of its associated structural characteristics (e.g., taller trees). Other studies have suggested that taller trees provide an increased surface area for feeding for bark-gleaning insectivores (e.g., Arriaga-Weiss *et al.* 2008). Moreover, *S. griseicapillus* favours lower landscape fragmentation with large remnants of older forests. Fragmentation, at the landscape level, has three main effects, habitat degradation in terms of quality and extent, separation of habitat fragments by sub-optimal or not optimal habitat, and increase of edge effects. Insectivores, especially forest-specialists, are prone to all three of these effects of fragmentation (Arriaga-Weiss *et al.* 2008).

Piranga roseogularis, endemic to the Yucatan Peninsula, is generally associated with mature, medium stature sub-deciduous and semi-evergreen forests in relatively humid areas of the Peninsula. We classified it as an arboreal insectivore since it mostly depends on invertebrates to feed its young (Wood *unpublished data*). In our study, its abundance increased with higher landscape connectivity, while decreasing with higher values of the edge density. These results suggest that the species prefers large patches of habitat that are contiguous to similar habitat types.

Additionally, we found differences in abundances among the vegetation classes for the other three species (i.e. *P. maculipectus*, *A. rufivirgatus* and *E. affinis*). However, we found no relationship between these three species abundances and the vegetation and landscape structure variables. Specifically, *P. maculipectus* and *A. rufivirgatus* showed differences in abundance between older and younger succession with a general pattern of decreasing species richness as forest age increased.

The aforementioned species are more closely associated with the edges of dense secondary growth forest and scrub with higher stem density (Vega *et al.* 2003; Wood 2005), which was higher in early succession than in older forests in our study area (Dupuy *et al.* 2012). *E. affinis*, a canopy frugivore, was significantly more abundant in older successional vegetation on flat terrain than in all other successional classes, in both the breeding and non-breeding periods. In our study area, mean height, basal area, stem density and species density of trees increased with successional age, and in particular canopy height increased in older forests on flat terrain (Dupuy *et al.* 2012). Moreover, in younger forests trees are less abundant (Dupuy *et al.* 2012).

Conservation implications

Tropical dry forests are under intense human pressure, which has led to an increase in secondary forests in the Yucatan Peninsula. Our findings suggests that bird communities, including different bird guilds and forest-dependent birds, are differentially affected by age of forest succession, and some of its concomitant vegetation structural characteristics, as well as by some landscape variables (e.g., fragmentation). Specifically, arboreal frugivores, bark-gleaning insectivores, and forest-dependent species are positively influenced by successional age, lower landscape fragmentation, and higher landscape connectivity. These findings suggest that higher conservation priority should be given to interconnected larger remnants of older forest, as species with restricted ecological traits (e.g., forest-dependent species) are highly sensitive to the loss and fragmentation of older forests.

Our study suggests that flat terrain, where human pressure is pronounced, has higher bird diversity in comparison to hilly terrain. Thus to maintain high diversity and the persistence of vulnerable species to habitat disturbance flat terrain should be given more or at least the same priority weight as the hilltop forests. Similarly, caution should be taken about the increasing amounts and intensity of land use change leading to forest clearing, which is occurring in the Yucatan Peninsula (Lawrence & Foster 2002) and may have negative impacts on bird communities.

Bird feeding guilds can provide important insights for understanding and assessing the conservation value of fragmented landscapes. However, in view of the fact that some species can

switch diets at different times of year, we caution against treating them as exclusive categories. Bark-gleaning insectivores and forest-dependent birds are highly sensitive to local disturbance, thus these groups are useful as ecological indicators of forest loss and degradation.

Acknowledgements

References

Arriaga-Weiss, S., S. Calmé & C. Kampichler. 2008. Bird communities in rainforest fragments: guild responses to habitat variables in Tabasco, México. *Biodiversity and Conservation* **17**: 173-190.

Anderson, D. R., K. P. Burnham & W. L. Thompson. 2000. Null hypothesis testing: problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**: 912-923.

Anderson, D. R. & K. P. Burnham. 2002. Avoiding pitfalls when using information-theoretic methods. *Journal of Wildlife Management* **66**: 912-918.

