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LIVE FENCES HAVE GREATER DIVERSITY OF BIRD ASSEMBLAGES THAN GALLERY FORESTS IN HUMAN-MODIFIED ECOSYSTEMS

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Abstract · Anthropogenic activities have led to changes in land use resulting in fragmented areas with a reduction of biodiversity and ecosystem services. Gallery forests and live fences are common elements in Neotropical agricultural landscapes that could contribute to the conservation of bird species and the services they provide. However, we need to better understand how different tree cover types influence bird assemblages in order to conserve biodiversity. I analyzed the diversity of bird assemblages in space and time across two cover types in three agricultural-livestock farms in Guanacaste, Costa Rica. Bird assemblages were sampled during 2019 using transects, covering both the dry and rainy season. I estimated richness and relative abundance of bird assemblages at each tree cover type and site. To characterize vegetation structure, I calculated plant richness, diameter at breast height and tree height. Patterns in bird diversity changed at a spatial scale, whereas remained similar in time. Bird assemblages had consistently higher richness and abundance in live fence than in gallery forest in the three study sites. In addition, live fences resulted in lower structural complexity compared to gallery forest, as indicated by lower plant richness and tree height. My results show that live fences play an important role for birds, allowing more diverse avian assemblages in human-modified ecosystems. Although live fences are less structurally complex and may offer less suitable habitats for birds than gallery forests, they might provide complementary food resources and act as stepping-stones for both resident and migratory bird species. Thus, live fences may perform as corridors for birds and increase connectivity in rural landscapes, which makes them an essential tool for bird conservation.

Resumen · Las cercas vivas tienen mayor diversidad de ensambles de aves que los bosques de galería en ecosistemas modificados por humanos
Las actividades antrópicas han provocado cambios en el uso de la tierra, que han resultado en áreas fragmentadas con una reducción en la biodiversidad y los servicios ecosistémicos. Los bosques de galería y las cercas vivas son elementos comunes en los paisajes agrícolas neotropicales que podrían contribuir con la conservación de las aves y los servicios ecosistémicos que brindan. Sin embargo, necesitamos comprender mejor cómo los diferentes tipos de cobertura arbórea influyen en los ensambles de aves para así conservar la biodiversidad. Analicé la diversidad de los ensambles de aves, tanto en el espacio como en el tiempo, en dos tipos de cobertura arbórea en tres fincas agrícola-ganaderas en Guanacaste, Costa Rica. Los ensambles de aves se muestrearon utilizando transectos en el 2019, que abarcaron tanto la estación seca como la lluviosa. Estimé la riqueza y abundancia relativa de los ensambles de aves en cada tipo de cobertura arbórea y sitio. Para caracterizar la estructura de la vegetación, calculé la riqueza de plantas, el diámetro a la altura del pecho y la altura de los árboles. Los patrones en la diversidad de aves cambiaron a escala espacial, mientras que permanecieron similares en el tiempo. Los ensambles de aves tuvieron una mayor riqueza y abundancia en cercas vivas que en bosques de galería en los tres sitios de estudio. Además, las cercas vivas resultaron en una menor complejidad estructural en comparación con el bosque de galería, como lo indica una menor riqueza de plantas y altura de los árboles. Estos resultados muestran que las cercas vivas desempeñan un rol importante para las aves, permitiendo ensambles de aves más diversos en ecosistemas modificados por humanos. Aunque las cercas vivas son menos complejas estructuralmente, por lo que ofrecerían hábitats menos adecuados para las aves que los bosques de galería, podrían proveer recursos alimenticios complementarios y actuar como escalones para especies de aves tanto residentes como migratorias. Por lo tanto, las cercas vivas pueden funcionar como corredores para las aves que aumentan la conectividad en los paisajes rurales, lo que las convierte en una herramienta fundamental para la conservación de las aves.

