AVIAN COMMUNITY CHARACTERISTICS AND DEMOGRAPHICS REVEAL HOW CONSERVATION VALUE OF REGENERATING TROPICAL DRY FORESTS CHANGES WITH FOREST AGE

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**ABSTRACT**

Expansion of secondary forests following the abandonment of agriculture may have important implications for bird conservation, but few studies have examined the dynamics of this process. We studied bird use of a chronosequence of differently-aged abandoned pastures regenerating to dry forest to better understand how the value of these habitats to birds changes over time. In a 5-yr study on Hispaniola, we recorded 7,315 net captures of 60 species of landbirds in sites that began the study at 2, 5, 10, and 20-yr post-abandonment, and in mature native dry forest. 25 species made up 97% of all net captures. Highest capture rates were in 2-yr and 5-yr old sites. Early-successional habitats had many over-wintering Neotropical migrants; among residents, granivores and frugivores predominated. In contrast, both the 20-yr old and mature forest sites had few migrants, more resident insectivores and omnivorous species, and a greater proportion of endemics. Age and sex ratios, body condition and site persistence suggest early successional sites were sub-optimal for over-wintering migrants; results for permanent residents varied among species. Remnant trees and understory shrubs in the agroecological matrix likely contributed to avian diversity in regenerating dry forest sites, and proximity to mature forest also likely affected the diversity and abundance of birds in regenerating habitat. Our study shows that regenerating forests do not fully compensate for loss of mature dry forest habitat; natural restoration of complex microhabitats in dry forest sites converted to agriculture may take decades or longer. The highest value of regenerating forests may be their role in creating a buffer zone that enhances biodiversity conservation by re-integrating these lands into the protected tracts of mature forest needed by the islands more unique and endemic bird species.

***Keywords:*** *agroecosystems, avian abundance, buffer zones, Dominican Republic, endemics, habitat change, Hispaniola, land use, landscape matrix, Neotropical migratory birds.*

**INTRODUCTION**

Human activity has directly affected half of the earth’s ice-free land surface, with approximately 40% of land now dedicated to agricultural crops or pasture (GEF 2012). The re

sulting expansion of degraded and deforested lands has important implications for long-term conservation of wildlife (Daily et al. 2001). But increasingly, attention is being paid to maximizing the conservation value of agricultural lands (Vandermeer and Perfecto 1997, Petit and Petit 2003), with investigations seeking to understand how birds respond to changes in land use in the agricultural matrix surrounding mature forest (Daily et al. 2001, Hughes et al. 2002, Sekercioglu et al. 2002). Several studies have shown that tropical forest birds are not entirely isolated from the agricultural matrix (Greenberg et al. 1997, Daily et al. 2001, Sekercioglu et al. 2007), and that this matrix may provide an important buffer between forested reserves and other, more intensive anthropogenic land uses (Lynagh and Urich 2002). The conservation of biodiversity, and even the functioning of national parks and reserves as repositories of species diversity, is thus increasingly seen to be dependent upon how we manage agricultural landscapes (Vandermeer and Perfecto 1997, Daily et al. 2001, Green et al. 2005, Sekercioglu et al. 2007).

As a component of the agricultural matrix, pastures are one of the most abundant agricultural habitats worldwide, but the potential conservation value of pastures has been generally overlooked (Harvey et al. 2006). Abandoned pastures also represent one of our best opportunities for restoration of forests, especially when some remnant tree cover has been retained. Shifting agricultural priorities and economic markets, as well as widespread slash-and-burn agricultural practices, can result in local or landscape-scale abandonment of pastures, resulting in a patchwork of pastures, scrub and early-successional regeneration within the agricultural matrix (Harvey et al. 2006). Studies have documented presence/absence or behavioral attributes of birds in scrub or agricultural habitats (Johnson and Sherry 2001, Komar 2006), but few researchers have evaluated the conservation value of regenerating pastures, and the employment of avian survival or other demographic variables in these studies is seldom realized despite its importance in assessing habitat quality for birds (but see Wunderle and Latta 2000, Johnson et al. 2006).

Pastures are also one of the most common land use types on the island of Hispaniola (Tolentino and Peña 1998). The island's two nations, Haiti and the Dominican Republic, harbor one of the most diverse assemblages of birds in the Caribbean, with more endemic bird species than any other Caribbean island. Its contribution to global biodiversity has earned Hispaniola the highest ranking of importance in a worldwide assessment of bird protection priorities (Stattersfield et al. 1998). Over-wintering Neotropical migratory birds are also an important seasonal component of the avifauna (Latta et al. 2006). Forest habitats are vital to the survival of many endemic and migrant bird species, but the loss of these habitats on Hispaniola has been estimated as >90% (Stattersfield et al. 1998). In response to this crisis, the Dominican government has established a number of protected areas. But the value of regenerating pastures and other agricultural lands, or how they can be managed or restored for birds, has received almost no attention.

The primary objectives of this research were to: (1) determine the abundance and diversity of birds across a chronosequence of different-aged dry forest regenerating from pastures; (2) determine how endemics, permanent residents, over-wintering migratory birds, and birds representing different foraging guilds respond to regenerating dry forest habitats; (3) determine if there are differences in demographic structure or site persistence among birds occurring in these early-successional habitats; and (4) compare these results to similar data from mature dry forests. Based on these findings, we discuss the conservation value of regenerating dry forest in an agroecological matrix.

