Bird communities in tropical agroforestry ecosystems: an underappreciated conservation resource

Skye M. Greenler & James J. Ebersole

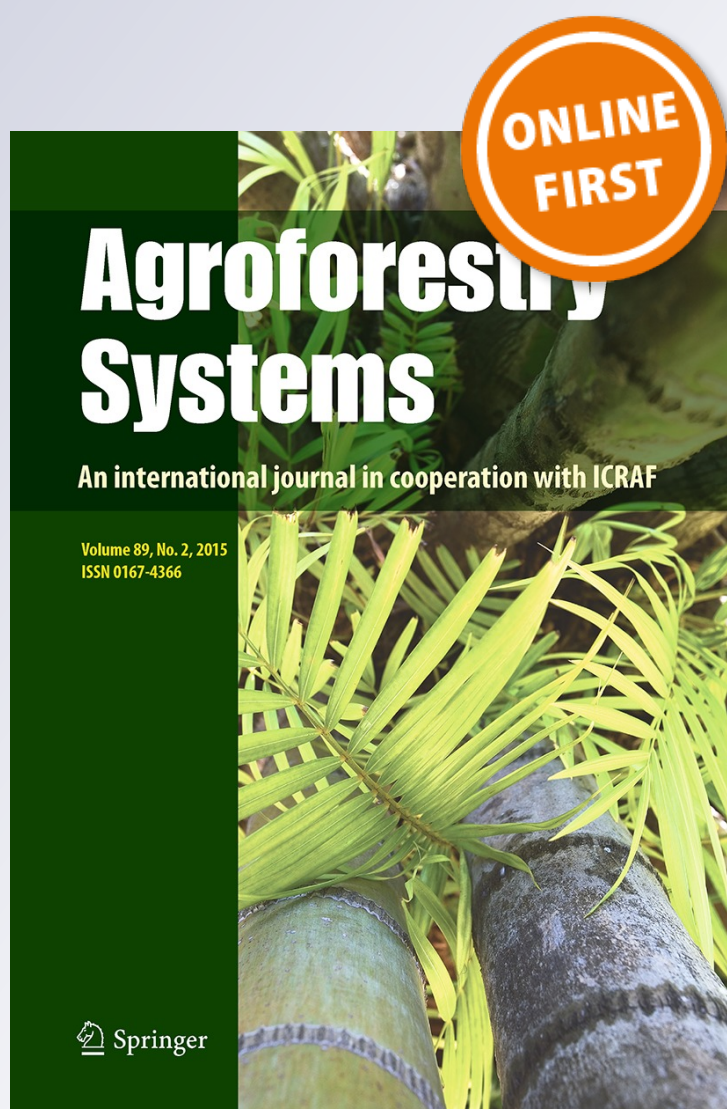ONLINE FIRST

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Abstract Tropical conservation and research focus primarily on protected areas and often ignore conservation values of surrounding agricultural lands. Understanding how species utilize agricultural land will maximize conservation efforts. We compared bird community composition in four habitats in northeastern Costa Rica: shade-grown cacao, live fences, riparian forest buffers, and preserved late-successional rainforest. Point counts over 2 months found 167 species from 36 families. Rainforest contained the most species unique to a habitat although richness per point was lower than in agricultural habitats. Half, 31, of the rainforest species did not occur in other habitats, while 106 species, mostly those preferring open areas, occurred in agroforest habitats but not rainforest. While agricultural habitats had fairly similar species composition to each other as determined by distance in an ordination, each also contained significant numbers, 9–30, of unique species. While intact rainforest remains central to conservation of tropical birds, agricultural lands with substantial trees, e.g., live fences, riparian buffers, and plantations with shade trees, can support a high richness of birds. These avian communities are not simply subsets of the rainforest species but include substantial numbers of unique species. Conservation contributions of these lands to species richness and complexity should be considered in conservation, and trees in these habitats preserved.

Introduction

For many years deforested agricultural land was not considered to have conservation value, but recent research shows that it may hold substantial biodiversity (Donald and Evans 2006). Understanding this conservation resource can help manage these lands effectively to maximize their conservation values as complements to the central importance of preserved areas (McIntyre and Hobbs 1999; Donald and Evans 2006; Koh and Ghazoul 2010; Mendenhall et al. 2012). In addition to direct value as habitat, the agricultural matrix around a preserved forest also influences preserve health, fragment recolonization, and bird movement (Stouffer and Bierregaard 1995;

S. M. Greenler (✉) · James J.Ebersole
Department of Organismic Biology and Ecology,
Colorado College, 14 E. Cache la Poudre St.,
Colorado Springs, CO 80903, USA
e-mail: skye.greenler@coloradocollege.edu;
skyegreenler@yahoo.com

Şekercioḡlu et al. 2002; Sigel et al. 2006; Laurance et al. 2012; Muhamad et al. 2013). However, only a few studies in Mexico (Estrada et al. 1997; Greenberg et al. 2000; Estrada and Coates-Estrada 2005), Nicaragua (Harvey et al. 2006), and Indonesia (Muhamad et al. 2013) have investigated differences in avian community composition among several agricultural habitats. To improve conservation management, we need to better understand bird communities of tropical agricultural lands and how they vary among different agricultural systems.

South and Central America are key locations to study the conservation value of agricultural land because this region loses approximately 4.4 million ha of forest cover annually and is a center of current extinctions (Wilson 1988; Bradshaw et al. 2009; Gardner et al. 2009; Eva et al. 2012). Deforestation has left Costa Rica with many discontinuous forest fragments surrounded by a complex agricultural mosaic (Bierregaard et al. 1992; Sigel et al. 2006). Fragmentation strongly affects Neotropical birds, which are generally specialized and use narrow microhabitats (Stouffer and Bierregaard 1995; Lindell et al. 2007; Ruiz-Guerra et al. 2012).

Island biogeography theory (MacArthur and Wilson 1967) has been used to describe species richness following forest fragmentation for decades (Mendenhall et al. 2014). However, it does not adequately describe the community composition following forest fragmentation because it accounts only for patch size and isolation and assumes the matrix is incapable of sustaining native species (Laurance 2008). Assuming a barren matrix and that species cannot adapt to altered habitat limits the conservation contributions of these areas (McIntyre and Hobbs 1999; Prevedello and Vieira 2010; Mendenhall et al. 2012).

Several types of tropical agroforest systems, including live fences, riparian forests, and shade-grown crops, have been touted to benefit avian conservation and functionally extend adjacent preserves (Van Bael et al. 2007; Seaman and Schulze 2010). Although not managed for conservation, these highly modified habitats may support some bird species (Gardner et al. 2009; Prevedello and Vieira 2010; Laurance et al. 2012; Kumaraswamy and Kunte 2013).

In this study we present data on bird community composition in a preserved, late successional rainforest; an organic, shade-grown cacao plantation; riparian forests; and live fence systems in northeastern Costa

Rica. We use these data to ask: (1) How do bird species assemblages differ among these agricultural habitats and the late-successional rainforest? (2) What families and guilds drive the differences in species assemblage among these habitats? Through these questions we explore the utility of the several community composition models in this system, address the conservation value of the existing agroforest ecosystem matrix, and make concrete conservation suggestions.

Methods

Study site

This study was completed in 10 km^2 landscape of mixed rainforest, pasture, agroforest, and monoculture in the Caribbean lowlands of northeastern Costa Rica (10°20″N, 83°20″W) (Fig. 1). The area is approximately 35 m above sea level and is in the premontane wet forest life zone (Holdridge 1967). Mean annual temperature is between 25 and 30 °C and mean annual precipitation is 6000 mm (Bermúdez and Hernández 2004). The study site is 2 km southwest of the Tortuguero National Park boundary and is essentially continuously connected to the park through privately preserved forests.

