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Diversity and habitat requirement of openland birds in a tropical countryside in south western Costa Rica

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Kurzfassung

Die Umwandlung von tropischen Regenwäldern in Landwirtschafts- und Weidelandschaften ist eine der Hauptursachen für den Verlust der biologischen Vielfalt. Hiervon betroffen sind insbesondere Vogelgemeinschaften in tropischen Ökosystemen. Diese Studie untersucht den Beitrag von Offenlandlebensräumen (Weiden, Brachflächen und Feuchtgebiete) zur biologischen Vielfalt der Vögel in der Region La Gamba im Südwesten Costa Ricas. Diese Lebensräume sind Teil des biologischen Korridors La Gamba. Die Forschung konzentriert sich auf die Frage, wie verschiedene Lebensraumtypen und -strukturen den Artenreichtum und die Zusammensetzung von Vogelgemeinschaften in vom Menschen veränderten Landschaften beeinflussen. Insgesamt wurden 29 Flächen untersucht, die anhand der Vegetationsstruktur und des Vorhandenseins von Wasser in offene, halboffene und feuchte Lebensräume eingeteilt wurden. Die Erhebungen wurden von November bis Dezember 2022 durchgeführt, wobei 130 Vogelarten aus 39 Familien erfasst wurden. Halboffene Lebensräume wiesen den höchsten Artenreichtum auf (121 Arten), gefolgt von offenen Lebensräumen (73 Arten) und Feuchtgebieten (68 Arten). Die Heterogenität der Lebensräume, insbesondere das Vorhandensein von Gehölzstrukturen und überschwemmten Gebieten, erhöhte den Artenreichtum deutlich über die Flächeneffekte hinaus. Die Analyse der Zusammensetzung der Lebensgemeinschaften ergab, dass Feuchtgebiete aufgrund von Überschwemmungen unterschiedliche Vogelarten beherbergen, während sich halboffene Lebensräume aufgrund ihrer strukturellen Komplexität als Hotspots für die biologische Vielfalt erwiesen. Offene Lebensräume hatten einen begrenzten ökologischen Wert, sie beherbergten weniger Arten und es fehlten wichtige Indikatorarten. Die Ergebnisse verdeutlichen, wie wichtig es ist, halboffene Lebensräume und Feuchtgebiete in landwirtschaftlichen Mosaiken zu erhalten, um die Artenvielfalt der Vögel zu fördern. Diese Studie zeigt, dass vielfältige Agrarlandschaften für den Vogelschutz wichtig sind, besonders in Regionen mit stark fragmentierten Wäldern.

Schlagwörter: Biodiversität, Artenvielfalt der Vögel, Lebensräume im Offenland, Zusammensetzung von Vogelgemeinschaften, vom Menschen geschaffene Lebensräume, Costa Rica, Biologischer Korridor La Gamba

Abstract

The transformation of tropical forests into agricultural and pastoral landscapes is a leading cause of biodiversity loss, particularly affecting avian communities in tropical ecosystems. This study investigates the contribution of open-land habitats (pastures, fallows, and wetlands) to avian biodiversity in the La Gamba region of southwestern Costa Rica, part of the La Gamba Biological Corridor. The research focuses on understanding how different habitat types and structures influence bird species richness and community composition in human-modified landscapes. A total of 29 countryside areas were surveyed, classified into open, semi-open, and wetland habitats based on vegetation structure and water presence. Bird surveys were conducted from November to December 2022, recording 130 bird species from 39 families. Semi-open habitats had the highest species richness (121 species), followed by open habitats (73 species) and wetlands (68 species). Habitat heterogeneity, in particular the presence of woody structures and flooded areas, significantly increased species richness beyond area effects. Community composition analysis revealed distinct bird assemblages in wetlands, driven by flooding, while semi-open habitats emerged as biodiversity hotspots due to their structural complexity. Open habitats had limited ecological value, supporting fewer species and lacking significant indicator species. The findings underscore the importance of maintaining semi-open habitats and wetlands within agricultural mosaics to support avian biodiversity. Conservation strategies should prioritize preserving or restoring woody structures and flooded areas to enhance habitat suitability for birds. This study demonstrates that diverse agricultural landscapes are important for bird conservation, especially in regions with highly fragmented forests.

Keywords: Avian Diversity, Tropical Countryside, Human-modified landscapes, Agricultural mosaics, Community Composition, Costa Rica, La Gamba Biological Corridor

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1. INTRODUCTION

The transformation of tropical forests into agricultural and pastoral lands is a principal driver of biodiversity loss, particularly affecting avian communities in tropical ecosystems (Myers *et al.*, 2000; Şekercioğlu *et al.*, 2019). While most forest species depending on relatively pristine forests experience population declines due to forest fragmentation and degradation, others, adapted to disturbed forests and being able to utilize semi-open ecosystems, can thrive in human-modified landscapes (Aubrecht and Schulze, 2008; Kitazawa *et al.*, 2019). In addition, extensively managed tropical farmland is itself characterized by its own set of species and can therefore contribute to regional bird diversity (Hendershot *et al.,* 2023). Understanding the role of these habitats in supporting avian biodiversity is thus essential for developing integrative conservation strategies that address the challenges of human-dominated landscapes.

In Costa Rica, agriculture and deforestation have reshaped much of the natural landscape, leading to a patchwork of forest remnants interspersed with open-land habitats (Zahawi *et al.*, 2015). At higher latitudes, such modified areas, which include abandoned farmlands, pastures, and seasonally flooded fields, can serve as important refuges for various bird species, particularly those that rely on grasslands, wetlands, or transitional ecosystems. Studies suggest that species richness in these areas often rivals that of more pristine habitats, underscoring the potential of managed agricultural landscapes to contribute to avian conservation efforts (Kitazawa *et al.*, 2019). However, there are few studies on the importance of such man-made open habitats for birds from tropical regions. Most of these studies only compared forests and/or agroforests and plantations with one certain openland habitat type (e.g. Schulze *et al.*, 2004).