**METHODS**

*Study sites*. We studied bird communities during the northern winters of 2003-04 through 2007-08 in the buffer zone of Sierra de Bahoruco National Park, Dominican Republic where a growing human population and associated agricultural activities often conflict with park protection goals. Four study sites of >15 ha were established at elevations of ~400 m within 2 km of the village of Mencia (18.176, -71.737). Sites were chosen based on age since disturbance (confirmed through interviews with landowners and long-term residents). The sites were originally cleared for agriculture (primarily beans, squash), and then utilized for occasional low-density grazing by small numbers of livestock. Remnant trees and living fences were characteristic of all sites. Sites contained two replicate mist netting arrays, and contiguous blocks of habitat for at least 150 m on each side minimized possible edge effects. Because of their proximity to one another, all sites shared a similar landscape matrix including mature forest, shade coffee, mixed agriculture, pasture and village. The study sites forming the chronosequence (with age since disturbance at initiation of study) were La Cueva (2-yr), La Caoba (5-yr), Morelia (10-yr), and El Corral (20-yr). A fifth site in mature dry forest studied during the winters of 1996-97 through 2000-01 represented native habitat of the Mencia sites prior to deforestation and served as the endpoint in the chronosequence. This control site, Aceitillar (18.098, -71.635), was located ~14 km east of Mencia and at a similar elevation (~350 m). The Aceitillar site was also affected by occasional grazing by stray cattle and tree cutting for charcoal, but represents some of the best remaining dry forest in the region.

*La Cueva (2-yr) and La Caoba (5-yr)*. Vegetation at these sites is similar and dominated by grasses, forbs, and woody shrubs in height categories <1.5 m, including *Chrysophyllum oliviforme*, *Guettarda preneloupii*, *Chromolaena odorata*, *Trichilia hirta*, *Eugenia monticola*, and *Ehretia tinifolia*. Trees are scarce but consist primarily of very young *Senna spectabilis* and scattered remnant *Bursera simaruba*. These sites have the lowest diversity and density of shrubs of all sites, as well as the lowest mean canopy height (3.6 m; 3.9 m) and canopy cover (18%; 22%).

*Morelia (10-yr)*. Vegetative cover occurs primarily in height categories <4.0 m. The diversity of shrub species is the highest of all study sites, and includes *Chrysophyllum oliviforme*, *Trichilia hirta*, *Psychotria berteroana*, *Piper aduncum*, and *Casearia aculeata*. Trees are small and dominated by *Senna spectabilis*, but include scattered *Bursera simaruba*, *Ocotea coriacea*, and *Zanthoxylum martinicense*. Mean canopy height is 5.2 m and mean canopy cover is 54%.

*El Corral (20-yr)*. Shrub density and diversity decrease but include *Trichilia hirta*, *Casearia aculeate*, *Eugenia monticola*, *Licaria triandra*, and *Nectandra hihua*. Mean canopy height (6.4 m) and canopy cover (76%) increases with trees that include *Eugenia monticola, Nectandra hihua, Licaria triandra, Acacia farnesiana*, *Leucaena leucocephala*, *Bauhinia divaricate,* and *Trichilia pallida*.

*Aceitillar*. The mature dry forest site has a mostly closed canopy (94%) with a mean tree height of 10.6 m, a few emergent trees, and an understory dominated by broadleaf shrubs. Trees include *Capparis ferruginea*, *Zizyphus rignoni*, *Bursera simaruba*, *Cameraria angustifolia*, *Cordia buchii*, and *Plumeria obtuse*.

*Sampling birds.* We conducted mist-netting in early- (November), mid- (December-January), and late-winter (January-February). At the Mencia sites we used 16 nets (12 m x 30 mm mesh) in each net array for three days: 3 hrs the first afternoon, all day the next day and 3 hrs on the final morning. At the Aceitillar site, we placed nets in two lines of 31 and 39 nets with each array covering 700 m. Weather permitting, netting began ~15 min after sunrise and ended at 1600. All mist-netted birds were identified to species, sexed and aged (juvenile: HY/SY, or adult: AHY/ASY) using plumage or molt limits (Latta et al. 2006, Pyle 1997). Birds were weighed with a Pesola spring balance (±0.5 g), and we measured wing chord (±0.5 mm) and tarsus length (±0.1 mm). Most birds were banded with a numbered metal band and three color bands to identify each individual. For birds too small to band (hummingbirds, todies) we clipped the outer primary feather so recaptures within a netting session could be identified. Abundances of birds are expressed as birds captured per 1000 mist-net hrs (mnh), where one 12-m mist net opened for 1 hr = 1 mnh.

Mist nets are subject to several biases (Remsen and Good 1996). This study minimized some of these problems: vegetation in these sites is relatively low, except in the mature dry forest; we limited analyses of net capture frequencies to within-species comparisons and assumed equal capture probabilities within species among sites; finally, our mist-netting schedule (2-3 days every six weeks) minimized net shyness of birds.