Bahadur, K. C. 2009. Improving landsat and IRS image classification: evaluation of unsupervised and supervised classification through band ratios and DEM in a mountainous Landscape in Nepal. *Remote Sensing* **1**: 1257-1272.

Blake, J. G. 1983. Trophic structure of bird communities in forest patches in East-Central Illinois. *Wilson Bulletin* **95**: 416-430.

Blake, J. G. & B. A. Loiselle. 2001. Bird assemblages in second-growth and old-growth forests, Costa rica: perspectives from mist nets and point counts. *BioOne* **118**: 304-326.

Brady, C. & R. Noske. 2009. Succession in bird and plant communities over a 24-year chronosequence of mine rehabilitation in the Australian monsoon tropics. *Restoration Ecology* **18**: 855-864.

Bu, W., R. Zang & Y. Ding. 2014. Functional diversity increases with species diversity along successional gradient in a secondary tropical lowland rainforest. *Tropical Ecology* **55**: 393-401.

Burnham, K. P. & D. R. Anderson. 1998. *Model Selection and Multimodel Inference: a Practical Information-Theoretic Approach*. Springer-Verlag, New York.

Chazdon, R., A. Redondo & B. Vilchez. 2005. Effects of climate and stand age on annual tree dynamics in tropical second-growth rain forests. *Ecology* **86**: 1808-1815.

Chazdon, R. L., C. A. Peres, D. Dent, D. Sheil, A. E. Lugo, D. Lamb, N. E. Stork & S. E. Miller. 2009. The potential for species conservation in tropical secondary forests. *Conservation Biology* **23**: 1406-1417.

Chesser, R. T., R. C. Banks, F. K. Barker, C. Cicero, J. L. Dunn, A. W. Kratter, I. J. Lovette, P. C. Rasmussen, J. V. Remsen Jr., J. D. Rising, D. F. Stotz & K. Winker. 2011. Fifty-second supplement to the American Ornithologist' Union. Check-list of North American birds. *The Auk* **128**: 600-613.

Dunn, R. R. 2004. Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* **18**: 302-309.

Dupuy, J. M., J. L. Hernández-Stefanoni, R. A. Hernández-Juárez, E. Tetetla-Rangel, J. O. López-Martínez, E. Leyequién-Abarca, F. Tun-Dzul & F. May-Pat. 2012. Patterns and correlates of tropical dry forest structure and composition in a highly replicated chronosequence in Yucatan, Mexico. *Biotropica* **44**: 151-162.

Fahrig, L. 2003. Effects of habitat fragmentation on biodiversity. *Annual Review of Ecology, Evolution and Systematics* **34**: 487-515.

FAO. 2007. *State of the World's Forests 2007*. Rome. Retrieved from htpp:\www.fao.org/docrep/009/a0773e/a0773e00.htm

Forshaw, J. M. & W. T. Cooper. 1977. *Parrots of the World*. T. H. F. Publications, Inc., N. J.

García, E. 1973. *Modificaciones al Sistema de Clasificación Climática de Köppen, México, D.F.* Instituto de Geografía, Universidad Autónoma de México, México.

Gray, M., S. Baldauf, P. Mayhew & J. Hill. 2007. The response of avian feeding guilds to tropical forest disturbance. *Conservation Biology* **21**: 133-141.

Greenberg, R. 1992. Forest migrants in non-forest habitats on the Yucatan Peninsula. pp. 273-286. *In:* J. M. Hagan III & D. W. Johnson (eds.) *Ecology and Conservation of Neotropical Migrant Landbirds*. Smithsonian Institution Press, Washington.

Gustafson, E. J. 1998. Quantifying landscape spatial patterns: What is the state of the art? *Ecosystems* **1**: 143-156.

Hargis, C. D., J. A. Bossonette & J. L. David. 1998. The

behaviour of landscape metrics commonly used in the study of habitat fragmentation. *Landscape Ecology* **13**: 167-186.

Hernández-Stefanoni, J. L., J. M. Dupuy, F. Tun-Dzul & F. May-Pat. 2011. Influence of landscape structure and stand age on species density and biomass of a tropical dry forest across spatial scales. *Landscape Ecology* **26**: 355-370.

Howell, S. & S. Webb. 1995. *A Guide to the Birds of México and Northern Central America.* Oxford University Press. Nueva York, E.U.A.