Key words: Agricultural-livestock farms · Agroecosystem · Avian communities · Biodiversity · Costa Rica · Species richness

INTRODUCTION

Neotropical forests are known to be highly biodiverse, but they are being rapidly transformed into fragmented landscapes consisting of scattered patches of native vegetation immersed in a matrix of human-dominated areas (Curtis et al. 2018). These forest patches can be part of protected areas and often remain isolated or with different degrees of connectivity among them. The replacement of original forests by extended and simplified agricultural systems results in species diversity loss and a decrease of their associated ecosystem services (Phillips et al. 2017, Sharma et al. 2019). Notably, birds are responsible for key ecological processes, such as pollination and seed-dispersal, that contribute to maintaining and enhancing biodiversity. These processes are highly relevant to implement habitat regeneration and restoration strategies aiming towards biological conser-

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vation (Traveset & Rodríguez-Pérez 2008).

Some farming production models have led to an anthropocentric matrix of large fields with little or no natural vegetation. However, there are models that allow for the preservation of different landscape features, such as gallery forests and live fences. These tree cover types may be crucial for avian diversity in agroecosystems, since they can offer shelter, food, and breeding resources for birds. Even more, a variety of tree cover types increases spatial heterogeneity in a given area, which is expected to favour biodiversity through partitioned niche space (MacArthur & MacArthur 1961, Horn & Mac Arthur 1972, Weisberg et al. 2014). Niche partitioning is a major mechanism leading to species coexistence and therefore, communities with high species richness. Moreover, different tree cover types in a specific area may significantly benefit avian diversity in human-modified environments (Hendershot et al. 2020).

Gallery forests in tropical agricultural landscapes are mostly narrow strips of forest associated with creeks and rivers. These riparian ecosystems may contain a large number of species and resources not otherwise available in areas dominated by pastures, in addition to performing important ecological functions (Veneklaas et al. 2005). In turn, live fences are lineal vegetation elements that may be natural remnants of the original forest, or may be planted to delineate property or act as wind and fire breaks (Molano et al. 2003). Both gallery forests and live fences are common elements in Neotropical agricultural landscapes that may play an important role in conservation of avian communities through landscape connectivity (Chacón León & Harvey 2006, Vilchez Mendoza et al. 2014). Some studies have characterized the structure, patterns, and evolution of the landscape, as well as the use of different tree cover types in agricultural areas. Otero & Onaindia (2009) found that live fences have an important positive effect on landscape structure and biodiversity. Other studies show higher bird diversity in forested than in non-forested habitats (Vilchez Mendoza et al. 2014, Lindell et al. 2004). In addition to spatial patterns in avian diversity, there is evidence of variation in temporal patterns, where birds are more abundant during a specific season across the year (Muñoz-Sáez et al. 2017). However, we still lack knowledge to better understand the relative importance of such different tree cover types on bird assemblages and its potential for biodiversity conservation (Chacón León & Harvey 2006).

The aim of this study was to investigate how bird assemblages in human-modified environments vary at a spatial and temporal scale. Specifically, I examined the variation in bird diversity and abundance across two tree cover types (live fences vs riparian forests) and seasons (dry vs rainy) in three agricultural livestock farms in the central region of the Nicoya Peninsula in Guanacaste, Costa Rica. I evaluated possible factors influencing this variation, such as vegetation structure and tree species phenology, to improve our understanding about landscape elements that may enhance diversity in avian communities.

METHODS

Study area. The project area extends from Nambí (10° 1'19"N, 85°30'15"W) to Hojancha (10°4´21"N, 85°25'31"W), within a radius of c. 9 km from the city of Nicoya, and between two National Parks (Barra Honda and Diriá). This area is part of the Guanacaste province in northwestern Costa Rica and corresponds to the Tropical Humid Forest life zone (Holdridge 1967). In this area, elevation ranges from 130 to 385 m a.s.l., while mean annual temperature averages 26.8 ° C and mean annual precipitation 2400 mm. The dry season extends from late December to early May, and the wettest months are July and October–November (Janzen 1983).