We classified birds captured in mist nets into groups based on diet on the basis of principal food items consumed in optimal habitats (Wunderle and Latta 1996). Groups included insectivores, nectarivores, granivores (including frugivores), carnivores, and omnivores. We grouped birds based on migratory status, including permanent residents and latitudinal migrants. We also classified birds by primary habitat, assigning all species to a single preferred habitat (secondary forest, deciduous forest, evergreen forest) based on Stotz et al. (1996).

*Demographics and site persistence*. Abundance data alone can be a misleading indicator of survival and habitat quality (James 1971). Moreover, among over-wintering migratory birds, dominance interactions result in many species segregating by sex and age class (Holmes et al. 1989; Latta and Faaborg 2002), so age- and sex-specific data on persistence of individual birds is needed to assess habitat quality (Faaborg et al. 2010). Over-winter site persistence was defined as the proportion of birds detected (by resighting or recapture) at any time >24 hr after initial capture. Following banding, each plot was systematically searched 56.5 ± 6.2 hr (SE) for color-banded individuals, with search areas extending ~100 m beyond plot boundaries. Although a few color-banded individuals may have remained unidentified, consistent resighting effort among sites and years insured comparability of results among habitats.

*Food resources.* Assessment of potential food items was focused on insect abundance as we sought to explain the distribution, in particular, of over-wintering migratory birds. Insects were sampled in December, January and February of years 1 and 2 with five yellow sticky traps placed at breast height for 48 hrs along a transect in each habitat. All insects 0.1–5.0 mm length were counted and pooled across sampling periods; the few larger insects were excluded because most wintering migrants consume primarily small arthropods (Greenberg 1995; Poulin and Lefebvre 1996). Leaf litter samples were collected in mid-winter (January) from n=30, 25-cm diameter circles in each site and placed into a sorting pan. All invertebrates <5.0 mm were counted and identified to order.

***Statistical analyses***

***General modeling approach***

Because succession from abandoned pasture to mature forests takes decades (DeWalt et al 2003) we use a chronosequence approach. While there are inherent limitations to exchanging space for time in this way, chronosequences are essential and robust tools for making inferences about successional processes (Walker et al 2010). Due to the nested structure of the chronosequence data we fit all regression and ANOVA-type models as generalized linear mixed models (GLMMs) with site (4 or 5 levels), year (5 to 11 levels), and bird species (x-y) as a random intercepts whenever appropriate. This results in a partially crossed random effects structure because all pasture sites were measured in all years, and most species occurred in most sites (Baayen et al. 2008). Models were fit in *R* 3.4.4 (R Core Team 2017) using the *lme4* package (Bates et al. 2015). Because of the relatively low number of levels to our random effects and the nested structure of the data we had to address several convergence issues. First, as is standard for GLMMs we centered our predictor variable “pasture age” around zero. Second, we used the *lme4* extension *blme* (Chung et al. 2013). This package facilitates model fitting by using a modified likelihood function (penalized likelihood) that is mathematically equivalent to using a weakly informative prior for the variance components in a Bayesian model. In particular, *blme* prevents variance components, such as variation between years, from erroneously being estimated as zero. Though this approach borrows from Bayesian approaches, inference is carried out using standard frequentists methods (Chung et al. 2013, Chung et al. 2015). To further avoid optimization problems we used the *all\_fit()* function in the *afex* package (Singman et al. 2018) to find a numeric optimizer that would not result in convergence warnings from the *lme4* package. The optimizers that produced satisfactory results were usually *Nelder\_Mead* and occasionally *nmkb* (Nelder-Mead using derivative-free optimization from the *dfoptim* package [Varadhan et al 2017]) . We confirmed that our final models met convergence criteria by checking convergence criteria as recommended in the *lme4* helpfile (accessed via “*?convergence”* in R).

It is sometimes recommended to simplify mixed models if random terms are not significant and to improve convergence (Matuschek et al. 2017; but see Bar et al. 2013). We had *a priori* expectations for there to be correlations within sites across years, and within years across sites, and we therefore did not feel it was appropriate to simplify our models and so used the quasi-Bayesian approach advocated by Chung et al. (2013).

To understand how bird communities and traits changed as pastures aged we generally fit two sets of models. First, we did regression-style modeling of continuous change over time as pastures aged from 2 to 24 years by using a GLMM to model difference between the La Cueva (2-6 years), La Caoba (5- 9 years), Morelia (10 – 14 years), and El Corral (20-24 years) sites. This first set of models did not include the mature forest site (Aceitillar) because to our knowledge this site has never been significantly disturbed. We used this approach to model both community-level data (e.g. species richness) and species-specific trends. For species-level models we included species as a random effect with a random slope. This allowed us to model both mean change averaged across all species as well as extract species-specific intercepts and slopes (BLUPS, Robins 1989) from the random effects.

This approach provides a number of advantages relative to building separate models for each species, including accounting for correlations across species due to common study years and sites shared across species, as well and joint modeling of shared characteristics of species (eg. migration behavior). These models can both improve power and estimation of trends for rarer species by sharing information across species (Gelman and Hill 2007). It can also reduce Type I errors by alleviating the need for corrections for multiple comparisons (Gelman et al 2012). This approach is becoming increasing popular for multi-species studies (Jackson et al 2012, Brouwer et al. 2017, Trevelline *submitted*).