Hutto, L., S. M. Pletschet & P. Hendricks. 1986. A fixed-radius point count method for nonbreeding and breeding season use. *The Auk* **103**: 593-602.

Ibarra-Macias, A., W. D. Robinson & M. S. Gaines. 2011. Experimental evaluation of bird movements in a fragmented neotropical landscape. *Biological Conservation* **144**: 703-712.

ITTO. 2002. *ITTO Guidelines for the Restoration, Management and Rehabilitation of Degraded and Secondary Tropical Forests.* ITTO Policy Development Series No. 13.84.

Johnson, J. B. & K. S. Omland. 2004. Model selection in ecology and evolution. *Trends in Ecology and Evolution* **19:** 101-108.

Kepler, C. B. & J. M. Scott. 1981. Reducing bird count variability by training observers. pp. 366-371. *In*: C. J. Ralph & J. M. Scott (eds.) *Estimating Numbers of Terrestrial Birds. Studies in Avian Biology.* Patuxent Wildlife Research Center.

Lentijo, G. & G. Kattan. 2005. Estratificación vertical de las aves en una plantación monoespecífica y en bosque nativo en la cordillera central de Colombia. *Ornitol Colomb* **3:** 51-61.

Laurance, W. F. & R. O. Bierregard Jr. 1997. *Tropical Forest Remnants: Ecology, Management and Conservation of Fragmented Communities.* Chicago University Press.

Lawrence, D. & D. Foster. 2002. Changes in forest biomass, litter dynamics and soils following shifting cultivation in southern Mexico: an overview. *Interciencia* **27**: 400-408.

Leyequien, E., J. Verrelst, M. Slot, G. Schaepman-Strub, I. Heitkönig & A. Skidmore. 2007. Capturing the fugitive: Applying remote sensing to terrestrial animal distribution and diversity. *International Journal of Applied Earth Observation and Geoinformation* **9:** 1-20.

Leyequien, E., W. F. De Boer & V. M. Toledo. 2010. Bird community composition in a shaded coffee agro-ecological matrix in Puebla, Mexico: the effects of landscape heterogeneity at multiple spatial scales. *Biotropica* **42**: 236-245.

Lynch, J. F. 1992. Distribution of overwintering Nearctic migrants in the Yucatan Peninsula II: Use of native and human-modified vegetation. pp. 178-196. *In*: J. M. Hagan III & D. W. Johnson (eds.) *Ecology and Conservation of Neotropical Migrant Landbirds.* Smithsonian Institution Press, Washington.

MacGarigal, K. & W. McComb.1995. Relationships between landscape structure and breeding birds in the Oregon coast range. *Ecological Monographs* **63:** 235-260.

MacGarigal, K. & S. Cushman. 2002. Comparative evaluation of experimental approaches to the study of habitat fragmentation effects. *Ecological Applications* **12:** 335-345.

MacGarigal, K., S. A. Cushman, M. C. Neel & E. Ene. 2002. *FRAGSTATS: Spatial Pattern Analysis for Categorical Maps.* University of Massachusetts.

Martinez-Beltran, C. & A. Calera-Belmonte. 2001. Irrigated crop area estimation using landsat TM imagery in La Mancha, Spain. *Photogrammetric Engineering & Remote Sensing* **67**: 1177-1184.

Mazerolle, M. J. & M. A. Villard. 1999. Patch characteristics and landscape context as predictor of species presence and abundance: A review. *Ecoscience* **6**: 117-124.

McCallum, D. A. 2005. A conceptual guide to detection probability for point counts and other count-based survey methods. pp. 754-761. *USDA Forest Service General Techincal Report (GTR)* PSW-GTR-191.

Milesi, F., L. Marone, J. López, V. Cueto & E. Mezquida. 2002. Gremios de manejo como indicadores de las condiciones del ambiente: un estudio del caso con aves y perturbaciones del hábitat en el monte central de Argentina. *École Astrale* **12**: 149-161.

Murphy, P. G. & A. E. Lugo. 1986. Ecology of tropical dry forest. *Annual Review of Ecology, Evolution and Systematics* **17**: 67-88.