The ecological roles of these countryside habitats are particularly relevant in regions where remaining forests are heavily fragmented. Open-land habitats provide foraging grounds and breeding sites, and act as movement corridors, thereby facilitating dispersal and gene flow across fragmented habitats, or act as dispersal barriers for forest specialists. In this context, understanding the habitat preferences and species composition of bird communities in open-land areas is essential for developing effective conservation strategies that integrate these secondary habitats within broader landscape-level management plans (Schlaepfer, 2002; Ceballos *et al.*, 2010).

Habitat heterogeneity is a critical factor influencing biodiversity patterns in modified landscapes. Benton *et al*. (2003) demonstrated that agricultural intensification often results in the homogenization of landscapes, a process strongly associated with declines in species richness. Conversely, heterogeneous habitats—characterized by vertical complexity, woody debris, and a mosaic of vegetation types—support diverse assemblages of species. Semi-open habitats, for instance, combine open spaces with scattered trees and shrubs, creating transitional ecosystems that provide essential foraging and nesting opportunities for both generalist and specialist birds (Hughes *et al.*, 2002; Luck *et al.*, 2003). These findings suggest that conservation strategies should prioritize maintaining or restoring structural diversity within agricultural mosaics.

This study examines the contribution of countryside habitats to avian biodiversity in southwestern Costa Rica's Golfo Dulce region, part of the La Gamba Biological Corridor. The focus is on assessing species richness and habitat utilization across different open-land habitats, including pastures, fallows, and wetland-like areas. By evaluating bird assemblages and identifying habitat features associated with higher species richness, this research aims to inform conservation practices that support avian diversity within agricultural landscapes.

In particular, we will address the following questions:

(1) To what extent do openland habitats contribute to the overall bird diversity of the La Gamba region?

(2) What habitat structures are shaping species richness and composition of bird assemblages as well as the occurrence of individual species in (semi-) open areas?

2.1 Study area and study sites

This study was conducted in the countryside landscape around the village La Gamba (N 8.708259°, W 83.185314°), situated between the Piedra Blancas National Park, the Golfito Forest Reserve and the mountain range Fila Cal in southwestern Costa Rica. The surroundings of La Gamba are characterized by pastures with small and elongated forest patches, strips of gallery forest, few big plantations (e.g. oil palm), old (and mostly abandoned cacao) agroforests and annual cultures (e.g. rice) (Seaman and Schulze, 2010; Höbinger *et al.*, 2012).

Costa Rica lies within the intertropical convergence zone (ITCZ) which is a major factor for precipitation levels and wet and dry seasons in the tropics. The major climatic characteristic for this region is first of all the high annual precipitation of 5.836 mm in La Gamba. Temperatures are uniform throughout the year with an average of 28.2 °C. The heaviest rainfall is recorded in September and October (Weissenhofer *et al.*, 2008a), which leads to partially flooded open agricultural areas.

The study area is part of the Biological Corridor La Gamba (COBIGA) (Weissenhofer *et al.*, 2008b) aiming to reconnect remaining forest areas by reforestation measures within the human-dominated landscape acting as barrier for dispersal of forest species. However, since some openland habitats may be valuable landscape elements for birds, an assessment of their contribution to maintaining avian biodiversity is urgently needed. Hence, in this study we surveyed bird assemblages in a diversity of different openland habitats ranging from pastures to fallows and swampy areas. When evaluating habitat preferences of (semi-)openland birds we will consider the landscape setting as well as vegetation structures (e.g. single trees, scrubs etc.) characterizing our study sites.

In total we surveyed 29 different areas (Fig. 1), which were classified into open, semi-open and wetland habitats (Table 1) using the following criteria: **Openland habitats** are lacking significant tree cover. **Semi-openland habitats** are characterized by a mix of open spaces and scattered trees or shrubs. **Wetland habitats** are characterized by the presence of standing water or water-saturated soils and inhabit a mix of open spaces and scattered trees or shrubs.

Figure 1: Map indicating all study sites. Orange: open habitats, green: semi-open habitats, blue: wetland habitats.

Table 1. Classification of the surveyed area (compare Fig. 1) into openland, semi-openland and wetland and their size.

Site code	Openland type	Size (ha)	Site code	Openland type	Size (ha)
1	semi-open	19.13	16	semi-open	7.15
2	semi-open	15.57	17	open	2.09
3	open	4.34	18	open	3.43
4	semi-open	3.10	19	semi-open	1.11
5	open	4.97	20	wetland	3.70
6	wetland	4.61	21	wetland	9.82
7	semi-open	1.88	22	wetland	5.09
8	semi-open	6.77	23	open	1.82
9	open	4.78	24	open	0.65
10	open	3.06	25	open	2.10
11	open	0.91	26	semi-open	5.49
12	semi-open	5.29	27	open	1.70
13	semi-open	1.51	28	semi-open	4.53
14	semi-open	3.90	29	semi-open	2.74
15	open	1.24			

2.2 Bird survey

Fieldwork was conducted from 03 November till 19 December 2022. All selected study sites were surveyed three times with an effort of 15 min per hectare. During this period all acoustically and visually detected birds were recorded and georeferenced using the app NaturaList. Surveys started at sunrise and ended around 10:30 am, thereby the period of highest bird activity was covered. Birds of smaller open land patches were recorded from the margin (e.g. from roads and paths) using a binocular and a scope. At larger study sites birds were observed from different points located at their margins and in the center of the areas always trying to avoid double counts.

2.3 Habitat variables

For understanding how avian diversity is distributed across tropical openland habitats, it was important to assess the effects of vegetation structure and land use. Therefore, the land use and the vegetation structure of the study sites were recorded on field maps during the bird surveys.

