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Consistency in bird use of tree cover across tropical agricultural landscapes

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Abstract. In tropical regions where forests have been replaced by agriculture, the future of biodiversity is increasingly dependent on the presence of remnant forest patches and on-farm tree cover within agricultural landscapes. While there is growing evidence of the importance of tree cover within agricultural landscapes, most studies have been conducted in a single landscape, making it difficult to ascertain whether the conservation value of different types of tree cover can be generalized across landscapes. To explore whether use of different forms of tree cover by birds is consistent across landscapes, we compared the number of individuals, species richness, and diversity of birds associated with different forms of tree cover in four agricultural landscapes in Central America, using a standardized methodology and sampling effort. In each landscape, we compared bird assemblages in six tree cover types (secondary forests, riparian forests, forest fallows, live fences, pastures with high tree cover, and pastures with low tree cover). We observed a total of 10 723 birds of 283 species, with 83–196 species per landscape. The specific patterns of bird species richness, number of individuals, and diversity associated with tree cover types varied across the four landscapes, but these variables were consistently higher in the forest forms of tree cover (riparian forests, secondary forests, and forest fallows) than in non-forest habitats. In addition, forest forms of tree cover had distinct species composition from non-forest forms in all landscapes. There was also consistency in the use of different types of tree cover by forest birds across the four landscapes, with higher richness and number of individuals of forest birds in forested than non-forested forms of tree cover, and more forest bird species in pastures with high tree cover than in pastures with low tree cover. Our findings indicate that riparian and secondary forests are consistently of higher value for bird conservation (particularly for forest species) than live fences and pastures with tree cover. Consequently, agricultural and land use policies that promote the retention of secondary and riparian forests and increase tree cover within pastures would greatly benefit bird conservation, regardless of the landscape in which they are applied.

Key words: birds; Costa Rica; live fences; matrix habitats; Nicaragua; production landscapes; riparian forests; secondary forest; trees in pasture.

Introduction

As tropical regions are deforested and cleared for agriculture and livestock production, the future of biodiversity conservation will increasingly depend on the ability of human-modified landscapes to conserve plant and animal diversity. This is particularly important in regions such as Central America (Harvey et al. 2008), where approximately 80% of the region's vegetation has been converted to pastures or cropland, many forest ecosystems (e.g., tropical dry forest) are under severe threat, and the existing protected areas are insufficient to conserve the region's unique biodiversity (Dinerstein et al. 1995, Dirzo et al. 2010). With pressure

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on the remaining forest expected to grow as agricultural land expands and agricultural production intensifies to meet an increasing demand for food (Godfray et al. 2010, Foresight 2011), efforts to conserve biodiversity will only be successful if, in addition to maintaining and enhancing the system of protected areas, the agricultural landscapes that replace the forests are managed to provide habitats, resources, and connectivity, and to ensure the continued persistence of forest species (Daily et al. 2003, Harvey et al. 2008).

There is now increasing evidence that agricultural landscapes that retain remnant forests and on-farm tree cover (such as riparian strips, live fences, windbreaks, or dispersed trees in pastures) can conserve diverse tropical bird assemblages, including some forest specialists (Petit and Petit 2003, Harvey et al. 2006, Şekercioğlu et al. 2007). For example, Estrada et al. (1997) reported that more than 70% of the bird species in Veracruz, Mexico, occur in agricultural landscapes, while in southern Costa Rica, nearly 50% of the bird species are present within human-dominated landscapes (Hughes et al. 2002). In addition, multiple studies have highlighted the importance of forest patches, riparian forests, and on-farm tree cover in providing habitats and resources for birds and for facilitating the movement of forest bird species across agricultural landscapes (e.g., Estrada et al. 2000, Fischer and Lindenmayer 2002, Luck and Daily 2003, Gillies and Cassady St. Clair 2008).

While it is generally recognized that diverse agricultural mosaics can play a key role in the conservation of bird diversity (Manning et al. 2006, Haslem and Bennett 2008), less is known about the specific conservation value of the different types of tree cover that typically occur within these landscapes. In particular, it is not clear whether the conservation value of particular types of tree cover (e.g., riparian forests, live fences, pastures with dispersed trees, etc.) is consistent across different agricultural landscapes and can therefore be generalized across agricultural landscapes, or whether the value of these habitat associations is specific to a given landscape. Understanding the consistency of bird use of different types of tree cover is critical for conservation efforts (Chan and Daily 2008), as this will determine whether coarse-grain or fine-scale conservation policies are needed for conserving biodiversity within agricultural landscapes. However, to date, most studies of bird assemblages in agricultural landscapes have only been conducted in a single landscape (but see Haslem and Bennett 2008), making it difficult to ascertain if the conservation value of different types of tree cover can be generalized.