In addition to our regression-style GLMMs we fit one-way ANOVA-style models which treated time since disturbance (age) as a categorical variable with five levels (4 pastures and 1 forest). These models allowed us to make comparisons between the four sites undergoing succession and the mature forest site at Aceitillar. The two youngest sites had shared values for 5 and 6-years post abandonment (Appendix 1) and so we removed the overlapping years for these sites. To assess change across this chronosequence we did an omnibus likelihood ratio test to determine if there was evidence for any difference between sites and the did a focused test for linear (contrast: -2, -1, 0, 1, 2) and quadratic (contrast: 2, -1, -2, -1, 2) trends across the chronosequence using a trend contrast (Rosenthal and Rosnow 1985; Gurevitch and Chester 1986). Trend tests were conducted using the *multcomp* package (Hothorn et al 2008).

This approach provides a number of advantages relative to building separate models for each species, including accounting for correlations across species due to common study years and sites shared across species and joint modeling of shared characteristics of species (eg. migration behavior). These models can both improve power by sharing information across species (“borrowing strength”; Gelman and Hill 2007) and reduce Type I errors without the need for corrections for multiple comparisons (Gelman et al 2012). This approach is becoming increasing popular for multi-species studies (Jackson et al 2012, Brouwer et al. 2017).

We calculated 95% confidence intervals (95% CI) around overall GLMM regression lines using the *predictInterval()* function in the *merTools* package (Knowles and Frederick 2016). Means for each site were estimated using the GLMM and confidence intervals approximated using standard errors (SE) from the model coefficients (95% CI = +/- 1.96\*SE). We built all plots using *ggplot2* (Whickham 2009) and *cowplot* (Wilke 2017).

***Rarefaction***We used rarefaction to compare species richness among sites, pooling data from across years. Rarefaction produces idealized species-accumulation curves that allow direct comparison of results among groups that differ in patterns of abundance or are sampled using different techniques (Gotelli and Colwell 2001). Rarefaction calculates the expected species richness of the different groups for a constant sampling effort, but does not provide an estimate of asymptotic richness. Rather, for each accumulation curve we calculated a Chao 1 non-parametric estimator of richness with its variance and 95% confidence interval (Chao 1984).

***Shannon Diversity, Dominance and Evenness***We calculated species richness and Shannon Diversity for each site each year of the study. We also calculated numerical dominance of species captured within each site, and Pielou’s evenness index (Magurran 1988) of the distribution of individuals among taxa (absolute evenness = 1.0). We converted diversity to the “effective number of species” by exponentiating species richness (Jost 2006) to represent true diversity with mathematical properties allowing comparison among groups. We modeled how these indices varied as pastures aged using regression and how they varied between age classes, including the mature forest at Aceitillar, as described above. We log transformed species diveristy and logit transformed evenness because it is a percentage (Warton and Hui 2011) and modeled both using a linear mixed model (LMM). Species richness was modeled using a Poisson GLMM with an observation-level random affect to account for overdispersion (Harrison 2014). All test statistics are reported for transformed data and analyses were re-run on untransformed data for plotting.

***Community Similarity (Jaccard and Sorenson Indices, NMDS)*** Foreach site we pooled data from across years and used Jaccard’s index to compare the similarity of communities based on presence/absence of species, and Sorenson’s measure to compare the similarity of sites based on the proportional abundance of species recorded, and the proportional abundance of birds in each diet category. Both indices were calculated using the *SimilarityPair()* function in the *SpadeR* package (Chao et al. 2016) We also used non-metric multidimensional scaling (NMDS) with a Bray-Curtis distance matrix in the vegan package (Oksanen et al. 2017) to visualize the overlap in community composition among the sites.

***Capture rates*** We modeled captures rates using a Poisson GLMM with an observation-level random effect to account for overdispersion (Harrison 2014). Overall regression vs. individual-level regression for BLUPs? Individual ANOVAs? Individual models with x^2 terms?

***Site persistence*** How defined? Defined the same for both direct site persistence analysis and body condition?

***Age ratio, sex ratio, migratory status, endemism*** We examined differences in the proportion of adults and the proportion of males among sites, and for significant heterogeneity in the proportion of species and individuals among sites grouped by migratory status and endemism. We analyzed all of these variables as binary data age with logistic regression GLMMs.

***Diet, habitat*** compositional analysis

We transformed the total number of each species into compositional data and applied the xxx transformation using the *compositions* package (van den Boogaart et al 2014).

***Body Condition*** To determine if body condition varied among sites we calculated the Scaled Mass Index (SMI or i, Peig and Green 2009). We used log-transformed body mass and wing chord measurements as our body size variables and the *smatr* package (Warton et al 2012) to calculate the scaling exponent *bSMA*. SMI was only calculated for individuals that could be classified as site persistent, either because they were resighted or recaptured within a single season or were observed in subsequent years. If a bird was captured more than once we only used mass and length data from its first capture. For each species we modeled whether SMA varied with pasture age using one-way ANOVA style models with site as a random effect and only considered species that occurred both in the pasture sites and the mature forest. [or was this done with just a lm() because the sample size was small?]

***Insect abundance*** To assess how insect abundance and diversity changed between sites we calculated total abundance of focal taxonomic groups in sticky traps and leaf litter samples, as well richness and diversity of taxonomic groups. Data were collected during two separate years but we did not incorporate this into our analysis. Instead we calculated means and standard deviations of each variable to assess general patterns of change. We also explored variation in insect communities across sites using naïve one-way multivariate analyses of variance (MANOVA) that treated each sample as independent.