To characterize our study area, a total of 10 habitat variables were recorded (Table 1). Three variables quantify the vertical structure of the herb layer and three variables characterizing the woody vegetation, e.g. the occurrence of small woodlots, the density of single trees and the density of living fences. Further, flooded areas were marked on field maps to estimate the percentage of flooded area for each study site.

To account for the influence of adjacent habitats, two variables were included: border forest and border oil palm. These variables measured the perimeter of the study site margin adjacent to forest or oil palm plantations, respectively. These variables were included because the proximity to forest edges or oil palm plantations can significantly influence bird communities by providing additional resources, shelter, or dispersal corridors, or conversely, by creating barriers or edge effects that alter species composition and diversity.

Table 2. Habitat variables recorded for each study area.

Habitat variable	Description and assessment method	Unit
meadow <10cm	Estimated meadow area with herb layer height of <10 cm.	% cover
meadow <50cm	Estimated meadow area with herb layer height between 10 and <50cm.	% cover
meadow >50cm	Estimated meadow area with herb layer height >50cm.	% cover
woodlot cover	Area covered by patches of small woodlots	% cover
flooded area	Estimated area flooded	% cover
single trees	Density of single trees	number of single trees/ha
living fences	Length of living fences	Living fence length/ha
border forest	Estimated study area margin with a border to forest measured in perimeter	% of study area margin
border oilpalm	Estimated study area margin with a border to forest measured in perimeter	% of study area margin

2.4 Analysis

To compare bird species richness between the three openland habitat types, abundance-based species accumulation curves and their 95 % confidence intervals were calculated with iNext Online (Chao *et al.* 2014, 2016). To evaluate if species assemblages of individual habitat types only represent subsets of the region's total richness of openland birds, a species accumulation curve was also calculated for the entire assemblage of study sites. All curves were extrapolated to twice the number of individuals counted.

To compare species richness between habitat types, the species richness was estimated for all sites for a shared sample size of 60 individuals by extrapolation or rarefaction of species accumulation curves, again calculated with iNext Online. Subsequently, a one-way ANOVA was used to test for differences in species richness predicted for a sample size of 60 individuals between openland habitat types.

To test for an effect of study area size on species richness a Pearson correlation was calculated. The residuals of a linear regression between species richness and study area size was used to quantify the deviation in species richness which cannot be explained by the species-area relationship. In advance, both variables were log-transformed. A one-way ANOVA was used to test for differences of the residuals between the openland habitat types. Again, all analyses were calculated using PAST 4.17.

A generalized linear model (GLM) was used to evaluate effects of habitat variables on the variance in site-specific species richness, which could not be explained by differences in study area size. However, due to multicollinearity of habitat variables and the risk of model over-parametrization a Principal Component Analysis (PCA) was calculated (using Varimax with Kaiser Normalization and rotation) to reduce the number of variables. Three principal components and the two variables border forest and border oil palm plantation (which were both not correlated with any other predictor variables) were then used as explanatory variables in the calculated GLM.

Community composition was analyzed using rank-abundance plots. Non-metric multidimensional scaling (NMDS) was used to visualize similarity relationships between surveyed sites. Therefore, Bray-Curtis dissimilarities were used, with square-root transformed abundances to increase the contribution of rarer species to the index value. With a stress value of <0.2, a two-dimensional ordination was accepted of reliably visualizing the true similarity relationships between assessed bird assemblages. To test for differences in species composition between openland habitat types a one-way ANOSIM was calculated. Spearman rank correlations were used to test for relationships between Dimension 1 and 2 values extracted from the NMDS ordination and habitat variables.

An Indicator Species Analysis (IndVal) was calculated (with 9,999 permutations) to identify indicator species associated with specific habitat types (Dufrene & Legendre, 1997).

If not mentioned otherwise, all analyses were calculated using PAST 4.17 (Hammer *et al*. 2001).

3.1 Species richness

A total of 130 bird species belonging to 39 different families were observed (Appendix A1). The most abundant species were Variable Seedeater (9.42% of counted individuals; Fig. 2), Bronzed Cowbird (9.31% of counted individuals; Fig. 3), and Western Cattle-Egret (6.43% of counted individuals; Fig. 4). We observed 121 species in semi-open habitats, 73 species in open habitats and 68 species in wetlands.

Figure 2: Variable Seedeater, La Gamba, 22.11.2022.

Figure 3: Bronzed Cowbird, La Gamba, 22.11.2022.

Figure 4: Western Cattle-Egret perching on the back of a cattle, La Gamba, 08.11.2022.

The abundance-based species accumulation curves for the three openland types indicate a significantly lower species richness of wetlands compared to semi-open and open study areas (Fig. 5). However, the wetland sites contributed to the overall richness since several bird species could only be recorded in this habitat type (Appendix A2).