Here, we compare number of bird individuals, species richness, diversity, and composition in different forms of tree cover across four pasture-dominated landscapes of Central America (two in Costa Rica, two in Nicaragua) to explore whether bird usage of tree cover types is consistent across different landscapes. We hypothesized that forest forms of tree cover (e.g., forest fragments and riparian forests) would consistently have higher bird species richness than non-forest forms of tree cover, due to their greater structural and floristic diversity. All four landscapes are dominated by pastures but retain a diverse, heterogeneous mixture of small secondary forest fragments, narrow riparian forests, forest fallows, and on-farm tree cover (in the form of dispersed trees and live fences in pastures). The specific objectives of our research were to (1) explore bird usage of tree cover types within individual agricultural landscapes and ascertain whether bird–habitat relationships were consistent across landscapes, and (2) explore the potential implications of our findings for conservation efforts. To our knowledge, our study is the first to compare bird–habitat relationships across multiple agricultural landscapes in the Neotropics, using a standardized, replicated methodology. The article also provides important guidelines for conservation efforts in the many regions of Central America that have already undergone wide-scale habitat conversion.

Methods

We studied the bird communities in four agricultural landscapes that were representative of the main cattle-producing regions of Central America. Two of the landscapes were located in Costa Rica (Cañas and Río Frío), and two in Nicaragua (Rivas and Matiguás). In each region, we chose an area of 10 000 to 16 000 ha as our study landscape. Cañas and Rivas were located in the tropical dry forest zone, Matiguás was in a transition zone between tropical dry forest and tropical humid forest, and Río Frío was located in a tropical wet forest zone (Fig. 1; Holdridge 1978). Distances between landscapes ranged from 93 km (Cañas and Río Frío) to 311 km (Río Frío and Matiguás). All four landscapes were dominated by cattle production, with pastures accounting for between 46% and 68% of each landscape (Table 1). In all landscapes, pastures retained significant tree cover, both in the form of dispersed trees (some relicts of the original forests, some from natural regeneration) as well as planted live fences. Additional details on the on-farm tree cover are available in Harvey et al. (2011; dispersed trees) and Harvey et al. (2005; live fences).

In each of the landscapes, we studied birds in six tree cover types: secondary forests (SF), riparian forests (RF), forest fallows (FF), pastures with high tree cover (16–25%; PH), pastures with low tree cover (<5%; PL), and live fences (LF). For each tree cover type, we randomly selected 7–8 plots, using satellite imagery, for a total of 46–48 plots per landscape and 190 plots across the four landscapes. Plots in the secondary forests, forest fallows, and pasture habitats were 100×100 m in size (1 ha), while the riparian forest plots were 500×20 m (1 ha). Live fence plots were 350 m long by 2 m wide.

We characterized the bird community using four point count stations per plot, spaced 100 m apart. In the square plots, the point counts were located in the four

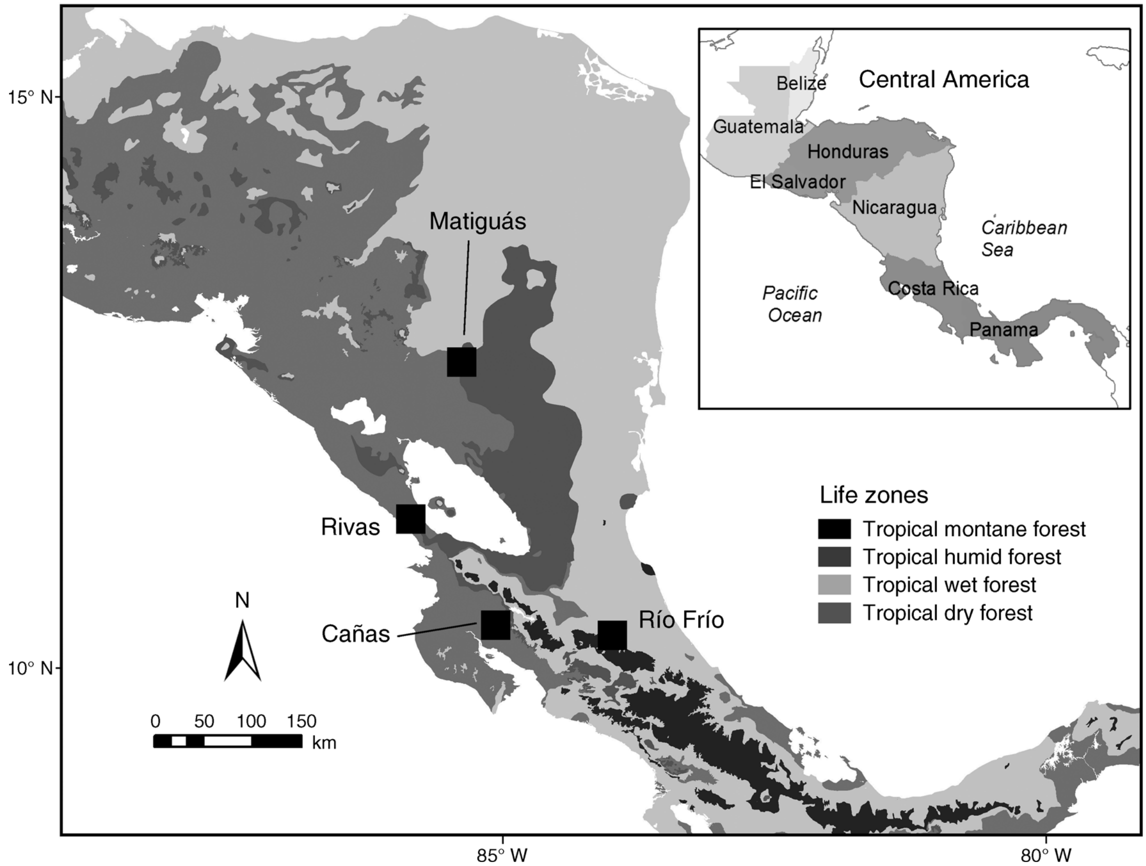

Fig. 1. Map of the four agricultural landscapes and life zones (Holdridge 1978) in Nicaragua and Costa Rica where bird assemblages were studied.

corners of the 1-ha plot, whereas in the linear plots, the point counts were located in a line. At each point, we observed birds for 10 minutes, between 06:00 and 07:40, which is the period of greatest morning activity. In each landscape, point counts were done by a single observer with significant knowledge of the avifauna and experience in the region. We registered all species occurring within a 25 m radius of the point (birds flying overhead

Table 1. An overview of the four agricultural landscapes in Central America where bird assemblages were studied.