The cacao plantation is 120 ha of organically managed, shade-grown cacao (*Theobroma cacao*). The canopy shade layer, primarily planted native and non-native trees with interspersed old-growth trees, provides approximately 40 % cover. Common shade trees in the cacao plantation are *Leucaena leucoephela*, *Eucalyptus deglupta*, *Cocos nucifera*, and banana (*Musa acuminata*). The farm is approximately 30 year old and was previously a wooded pasture with areas of secondary growth forest (Geovanny Herrera, pers. comm.). Cacao trees are evenly spaced on a 3 m × 3 m grid and are trimmed to a maximum height of 3–4 m. The understory of grass or cacao litter is continuously trimmed. Multiple small creeks and drainage ditches cross the plantation.

Riparian forests were studied on two reaches of a stream, both bordered by pasture, and extended approximately 15 m away from the creek bank as regulated by Costa Rican law for the protection of riparian forests (Asemblea Legislativa de la Republica de Costa Rica, 1997, No. 7575 Ley Forestal; Seaman and Schulze 2010). Although not all managers follow

these requirements, the riparian forests we studied do extend approximately 15 m from the creek bank. They contain primarily successional native and introduced trees with scattered old growth trees. The most prominent tree species are *Cordia alliodora*, *Piper auratum*, *Pterocarpus officinalis*, *Posoqueria grandiflora*, *Cecropia obtusifolia*, and *Carica papaya*.

The live fences in this study are intentionally planted single rows of various tree species, which are used as living posts and strung with barbed wire. This common agricultural practice in Central America delineates field boundaries and partitions pastures. Trees in the live fences are primarily *Castilla elastica*, *Erythrina poeppigiana*, *Ficus wreckleana*, *Spondias mombin*, and *Cordia alliodora*. Trees are 1–3 m apart, and 3–7 m tall, and the 2–6 m wide canopy is usually contiguous the length of the fence. We sampled live fences in two pastures, one of which is wetter and as a result had more waterfowl.

The late successional forest (hereafter rainforest) is privately conserved and has never been clear-cut but was selectively logged over 40 years ago (Geovanny Herrera, pers. comm.) and is in a late stage of succession according to the criteria of Gutiérrez and Huth (2012). The rainforest has a closed canopy 30–50 m high, highly variable understory and sub-canopy cover, and trees in all life stages. The hilly, steep terrain makes it essentially unusable for agriculture. There is a sharp border between the rainforest and adjacent pasture and African palm plantations. The forest is not currently managed or used for any economic venture (Geovanny Herrera, pers. comm.).

The four habitats studied are mostly surrounded by pasture, banana (*Musa acuminata*), pineapple (*Ananas comosus*), and African palm (*Elaeis guineensi*) monocultures.

Data collection

Bird populations were sampled using the fixed-radius, point-count method (Hutto et al. 1986) along two sampling lines in each of the four habitats. Each sampling line had 10 permanent point-count stations at least 100 m apart in the cacao plantation, riparian forests, and rainforest, and >80 m apart in live fences.

Two permanent sampling lines were established in each habitat at the beginning of the study. Sampling lines in the cacao plantation were roughly parallel, straight lines 85 m and 68 m on either side of a main access path. The two riparian forest sampling lines followed the stream. Rainforest sampling lines followed animal trails due to ease of access in the steep terrain. Sampling lines for live fences were straight lines perpendicular to fences in a silvopasture; each point count was on a different live fence in the same pasture. Distances between stations in live fences varied, but placement on different fences ensured independence. All sampling lines were at least 100 m from the edge of the habitat (Fig. 1). Each line was sampled four times over 44 days in March and April 2013 for a total of 40 counts/sampling line and 80 counts/habitat.

We used 25-m fixed radius counts because they are small enough to compare bird abundances among a variety of habitats (Hutto et al. 1986). On a given morning, between 0600 and 1000, we surveyed the ten points on one line. At each point the bird species present were recorded (presence/absence) visually and aurally for 10 min. Birds flushed from the measurement area on approach were counted, and birds flying
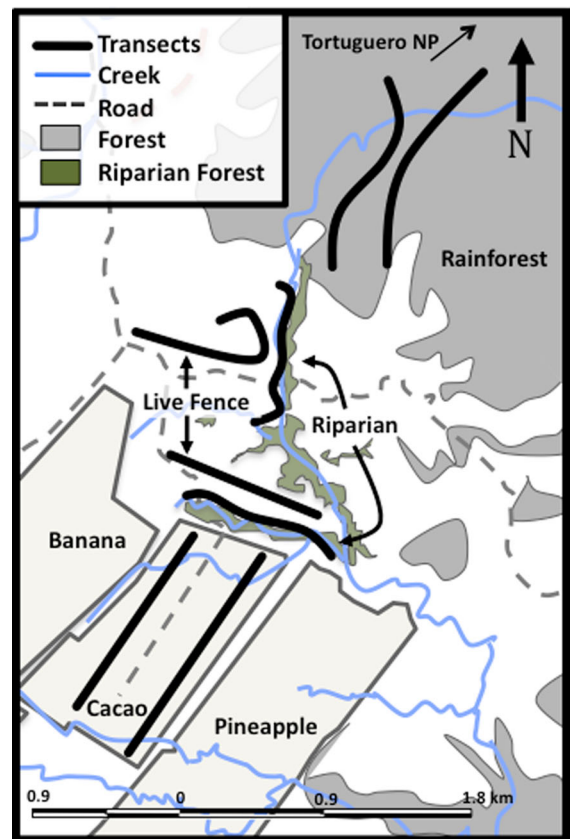
Fig. 1 Map of study area and sampling lines, adapted from Vaughan et al. (2007) and Google maps

above the canopy or across the landscape were not counted. We did not collect data rainy days, consistent with the procedure of Ralph et al. (1993).

Birds were identified visually using Garrigues and Dean (2007) and Stiles et al. (1989) and aurally from memory and by comparing field recordings to known recordings.

In the live fences some of the measurement area was pasture adjacent to the fence so the location of each bird was noted as in the live fence or in pasture after Estrada et al. (1997), Estrada and Coates-Estrada (2005), and Cerezo et al. (2009). In the cacao plantation we noted if birds were in shade trees or cacao trees. Since the rainforest canopy is much higher than the agroforest habitats, rainforest canopy birds are likely undercounted in this study.

Statistical analysis

We measured sampling effort completeness with species accumulation curves for each of the eight sampling lines over the study (online resource A in ESM).

We grouped identified species into 36 families and 14 diet guilds using Gentry (1990) and Stiles et al. (1989) (online resource B in ESM) and analyzed each group separately. We did not statistically test families or diet guilds that contained <3 % of the total species or individuals identified because sample sizes were too small. Analyses within a grouping (family or diet) are independent, but since the same data were grouped in two ways, statistical tests across the groups are not completely independent.

Since data collection occurred during spring migration, observations include migrants. Several species in Costa Rica have both migratory and resident populations, which are difficult or impossible to distinguish in the field. For species with both migrant and resident individuals, half of individuals were considered migrants.