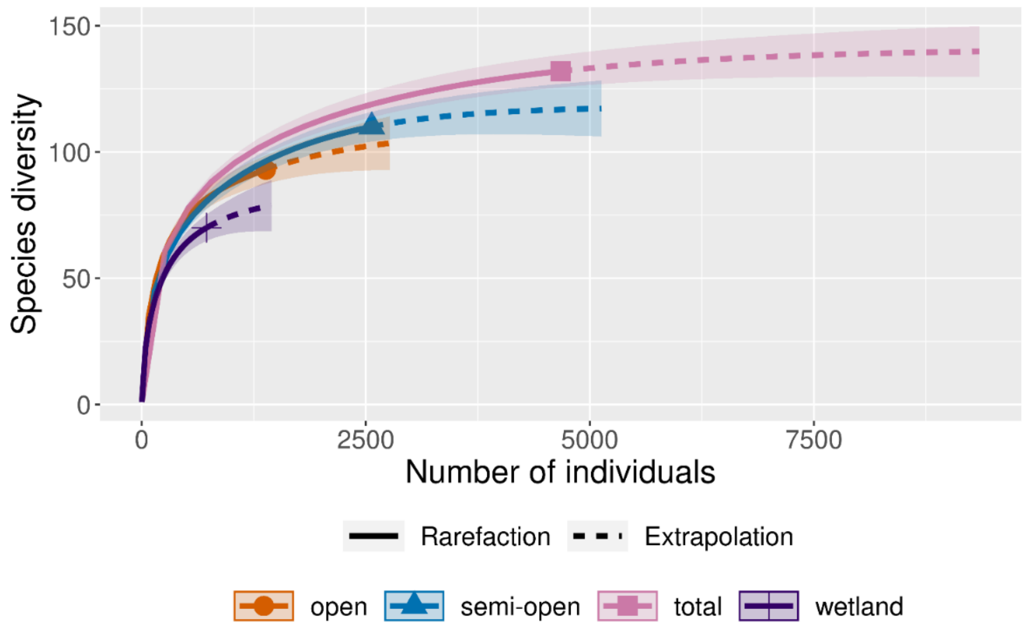

Figure 5: Species accumulation curves (±95% CI) for the three openland types and all study areas combined. Broken lines indicate extrapolated parts of the curves.

Mean species richness per study site predicted for a shared sample size of 60 individuals proved being similar for the three habitat types ranging between 21.30 and 23.73 species (Fig. 6; one-way ANOVA: $F_2 = 1.114$, $p = 0.3434$).

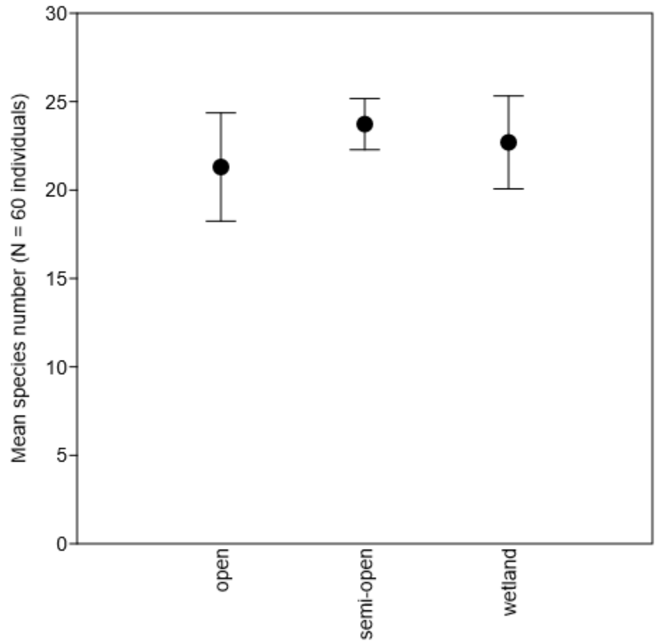

Figure 6: Fig. Mean species richness (± 95% CI), predicted for a shared sample size of 60 individuals of the three openland types.

Recorded species richness increased significantly with the size of the surveyed areas (Pearson correlation: r = 0.458, p = 0.0124; Fig. 4). However, the low coefficient of determination (r^2 = 0.210) indicates that several other factors beside area effects are shaping the species richness.

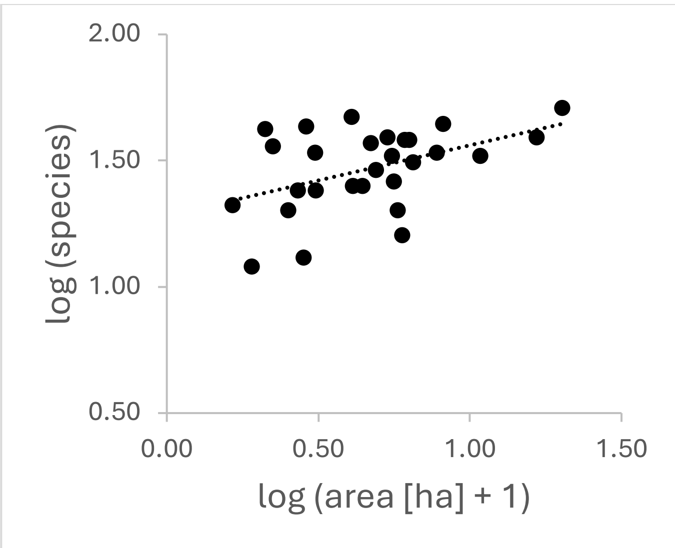

Figure 7: Species-area relationship of the surveyed areas (N = 29) visualized by a linear regression line.

Also mean residuals of the species area-relationship did not differ significantly between habitat types (one-way ANOVA: $F_2 = 1.102$, $p = 0.3474$; Fig. 8).

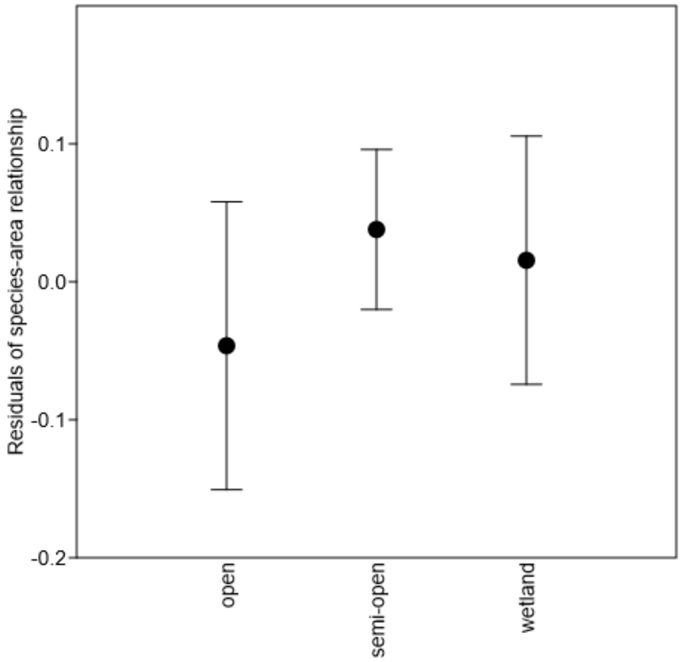

Figure 8: Mean residuals (± 95% CI) of the species-areal relationship of the three habitat types.