Nichols, J. D., J. E. Hines, J. R. Sauer, F. W. Fallon, J. E. Fallon & P. J. Heglund. 2000. A double-observer approach for estimating detection probability and abundance from point counts. *The Auk* **117:** 393-408.

Pearman, P. B. 2002. The scale of community structure: habitat variation and avian guilds in tropical forest understorey. *Ecological Monographs* **72**: 19-39.

Petit, D., J. Lynch, R. Hutto, J. Blake & R. Waide. 1995. Habitat use and conservation in the neotropics. pp. 145-197. *In*: T. Martin & D. Finch (eds.) *Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues.* Oxford University Press, Nueva York.

Pineda-Diaz, E., J. L. León-Cortés & J. L. Rangel-Salazar. 2012. Diversity of bird feeding guilds in

relation to habitat heterogeneity and land-use cover in a human-modified landscape in southern Mexico. *Journal of Tropical Ecology* **28**: 369-376.

Ralph, J., G. G. Geupel, P. Pale, T. Martin, D. Desante & B. Mila. 1996. *Manual de Métodos de Campo Para el Monitoreo de Aves Terrestres*. United State Department of Agriculture. California, E.U.A.

Raman, S., G. Rawat & J. Johnsingh. 1998. Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, Nortn-east India. *Journal of Applied Ecology* **35:** 214-231.

Rappole, J. H., K. Winker & G. V. N. Powell. 1998. Migratory bird habitat use in southern Mexico: Mist nets versus point counts. *Journal of Field Ornithology* **69:** 635-643.

Salgado-Ortiz, J. 2000.*Slash-and-Burn Disturbance and Patterns of Avian Diversity at the Calakmul Biosphere Reserve, Campeche, Mexico: the Conservation Implications of a Hábitat Mosaic*. Dept. of Biology, Queen's University, Kingston, Ontario, Canada.

Shibata, R. 1989. Statistical aspects of model selection. pp. 215-240. *In:* J. C. Willems (ed.) *From Data Model*. Springer-Verlag, London.

Smith, A., J. Salgado & R. Robertson. 2001. Distribution patterns of migrant and resident birds in successional forests of the Yucatan Peninsula, Mexico. *Biotropica* **33:** 153-170.

Stouffer, P., R. O. Bierregaard, C. Strong & T. Lovejoy. 2006. Long-term landscape change and bird abundance in amazonian rainforest fragments. *Conservation Biology* **20:** 1212-1223.

Thompson, F. R. III, J. R. Probst & M. G. Raphael. 1995. Impacts of silviculture: overview and management. pp. 201-219. *In*: T. E. Martin & D. M. Finch (eds.) *Ecology and Management of Neotropical Migratory Birds: a Synthesis and Review of Critical Issues*. Oxford University Press, New York.

Thornton, D. H., L. C. Branch & M. E. Sunquist. 2011. The influence of landscape, patch, and within-patch factors on species presence and abundance: a review of focal patch studies. *Landscape Ecology* **26**: 7-18.

Vega, J., J. Rappole & P. Escalante. 2003. Identificación del hábitat de ocho especies de aves tropicales mediante análisis de regresión, en los Tuxtlas, Veracruz, México. *Anales del Instituto de Biología, Universidad Nacional Autónoma de México, Series Zoología* **74:** 195-201.

Vergara, P. & J. Armesto. 2009. Responses of Chilean forest birds to anthropogenic habitat fragmentation across spatial scales. *Landscape Ecology* **24:** 25-38.

Volpato, G., E. V. López, L. B. Mendonca, R. Bocon, M. B. Bisheimer, P. P. Serafini & L. D. Anjos. 2009. The use of the point count method for bird survey in the Atlantic forest. *Zoología* **26**:74-78.

Wang, Y. & D. M. Finch. 2002. Consistency of mist netting and point counts in assessing landbird species richness and relative abundance during migration. *The Condor* **104:** 59-72.

Warkentin, I. G., R. Greenberg & J. Salgado-Ortiz. 1995. Songbird use of gavllery woodlands in recently cleared and older settled landscapes of the Selva Lacandona, Chiapas, Mexico. *Conservation Biology* **9**: 1095-1106.

Whittingham, M. J. & K. L. Evans. 2004. The effects of habitat structure on predation risk of birds in agricultural landscapes. *Ibis* **146:** 210-220.