We used repeated measures ANOVA to test for differences, per point count, in (1) species richness, (2) number of migrant species, (3) number of species in each diet guild, and (4) number of species within each family. The statistical model used habitat as a fixed effect, sampling line as a random effect nested within habitat, time, and habitat by time interaction. When the overall ANOVA was significant, we used Tukey's multiple range tests to determine which pairs of habitats differed. We tested assumptions of ANOVA by assessing normality of residuals with the Anderson–Darling test and by examining normality plots. Residuals were normally distributed for all variables except the wren family. The leptokurtosis of this variable was removed by taking the cube root of the difference between each value and the mean. We did not test homoscedasticity because inequality of variances does not affect P values of ANOVA when sample sizes are equal (Scheffé 1959). We did not adjust P values for the number of tests in the study. ANOVAs were completed with Minitab version 16 (Minitab Corp. 2013, State College, PA) and Tukey's multiple range tests were completed with SPSS version 21 (IBM Corp. 2012, Armonk, NY). Online resource C in ESM contains all habitat means, F ratios, P values, and error mean squares for habitat differences. Online resource D contains all F ratios, P values, and error mean squares for habitat by time interaction, sampling line within habitat, and time.

To assess the differences in bird community composition we used detrended correspondence analysis (DCA) of the quantitative sampling line-by-bird species matrix (167 species by eight sampling lines) and point-by-bird species matrix (167 species by 80 points) (PC-ORD 6, McCune and Mefford 2011). DCA arranges samples in an n-dimensional (in this case n = 167) species space and finds axes that account for the maximum variation in the data set so that so that samples similar in species composition appear closer to each other in a 2 or 3-D representation (Barnes and De Grave 2001). The DCA was run with 443 and 1057 (respectively) non-zero data items, no randomization tests, no down weighting of rare species, and rescaling of axes with 30 segments at a threshold of 0.

Results

Species richness

We recorded 1417 individuals of 167 species from 35 families. Species accumulation curves approached asymptotes by the end of the study, demonstrating adequate sampling (online resource A in ESM).

We recorded the most species, 95, in riparian forests, followed by 83 in live fences. Rainforest and cacao plantation had fewer species, 61 and 60 respectively. Half of the total species identified, 85, were identified in only one of the habitats. Rainforest

had the most unique species, 30; there were 23 unique species in both riparian forests and live fences; and only nine in the cacao plantation.

Mean number of species identified per point was greatest in live fences, intermediate in riparian forest and the cacao plantation, and lowest in rainforest ($F_{3,4} = 50.90$, $P = 0.001$, Fig. 2). There were no significant differences in number of species between sampling lines within habitats or with time and no habitat by time interaction (online resource D in ESM).

Species composition: detrended correspondence analysis

A two-dimensional DCA explained a high proportion of the variation in the sampling line-by-species data
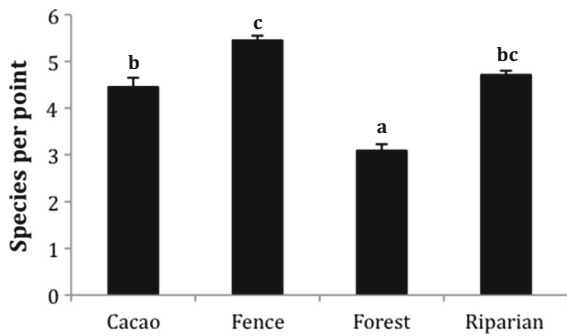
Fig. 2 Mean (±SE) number of bird species identified per point by habitat. *Letters* indicate significant differences between habitats determined by Tukey HSD 95 % confidence interval
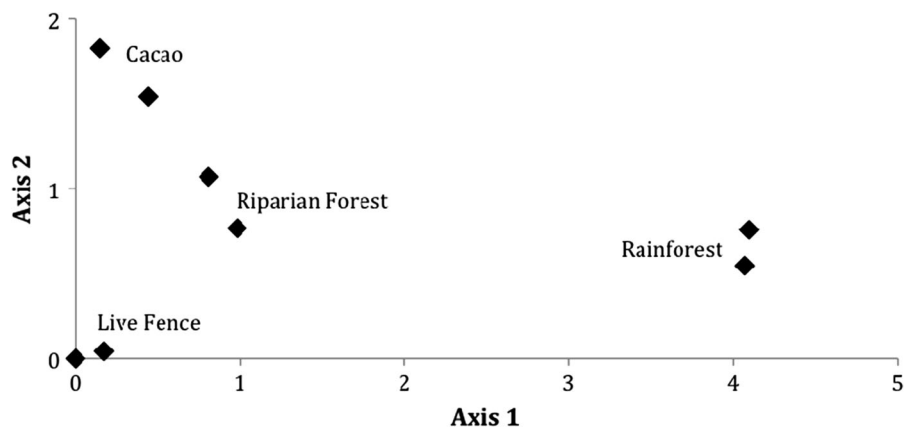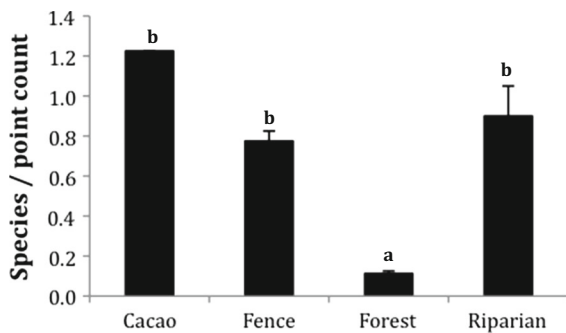
matrix. The DCA separated the four habitats and also showed that the two sampling lines within each habitat were quite similar in species composition. The first axis (eigenvalue = 0.737) separated the rainforest from the three agricultural habitats. The second axis (eigenvalue = 0.257) separated the agricultural habitats, with riparian forests intermediate in species composition between the cacao plantation and live fence (Fig. 3). We did not use the third axis because of its low eigenvalue (0.105). The total variance in the data set was 1.7890.

The ordination separated the rainforest by 3–4 standard deviations from the three agricultural habitats. Since, on average, species appear, rise to a maximum, and disappear over about 4 SD of a DCA axis (Hill and Gauch 1980), these distances show that the agricultural habitats support a substantially different avian community than the rainforest. Avian communities in the riparian forests were slightly more similar to the rainforest than the other two agricultural habitats, perhaps because the riparian forest structure is more similar to that of the rainforest.

Bird communities in the agricultural habitats were more similar, 1–1.5 SD apart, to each other than to the rainforest. Because 1 SD represents a community similarity of about 50 % (Hill and Gauch 1980), this indicates that the agricultural habitats support moderately similar but still biologically distinct bird communities.

A two-dimensional point-by-species DCA showed similar overall patterns but with more variation (online resource E in ESM). The rainforest showed more

Fig. 3 Detrended correspondence analysis of quantitative abundances of bird species in eight sampling lines. Units of axis *1* and *2* are standard deviations

Fig. 4 Mean (±SE) number of migrant species identified per point by habitat. *Letters* indicate significant differences between habitats determined by Tukey HSD 95 % confidence interval. (Absence of *error bars* indicates all values were identical)

within-habitat variation than the agricultural habitats. The greatest difference between an agricultural and rainforest point is 6.4 SD on the first axis (eigenvalue = 0.772). The second axis is also longer with a range of 4.3 SD (eigenvalue = 0.429) and primarily separated rainforest points. This is not unexpected because the habitats were not completely homogeneous and different points had different resources and disturbances. There were no noticeable differences between the two sampling lines in a habitat.

Migrant species

Migratory species occurred more frequently, on a per point count basis, in the cacao plantation, riparian forests, and live fences than in rainforest ($F_{3,4} = 34.72$, $P = 0.003$, Fig. 4). This suggests that migratory species prefer the structure and resources in the human-influenced agroforest ecosystems to the relatively undisturbed rainforest. Effects of sampling line, time, and habitat by time interaction were not significant (online resource D in ESM).