Field data collection was conducted in three farms in the localities of Nambí, Dulce Nombre, and Hojancha. Each farm included the two tree cover types of interest: gallery forest and live fence. The main productive activity in the farms is livestock, and to a lesser extent, corn, fruit trees, and Tek (*Tectona grandis*) plantations. Both gallery forests and live fences include native plants such as Jocote (*Spondias purpurea*, Anacardiaceae) and naked Indian (*Bursera simaruba*, Burseraceae), among other species.

Data collection. Fieldwork was conducted from January to August 2019, covering both dry and rainy seasons. Data on composition, richness and abundance of bird assemblages were collected across a total of 36 field samplings by visiting each farm 12 times (six times per season). In addition, plant richness, species phenology and vegetation structure were also sampled.

To record data on bird and plant communities, I established four transects of 100 m by 40 m at each of the studied farms (two per tree cover type). Transect locations were separated at least by 50 m and chosen to cover a representative sample of vegetation in the two tree cover types according to the availability at each farm. Along these transects, bird samplings were conducted once a month at two times of the day: morning (6:00–9:30 h) and afternoon (13:00–16:30 h), with a total of seven hours of observation per day at each farm. Birds were recorded by sight and vocalizations by two observers walking slowly along each transect. All birds were identified to species according to Stiles & Skutch (1989). Within the same transects, plants were identified when diameter at breast height (DBH) was greater than 15 cm, and I measured their DBH and maximum tree height. To identify plant species as potential resources for birds (i.e., in flowering or fruiting stage), phenological data were collected by recording flowering and fruiting of tree species.

Data analysis. To describe the taxonomic diversity of avian assemblages, I calculated the richness and relative abundance of bird species for each tree cover type, site, and sampling. The total number of individuals of each species observed across the four transects was used as an estimate of species abundance. To avoid overestimation of bird abundance, the number of individuals recorded during the morning count in the four transects was summed separately from those recorded during the afternoon count. From these two counts, the maximum number of birds for each bird species was considered as its abundance. Richness of the assemblage was estimated as the total number of observed species in each sampling day, at each tree cover type and at each farm. This means that to account for variability in species richness across time, I estimated the number of species at each date of sampling.

To analyze variations in bird assemblages across space and time, I fitted two separated generalized linear models

Table 1. Best models statistics describing the relationship between two metrics of bird assemblage and predictor variables in three agricultural-livestock farms located in the central region of the Nicoya Peninsula in Guanacaste, Costa Rica. Richness or overall bird abundance across sampling periods were included as response variable, whereas tree cover type and the three study sites were included as fixed effects. The reference level (intercept) in the two models was bird assemblage at Dulce Nombre and gallery forest. Shown are model estimate (β), *t* statistic, and *P* value; the coefficient of determination R^2 was 0.74 in the two models. Models with significant relationships between metric of bird assemblage and predictor variables are shown in bold ($P < 0.05$).

	Bird richness model			**Bird abundance model**		
Predictor	**β**	***t***	***P***	**β**	***t***	***P***
Intercept	2.93	34.47	**<0.001**	3.67	34.31	**<0.001**
Hojancha	0.11	1.22	0.230	0.08	0.75	0.460
Nambí	–0.33	–3.26	**0.003**	–0.09	–0.79	0.435
Live fence	0.58	6.99	**<0.001**	0.98	9.69	**<0.001**