Parameter	Cañas, Costa Rica	Río Frío, Costa Rica	Rivas, Nicaragua	Matiguás, Nicaragua
Study area (ha)	13 051	15 987	11 621	10 108
Holdridge life zone	tropical dry forest	tropical wet forest	tropical dry forest	transition from tropical dry forest to tropical humid forest
Mean annual rainfall (mm)	1 544	4 120	1 400	1 800
Main cattle production system	beef	dairy (some beef and dual purpose)	dual purpose cattle and agriculture	dual purpose cattle (with some agriculture)
Land covered by pasture	48	47	57	68
Land covered by secondary forests	15	16	16	7
Dispersed tree density (trees/ha of pasture)†	8.0 ± 1.0	23.1 ± 3.4	16.9 ± 5.1	33.4 ± 6.1
Live fence density (km/ha of pasture)†	0.14 ± 0.02	0.34 ± 0.05	0.21 ± 0.04	0.16 ± 0.22

Note: Data on the density of live fences and dispersed trees come from Harvey et al. (2005) and Harvey et al. (2011), respectively.
† Values are means ± SE.

were not included), during two consecutive days, for a total of 80 minutes of observation per plot, and a total sampling effort of 15 200 minutes (80 minutes/plot over 190 plots). Data collection occurred in the Rivas and Cañas sites during 2002 and 2003, while data collection in Matiguás and Río Frío was conducted in 2003 and 2004. In each sampling excursion, one plot of each type of tree cover was sampled in random order. Birds were identified using a bird guide of Costa Rica (Stiles and Skutch 1989). We classified birds as "forest birds" based on Stiles and Skutch (1989) and Stotz et al. (1996), including species that were listed as dependent on intact primary forest as well as those present in secondary forests and riparian forest. Nomenclature follows Martínez-Sánchez (2007).

Data analysis

For each of the 190 plots where birds were sampled, we calculated the total number of individuals, the observed species richness, and the Shannon diversity index (referred to hereafter as diversity), as well as the number of species and individuals of forest birds present in each tree cover. We also estimated the overall landscape species richness, using Chao 1 species richness estimator (Colwell and Coddington 1994, Oksanen et al. 2011).

In each individual landscape, we used an analysis of variance (ANOVA) to detect differences in the bird assemblages (e.g., observed species richness, number of individuals, and diversity of all birds, as well as the richness and number of individuals of forest birds) across habitat types. Preliminary analyses indicated that results were similar regardless of whether migratory birds were included or not; henceforth all analyses reported here include all birds observed (i.e., both migratory and resident birds).

To compare the relationships between bird communities (species richness, number of individuals, diversity, and richness and number of individuals of forest bird species) and different tree cover types across the four landscapes, we performed an ANOVA for a generalized block design using a linear mixed model (Pinheiro and Bates 2000, Di Rienzo et al. 2009), where individual landscapes (blocks) were considered as a random effect. All data were tested for normality using the Shapiro-Wilks test prior to any statistical test. Due to lack of normality, the number of individuals was transformed using natural logarithm, while species richness and number of individuals of forest species variables were rank transformed. All analyses were conducted using InfoStat version 2009 (Di Rienzo et al. 2009).

Moreover, to compare the species composition of birds across different types of tree cover within each landscape, we performed a principal coordinates analysis using the capscale function from the vegan library in R (Oksanen et al. 2011). We used Bray Curtis as a measure of dissimilarity (Legendre and Legendre 1998, McCune and Grace 2002). The performance of the ordination was assessed using the variance explained by each axis and a goodness-of-fit test based on an analysis of variance using anova.cca function with 999 permutations in the R vegan library (R Development Core Team 2009).

Results

We observed a total of 10 723 birds of 283 species in the four agricultural landscapes (Appendix A), of which 42 species (1114 birds) were migratory. The greatest number of birds was observed in Río Frío, the tropical wet forest site (4588 birds), followed by Cañas (Table 2). The observed bird species richness ranged from 83 to 196 per landscape (with Río Frío having the highest), while the estimated species richness (Chao 1) ranged from 100 to 239. In all four landscapes, the total bird species richness observed was generally highest in forest tree cover (SF, RF, FF), and lowest in either pastures with low tree cover or live fences.

Many species in each landscape (from 29% to 43%) were found in a single tree cover type. However, there was also a subset of bird species in each landscape (8–17%) that were found in all six habitat types. Examples of species that were commonly found in all six tree covers include *Campylorhynchus rufinucha*, *Cyanocorax morio*, *Euphonia hirundinacea*, *Melanerpes hoffmannii*, *Psarocolius montezuma*, *Troglodytes aedon*, and *Trogon melanocephalus*, all of which are known to be generalist species (Stiles 1985).