Differences in families among habitats

The number of species per point count in seven families, Cardinalidae, sparrows (Emberizidae), ovenbirds (Furnariidae), new world warblers (Parulidae), tanagers (Thraupidae), wrens (Troglodyridae), and flycatchers (Tyrannidae), varied significantly between at least two of the habitats. The five families pigeons and doves (Columbidae), Icteridae, woodpeckers (Picidae), parrots (Psittacidae), and hummingbirds

Fig. 5 Mean (±SE) number of bird species identified per ▶ point by habitat for the 12 most common families. *Letters* indicate significant differences between habitats determined by Tukey HSD 95 % confidence interval. (Absence of *error bars* indicates all values were identical). Note varying y-axis scales

(Trochilidae) did not show differences in number of species among habitats (Fig. 5).

Live fences had significantly more flycatchers per point count than the cacao plantation and riparian forests, which both contained more than the rainforest ($F_{3,4} = 68.85$, $P = 0.001$, Fig. 5). This trend follows the amount of open space in the four habitats, which decreases from live fences to rainforest, and corresponds to flycatchers' need for open spaces to hunt insects and for tree cover for perching and protection.

Similar patterns were seen in the new world warblers, with the cacao plantation having a greater number of species per point count than live fence or riparian forests and rainforest having the fewest ($F_{3,4} = 48.14$, $P = 0.001$, Fig. 5). 80 % of the new world warblers we identified are migrants, which suggests the same reasons for the differences as in migratory species.

Live fences and riparian forests had significantly more tanager species per point count than rainforest while the cacao plantation was not different from other habitats ($F_{3,4} = 13.37$, $P = 0.015$, Fig. 5). The tanager species identified in this study tend to use young and old second-growth forests, pastures, plantations, and forests edges and gaps (Gentry 1990). This suggests that, before human modification of the landscape, this family used natural gaps, open areas, and savannas, which are now mostly replaced with agroforests.

Rainforest had more wren species per point count than cacao plantation or riparian forests ($F_{3,4} = 12.14$, $P = 0.018$, Fig. 5). The only wren species recorded in the cacao plantation and live fences was the House Wren (*Troglodytes aedon*), and no House Wrens were recorded in the rainforest. Only four wren individuals were recorded in riparian forests over the course of the study. With the exception of House Wrens, it appears that species within this family do not thrive in any agroforest ecosystem.
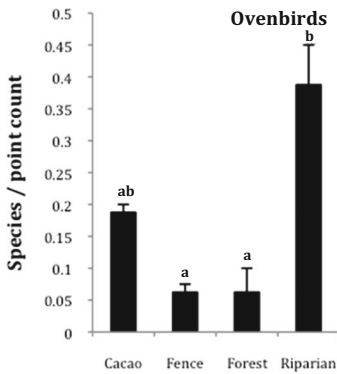
Diet guild differences