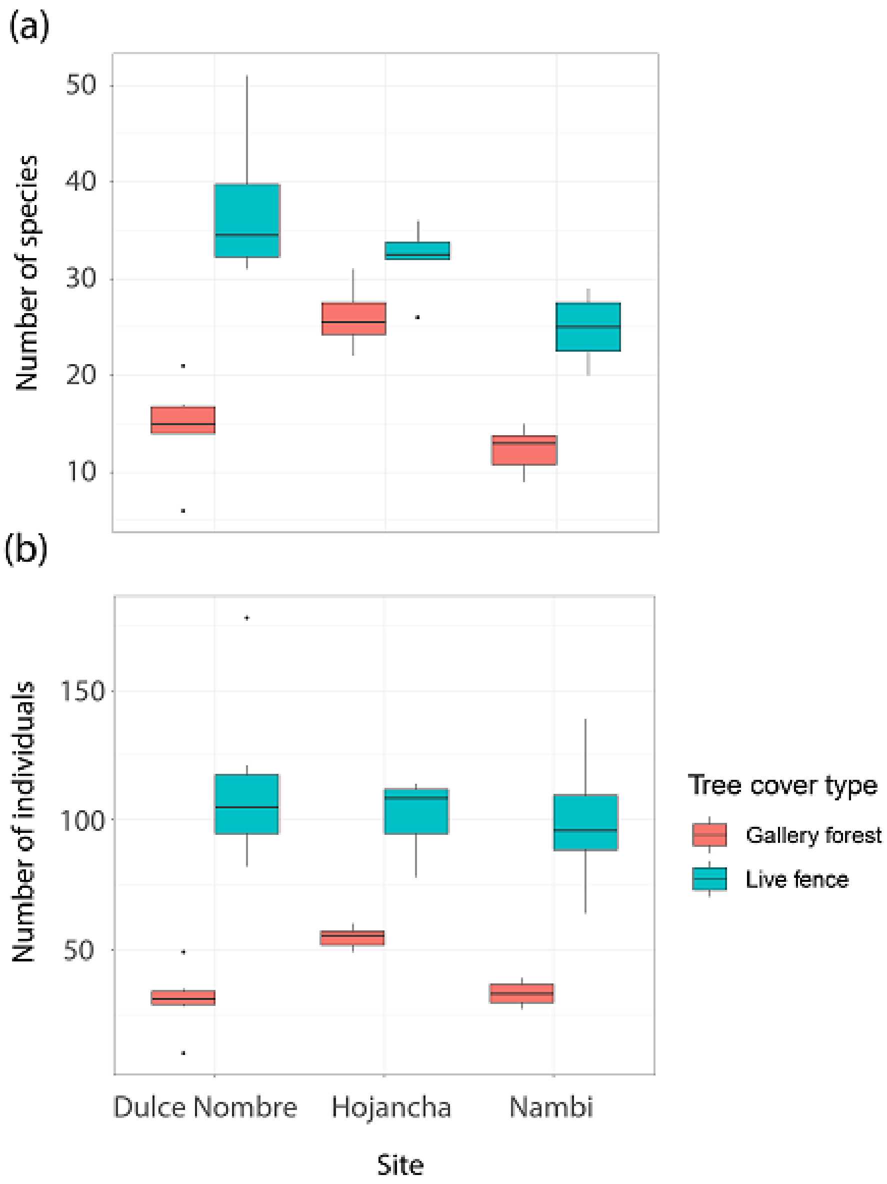

Figure 1. (a) Richness of bird assemblages and (b) overall bird abundance in two tree cover types in three agricultural livestock farms located in the central region of the Nicoya Peninsula in Guanacaste, Costa Rica. Variability per tree cover and site corresponds to the temporal variability among sampling days, horizontal lines across boxes are medians, boxes indicate 25th and 75th percentiles, ends of the vertical lines indicate the data range, and circles are outliers.

(GLM), including richness or overall bird abundance as response variable, and tree cover type, study site, and season as fixed effects:

$$\text{number bird species} \sim \text{tree cover type} + \text{site} + \text{season}. \quad (1)$$

Since both richness and abundance were overdispersed count data, I used quasi-Poisson regression models because its distribution is appropriate for dealing with this kind of data, where an extra dispersion parameter is fitted to account for the extra variance in the model (see Hoef & Boveng 2007). I used the automated selection to identify the most parsimonious model according to the corrected Akaike information criterion (ΔAIC_c to all other models >2) and weight of the model.