Due to multicollinearity of the meadow and woody structure habitat variables a PCA was calculated. The first three principal components already explained 78.45 % of the variance (Tab. 3). Hence, only these three components were considered in further analyses.

Table 3: Results of principal component analysis (PCA) (Varimax with Kaiser Normalization and rotation) considering meadow and woody structure variables.

Component	Eigenvalues	% of variance	Cumulative %
1	2.806	40.079	40.079
2	1.585	22.637	62.716
3	1.101	15.733	78.450
4	0.732	10.461	88.911
5	0.409	5.842	94.753
6	0.367	5.247	100.000
7	-6.287E-17	-8.981E-16	100.000

The three principal components were identified as follows: PC1 is characterized by meadow height (contrasting short meadows <10 cm with tall meadows <50 cm), PC2 represents woody structures (including living fence and single tree density), and PC3 reflects the extent of flooded areas (Tab. 4).

Table 4: Factor loadings of habitat variables on the first three components of a PCA (Rotation method: Varimax with Kaiser Normalization; compare Table 3). Marked cells indicate high factor loadings (>|0.8|).

	Components		
Habitat variables	PC 1	PC 2	PC 3
living fences	.072	.863	-.084
single trees	.006	.869	.014
meadow <10cm	-.917	-.218	-.326
meadow <50cm	.628	.560	-.052
meadow >50cm	.911	-.183	-.161
woodlot cover	.418	.375	.435
flooded area	-.032	-.158	.924

			95% Wald Confidence Interval		Hypothesis Test		
Parameter	B	Std. Error	Lower	Upper	Wald Chi-Square	df	Sig.
(Intercept)	.005	.0294	-.053	.062	.024	1	.877
border forest	.000	.0015	-.003	.003	.006	1	.936
border oilpalm	-.001	.0016	-.004	.003	.129	1	.720
PC1	.037	.0222	-.007	.080	2.748	1	.097
PC2	.069	.0225	.025	.113	9.359	1	.002
PC3	.019	.0222	-.024	.063	.736	1	.391
(Scale)	0.14[a]	.0036	.008	.023			

Dependent Variable: Residuals

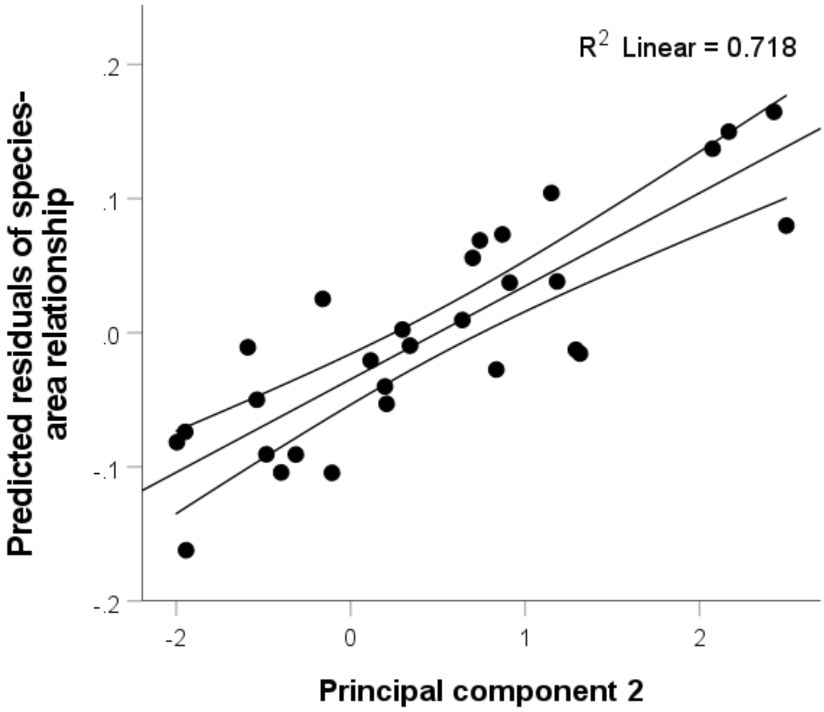

Figure 9: Predicted relationship between residuals of species-area relationship and principal component 2 (≈density of living fences and single trees) of a PCA on habitat variables visualized by a linear regression (±95% CI) (R^2 = 0.718).

3.2 Community composition

The bird assemblages of the three openland types are characterized by a relatively similar rank-abundance structure (Fig. 10). Further, species composition did not differ between the openland habitat types (one-way ANOSIM: R = 0.057, p = 0.1893), although the NMDS ordination based on Bray-Curtis dissimilarities indicates that wetlands may be characterized by a partly distinct species composition (Fig. 11). This is also confirmed by a significant correlation between the Dimension 1 values of the NMDS and PC3 (≈flooded area) (Table 6).

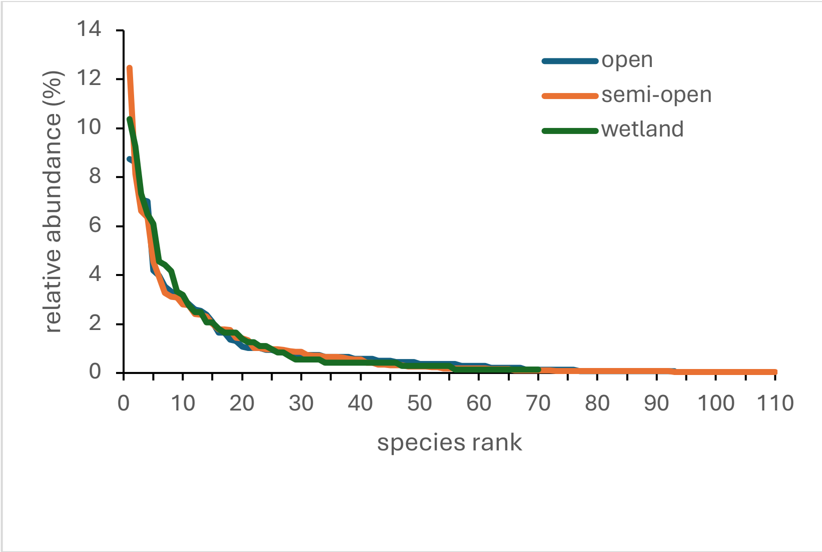

Figure 10. Rank-abundance plot for bird assemblages of open habitats, semi-open habitats, and wetland habitats.