The six diet guilds (a) fruits or fruits and seeds; (b) large insects, small vertebrates; (c) nectar, small
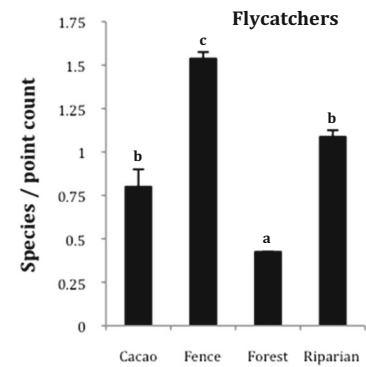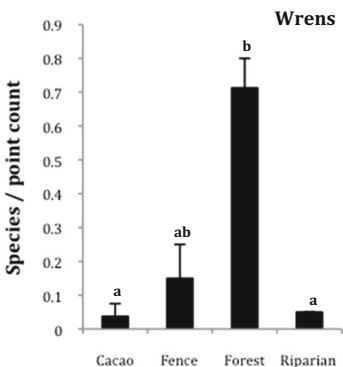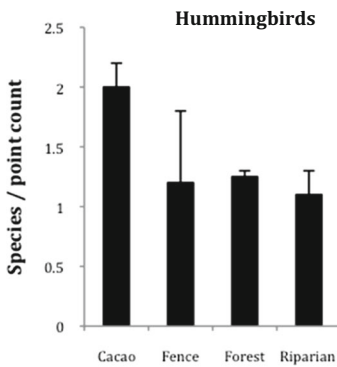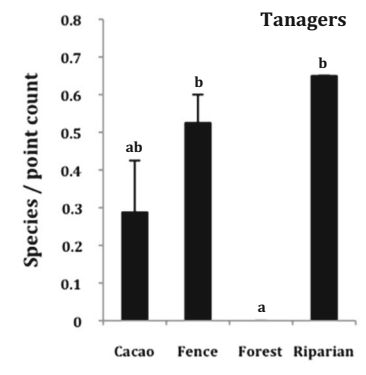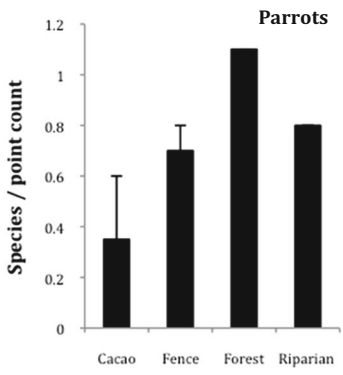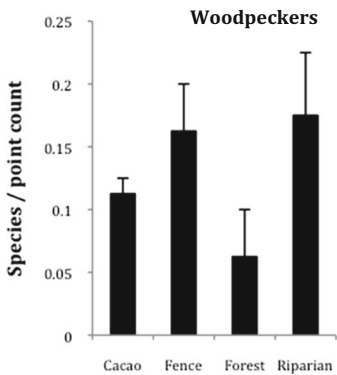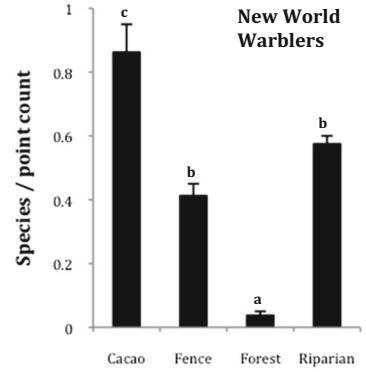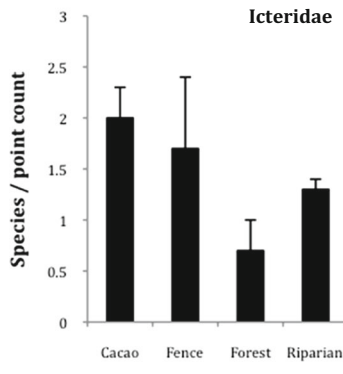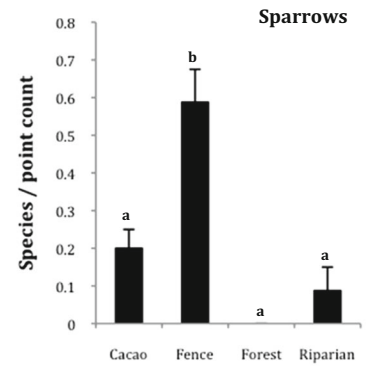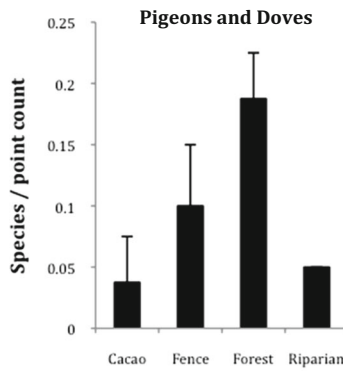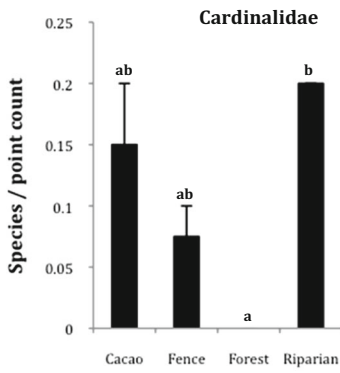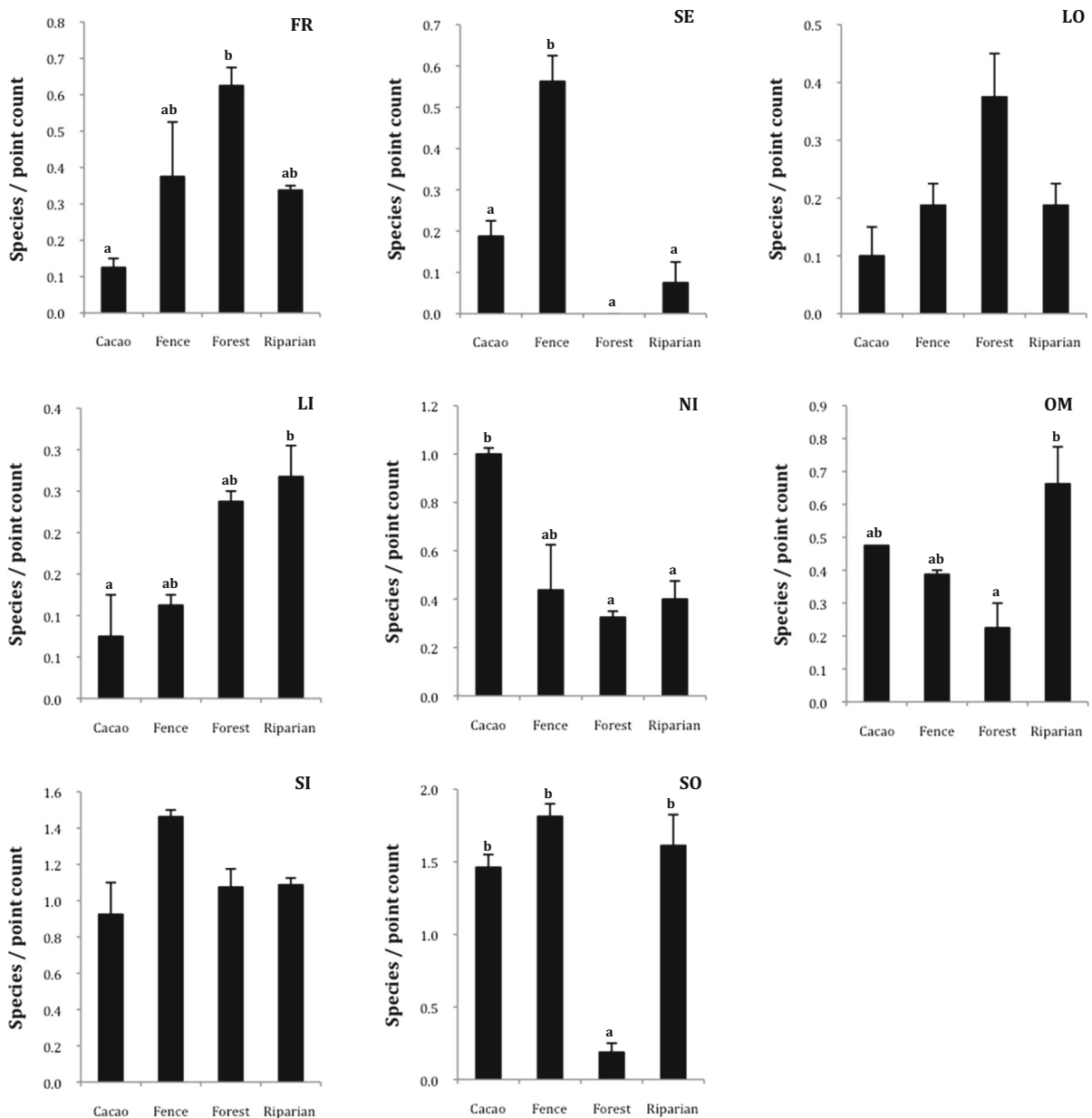
Fig. 6 Mean (±SE) number of bird species identified per point by habitat for the eight most common diet guilds. *Letters* indicate significant differences between habitats determined by Tukey HSD 95 % confidence interval. Note varying y-axis scales. *FR* fruits or fruits and seeds, *SE* grass seeds, *LO* large insects, fruit, and small vertebrates, *LI* large insects, small vertebrates, *NI* nectar, small insects/spiders, *OM* omnivore, *SI* small insects, *SO* small insects and fruit

insects/spiders; (d) omnivore; (e) grass seeds; and (f) small insects and fruits varied significantly in number of species per point count between at least two habitats. The two diet guilds (a) large insects, fruits and small vertebrates and (b) small insects did not vary among habitats (Fig. 6).

Live fences had significantly more species per point count in the grass seeds diet than rainforest, riparian forests, or cacao plantation ($F_{3,4} = 31.92$, $P = 0.003$, Fig. 6), which corresponds with birds foraging in open fields and returning to trees or shrubs for cover (pers. obv.). The sparrow family showed the same pattern

because there was 96 % overlap of individual observations between the two groups (these were the only two groups with such high overlap between family and diet guild).

There were significantly more species per point count within the guild that eats large insects and small vertebrates in riparian forests than in the cacao plantation, and rainforest and live fences were intermediate in this parameter and not different from the other habitats ($F_{3,4} = 9.62$, $P = 0.027$, Fig. 6). This suggests that because of large insect availability, vegetation structure, water availability, plant diversity, or other unknown factors the riparian forests support more species per point count from this diet guild despite appearing to be structurally similar to the cacao plantation.

In contrast, the cacao plantation contained significantly more species in the nectar, small insects/spiders guild than riparian forests or rainforest while the live fence habitat was not different from other habitats ($F_{3,4} = 9.13$, $P = 0.029$, Fig. 6). Birds in this guild were not feeding directly on the nectar from cacao trees, because cacao flowers are very small and are pollinated by tiny midges (de Schawe et al. 2013). These patterns are not easily explained because one might assume that a habitat (riparian forest) that supported a high number of birds that eat large insects would also support a high number of birds that eat nectar and small insects. This highlights that subtle differences in plant species composition, vegetation structure, management, and other unknown factors can lead to similar habitats supporting different bird species.

There were more species in the fruit or fruits and seeds diet in rainforest than in the cacao plantation ($F_{3,4} = 6.52$, $P = 0.051$, Fig. 6), likely because the cacao plantation simply does not have enough fruiting trees to support a large population of birds that exclusively eat fruit. Additionally, workers on the cacao plantation frequently harvest the fruit from the fruiting canopy trees before the birds have access to it (pers. obv.).

Sampling line, time, and habitat by time interactions

Significant effects of sampling line nested within habitat occurred only for the sparrow family ($F_{4,12} = 5.00$, $P = 0.013$) and grass seed diet ($F_{4,12} = 3.95$, $P = 0.029$). When examined graphically, these differences between sampling lines occurred only in the

live fences, likely because one of the fields was wetter than the other, which decreased the abundance of sparrows and seed eaters that live on the ground and increased the bird species that respond positively to water.