Wood, P. A., D. K. Dawson, J. R. Sauer & M. Wilson. 2005. Predicting bird response to alternative management scenarios on a ranch in Campeche, Mexico. pp. 101-106. *In*: C. J. Ralph & T. D. Rich (eds.) *Bird Conservation Implementation and Integration in the Americas: Proceedings of the Third International Partners in Flight Conference*, Vol. 1. Asilomar, California.

Zar, J. H. 1999. *Biostatistical Analysis*. 4th edn.Prentice Hall, NJ, USA.

Zhu, X. 2013. Land cover classification using moderate resolution satellite imagery and random forests with post-hoc smoothing. *Journal of Spatial Science* **58:** 323-337.

Appendix 1. Location of the training sites before applying supervised classification to the spot imagery. Vegetation class 1 = 3-8 y-old secondary forest, vegetation class 2= 9-15 y-old secondary forest, vegetation class 3 >15 y-old secondary forest on flat areas, and vegetation class 4 >15 y-old secondary forest on hills.
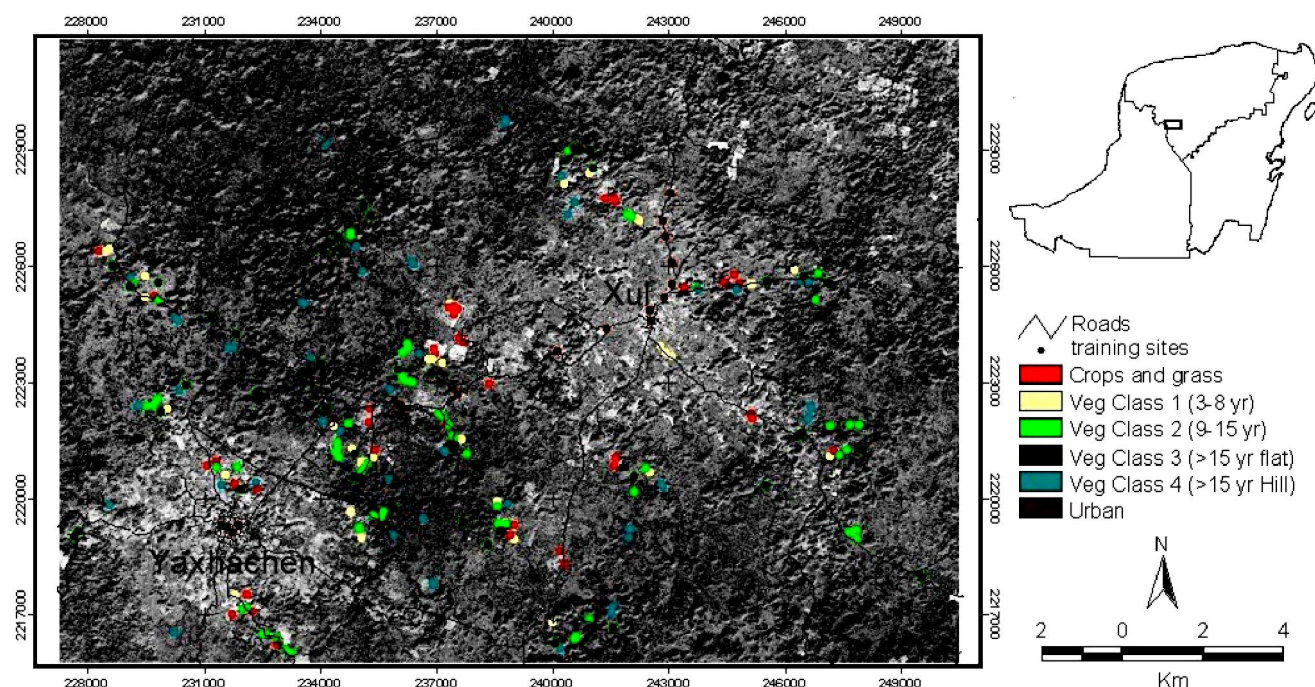
Appendix 2. Description of all landscape metrics included in the pairwise Pearson correlation analyses to choose those metrics with the minimum correlations