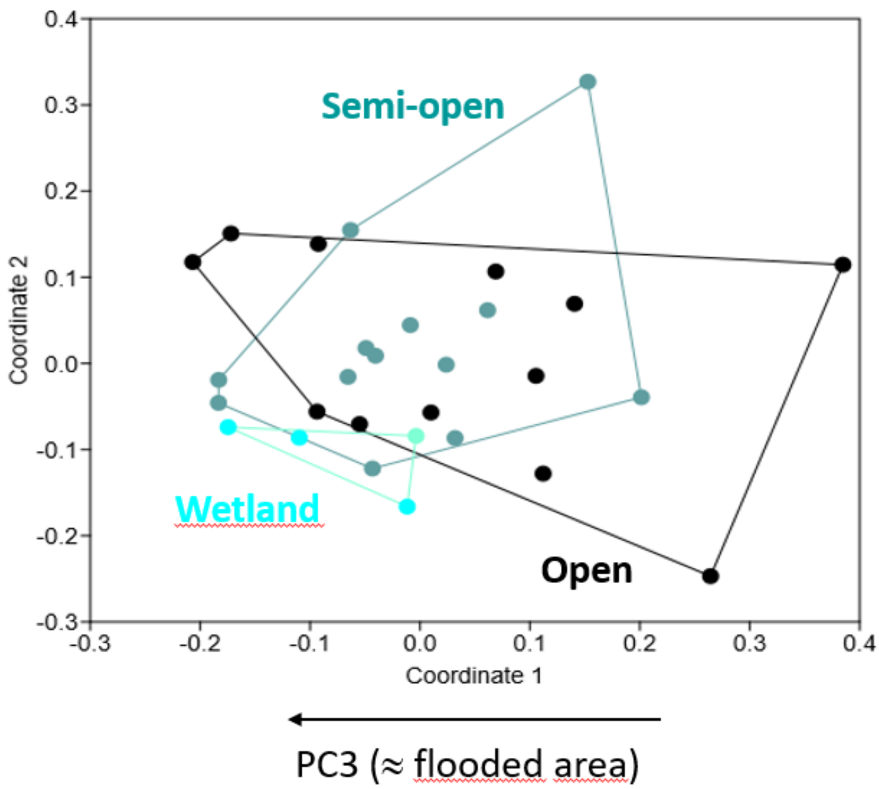

Figure 11: Fig. NMDS ordination visualizing similarity relationships of bird assemblages (based on Bray-Curtis dissimilarities; using square-root transformed abundances) of all sampled study sites (stress = 0.257). Habitat type affiliation of study sites is indicated by different colors of points. The arrow below the x axis indicates the significant negative correlation between coordinate 1 values and the PC3 values of a PCA on habitat variables (Tab. 6).

Table 6: Results of spearman's rank correlations between the dimension 1 and 2 values of a NMDS on similarity relationships between bird assemblages of the sampled study sites (Fig. 11) and habitat variables. Flooding (PC3) significantly influence wetland bird assemblages (p=0.025).

Predictor variables	NMDS_Dimension1	NMDS_Dimension2
border forest	r_s = 0.355 p = 0.058	r_s = -0.046 p = 0.811
Border oil palm	r_s = 0.367 p = 0.050	r_s = 0.070 p = 0.717
PC1	r_s = -0.357 p = 0.058	r_s = 0.182 p = 0.344
PC2	r_s = 0.296 p = 0.120	r_s = 0.335 p = 0.076
PC3	r_s = -.416* p = **0.025**	r_s = -0.086 p = 0.658

3.3 Indicator species for openland habitats

While 11 and 8 species were identified as indicator birds for semi open and wetland areas, respectively, none was highlighted for the open areas (Fig. 11).