**RESULTS**

*Patterns of bird distribution*. Through 40,723 mnh we recorded 7,315 captures of 60 species (Table 1). 25 species of birds with >30 captures each composed 96.9% of all captures, but capture rates were higher in the 2-yr and 5-yr old sites (231.5 and 236.0 birds/1000 mnh, respectively) than in the 10-yr and 20-yr old sites (152.5 and 132.9 birds/1000 mnh, respectively), or the mature dry forest (155.4 birds/1000 mnh).

Rarefaction curves indicated that sampling intensity was appropriate, with curves for each site approaching an asymptote (Fig. 1). Observed species richness was highest in the three youngest sites and lowest in the 20-yr old habitat, with intermediate richness in the mature dry forest (Fig. 1; Table 2). Shannon Diversity Index suggested that the three early-successional habitats were most diverse; lowest diversity was in the mature dry forest (Table 2). The effective number of species showed a similar pattern (Table 2), but Chao 1 non-parametric estimates of species richness indicate no significant difference in richness among sites (Table 2).

Regression analysis indicated that species richness and diversity decreased both increased significantly as time since abandonment increased (Figure 2; Table 2). ANOVA trend analysis indicated that these trends continued through the mature forest stage. Evenness of bird captures was generally high and similar among sites (Table 2). In all cases, evenness ranged from 0.74-0.82, with the lowest measure of evenness in mature dry forest. Regression analysis indicates that evenness increased significantly post-abandonment but was lower at the mature forest site.

The extent of numerical **dominance** of species within a site also suggests the degree of evenness (Table 3); five species accounted for 47.9–52.9% of captures in all early-successional habitats, whereas five species accounted for 61.1% of captures in mature dry forest. Although Greater Antillean Bullfinch (scientific names of all birds appear in Table 1) appeared as one of the five most abundant species in all habitats, other species contributed to among habitat differences in numerical dominance. For example, Yellow-faced Grassquit and Common-Ground Dove were among the most common species in the 2-yr and 5-yr old sites, with Ovenbird most abundant in the 10-yr and 20-yr old sites, and Bananaquit, Black-crowned Palm-Tanager, and Green-tailed Ground-Tanager largely restricted to the oldest sites.

Similarity indices based on species presence/absence were only moderately high with scores of 0.57–0.71 for habitat pairs (Table 4); scores tended to be higher between similarly-aged sites. Similarity indices based on the proportional abundances of individuals mist-netted (Table 4) were somewhat higher than scores based on presence/absence, and ranged up to 0.81. These scores generally point towards the uniqueness of the mature dry forest site apart from early successional habitats.

Of the 60 species recorded, 13 (22%) were endemic residents and 22 (37%) were latitudinal migrants (Table 1). The **proportion of endemic species** ranged from 21-25% of species captured within a site, and did not vary significantly (*G*4=0.182, *P*<0.996). But the proportion of endemic individuals ranged from 15-29% of all individuals captured within a site, and did vary significantly (*G*4=101.7, *P*<0.001) with the greatest numbers in the 20-yr and mature forest habitats (Table 2). The **proportion of migrants** varied from 26-40% and was not significantly different (*G*4=2.445, *P*=0.655), however, this result may have been influenced by a few rare species. The proportion of migrant individuals detected varied from 22-38% and was significantly different among sites (*G*4=136.7, *P*<0.001). Migrants were proportionately more abundant in the 5-yr and 10-yr sites with more dense shrubs, and less common in the 2-yr old and mature forest habitats (Table 2).

Presence/absence data suggest that most species occurring at our study sites were generalists. Of the 60 recorded species, 21 of 25 species with n>30 captures were recorded in all five sites (Table 1). Hispaniolan Lizard-Cuckoo and Black-crowned Palm-Tanager appeared to be true generalists in these habitats with no significant differences in capture rates among sites. However, others showed significant differences in abundance among sites (Table 1). Among residents, six species appeared to prefer the early-successional sites. These included Common Ground-Dove, Hispaniolan Emerald, Northern Mockingbird, Hispaniolan Spindalis, and Yellow-faced and Black-faced grassquits. In contrast, 3 species showed higher capture rates in more mature, forested sites. These included Key West Quail-Dove, Green-tailed Ground-Tanager, and Greater Antillean Bullfinch.

Neotropical migrants varied in their response to pasture age. Capture rates of Ovenbirds, Black-throated Blue Warblers and Black and White Warblers all increased significantly as pastures aged (Figure 3). Only Cape-May Warblers capture rates declined significantly, though Prairie Warblers, Palm Warblers, and American Redstarts all showed marginal declines. Among residents, only the Hispanolean Least Cuckoo capture rates increased as pasture age increased, Though several other species increased marginally. Only Capture rates of Yellow-faced Grassquits and Bananquits declined significantly with capture age,, though several other species showed marginal declines.