Set of variables	Description	Code
Landscape structure set		
Proportional abundance of each patch type	High values indicate dominance of certain succession patch type	PLAND
Patch density	High values indicate higher number of small patches per area unit	PD
Edge density at the class level	High values indicate higher edge density per successional class	ED
Overall shape complexity	High values indicate more irregular patch shape	SHAPE
Patch isolation	High values indicate a greater patch isolation (same patch type)	ENN
Edge contrast	High values indicate higher landscape fragmentation	TECI
Shape	Measures the complexity of patch shape compared to a standard shape	SHAPE
Core area	Quantifies the percentage of the patch that is comprised of core area	CA
Proximity index	The index distinguishes sparse distributions of small habitat patches from configurations where the habitat forms a complex cluster of larger patches.	PROX
Similarity	Percent of the landscape occupied by the same patch type as the patch	SIMI
Core area	Quantifies the percentage of the patch that is comprised of core area	CA
Contagion	Measures the extent to which landscape elements (patch types) are aggregated or clumped (i.e., dispersion)	CONTAG

Appendix 3. Description of biophysical variables grouped into three sets of variables: vegetation structure, landscape structure, and spatial structure of sampling sites.

Set of variables	Description	Code
Vegetation set		
Stand age	Age after abandonment following slash-and-burn shifting cultivation	AGE
Height of the ten top higher stems	Average height of the ten top highest stems (m) per plot	CANOPY HEIGHT
Landscape structure set		
Proportional abundance of each patch type	High values indicate dominance of certain succession patch type	PLAND
Patch density	High values indicate higher number of small patches per area unit	PD
Edge density at the class level	High values indicate higher edge density per successional class	ED
Overall shape complexity	High values indicate more irregular patch shape	SHAPE
Edge contrast	High values indicate higher landscape fragmentation	TECI
Proximity index	The index distinguishes sparse distributions of small habitat patches from configurations where the habitat forms a complex cluster of larger patches.	PROXI
Similarity	Percent of the landscape occupied by the same patch type as the patch	SIMI

Appendix 4. Error matrix for the land cover map of the study area.

Classes	Plots sampled at field							User's Accuracy
	Agricultural fields	3-8 y-old	9-14 y-old	>15 yr-old on flat areas	>15 y-old on hills	Urban areas	Total	
Agricultural fields	23	2	1		1		27	85.2
3-8 y-old		24	4	3	1		32	75.0
9-14 yr-old		2	27	2	3		34	79.4
>15 yr-old on flat areas		2	6	31	8		47	66.0
>15 yr-old on hills		1	2	14	36		53	67.9
urban areas						20	20	100.0
Total	23	31	40	50	49	20	213	
Producer's accuracy	100.0	77.4	67.5	62.0	73.5	100.0		Accuracy = 75.6
								Kappa = 0.70

Appendix 5. List of registered species: Status: B = Breeding and NB = Non-breeding. *Forest-dependent species and †individual species that are of conservation interest. Nomenclature based on the 54th supplement of the American ornithologists' union (Chesser *et al.* 2013).