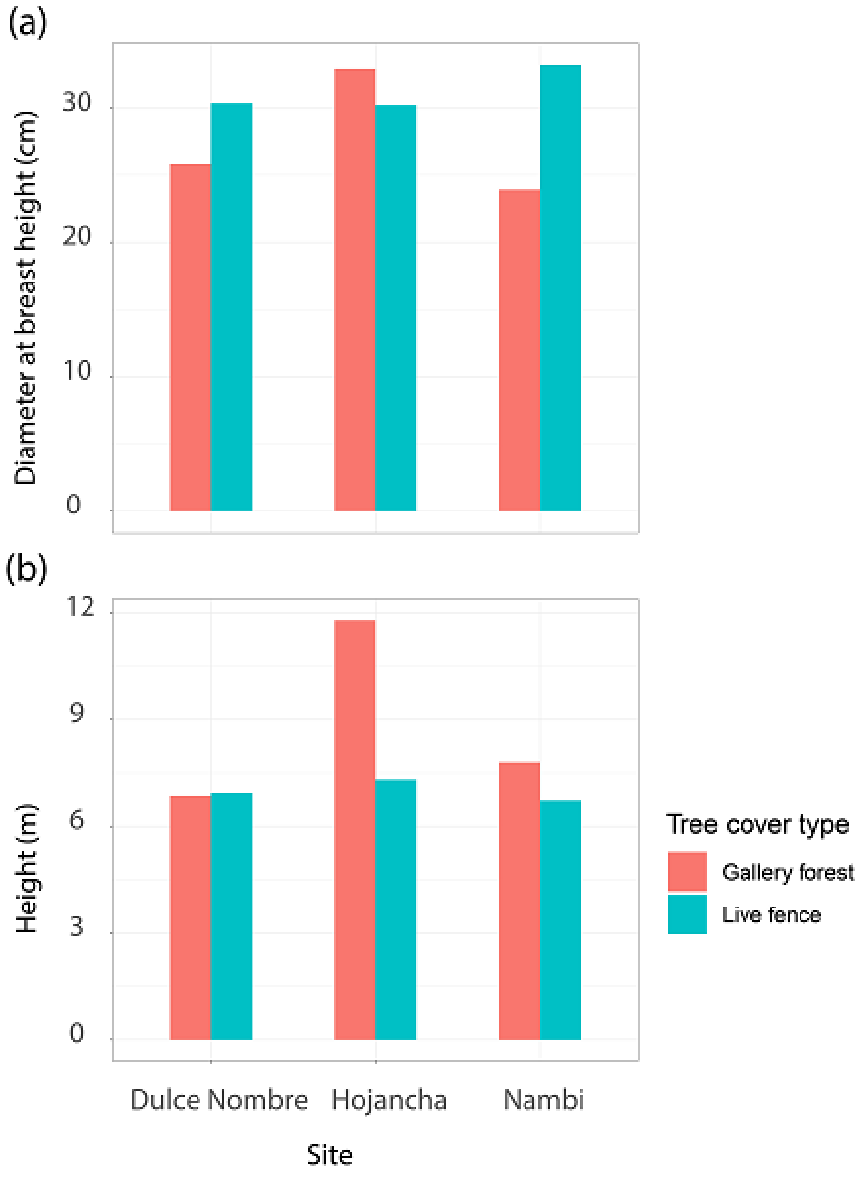

Figure 2. (a) Mean values of diameters at breast height (DHB) and (b) tree height in two tree cover types in three agricultural livestock farms located in the central region of the Nicoya Peninsula, Guanacaste, Costa Rica. Results from linear mixed effect models indicate similar DHBs among tree cover types (β = 0.63, t = 1.67, P = 0.107, R^2 = 0.14), while tree height was lower in live fence compared to gallery forest (β = –0.9765, t = –2.78, P = 0.010, R^2 = 0.21)

To quantify vegetation structure, I performed two separate linear mixed effect models (LMM) including DBH or tree height as response variable, and tree cover type and site as fixed effects. To account for variability across sampling transects, I included it as a random effect in the models:

$$\text{DBH} \sim \text{tree cover type} + \text{site} + (1|\text{transect}). \quad (2)$$

In both LMMs, parameter estimates were based on scaled values (mean zero and unit variance) to make models more comparable. To test variation in plant richness, I fitted a generalized linear mixed model (GLMM) with Poisson distribution of errors, with the number of plant species as the response variable, tree cover type as fixed effect, and sampling transect as random effect. This model can be represented as:

$$\text{number plant species} \sim \text{tree cover type} + (1|\text{transect}). \quad (3)$$

To assess the influence of resource availability on bird assemblages in the two cover types and sites, I performed a second GLMM with the same structure as (3), but only including those plant species that had flowers or fruits during the dry and rainy season along the study. I used automated model selection as outlined previously to choose the best fitting models.