Across the four landscapes, forest bird species represented a total of 136 species and just over one-quarter of all birds observed (Appendix A). Some examples of forest birds species found in the agricultural landscape included *Myrmeciza exsul*, *Myrmeciza inmaculata*, *Cercomacra tyrannina*, *Gymnopithys leucapsis*, *Microrhopias quixensis*, *Cymbilaimus lineatus*, *Henicorhina leucosticta*, *Automolus ochralaemus*, and *Lepidocolaptes souleyetii*, among others.

General patterns of bird use of different types of tree cover

When the bird use of different types of tree cover was analyzed within individual landscapes, three of the landscapes showed clear patterns of bird use of certain types of tree cover, while one (Cañas) did not (Fig. 2, Appendix B). In Río Frío, pastures with low tree cover had fewer bird species than all other tree cover types ($F_{5,42} = 3.74$, $P = 0.0069$). In Rivas, riparian forests had greater species richness than live fences and the two types of pastures; in addition, secondary forests and forest fallows had greater species richness than live fences and pastures with low tree cover, and pastures with high tree cover had more species than live fences or pastures with low tree cover ($F_{5,42} = 8.17$, $P < 0.0001$). In Matiguás, species richness was higher in secondary forests than in either live fences or pastures with low tree cover ($F_{5,42} = 2.56$, $P = 0.0410$). Number of bird individuals differed among tree cover types in the Río

TABLE 2. Total species richness and abundance of birds observed in different types of tree cover in four agricultural landscapes of Central America.

	Tree cover types						
Variable	SF	RF	FF	LF	PH	PL	Total
Cañas							
Individuals	385	419	393	353	356	466	2372
Species	54	56	56	46	45	42	107 (133)
Sampling effort	7	7	8	8	8	8	46
Río Frío							
Individuals	650	837	890	778	941	492	4588
Species	99	100	110	90	89	70	196 (239)
Sampling effort	8	8	8	8	8	8	48
Rivas							
Individuals	369	486	340	199	253	193	1840
Species	49	43	43	34	41	36	83 (100)
Sampling effort	8	8	8	8	8	8	48
Matiguás							
Individuals	317	361	310	233	423	279	1923
Species	71	74	63	47	53	51	137 (177)
Sampling effort	8	8	8	8	8	8	48
Total							
Individuals	1721	2103	1933	1563	1973	1430	10 723
Species	177	172	169	131	138	110	283

Notes: The total sampling effort refers to the number of plots sampled. Each plot was sampled for a total of 80 minutes. In the Total column, the numbers in parenthesis indicate the total estimated species richness at the landscape level, based on Chao 1. Tree cover types are: SF, secondary forests; RF, riparian forests; FF, forest fallows; LF, live fences; PH, pastures with high tree cover; PL, pastures with low tree cover.