Order	Family	Species	Status	Guild	Stratum	Code
Galliformes	Odontophoridae	*Dactylortyx thoracicus**	B	Granivore	Terrestrial	TG
Columbiformes	Columbidae	*Patagioenas flavirostris†*	B	Frugivore	Arboreal	AF
	Columbidae	*Columbina passerina*	B	Granivore	Terrestrial	TG
	Columbidae	*Columbina talpacoti*	B	Granivore	Terrestrial	TG
	Columbidae	*Leptotila verreauxi†*	B	Granivore	Terrestrial	TG
	Columbidae	*Leptotila jamaicensis*	B	Granivore	Terrestrial	TG
Psittaciformes	Psittacidae	*Aratinga nana*	B	Frugivore	Arboreal	AF
	Psittacidae	*Amazona albifrons*	B	Frugivore	Arboreal	AF
Cuculiformes	Cuculidae	*Piaya cayana*	B	Insectivore	Arboreal	AF
	Cuculidae	*Dromococcyx phasianellus**	B	Insectivore	Ground-foraging	GFI
Trogoniformes	Trogonidae	*Trogon melanocephalus*	B	Insectivore	Arboreal	AI
	Trogonidae	*Trogon caligatus**	B	Insectivore	Arboreal	AI
Coraciiformes	Momotidae	*Momotus momota**	B	Insectivore	Arboreal	AI
	Momotidae	*Eumomota superciliosa*	B	Insectivore	Arboreal	AI
Piciformes	Picidae	*Melanerpes pygmaeus**	B	Insectivore	Bark-gleaning	BGI
	Picidae	*Melanerpes aurifrons*	B	Insectivore	Bark-gleaning	BGI
	Picidae	*Picoides scalaris**	B	Insectivore	Bark-gleaning	BGI
	Picidae	*Veniliornis fumigatus**	B	Insectivore	Bark-gleaning	BGI
	Picidae	*Colaptes rubiginosus**	B	Insectivore	Bark-gleaning	BGI
	Picidae	*Dryocopus lineatus**	B	Insectivore	Bark-gleaning	BGI
Passeriformes	Furnariidae	*Dendrocincla anabatina**	B	Insectivore	Bark-gleaning	BGI
	Furnariidae	*Dendrocincla homochroa**	B	Insectivore	Bark-gleaning	BGI
	Furnariidae	*Sittasomus griseicapillus*†*	B	Insectivore	Bark-gleaning	BGI
	Furnariidae	*Xiphorhynchus flavigaster*†*	B	Insectivore	Bark-gleaning	BGI
	Thamnophilidae	*Thamnophilus doliatus*	B	Insectivore	Shrub	SI
	Tyrannidae	*Camptostoma imberbe*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Myiopagis viridicata**	B	Insectivore	Arboreal	AI
	Tyrannidae	*Elaenia flavogaster*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Oncostoma cinereigulare**	B	Insectivore	Arboreal	AI
	Tyrannidae	*Tolmomyias sulphurescens**	B	Insectivore	Arboreal	AI
	Tyrannidae	*Platyrinchus cancrominus*†*	B	Insectivore	Understorey	UI
	Tyrannidae	*Contopus virens*	NB	Insectivore	Arboreal	AI
	Tyrannidae	*Contopus cinereum*	B	Insectivore	Aboreal	AI
	Tyrannidae	*Empidonax minimus*	NB	Insectivore	Arboreal	AI
	Tyrannidae	*Attila spadiceus*†*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Myiarchus yucatanensis†*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Myiarchus tuberculifer*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Myiarchus tyrannulus*	B	Insectivore	Arboreal	AI

Appendix 5. Continued.