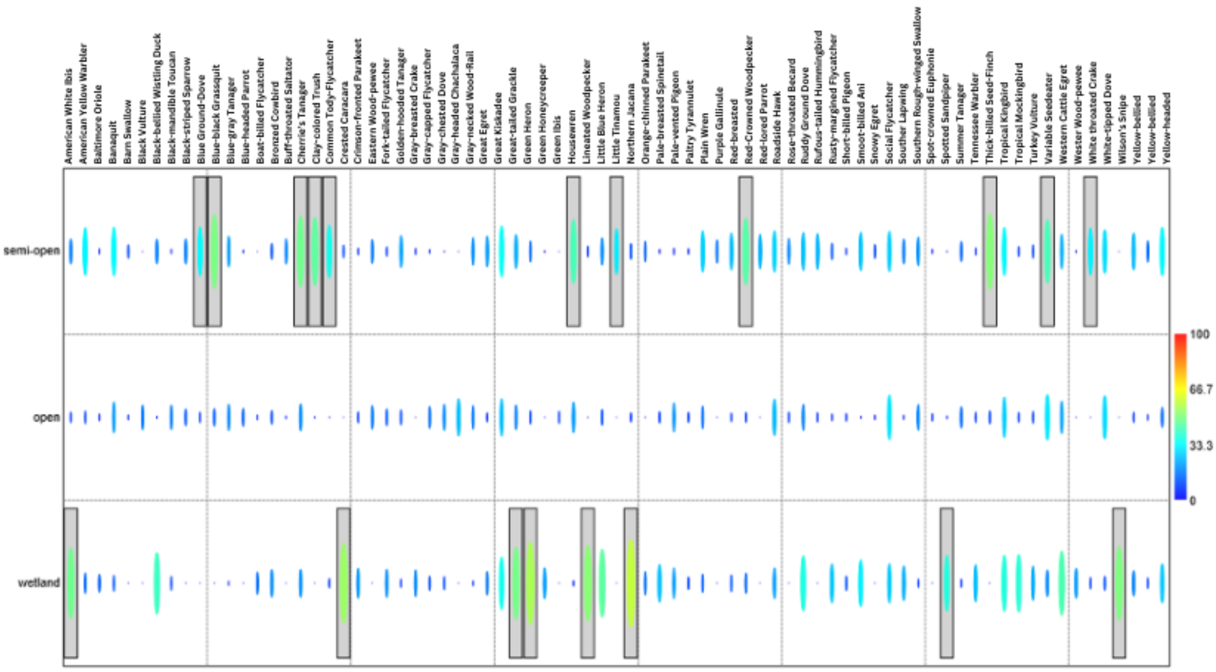

Figure 11: Results of an Indicator Species Analysis (IndVal). The indicator values of species (ranging from *0 to 100*) are indicated by different colors. Statistical *significances (p values) of* species' *indicator values* for the three openland types are indicated by gray boxes.

4. DISCUSSION

The high number of bird species recorded during this study at La Gamba highlights the ecological significance of openland habitats in supporting avian biodiversity in the region of southwestern Costa Rica. Semi-open habitats, characterized by scattered trees and shrubs, supported the highest species richness among the surveyed habitat types. This aligns with findings from Johnson *et al*. (2011) and Hughes *et al*. (2002), who emphasized that structurally diverse landscapes enhance habitat suitability for birds. In contrast, entirely open areas exhibited limited ecological value, lacking significant indicator species and the structural complexity required to support diverse avian assemblages. Wetlands provide critical resources for resident (e.g. Green Heron and Northern Jacana) and migratory species (e.g. Spotted Sandpiper and Wilson's Snipe).

The role of open-land habitats in the overall bird diversity

The La Gamba region is known for its rich avian diversity, with Graham Tebb's checklist (2008) documenting over 400 bird species in the area. In this study, we recorded 130 bird species, representing approximately 32.5% of the region's total avian diversity. This significant proportion underscores the importance of openland habitats, particularly semi-open and wetland areas, in supporting a substantial fraction of the region's birdlife. While forests remain critical for many forest-dependent species, our findings suggest that openland habitats, especially those with structural complexity, play a complementary role in maintaining regional biodiversity. This is particularly relevant in fragmented landscapes where forest remnants are interspersed with agricultural and pastoral lands.

The role of habitat heterogeneity

Habitat heterogeneity is a well-documented driver of biodiversity. Benton *et al.* (2003) argued that the loss of ecological heterogeneity, primarily due to agricultural intensification, is a major contributor to biodiversity decline. Promoting heterogeneity at multiple spatial scales is essential to mitigating this trend. Our findings reinforce this perspective, as the presence of vertical structures, woody debris, and vegetation mosaics in semi-open and wetland habitats was strongly correlated with increased avian richness and diversity. Similarly, Daily *et al.* (2001) observed that structurally complex agricultural landscapes in Costa Rica support significant avifauna, underscoring the importance of maintaining diverse habitats within human-modified landscapes.

Wetlands as unique habitats

Wetlands emerged as unique and ecologically vital habitats, hosting specialized waterbirds and other indicator species such as the Lineated Woodpecker, which relies on dead trees for nesting, and migratory species like the Wilson's Snipe. Partially submerged meadows provide essential resources for local breeding birds and overwintering migrants (Hughes *et al.*, 2002). The structural complexity of wetlands, including standing water and woody structures, contributes significantly to avian species composition, emphasizing the need for prioritizing their conservation within agricultural landscapes.

Indicator species like the Lineated Woodpecker and Wilson's Snipe can serve as proxies for habitat quality. The presence of these species may suggest healthy, functioning ecosystems with adequate resources for foraging, nesting and shelter. For example, the Lineated Woodpecker's reliance on dead trees highlights the importance of maintaining snags and woody debris in wetland habitats, while the Wilson's Snipe's presence indicates suitable wetland conditions for migratory stopovers.

Semi-open Habitats as biodiversity hotspots

Semi-open habitats, created through natural processes like tree falls and anthropogenic activities like agriculture, support diverse bird communities by providing transitional landscapes. Şekercioğlu *et al.* (2007) demonstrated that certain bird species can adapt to deforested agricultural areas if remnant trees and shrubs are preserved. Our study corroborates those findings, emphasizing that semi-open habitats serve as biodiversity

hotspots for both generalist and specialist species. Luck and Daily (2003) also highlighted the conservation value of low-intensity agricultural practices incorporating remnant trees and living fences, which provide critical resources for frugivores and insectivores.
Unlike entirely open habitats, semi-open areas offer essential foraging opportunities and nesting sites for species adapted to transitional landscapes. These findings align with the concept that semi-open habitats have historically existed in Central America, shaped by both natural and anthropogenic processes (Filippelli *et al.,* 2010). Human activities, including indigenous land use and more recent agricultural practices, have expanded the prevalence of such habitats, enabling species to adapt and thrive.

Historical and anthropogenic influences

Historical evidence underscores the profound influence of human activity on Central American landscapes. Sedimentary records from Laguna Zoncho indicate that land use practices, such as forest thinning, agriculture, and fire management have shaped these landscapes for over 3,000 years (Filippelli *et al.,* 2010). These practices facilitate the southward migration of bird species adapted to prairie-like environments. Daily *et al.* (2001) noted that Costa Rica's agricultural matrix continues to support a significant proportion of its avifauna, particularly in areas where traditional land-use practices maintain structural diversity.