[Overall capture rates declined marginally as pastured aged; not sure if this is interesting; code has issue that I need to fix]

[Can look at species-specific trends that incorporate Aceitillar but these are often complex. BAWW shows a consistent increase from the pasture sites continuing on to Aceitillar. COYE are PAWA are both abundant at a single pasture site. OVEN and BTBW both show overall linear trends when you just look at the pasture sites, but if you consider Aceitillar there is evidence that their abundance actually peaks for the middle-aged pasture.]

Among over-wintering Neotropical migratory birds, Common Yellowthroat, American Redstart, Cape May Warbler, Palm Warbler, and Prairie Warbler showed significantly higher **capture rates** in younger habitats (Table 1). Only Black-and-white Warbler appeared to prefer the more mature habitats with highest capture rates in 20-yr old and mature forest sites (Table 1).

Neotropical migratory species often segregate by **sex or age** on the over-wintering grounds. We reliably determined sex of six species that were mist-netted with adequate sample sizes for analysis, including Black-and-White Warbler, Common Yellowthroat, American Redstart, and Cape May, Black-throated Blue, and Prairie warblers. There was no significant difference in the proportion of males among sites for any of these species (Table 5). In addition, there was no significant difference in the proportion of AHY individuals for any of these species, or for Ovenbird or Palm Warbler (Table 5).

The proportion of species of different **diet categories** did not vary significantly among sites (Fisher’s Exact Test, *P*=0.997), but the number of individuals in each diet category did (*G*16=820.1, *P*<0.001). Capture data (Fig. 2a) showed that granivores (combined with frugivores) predominated in early successional habitats, while more mature sites tended to be dominated by insectivores and omnivores. Nectarivores were present in all sites but also made up a greater proportion of all individuals in the mature dry forest.

**Preferred habitats** of mist-netted species was not significantly different among sites (Fisher’s Exact Test, *P*=0.945), but the preferred habitats of individuals did vary significantly among sites (*G*8=607.3, *P*<0.001). Early-successional sites were dominated by a greater proportion of individuals favoring pastures, scrub, and secondary forest, while the mature forest was dominated by individuals favoring evergreen forest habitats (Fig. 2b).

***Site Persistence and Body Condition*.** We used site persistence as our proxy for survival and then assessed whether the proportion of site persistent birds varied among sites. We found no significant difference in the proportion of site persistent individuals for any of the eight migratory species for which we had sufficient data for analysis (Table 5). Site persistence was generally low when averaged across all regenerating dry forest sites for Ovenbird (58.9%), Black-and-white Warbler (75.7%), Common Yellowthroat (57.9%), American Redstart (57.3%), Cape May Warbler (36.1%), Black-throated Blue Warbler (50.6%), Palm Warbler (32.5%), and Prairie Warbler (66.2%).

Among resident species, we found a significant difference in site persistence among habitats for four species. These species included Northern Mockingbird, Black-crowned Palm-Tanager, Yellow-faced Grassquit, and Greater Antillean Bullfinch (Table 6). In each case site persistence was higher in younger sites than older sites.

Site persistence may be related to food availability; flying insects caught on sticky traps were most abundant in mature forest and least abundant in the 2-yr habitat (Fig. 3a), with types of insects captured varying significantly among sites (*G*12=116.4, *P*<0.001). Younger sites tended to have a greater proportion of homopterans and coleopterans, while older sites had a greater proportion of dipterans (Fig. 3a). Leaf litter samples recorded similar numbers of arthropods in all sites except for mature forest where numbers were depressed (Fig. 3b). The types of arthropods recorded in leaf litter samples varied significantly among sites (*G*12=106.7, *P*<0.001), with older habitats dominated by ants and spiders, and younger habitats characterized by a wide variety of insects (Fig. 3b).

***Body condition***

***Body Condition*** Body condition of site persistent individuals of 15 species was compared across sites by analyzing variation in body mass adjusted for body size (Fig. 4). As pasture sites matured body regression analysis indicated that condition increased significantly for Hispaniolan Least Cuckoo and decreased for Red-Legged Thrush (Figure x). For specie that occurred in both abandoned pastures and the mature forest site, ANOVA trend analysis [note – b/c sample size was small these were done using just a lm!!!!] indicated that Bananquits peaked in abundance at moderately old pasture and decline in condition in old pastures and in mature forest (Linear trend: t = -2.65, p = 0.009; quadratic trend: t = -2.51, p = 0.012; Table x; include figures?). Black-crowned palm tanagers did not show significant decline in regression analysis (beta = x, SE, p = 0) but did when considering the mature forest site (Linear trend: t = -3.4, p = 0.001). Similarly the abundance of the GABU was faily constant as pastures aged ( beta = x, SE, p = 0) but decline significantly at the mature site (Linear trend: t = -3.4, p = 0.001; quadratic trend: t = -2.3, p = 0.023; Table x; include figures?; contrast between oldest pature and Aceitllar?). GRWA should a similar pattern, with relative constant condition as pastures aged but condition decline for birds at the mature forest site (Linear trend: t = -2.32, p = 0.021; quadratic trend: t = -1.7, p = 0.09; Table x; include figures?; contrast between oldest pature and Aceitllar? Among over-wintering migratory birds adjusted body mass did not vary significantly across sites (Fig. 4, Table x).