Significant variation with time was found in the New World warblers ($F_{3,12} = 3.67$, $P = 0.044$); hummingbirds ($F_{3,12} = 4.18$, $P = 0.031$); nectar, small insects/spiders diet ($F_{3,12} = 5.37$, $P = 0.014$); and grass seed diet ($F_{3,12} = 4.74$, $P = 0.021$). The variation was not a simple increase or decrease through time. Departure of migrants through the study period likely explains why New World warblers and nectar and small insects/spiders diet showed differences since these groups contain a large proportion of migrants (97 and 27 % respectively). We cannot explain why the hummingbird family and grass seed diet varied with time.

Significant habitat by time interactions occurred in flycatchers ($F_{9,12} = 3.44$, $P = 0.025$, Fig. 5); sparrows; ($F_{9,12} = 5.65$, $P = 0.004$, Fig. 5); nectar, small insects/spiders diet ($F_{9,12} = 5.37$, $P = 0.05$, Fig. 6); and grass seed diet ($F_{9,12} = 7.75$, $P = 0.001$, Fig. 6), which we cannot explain.

Use of live fence trees and cacao plantation shade trees

In the live fence habitat only 16 of 83 species were seen using the adjacent pasture. Of these 16, only 10 species were on the ground ≥ 50 % of occurrences.

In the cacao plantation, most species and individuals occurred in the shade trees rather than cacao trees. Of the 60 species in this habitat, 38 were identified only in the shade trees. Of the 22 species identified in the cacao trees, only 10 were in cacao trees in ≥ 50 % of occurrences.

Discussion

All habitats contribute to regional complexity and conservation

The ordination and ANOVA results show that the avifauna of the rainforest differs substantially from the agroforest ecosystems. Only 31 of the 61 species identified in the rainforest were identified in another habitat, indicating high value of the intact forest. These species are likely unable to survive outside of

the preserved rainforest. However, 106 species were identified in at least one of the agroforest ecosystems were not identified in the rainforest. Additionally, no birds from tanager, sparrow, or Cardinalidae families and grass seed diet were identified in the rainforest but were identified frequently in the other habitats. While slight undercounting likely occurred in the rainforest due to decreased detection probability, this limitation would apply mostly to canopy birds and not the groups above.

The majority of the species identified in our study were abundant or common according to Stiles et al. (1989) and were listed as species of least concern on the ICUN red list (IUCN 2014) (online resource B in ESM). Only four species we identified were listed as near threatened: *Amazona farinose* (Mealy Parrot), *Tinamus major* (Great Tinamou), *Ramphastos ambiguous* (Chestnut-Mandibled Toucan), and *Contopus cooperi* (Olive-Sided Flycatcher). All except for *Amazona farinose* were identified only in the rainforest. This corresponds to research showing that most threatened or endangered birds do not adapt well to agricultural habitats (Sodhi et al. 2008).

The landscape mix of preserved forest and varied agricultural landscape supports a higher bird species richness than any of the individual systems would on their own. The three agroforest habitats also support different species compositions and appear to provide diverse resources for different types of birds. While previous studies have compared species richness among habitats, few have examined if the similar richness represents a similar community composition (Estrada et al. 1997; Greenberg et al. 2000; Estrada and Coates-Estrada 2005; Muhamad et al. 2013).

The three agroforest systems provide habitat for many migrant species while the rainforest apparently does not. The patchy and semi-open structure of the agroforests may be more similar to the structure of the northern forests where many migrants summer.

While the agroforests support high species richness, many of these species are not rainforest species. Before large-scale anthropogenic deforestation these species likely inhabited forest edges, gaps, dry forests, and savannas in the region. Most tropical forest ecosystems were likely not originally homogenous and contained naturally isolated forest fragments and savannas (Ratter et al. 1997; Dos Anjos and Boçon 1999; Tubelis and Tomás 1999; Pavlacky and Anderson 2007; Ospina et al. 2012). These areas have been essentially completely converted to agriculture and cover less than 1 % of their former range due to their ease of development and more fertile soils (Janzen 1988; Maass 1995; Gillespie et al. 2006; Stevens 2001). Thus, open agricultural matrices may provide habitat for species whose habitat was destroyed elsewhere.

Many agricultural landscapes in Central America and other tropical areas are not adjacent to a large protected area like Tortugero National Park, which may act as an important source of birds to our study system. Agricultural areas far from large preserves may have lower species richness and different community composition, but differences among agricultural habitats and conservation value would likely persist. In this study each agroforest ecosystem had species not found in the other ecosystems (23 in the riparian forests, 23 in the live fences, and nine in the cacao plantation). Each of these systems contributes to avifauna in the region, and it is important to recognize the value of all of the components of a landscape mosaic in conservation. To maximize conservation benefits of these habitats, they need to be considered in conjunction with one another and the intact rainforest.

Community composition models in agroforest ecosystems

Many have often implicitly assumed that agricultural land surrounding a relatively undisturbed habitat patch has a species richness that is less than and a subset of the patch (Fahrig 2013), but our data do not support this. Our data suggest that cacao plantations, riparian forests, and live fences have higher species richness than the rainforest. And while the agroforest habitats did contain some of the species found in the rainforest, they also contained many unique species not found in the rainforest. Additionally even habitats that had a similar number of species per point (riparian forests and cacao plantation and riparian forests and live fence) had distinct species assemblages. Using island biogeography theory to explore forest fragmentation dynamics in this system would likely produce incorrect conclusions by focusing too tightly on the rainforest and discounting the contributions of agricultural matrix (Koh and Ghazoul 2010).

Given this study's relatively small area, 10 km^2, and that birds are mobile organisms, all species hypothetically had equal access to the habitats but

showed strong habitat preferences. Since the agricultural lands in this study are more appropriately viewed as distinct habitats with unique species assemblages rather than a matrix around the rainforest, island biogeography theory is not adequate and could limit conservation. Other theories that could better explain community composition patterns important for conservation among agricultural habitats include patch dynamics, mass effect (source–sink), niche theory, and environmental filtering (Jonsson et al. 2011; Livingston et al. 2013).

Patch dynamics and mass effect do not appear to explain community composition in this system. The patch dynamics model assumes that habitat patches are in a natural state of transition, which is not applicable in agricultural land because ongoing maintenance maintains a single state (Pavlacky and Anderson 2007; Moustakas et al. 2009). Mass effect also fails to explain species composition of these habitats because it assumes that constant dispersal from the rainforest drives agroforest community assembly. Since we found many species in the agroforests not in the rainforest, this model falls short (Foppen et al. 2000; Livingston et al. 2013).

Environmental filtering and niche theory better explain community composition in these agroforest habitats. Environmental filtering (species sorting) proposes that communities assemble through a hierarchy of filters from the regional species pool into the observed species pool (Livingston et al. 2013; Lusk et al. 2013). After sorting, communities are composed of species pre-adapted to specific conditions and therefore have similar functional traits (Mayfield et al. 2009; Meynard et al. 2011; Wiescher et al. 2012; Chalmandrier et al. 2013). Niche theory states that the specific environment conditions a species requires for positive growth determines where it can live. Species occupy different niches to minimize negative interactions with each other, which maximizes diversity on a community scale (Grinnell 1917; Leibold 1995; Kylafis and Loreau 2011; Özkan et al. 2013). Niche theory is thought to operate on a smaller scale than environmental filtering (Maitner et al. 2012).

In this system it appears that environmental filtering, at a larger scale, and niche theory, at a smaller scale, provide best explanations for community composition. We hypothesize that environmental filtering explains why half the species identified in the rainforest were not identified in any other habitat.