All statistical analyses were conducted with R programming environment (version 4.0.3, R Development Core Team 2020). I used the function *glm* in the package “lme4” (Bates et al. 2014) to perform GLMs, the function *dredge* in the package “MuMIn” (Barton 2020) for automated model selection, and the function *ggplot* in the package “ggplot2” (Wickham 2016) for figures. I estimated the proportion of variance in the dependent variables explained by the fixed factors in the GLMs with the coefficient of determination R^2, using the function *rsq* in the “rsq*”* package (Zhang 2017, 2021), and for the LMM using the function *r.squaredGLMM* in the "MuMIn" package (Nakagawa et al. 2017, Barton 2020).

RESULTS

A total of 2,600 individuals of 114 bird species belonging to 36 families and 18 orders were recorded at the three study sites, out of which 102 were resident and 12 were migratory species (for the complete species list, see Supplementary Table 1). The most abundant species were *Amazona albifrons* (Psittacidae), *Crotophaga sulcirostris* (Cuculidae), and *Campylorhynchus rufinucha* (Troglodytidae), which together made up 22% of all individuals recorded. The best fitting model excluded season as predictor in both the richness and abundance models (ΔAICc = 1.10, weight = 0.37 and ΔAICc = 0, weight = 0.73, respectively), indicating that the number of species and individuals at each site and tree cover type did not vary between the dry and rainy seasons. Richness of bird assemblages was lower in Nambí compared to Dulce Nombre and Hojancha, whereas bird abundance was similar among the sites (Table 1), ranging from 1,115 to 1,188 individuals. In the three sites, live fence was the tree cover type with the highest richness and overall bird abundance compared to gallery forest (Table 1; Figure 1a, 1b). Both gallery forest and live fence had the same number of migratory species (N = 12) and very similar species composition (only one species in live fence was not common to gallery forest and *vice versa*), but live fences had over four times more abundance than gallery forests. The most abundant migratory species in live fences were the nectarivores *Archilochus colubris* and *Icterus galbula*, which accounted for 49% of the records in this tree cover type. For these species, a total of 12 flower-bird interactions were observed in five species of trees in live fences, whereas only one interaction was recorded in gallery forest.

In the three sites, a total of 471 trees were recorded, which represent 52 species from 26 families and 14 orders (Supplementary Table 2). The most common species were *B. simaruba* (Burseraceae), *Guazuma ulmifolia* (Malvaceae) and *Gmelina arborea* (Lamiaceae). Mean DBH ± SE was 29.7 ± 0.32 cm, whereas mean tree height ± SE was 7.8 ± 0.08 m across sites and tree cover types. Best fitting models for both DBH and tree height only included tree cover type as fixed effect (ΔAICc = 1.97, weight = 0.23 and ΔAICc = 0.42, weight = 0.40, respectively). DBHs were similar among tree cover types (Figure 2a), while tree height was lower in live fence compared to gallery forest (Figure 2b). Plant richness varied significantly between the two tree cover types ($\beta = -0.7209$, $t = -4.32$, $P < 0.001$), with an average of 15 and 7 species in gallery forest and live fence, respectively. Richness of flowering/fruiting plants did not change significantly across sites or tree cover types ($\beta = -0.2151$, $z = -0.94$, $P = 0.347$, $R^2 = 0.06$).

DISCUSSION

Land use change has caused the transformation of original forested Neotropical regions into fragmented landscapes, leading to substantial shifts in biodiversity and related ecosystem services (Phillips et al. 2017, Sharma et al. 2019). By comparing the bird assemblages associated to two tree cover types in agricultural livestock farms in a human-modified landscape, I found that patterns in bird richness and abundance changed at a spatial scale, whereas it remained similar in time. Specifically, live fences had higher richness and bird abundance compared to gallery forests, which was consistent across the three studied farms. These results suggest an important role of live fences for bird species, allowing more diverse avian communities in agroecosystems.