**DISCUSSION**

Despite the similarity in species richness and diversity across these sites, we found that early successional and mature dry forests provide habitat for unique sets of permanent resident and over-wintering migratory birds. By looking beyond simple presence/absence, most species showed a preference for either relatively younger or generally older habitats. These differences were likely driven by differences in resource availability, as trophic composition differed between young and old sites, reflecting differences in availability of resources or foraging sites (Blake and Loiselle 1991, 2001).

Many of the species occurring in the early-successional sites are considered typical of open areas and young, shrubby second-growth, and are granivores or frugivores. These species include Common Ground-Dove, and Yellow-faced and Black-faced grassquits. In addition, the few island nectarivores frequently had higher capture rates in early successional sites; the Antillean Mango, Hispaniolan Emerald, Cape May Warbler, and Bananaquit took advantage in particular of remnant *Bursera* trees, prolifically flowering *Senna* trees, and other understory vegetation. These results are consistent with other studies that show bird assemblages in tropical agroecosystems are composed of disproportionately more frugivorous and nectarivorous birds and fewer insectivorous species than native forest (Tscharntke et al. 2008). Results showing significantly higher adjusted body mass in early-successional habitats for the Bananaquit and the omnivorous Black-crowned Palm-Tanager reflect similar patterns in site persistence for these species, and help explain why tropical agroecosystems, including regenerating pastures, are composed of disproportionately more omnivorous and nectarivorous birds, and fewer insectivores compared to native forest (Karr et al. 1990, Blake and Loiselle 2001, Tscharntke et al. 2008).

In addition to supporting species typically associated with early-successional habitats, shrubs have also been shown to provide seasonal opportunities for foraging on fruit and critical cover for birds thought of as primary forest species (Anders et al. 1998, Streby et al. 2011, Stoleson 2013). For example, the occasional presence in early-successional habitats of species such as White-fronted Quail-Dove, Ruddy Quail-Dove, and Rufous-throated Solitaire, typical of primary forest, suggests that individuals may move from nearby older forests in the landscape matrix, and into early-successional habitats temporarily to take advantage of unique resources (Blake and Loiselle 1991).

The 20-yr old and mature forest sites were, in contrast, distinguished by insectivores, such as Ovenbird and Green-tailed Ground-Tanager, as well as more omnivorous species, such as Greater Antillean Bullfinch, as seen in other tropical forested habitats (Blake and Loiselle 2001). High insect abundance in mature dry forest, in particular, may explain the relatively high capture rates of such species as Hispaniolan Pewee, Black-and-white Warbler, and Green-tailed Ground-Tanager, but fail to explain lower adjusted body mass in this same habitat. The ground-tanager, a species which forages low in the understory (Latta et al. 2006), may respond negatively to depressed numbers of ground-dwelling insects, as did the Ovenbird, since our studies revealed lower counts of arthropods in leaf litter samples in mature dry forest. In addition, many of these ground-dwelling insects, such as ants, are considered less palatable for birds (Zach and Falls 1979, Bell 1990).

An especially important finding from our study is that Hispaniolan endemics comprise a greater proportion of mist net captures in the oldest habitats, and especially in mature dry forest. While some endemics, such as Hispaniolan Lizard-Cuckoo and Black-crowned Palm-Tanager, appear to be true generalists across the studied habitats, older sites were characterized by robust populations of several more unique species, such as Key West Quail-Dove, Green-tailed Ground-Tanager, and Greater Antillean Bullfinch. The uniqueness of these older habitats is apparent in results from the Sorenson Index which emphasizes the relatively low similarity of the 20-yr old and mature forest habitat to other sites. Our findings are similar to those of MacGregor-Fors and Schondube (2011) who also found that simplified agricultural landscapes such as cattle pastures had bird communities with endemic species poorly represented compared to tropical dry forests in Mexico.

Over-wintering migrants are an especially significant portion of the avian community in the 5-yr and 10-yr old sites with a dense understory. These include species known to prefer shrubby and open habitats, such as Common Yellowthroat (Lynch 1992), Palm Warbler (Latta 2003) and Prairie Warbler (Latta and Faaborg 2001), but also the frequently nectarivorous Cape May Warbler (Latta and Faaborg 2002), which took advantage of abundant flowering trees and shrubs, including *Senna* and *Bursera*. Only the ground-foraging Ovenbird, which prefers shaded sites with abundant leaf litter, and Black-and-white Warbler, which forages for arthropods on trunks and branches of larger trees (Wunderle and Latta 1996), favored mature forest sites. Our results support the conclusion that second-growth and other disturbed habitats can be important to many species of long-distance migrants (Lynch 1992, Wunderle and Waide 1993).

However, regenerating dry forest appears to be relatively suboptimal-quality habitat for latitudinal migrants based on age and sex ratios and site persistence. A preponderance of male and AHY migrants has been used as an indicator of high-quality habitat for many species (Faaborg et al. 2010), and segregation has been demonstrated previously for American Redstart, Cape May Warbler, Black-throated Blue Warbler, and Prairie Warbler (Faaborg et al. 2010). Among migrants in this study we found populations tended to be dominated by females and HY/SY individuals, suggesting that these early successional habitats may be of relatively low quality for these species. This conclusion is supported by low rates of site persistence for these species when compared with comparable data from previous studies. For example, site persistence of warblers wintering in native forests and shade coffee plantations range from 52-80% for American Redstart (Holmes et al. 1989, Sherry and Holmes 1996, Wunderle and Latta 2000), 42-85% for Black-throated Blue Warbler (Holmes et al. 1989, Wunderle and Latta 2000), 61-82% for Black-and-white Warbler (Wunderle and Latta 2000), 67-88% for Cape May Warbler (Latta and Faaborg 2002), and 75-84% for Prairie Warbler (Latta and Faaborg 2001). In all cases, warblers over-wintering in our early-successional sites exhibited site persistence levels at the low end of these ranges.