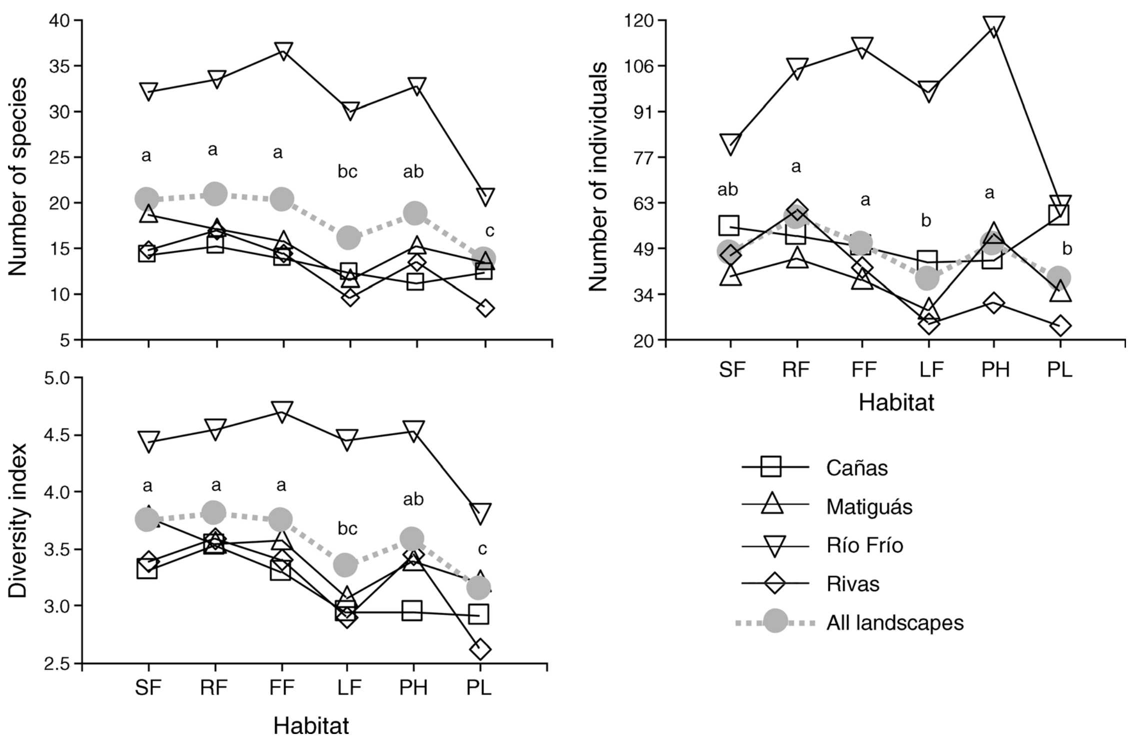

FIG. 2. Number of species, individuals, and diversity of birds present in six tree cover types (secondary forests [SF], riparian forests [RF], forest fallows [FF], live fences [LF], pastures with high tree cover [PH], and pastures with low tree cover [PL]) in four agricultural landscapes of Central America (Cañas, Río Frío, Rivas, and Matiguás). Plotted values are means. The dotted line represents the means for all four landscapes combined, with different letters indicating significant differences ($P < 0.05$) among the different tree cover types.

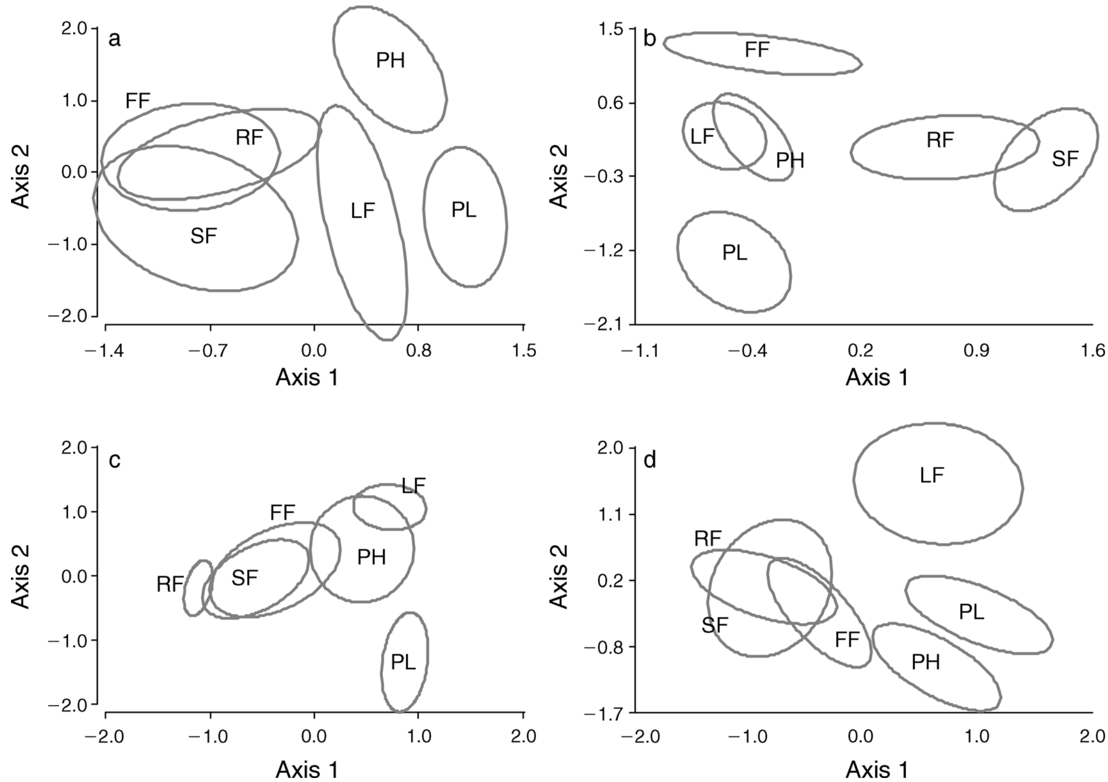

FIG. 3. Ordination of tree cover types based on bird species composition observed in six different types of tree cover in four agricultural landscapes (a, Cañas; b, Río Frío; c, Rivas; d, Matiguás), using Bray Curtis dissimilarity. The ellipses represent the confidence interval at 95% for each habitat.

Frío ($F_{5,42} = 3.09$, $P = 0.0184$), Rivas ($F_{5,42} = 10.4$, $P < 0.0001$) and Matiguás landscapes ($F_{5,42} = 3.38$, $P = 0.0061$), but not in Cañas. Bird diversity differed among tree cover types only in the Rivas landscape (Fig. 2, Appendix B).

When we combined the data from all four landscapes and analyzed patterns of bird–tree-cover associations across the landscapes (using an ANOVA, with landscapes considered as blocks), there were differences in bird species richness, number of individuals, and diversity across different tree cover type across landscapes (Fig. 2, Appendix B). Secondary forests, riparian forests, and forest fallows had greater bird species richness than live fences and pastures with low tree cover. In addition, pastures with high tree cover had greater bird species richness than pastures with low tree cover. Overall bird number of individuals was greater in the riparian forests, forest fallows, and pastures with high tree cover than in live fences and pastures with low tree cover. Bird diversity was higher in secondary forests, riparian forests, and forest fallows than in live fences and pastures with low tree cover, and pastures with high tree cover had greater bird diversity than pastures with low tree cover.