The drastic change in both biotic and abiotic factors between the rainforest and agroforests likely filters out many of the forest species that cannot tolerate the conditions in the agroforest habitats. Under this interpretation these differences would also explain why some species occur in agroforests but not in the rainforest. Niche theory may explain the more subtle variation among agroforest habitats, which initially appear similar in vegetation structure but have different species compositions. The more subtle variation in specific environmental conditions among the agroforest habitats likely allow species to occupy different niches, leading to the high functional diversity in this system (Leibold 1995; Kylafis and Loreau 2011; Özkan et al. 2013). Further research is needed to fully test and explore the dynamics of these models in fragmented agroforest ecosystems.

Importance of trees

In live fences, only 12 % of species were identified in ≥50 % of occurrences on the ground rather than on the live fence, showing that trees in the live fence provide important habitat for the majority of the birds in this habitat. Most individuals on the ground were water birds, which did not frequently use the fence. The non-water birds identified on both the ground and in the live fences were frequently foraging for seeds in the pasture grass and would then return to the live fence. Estrada et al. (1997) and Estrada and Coates-Estrada (2005) found similar results in live fences in Central Mexico.

Only 37 % of the species in the cacao plantation occurred in the cacao trees in ≥50 % of occurrences; the rest mainly used the shade trees. In cacao plantations in Panama Van Bael et al. (2007) also recorded a greater number of birds in the shade trees and concluded that the canopy cover, depth, cacao tree density, shade tree species diversity, and shade tree height all positively correlated with species richness. Thus, shade trees clearly play a critical role in conservation of birds in a cacao agroforest ecosystem. A cacao monoculture under artificial shade or no shade would likely support a much smaller number and diversity of birds.

The trees preserved in riparian areas by Costa Rican legislation have provided habitat for many birds that would not live in the area otherwise. The riparian forests contained 23 bird species not found in other

habitats, and these would likely not be present, or present in significantly reduced numbers, without the riparian forests.

Management implications and future study

In a study of global biodiversity loss, Dirzo and Raven (2003) found that habitat loss and degradation affected 88 % of threatened bird species and that agriculture caused 70 % of these losses. Clearly, preserving large tracts of remaining forest takes first priority. However, since riparian forests, live fences, and cacao plantations provide habitat to a wide variety of forest and non-forest birds, these agricultural habitats also play an important role in preserving species diversity in this fragmented system and should be considered when assessing the conservation value of tropical areas.

As the human population continues to grow, the amount of land in agriculture will likely increase. Future conservation efforts should explicitly consider the contributions of agricultural land when making decisions rather than focusing solely on protected areas. Further research on these agricultural habitats within their landscape context will elucidate their roles in maintaining ecosystem functions and providing habitat for a variety of taxa.

Agricultural land will never have the full value of intact rainforest, but promoting a varied agricultural landscape and maintaining trees within agricultural systems will aid greatly in avian conservation on a landscape scale. Using live fences rather than wood or metal fence posts, preserving riparian forest buffers, and growing cacao under native shade trees will create important habitat for a wide range of bird species. Encouraging these small-scale agroforests over large-scale monoculture is paramount. With proper management, some rainforest and gap species can be conserved while still allowing human communities to benefit economically from the land. Maintaining these habitats with their considerable conservation value within an agriculture landscape will become increasingly important as the global population grows and the pressure to convert forested areas into agricultural land intensifies.

References

Barnes DKA, De Grave S (2001) Ecological biogeography of southern polar encrusting faunas. J Biogeogr 28(3):359–365

Bermúdez FA, Hernández CH (2004) Plan de Manejo del Parque Nacional Tortuguero. Área de Conservación Tortuguero. Ministerio de Ambiente y Energía, San Jose, Costa Rica

Bierregaard R, Lovejoy T, Kapos V, Dossantos A, Hutchings R (1992) The biological dynamics of tropical rain-forest fragments. Bioscience 42(11):859–866

Bradshaw CJ, Sodhi NS, Brook BW (2009) Tropical turmoil: a biodiversity tragedy in progress. Front Ecol Environ 7(2):79–87

Cerezo A, Robbins CS, Dowell B (2009) Modified-habitat use by tropical forest-dependent birds in the Caribbean region of Guatemala. Revista de Biología Tropical 57(1/2):401–419

Chalmandrier L, Münkemüller T et al (2013) A family of null models to distinguish between environmental filtering and biotic interactions in functional diversity patterns. J Veg Sci 24(5):853–864

de Schawe CC, Durka W, Tscharntke T, Hensen I, Kessler M (2013) Gene flow and genetic diversity in cultivated and wild cacao (*Theobroma cacao*) in Bolivia. Am J Bot 100(11):2271–2279

Dirzo R, Raven PH (2003) Global state of biodiversity and loss. Annu Rev Environ Resour 28(1):137–167

Donald PF, Evans AD (2006) Habitat connectivity and matrix restoration: the wider implications of agri-environment schemes. J Appl Ecol 43(2):209–218

Dos Anjos L, Boçon R (1999) Bird communities in natural forest patches in southern Brazil. Wilson Bull 111(3):397–414

Estrada A, Coates-Estrada R (2005) Diversity of neotropical migratory landbird species assemblages in forest fragments and man-made vegetation in Los Tuxtlas, Mexico. Biodivers Conserv 14(7):1719–1734

Estrada A, Coates-Estrada R, Meritt DA Jr (1997) Anthropogenic landscape changes and avian diversity at Los Tuxtlas, Mexico. Biodivers Conserv 6(1):19–43

Eva HD, Achard F et al (2012) Forest cover changes in tropical South and Central America from 1990 to 2005 and related carbon emissions and removals. Remote Sens 4(5):1369–1391

Fahrig L (2013) Rethinking patch size and isolation effects: the habitat amount hypothesis. J Biogeogr 40(9):1649–1663

Foppen RP, Chardon JP, Liefveld W (2000) Understanding the role of sink patches in source–sink metapopulations: reed warbler in an agricultural landscape. Conserv Biol 14(6):1881–1892

Gardner TA, Barlow J et al (2009) Prospects for tropical forest biodiversity in a human-modified world. Ecol Lett 12(6):561–582

Garrigues R, Dean R (2007) The birds of Costa Rica. Comstock, Ithaca, NY

Gentry AH (1990) Four neotropical rainforests. Yale University Press, New Haven, CT (Association for Tropical Biology, American Institute of Biological Sciences. Organization for Tropical Studies)

Gillespie TW, Zutta BR, Early MK, Saatchi S (2006) Predicting and quantifying the structure of tropical dry forests in south

Florida and the neotropics using spaceborne imagery. Glob Ecol Biogeogr 15(3):225–236

Greenberg R, Bichier P, Angón AC (2000) The conservation value for birds of cacao plantations with diverse planted shade in Tabasco, Mexico. Anim Conserv 3(2):105–112

Grinnell J (1917) The niche-relationships of the California Thrasher. Auk 34(4):427–433

Gutiérrez AG, Huth A (2012) Successional stages of primary temperate rainforests of Chiloé Island, Chile. Perspect Plant Ecol Evol Syst 14(4):243–256

Harvey CA, Medina A et al (2006) Patterns of animal diversity in different forms of tree cover in agricultural landscapes. J Appl Ecol 16(5):1986–1999

Hill MO, Gauch HG (1980) Detrended correspondence analysis: an improved ordination technique. Vegetatio 42(1–3):47–58

Holdridge LR (1967) Life zone ecology. Tropical Science Center, San Jose, Costa Rica