*Conservation implications*. Many previous studies of the impact of anthropogenic habitat change on birds have focused on the impact of deforestation and fragmentation of primary forests on species and communities and the associated loss of biodiversity from these landscapes (Stouffer and Bierregaard 1995, Sekercioglu et al. 2002). Relatively few studies, however, have looked at the inverse questions: i.e., what is the pattern of regained bird diversity as agricultural lands are abandoned, when do regenerating forests attain equivalent ecological value for birds found in mature forest, and what components of the agricultural matrix support higher biodiversity?

Results from this study suggest the importance of remnant trees in contributing to avian diversity in our regenerating dry forest sites. While tree cover in the agroecological matrix may typically be thought of in terms of remaining blocks of primary forest, even in a landscape dominated by agriculture, individual trees may be retained for fruit, shade, or other functions (Harvey et al. 2006). These trees may then serve birds as dietary resources (Sekercioglu et al. 2007), shelter (MacGregor-Fors and Schondube 2011), stepping stones between forest patches (Graham 2001, Sekercioglu et al. 2007), and microclimatic refuges (Greenberg et al. 1997, Sekercioglu et al. 2007). In our work, avian species richness did not vary among sites, in part because we found numerous granivores, omnivores, and nectarivores even in our youngest sites. Despite the difference in age of regenerating pastures, bird species were likely attracted especially to the abundant flowers and fruit of remnant trees remaining in all of the abandoned pastures. Modest numbers of trees have been shown to be important for birds even in an agricultural countryside (Harvey et al. 2006, Estrada et al. 1997, Sekercioglu et al. 2007), suggesting that agricultural efforts and restoration methods that promote the retention of remnant trees in the landscape can have a very positive impact on many bird species.

But not all remnant trees are considered equal for avian diversity in an agricultural matrix. Some tree species have been shown to have unusually high value for birds (Wunderle and Latta 1996, MacGregor-Fors and Schondube 2011). For example, Greenberg et al. (1997) found *Acacia*, a legume like *Senna,* supported both the highest density and diversity of migratory birds compared to other habitats in Mexico, and the value of *Bursera*, a species also prominent in our sites, has been established for a variety of bird species in several situations (Greenberg et al. 1995, Latta et al. 2001). As a result, not only is the distribution of remnant and regenerating trees important to the diversity and abundance of birds in the Mencia landscape, but the prominent presence of legumes and *Bursera* added positively to that impact.

In addition to remnant trees, shrub understory also plays a role in supporting a diverse avian community. This study emphasizes the importance of shrubby pastures to a wide variety of birds, and reinforces the suggestion that the loss of pastures which include shrubs and trees is associated with the decline of many agricultural bird species (Pärt and Söderström 1999, Heikkinen et al. 2004). Latitudinal migrants were an especially significant portion of the avian community in the 5-yr and 10-yr old sites with more dense shrubs. Nevertheless, age and sex ratios, and relatively low site persistence suggests that this shrubby habitat may be comparatively low quality for species such as Common Yellowthroat, American Redstart, Cape May Warbler, Palm Warbler, and Prairie Warbler, and this deserves additional study.

Finally, although protecting natural vegetation is essential for the preservation of major elements of biodiversity (Bruner et al. 2001, McKinney 2002, Sekercioglu et al. 2004), our results suggest that the agricultural matrix can provide habitat for some birds in the buffer zone of forested protected areas. Discussions of buffering the effects of agriculture on protected areas have often focused on providing a mature forest matrix to facilitate the movement or dispersal of forest species (Vandermeer and Perfecto 2007, Burkey 1989, Vandermeer and Carvajal 2001). Until now much less has been written on how the agroecological matrix itself, and early successional regeneration, can provide habitat for birds (but see MacGregor-Fors and Schondube 2011). However, care should be taken to examine body condition and demographic rates as we do here in assessing the value of these early successional habitats.

In conclusion, this study shows that the regenerating forests that we examined failed to compensate for the loss of mature dry forest habitat, as indicated by distinct suites of bird species in the contrasting habitats, including the presence of some unique Hispaniolan endemics in mature habitats. Remnant overstory trees and dense understory in early successional regenerating pastures, however, do provide habitat for a suite of species, including many over-wintering migrants. But demographic and site persistence data suggest that these habitats may not be optimal for many migrants in particular. Because some of our regenerating sites were 20 yr old and still failed to replicate mature dry forest habitat, regaining complex microhabitats and structures such as canopy closure in these dry forest sites may take decades or longer. Therefore, while early successional habitats may be viewed as part of a complex mosaic of habitats capable of attracting many birds, perhaps their greatest value is as a component of the buffer zone, enhancing biodiversity conservation through integration with protected areas which themselves contain mature forests that harbor more unique, often endemic, bird species.

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