In addition, the ordination of species composition for all birds observed in different tree cover types showed clear distinctions between forest and other tree cover types in all landscapes (Fig. 3). In all four landscapes, secondary forests and riparian forests were grouped together, and in three of the four landscapes, these forested habitats also had a high affinity with forest fallows. There was no overlap among forest and non-forest tree cover types in three landscapes and only a modest overlap between pastures with high tree cover and forest fallows in Rivas. The pasture and live fence habitats had a distinct species composition from the forested habitats; in addition, in all four landscapes, pastures with low tree cover were separated from all other habitats, reflecting their much less diverse species composition. Interestingly, in all four landscapes, pastures with high tree cover consistently had distinct bird assemblages from pastures with low tree cover.

Forest bird use of different types of tree cover

The number of forest bird species varied among tree cover types in all four landscapes (Cañas $F_{5,40} = 6.07$, $P = 0.0003$; Río Frío $F_{5,42} = 6.99$, $P = 0.0001$; Rivas $F_{5,42} = 23.38$, $P < 0.0001$; Matiguás $F_{5,42} = 2.40$, $P = 0.0500$),

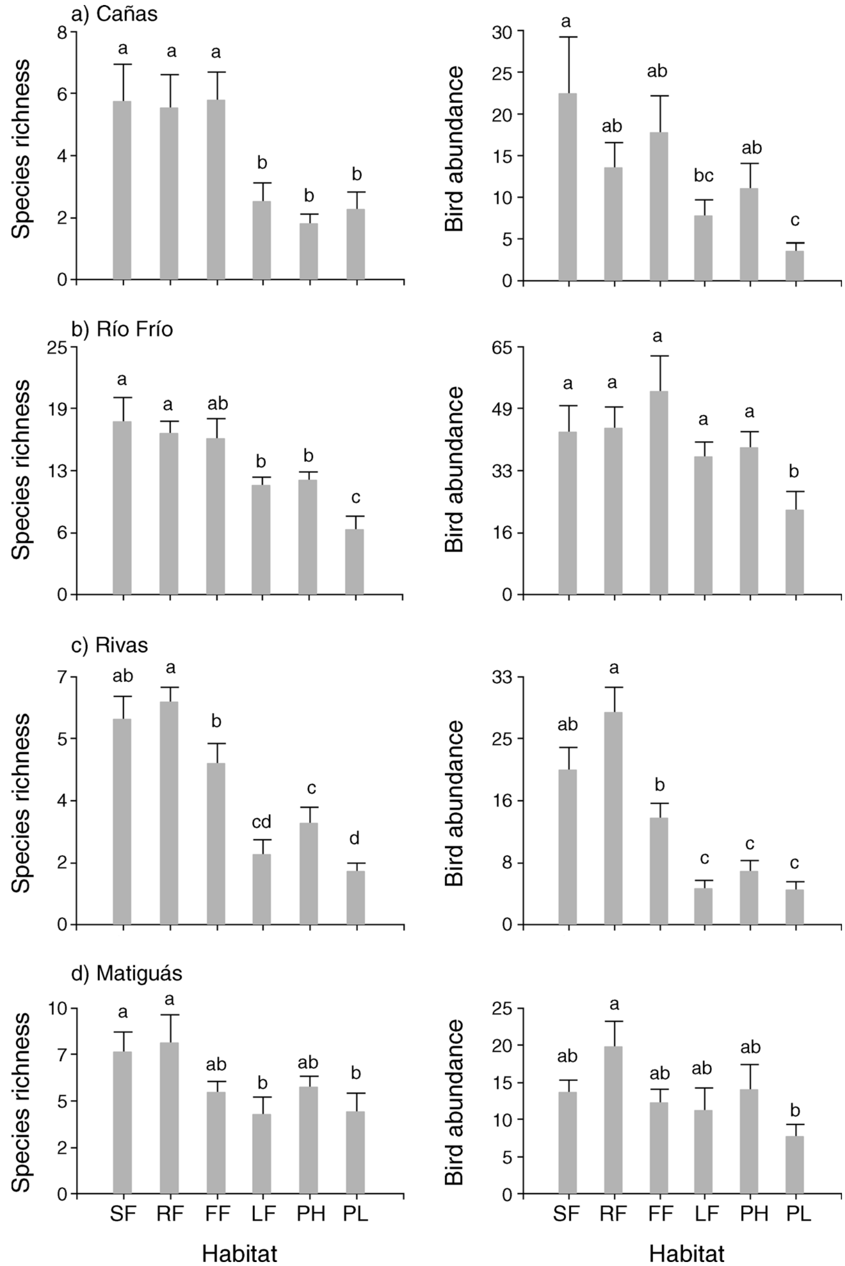

FIG. 4. Species richness and abundance of forest birds (mean + SE) observed in different types of tree cover for four agricultural landscapes of Central America: (a) Cañas, (b) Río Frío, (c) Rivas, and (d) Matiguás. Different letters indicate significant differences among means, with $P < 0.05$, based on one-way ANOVAs.

with a consistent pattern of higher forest bird species richness in secondary forests and riparian forests than in pastures with low tree cover and live fences (Fig. 4). Forest bird number of individuals also varied consistently among tree cover types. There were differences in all landscapes (Cañas $F_{5,40} = 5.16$, $P = 0.0009$; Río Frío $F_{5,42} = 2.74$, $P = 0.0312$; Rivas $F_{5,42} = 15.39$, $P < 0.0001$; Matiguás $F_{5,42} = 2.36$, $P = 0.0501$). In all landscapes, there was a general pattern of secondary forests/riparian forests having greater forest bird number of individuals than pastures with low tree cover (Fig. 4).