Hutto RL, Pletschet SM, Hendricks P (1986) A fixed-radius point count method for nonbreeding and breeding season use. Auk 103:593–602

IBM Corp. Released (2012) IBM SPSS statistics for Windows, version 21.0. IBM Corp., Armonk, NY

IUCN (2014) The IUCN red list of threatened species. Version 2014.3. http://www.iucnredlist.org. Accessed 25 Jan 2015

Janzen DH (1988) Management of habitat fragments in a tropical dry forest: growth. Ann Mo Bot Gard 75:105–116

Jonsson M, Englund G, Wardle DA (2011) Direct and indirect effects of area, energy and habitat heterogeneity on breeding bird communities. J Biogeogr 38(6):1186–1196

Koh LP, Ghazoul J (2010) A matrix-calibrated species-area model for predicting biodiversity losses due to land-use change. Conserv Biol 24(4):994–1001

Kumaraswamy S, Kunte K (2013) Integrating biodiversity and conservation with modern agricultural landscapes. Biodivers Conserv 22(12):2735–2750

Kylafis G, Loreau M (2011) Niche construction in the light of niche theory. Ecol Lett 14(2):82–90

Laurance WF (2008) Theory meets reality: how habitat fragmentation research has transcended island biogeographic theory. Biol Conserv 141(7):1731–1744

Laurance WF, Useche DC et al (2012) Averting biodiversity collapse in tropical forest protected areas. Nature 489(7415):290–294

Leibold MA (1995) The niche concept revisited: mechanistic models and community context. Ecology 76(5):1371–1382

Lindell CA, Riffell SK et al (2007) Edge responses of tropical and temperate birds. Wilson J Ornithol 119(2):205–220

Livingston G, Philpott SM, Rodriguez MA (2013) Do species sorting and mass effects drive assembly in tropical agroecological landscape mosaics? Biotropica 45(1):10–17

Lusk CH, Kaneko T, Grierson E, Clearwater M (2013) Correlates of tree species sorting along a temperature gradient in New Zealand rain forests: seedling functional traits, growth and shade tolerance. J Ecol 101(6):1531–1541

Maass J (1995) Conversion of tropical dry forest to pasture and agriculture. In: Bullock SH, Mooney HA, Medina E (eds) Seasonally dry tropical forests. Cambridge University Press, Cambridge, MA, p 399

MacArthur RH, Wilson EO (1967) The theory of island biogeography. Princeton University Press, Princeton, NJ

Maitner BS, Rudgers JA, Dunham AE, Whitney KD (2012) Patterns of bird invasion are consistent with environmental filtering. Ecography 35(7):614–623

Mayfield MM, Boni MF, Ackerly DD (2009) Traits, habitats, and clades: identifying traits of potential importance to environmental filtering. Am Nat 174(1):E1–E22

McCune B, Mefford MJ (2011) PC-ORD. Multivariate Analysis of Ecological Data. Version 6. MjM Software, Gleneden Beach, OR, USA

McIntyre S, Hobbs R (1999) A framework for conceptualizing human effects on landscapes and its relevance to management and research models. Conserv Biol 13(6):1282–1292

Mendenhall CD, Daily GC, Ehrlich PR (2012) Improving estimates of biodiversity loss. Biol Conserv 151(1):32–34

Mendenhall CD, Karp DS, Meyer CFJ, Hadly EA, Daily GC (2014) Predicting biodiversity change and averting collapse in agricultural landscapes. Nature 509(7499):213–217

Meynard CN, Devictor V, Mouillot D, Thuiller W, Jiguet F, Mouquet N (2011) Beyond taxonomic diversity patterns: how do α, β and γ components of bird functional and phylogenetic diversity respond to environmental gradients across France? Glob Ecol Biogeogr 20(6):893–903

Minitab, Inc. (2013) Minitab 16 Statistical Software. Minitab, Inc., State College, PA

Moustakas A, Sakkos K et al (2009) Are savannas patch-dynamic systems? A landscape model. Ecol Model 220(24):3576–3588

Muhamad D, Okubo S, Miyashita T, Takeuchi K (2013) Effects of habitat type, vegetation structure, and proximity to forests on bird species richness in a forest–agricultural landscape of West Java, Indonesia. Agrofor Syst 87(6):1247–1260

Ospina S, Rusch GM, Pezo D, Casanoves F, Sinclair FL (2012) More stable productivity of semi-natural grasslands than sown pastures in a seasonally dry climate. PLoS ONE 7(5):e35555

Özkan K, Svenning J, Jeppesen E (2013) Environmental species sorting dominates forest-bird community assembly across scales. J Anim Ecol 82(1):266–274

Pavlacky D, Anderson S (2007) Does avian species richness in natural patch mosaics follow the forest fragmentation paradigm? Anim Conserv 10(1):57–68

Prevedello JA, Vieira MV (2010) Does the type of matrix matter? A quantitative review of the evidence. Biodivers Conserv 19(5):1205–1223

Ralph CJ, Geupel GR, Pyle P, Martin TE, DeSante DF (1993) Handbook of field methods for monitoring landbirds. USDA Forest Service/UNL Faculty Publications, Berkley, CA

Ratter J, Ribeiro J, Bridgewater S (1997) The Brazilian cerrado vegetation and threats to its biodiversity. Ann Bot 80(3):223–230

Ruiz-Guerra B, Renton K, Dirzo R (2012) Consequences of fragmentation of tropical moist forest for birds and their role in predation of herbivorous insects. Biotropica 44(2):228–236

Scheffé H (1959) The analysis of variance. Wiley, New York

Seaman BS, Schulze CH (2010) The importance of gallery forests in the tropical lowlands of Costa Rica for understory forest birds. Biol Conserv 143(2):391–398

Şekercioğlu ÇH, Ehrlich PR et al (2002) Disappearance of insectivorous birds from tropical forest fragments. Proc Natl Acad Sci USA 99(1):263–267

Sigel BJ, Sherry TW, Young BE (2006) Avian community response to lowland tropical rainforest isolation: 40 years of change at La Selva Biological Station, Costa Rica. Conserv Biol 20(1):111–121

Sodhi NS, Posa MRC, Lee TM, Warkentin IG (2008) Perspectives in ornithology: effects of disturbance or loss of tropical rainforest on birds. Auk 125(3):511–519

Stevens WD (2001) Flora de Nicaragua, introducción, gimnospermas y angiospermas (Acanthaceae—Euphorbiaceae), vol 85., Mongr Syst Bot Missouri Botanical Garden, St. Louis, MO

Stiles FG, Skutch AF, Gardner D (1989) A guide to the birds of Costa Rica. Christopher Helm, London

Stouffer P, Bierregaard R (1995) Use of Amazonian forest fragments by understory insectivorous birds. Ecology 76(8):2429–2445

Tubelis DP, Tomás WM (1999) Distribution of birds in a naturally patchy forest environment in the Pantanal wetland, Brazil. Ararajuba 7(2):81–89

Van Bael SA, Bichier P, Ochoa I, Greenberg R (2007) Bird diversity in cacao farms and forest fragments of western Panama. Biodivers Conserv 16(8):2245–2256

Vaughan C, Ramírez O, Herrera G, Guries R (2007) Spatial ecology and conservation of two sloth species in a cacao landscape in Limón, Costa Rica. Biodivers Conserv 16(8):2293–2310

Wilson EO (1988) The current state of biological diversity. Biodiversity 521(1):3–18

Wiescher PT, Pearce-Duvet JMC, Feener DH (2012) Assembling an ant community: species functional traits reflect environmental filtering. Oecologia 169(4):1063–1074