Order	Family	Species	Status	Guild	Stratum	Code
	Tyrannidae	*Pitangus sulphuratus*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Megarynchus pitangua*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Myiozetetes similis*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Tyrannus melancholicus*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Tyrannus couchii*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Pachyrampus major**	B	Insectivore	Arboreal	AI
	Tyrannidae	*Pachyrampus aglaiae*	B	Insectivore	Arboreal	AI
	Tyrannidae	*Tityra semifasciata**	B	Insectivore	Arboreal	AI
	Tyrannidae	*Tityra inquisitor**	B	Insectivore	Arboreal	AI
	Vireonidae	*Vireo griseus*	NB	Frugivore	Arboreal	AF
	Vireonidae	*Vireo pallens*	B	Insectivore	Arboreal	AI
	Vireonidae	*Vireo flavifrons*	M	Insectivore	Arboreal	AI
	Vireonidae	*Hylophilus decurtatus**	B	Insectivore	Arboreal	AI
	Vireonidae	*Cyclarhis gujanensis*	B	Insectivore	Arboreal	AI
	Corvidae	*Psilorhinus morio*	B	Insectivore	Arboreal	AI
	Corvidae	*Cyanocorax yncas*	B	Insectivore	Arboreal	AI
	Corvidae	*Cyanocorax yuctanicus*	B	Insectivore	Arboreal	AI
	Troglodytiidae	*Pheugopedius maculipectus†*	B	Insectivore	Shrub	SI
	Troglodytiidae	*Thryothorus ludovicianus*	B	Insectivore	Shrub	SI
	Troglodytiidae	*Uropsila leucogastra*	B	Insectivore	Arboreal	AI
	Polioptilidae	*Rhamphocaenus melanurus**	B	Insectivore	Arboreal	AI
	Polioptilidae	*Polioptila caerulea*	B	Insectivore	Arboreal	AI
	Polioptilidae	*Polioptila plúmbea**	B	Insectivore	Arboreal	AI
	Turdidae	*Hylocichla mustelina*	NB	Insectivore	Ground-foraging	GFI
	Turdidae	*Turdus grayi*	B	Frugivore	Arboreal	AF
	Mimidae	*Melanoptila glabrirostris*	B	Frugivore	Arboreal	AF
	Mimidae	*Dumetella carolinensis†*	NB	Frugivore	Shrub	SF
	Parulidae	*Vermivora cyanoptera*	NB	Insectivore	Arboreal	AI
	Parulidae	*Oreothlypis peregrina*	NB	Insectivore	Arboreal	AI
	Parulidae	*Setophaga americana*	NB	Insectivore	Arboreal	AI
	Parulidae	*Setophaga magnolia*	NB	Insectivore	Arboreal	AI
	Parulidae	*Setophaga caerulescens*	NB	Insectivore	Arboreal	AI
	Parulidae	*Setophaga virens*	NB	Insectivore	Arboreal	AI
	Parulidae	*Setophaga dominica*	NB	Insectivore	Arboreal	AI
	Parulidae	*Mniotilta varia*	NB	Insectivore	Arboreal	AI
	Parulidae	*Setophaga ruticilla*	NB	Insectivore	Arboreal	AI
	Parulidae	*Seiurus aurocapilla*	NB	Insectivore	Ground-foraging	GFI
	Parulidae	*Geothlypis trichas*	NB	Insectivore	Shrub	SI
	Parulidae	*Setophaga citrina*	NB	Insectivore	Shrub	SI
	Thraupidae	*Eucometis penicillata**	B	Insectivore	Ground-foraging	GFI
	Thraupidae	*Cyanerpes cyaneus*	B	Insectivore	Arboreal	AI

Appendix 5. Continued.

Order	Family	Species	Status	Guild	Stratum	Code
	Emberizidae	*Volatinia jacarina*	B	Granivore	Terrestrial	TG
	Emberizidae	*Sporophila torqueola*	B	Granivore	Understorey	UI
	Emberizidae	*Tiaris olivaceus*	B	Granivore	Understorey	UI
	Emberizidae	*Arremonops rufivirgatus†*	B	Insectivore	Ground-foraging	GFI
	Emberizidae	*Arremonops chloronotus*†*	B	Insectivore	Ground-foraging	GFI
	Cardinalidae	*Cyanocompsa parellina*†*	B	Insectivore	Arboreal	AI
	Cardinalidae	*Passerina cyanea*	NB	Granivore	Terrestrial	TG
	Cardinalidae	*Granatellus sallaei**	B	Insectivore	Arboreal	AI
	Cardinalidae	*Habia fuscicauda**	B	Insectivore	Ground-foraging	GFI
	Cardinalidae	*Piranga roseogularis**	B	Insectivore	Arboreal	AI
	Cardinalidae	*Piranga rubra*	NB	Insectivore	Arboreal	AI
	Insertae	*Saltator coerulescens*	B	Frugivore	Understorey	UF
	Insertae	*Saltator atriceps†*	B	Frugivore	Understorey	UF
	Icteridae	*Dives dives*	B	Insectivore	Arboreal	AI
	Icteridae	*Molothrus aeneus*	B	Granivore	Terrestrial	TG
	Icteridae	*Icterus prosthemelas*	B	Omnivore	Arboreal	AO
	Icteridae	*Icterus cucullatus*	B	Omnivore	Arboreal	AO
	Icteridae	*Icterus chrysater*	B	Omnivore	Arboreal	AO
	Icteridae	*Icterus mesomelas*	B	Omnivore	Arboreal	AO
	Icteridae	*Icterus auratus†*	B	Omnivore	Arboreal	AO
	Icteridae	*Icterus gularis†*	B	Omnivore	Arboreal	AO
	Icteridae	*Amblycercus holosericeus†*	B	Insectivore	Shrub	SI
	Fringillidae	*Euphonia affinis†*	B	Frugivore	Arboreal	AF
	Fringillidae	*Euphonia hirundinacea*	B	Frugivore	Arboreal	AF