When the data from the four landscapes was combined and analyzed jointly (using an ANOVA with landscapes considered as blocks), the associations of forest birds with different types of tree cover types became even clearer (Fig. 5). There were more forest bird species and individuals in secondary forests, riparian forests, and forest fallows than in live fences and the two types of pastures ($F_{5, 181} = 19.74$, $P < 0.0001$ and $F_{5, 182} = 12.58$, $P < 0.0001$, respectively). Pastures with high tree cover had more forest bird species than pastures with low tree cover.

Discussion

By comparing the associations of bird assemblages with different types of tree cover across four Neotropical agricultural landscapes, we have demonstrated for the first time that the conservation value of certain types of tree cover for bird assemblages can be generalized across different agricultural landscapes, especially for forest bird species. In particular, our results suggest a general pattern of greater bird species richness and number of individuals in forested habitats (secondary forests, riparian forests, and forest fallows) relative to live fences and pastures with trees. This pattern was evident (and significant) in three of the landscapes studied (Rivas, Río Frío, and Matiguás), but not in Cañas, where no differences in bird assemblages across different tree cover types were detected. However, when the four landscapes were analyzed as a single data set, the patterns were highly significant, with secondary forests, riparian forests, and forest fallows all having greater species richness and number of individuals than live fences and pastures with low tree cover. Another consistent pattern was the higher species richness and diversity of birds in pastures with high tree cover relative to pastures with low tree cover; a pattern that was evident in analyses of three of the individual landscapes, as well as in the overall analysis combining data from all four landscapes. Our data also showed that forest types of tree cover consistently harbored different bird assemblages than the non-forest habitats, with secondary forests and riparian forests having very distinct species composition from the live fences and pastures with trees. These patterns were evident in all four of the studied landscapes, again highlighting the consistency of bird associations with different types of tree cover across landscapes.

These results suggest that it may sometimes be difficult to distinguish the conservation value of particular types of tree cover for bird assemblages based on information from any particular landscape, so caution should be taken when generalizing findings from a single landscape to agricultural landscapes elsewhere. For example, if we had only analyzed data from the Cañas landscape, we would have concluded that the relationships between tree cover types and bird assemblages were unclear. However, as we have shown, there is remarkable consistency in the contributions that certain types of tree cover (particularly secondary forests and riparian forests) make to bird diversity, which are clearly evident when multiple landscapes are considered.

Perhaps of even more importance to conservation efforts, the number of individuals and species richness of forest birds (which are typically of greatest conservation concern) showed even clearer associations with tree cover types. In all four landscapes, there were consistent patterns of greater species richness and number of individuals of forest birds in secondary forests, riparian forests, and forest fallows than pastures and live fences. The analysis of data combined from all four landscapes confirmed this pattern, and also highlighted the important positive effect of increasing tree density within pastures on bird assemblages.

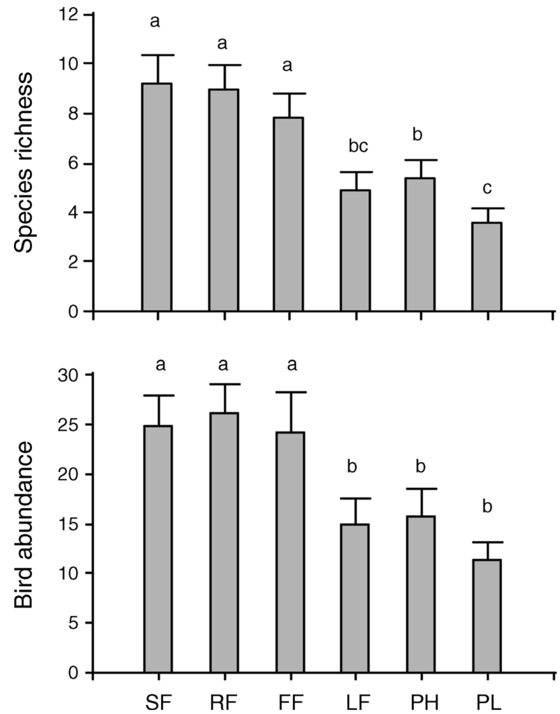

Fig. 5. Number of species and individuals (mean + SE) of forest birds present in six tree cover types for four agricultural landscapes of Central America. Bars with different letters are significantly different ($P < 0.05$).

While previous studies of bird assemblages in agricultural landscapes in the Neotropics have similarly noted more individuals and species of forest birds in the forest habitats within these landscapes (e.g., Petit et al. 1999, Daily et al. 2001), as well as the positive effect of increased tree cover within pastures on bird communities (e.g., Estrada et al. 1997), our study is the first to use data from multiple landscapes (all surveyed with the same methodology and same sampling intensity) to statistically demonstrate the consistency of these patterns across different agricultural landscapes.