Live fences usually cover only small portions of the total landscape (e.g., between 2 and 4.6%; Chacón León & Harvey 2006, Otero & Onaindia 2009). Moreover, live fences are characterized by their structural simplicity, as indicated by the vegetation measures in mine (lower plant richness and tree height) and other studies (Estrada et al. 2000, Pulido-Santacruz & Renjifo 2011). In contrast, forested patches, such as gallery forests, have a greater structural complexity of vegetation that can provide more resources for birds than live fences, and hence support a higher bird richness and abundance (Khanaposhtani et al. 2012). This idea is in line with Vilchez Mendoza et al. (2014), who found higher bird richness and abundance in gallery forests than in live fences across four agricultural landscapes throughout Nicaragua and Costa Rica. A greater number of bird species and individuals in live fences in my study, compared to gallery forests, reveal that factors other than vegetation structure may be related to the differential use of tree cover types by birds, such as food resources and connectivity through landscape (Harvey et al. 2005, Pulido-Santacruz & Renjifo 2011). Although live fences may be less suitable for sustained living because of the lower complexity in vegetation structure and high exposure, they might provide complementary food resources to remnant forests for both resident and migratory birds (Harvey et al. 2004). This may be especially important if gallery forests are scarce or saturated with bird populations, in which case live fences might be acting as sink habitats for some bird species (Pulliam 1996).

The greater number of migratory birds in live fences, compared to gallery forests, was given mainly by two nectarivore species. These species were observed visiting flowers from tree species typically found in live fences, such as *Poincianella eriostachys* and *Gliricidia sepium*, suggesting that this tree cover type might offer more flower resources than the gallery forest. Although I did not find differences in the number of trees in flowering stage between the two tree cover types, great variation exists in flower resources among plant species visited by nectarivore birds in terms of both number of flowers and nectar quantity (McDade 2004, Maglianesi et al. 2020). Thus, further studies analyzing these variables are needed to test whether trees in live fences may be a critical supply of food resources for migratory nectarivore birds. In addition to providing food resources to birds, live fences might be important as stepping-stones across landscapes (Helzer & Jelinski 1999, Fahrig 2013, Acevedo-Charry & Aide 2019). Thereby, bird species differing in dietary habits and mobility can still persist in human-dominated landscapes (Estrada et al. 1997, Acevedo-Charry & Aide 2019).

Connectivity, a central concept in landscape ecology, is related to the movement of organisms as driven by landscape structure (Burel & Baudry 2005). As live fences could act as corridors, facilitating movement and dispersal for many bird species, they contribute to genetic diversity of populations, which is important for the long-term conservation of bird species (Gómez-Fernández et al. 2016). An interconnected network of natural habitats represents a main prerequisite for biodiversity conservation on a landscape scale (Haddad et al., 2015, Lamy et al. 2016). More diverse bird assemblages in live fences compared to gallery forests, in spite of lower plant richness and overall higher simplicity in my study, suggest that live fences represent places where bird species would be the most likely to transit the landscape. Thus, live fences may act as important corridors for bird species and increase connectivity in rural landscapes, which make them an important tool for biodiversity conservation (Pulido-Santacruz & Renjifo 2011).

Finally, in Neotropical regions where highly diverse forests have been replaced by agricultural lands, the future of biodiversity is increasingly dependent on the presence of remnant forest patches and other tree-cover types within human-dominated landscapes. I found a consistent pattern of greater richness and abundance of bird assemblages in live fences compared to gallery forests across three agricultural-livestock farms. These findings show that live fences play an important role for bird diversity in the studied landscape, which may be related to the provision of food resources and greater connectivity in agricultural landscapes. Consequently, farming production models that promote the increase of live fences within pasture lands would greatly benefit bird conservation. My results should be expanded by investigating the composition of live fences, with special attention to those plant species that may offer food and breeding resources for birds.

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