Conservation implications

The fact that forested habitats within agricultural landscapes were consistently used by more bird species and individuals, and particularly by more forest birds, than were non-forested habitats indicates that it is appropriate to develop coarse-grain regional recommendations for bird conservation in agricultural landscapes across the region, rather than developing specific conservation plans for individual landscapes. While there may be a need for individualized conservation plans in specific landscapes to conserve specific species of particular concern or to address unique drivers of biodiversity loss that are unique to that landscape (Simberloff 1998), our results suggest it is possible to develop regional conservation strategies that would effectively promote bird conservation across the agricultural landscapes that dominate much of Central America (Harvey et al. 2008).

Such a strategy would need to focus on two key elements: (1) conserving the remaining forest habitats (including patches of secondary forest, riparian forests, and forest fallows) within the agricultural matrix and preventing their further degradation, and (2) increasing tree cover and diversity within pastures. The conservation of remaining forest cover within agricultural landscapes is critical not only for birds (e.g., Estrada et al. 1997, Daily et al. 2001, Luck and Daily 2003, Şekercioğlu et al. 2007), but also for dung beetles (Estrada and Coates-Estrada 2002), bats (Estrada and Coates-Estrada 2001), terrestrial mammals (Daily et al. 2003), and trees (e.g., Chazdon et al. 2009), among other taxonomic groups, and should form the cornerstone of any conservation efforts. It will also be key to ensure that the remaining forest fragments and riparian areas are protected from further degradation, particularly from cattle grazing and fires. In all four landscapes where we worked, most of the riparian forests were highly impacted by cattle grazing, with compacted soils, limited regeneration in the understory, and water with heavy sediment loads, and this may negatively impact the existing bird assemblages (Martin and McIntyre 2007). Restricting cattle entry into riparian forests and remaining forest patches and reducing grazing pressure would be expected to allow regeneration of understory and so enhance their conservation value not only for birds, but also other taxa that are dependent on diverse forest understories (Saab and Petit 1992, Martin and McIntyre 2007).

Regional conservation efforts also need to recognize the importance of maintaining and increasing tree cover within the pasture matrix. While dispersed trees and live fences consistently had fewer bird species and fewer forest species than the forest habitats, both of these types of on-farm cover are used by a large number of species; across the four landscapes, we recorded a total 159 species of birds visiting dispersed trees in pastures and 131 species visiting live fences. Both dispersed trees and live fences serve as additional habitat, foraging sites, display posts, and stepping stones for birds, while also enhancing the connectivity of on-farm tree cover and creating a more heterogeneous and fine-grained landscape (Chacon and Harvey 2006), which may benefit forest-dependent species. Efforts to enhance the conservation value of pastures should prioritize conserving large remnant trees, increasing tree diversity, and promoting natural regeneration within pastures (Esquivel et al. 2008, Harvey et al. 2011, Murgueitio et al. 2011). Emphasis should also be placed on increasing tree density within pastures, as our results clearly show that pastures with higher tree densities harbor a greater variety of bird species, and, in particular, more forest bird species. The conservation value of live fences could also be enhanced by including additional tree species within the live fences (beyond the few species, *Gliricidia sepium*, *Bursera simarouba*, *Erythrina costaricensis*, and *Pachira quinata*, which currently dominate these elements [Harvey et al. 2005]), reducing the frequency and severity of pruning to ensure that they provide year-round habitat to birds, and increasing the density of live fences within the landscape, thereby increasing structural connectivity (Chacón and Harvey 2006). However, these changes in the management of live fences and trees within pastures could potentially result in tradeoffs with pasture productivity (Harvey et al. 2005, Murgueitio et al. 2011) and need further examination.

While the necessary components of a regional plan for bird conservation within agricultural landscapes are evident, what is less clear is how these recommendations can be effectively implemented. In most Central American countries, efforts for biodiversity conservation, including bird conservation, are still focused primarily on remaining intact forest, and pay little attention to conservation needs within the agricultural landscapes (Harvey et al. 2008). The few strategies that take into account the potential value of on-farm tree cover for conservation, such as the payment for ecosystem service program in Costa Rica that allows farmers to receive payments for conserving forest and other on-farm tree cover (FONAFIFO 2000, Pagiola 2008), are often underfunded and, therefore, unable to reach large areas of agricultural landscapes that could be managed for conservation purposes. In addition, while many countries have laws stipulating the conservation of riparian areas within agricultural landscapes, these laws are rarely enforced and, therefore, ineffective.

There is an urgent need both for greater recognition of the importance of tropical agricultural landscapes for biodiversity conservation, as well as political willingness to develop incentives that encourage farmers to retain forest and tree cover within their farms. The current request by the Convention of Biological Diversity for countries to develop their new strategies for biodiversity conservation and to explore how they will meet the new Aichi Targets (Convention on Biological Diversity 2011) provides one immediate opportunity for taking these ideas into account and developing national or even regional strategies that prioritize the conservation of forest fragments and riparian forests within agricultural landscapes. However, urgent action is needed to ensure that tropical agricultural landscapes retain forest and on-farm tree cover and continue to contribute to biodiversity conservation efforts.

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Supplemental Material

Appendix A

List of bird species found in four agricultural landscapes in Central America, indicating whether the bird species is migratory or resident, and the habitats in which they were found (*Ecological Archives* A024-009-A1).

Appendix B

Mean species richness, abundance, Shannon diversity, and equity of birds observed in different tree cover types for four agricultural landscapes in Central America (*Ecological Archives* A024-009-A2).