Species benefiting from deforestation include those adapted to disturbed or open environments. Many open-land species are generalists or grassland-associated birds that have migrated from northern prairies or arid regions. Their ability to exploit artificial landscapes, such as pastures and heavily grazed fields, has enabled them to establish populations in areas previously dominated by dense forests. However, entirely open landscapes, devoid of woody structures or vegetation heterogeneity, were found to have limited ecological value, supporting only a narrow range of species.

Costa Rica's landscape has been significantly shaped by human activity over the past centuries, from pre-Columbian agriculture to modern farming practices. Indigenous land use, including the integration of fruit trees and agroforestry, has historically contributed to the creation of semi-open landscapes (Filippelli *et al.,* 2010). Modern farming practices, such as the use of living fences, continue to reflect this cultural legacy while supporting biodiversity. Luck and Daily (2003) observed that isolated fruiting trees and living fences in agricultural landscapes provide critical resources for frugivores, enhancing their capacity to persist in human-modified environments.

Ecosystem services provided by avian communities

Birds in semi-open and wetland habitats provide essential ecosystem services that benefit both natural ecosystems and human communities. For example, insectivorous birds contribute to pest control in agricultural landscapes, reducing the need for chemical pesticides (Şekercioğlu *et al.,* 2016). Frugivorous birds play a critical role in seed dispersal, facilitating forest regeneration and maintaining plant diversity (Whelan *et al.*, 2008). Additionally, wetland birds, such as herons and egrets, contribute to nutrient cycling and water quality regulation through their foraging activities (Green *et al.,* 2017). Recognizing these ecosystem services underscores the importance of conserving avian habitats for both ecological reasons and human well-being.

Conservation implications and future research

The findings of this study highlight the importance of conserving semi-open and wetland habitats within agricultural mosaics. Wetlands, with their distinctive species assemblages, serve as critical refuges for resident and migratory birds. Semi-open landscapes, characterized by features like scattered trees and living fences, provide valuable resources for species requiring open spaces and vertical structures. Conservation strategies should prioritize maintaining these habitat features, recognizing their role in supporting biodiversity.

Future research should explore the long-term effects of land-use changes on tropical avian communities and investigate the potential for restoring semi-open habitats in degraded areas. Luck and Daily (2003) suggested that low-intensity agricultural practices and agroforestry systems could facilitate seed dispersal and support biodiversity. Additionally, studies examining the population dynamics of species in source and sink habitats, as described by Arlt *et al.* (2008), could provide further insights into the sustainability of conservation strategies. By integrating these findings into conservation planning, the La Gamba region can serve as a model for sustainable land management that supports both biodiversity and agricultural productivity.

REFERENCES

Arlt, D., Forslund, P., Jeppson, T. and Pärt, T. (2008): Habitat-specific population growth of a farmland bird. PLoS ONE, 3(8): e3006.

Aubrecht, G. and Schulze, C.H. (2008): Birds of La Gamba – a call for research and scientific collaboration. Pp. 349–351. In Weissenhofer, A., Huber, W., Mayer, V., Pamperl, S., Weber, A. & Aubrecht, G. (eds.), Natural and Cultural History of the Golfo Dulce Region, Costa Rica. Stapfia 88. Biologiezentrum des Oberösterreichischen Landesmuseums, Linz.

Benton, T.G., Vickery, J.A. and Wilson, J.D. (2003): Farmland biodiversity: Is habitat heterogeneity the key? Trends in Ecology and Evolution 18: 182–188.

Ceballos, G., Ehrlich, P.R. and García, A. (2010): The sixth extinction crisis: Loss of animal populations and species. Journal of Cosmology 8(1821): 31.

Chao, A., Gotelli, N.J., Hsieh, T.C., Sander, E.L., Ma, K.H., Colwell, R.K. and Ellison, A.M. (2014): Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs 84: 45-67.

Chao, A., Ma, K.H. and Hsieh, T.C. (2016): iNEXT (iNterpolation and EXTrapolation) Online: Software for Interpolation and Extrapolation of Species Diversity. Program and User's Guide. http://chao.stat.nthu.edu.tw/wordpress/software_download/inext-online/. (last access: 27 February 2025)

Daily, G.C., Ehrlich, P.R., and Sánchez-Azofeifa, G.A. (2001): Countryside biogeography: Use of human-dominated habitats by the avifauna of southern Costa Rica. Ecological Applications 11(1): 1–13.

Dufrene, M. and Legendre, P. (1997): Species assemblages and indicator species: The need for a flexible asymmetrical approach. Ecological Monographs, 67(3): 345.

Filippelli, G.M., Souch, C., Horn, S.P. and Newkirk, D. (2010): The pre-Colombian footprint on terrestrial nutrient cycling in Costa Rica: Insights from phosphorus in a lake sediment record. Journal of Paleolimnology 43(4): 843–856.

Graham, T. (2008): The birds of La Gamba. Stapfia. 88. 353-380

Green, A.J., Elmberg, J. and Lovas-Kiss, Á. (2017): Beyond seed dispersal: The role of waterbirds in wetland ecosystems. Aquatic Conservation: Marine and Freshwater Ecosystems 27(1): 5-10.

Hammer, O., Harper, D.A.T. and Ryan, P.D. (2001): PAST: Paleontological Statistics Software Package for Education and Data Analysis. Palaeontologia Electronica 4(1): 1.

Hendershot, J.N., Echeverri, A., Frishkoff, L.O., Zook, J.R., Fukami, T. and Daily, G.C. (2023): Diversified farms bolster forest-bird populations despite ongoing declines in tropical forests. PNAS 120(37): e2303937120.

Höbinger, T., Schindler, S., Seaman, B.S., Wrbka, T. and Weissenhofer, A. (2012): Impact of oil palm plantations on the structure of the agroforestry mosaic of La Gamba, southern Costa Rica: Potential implications for biodiversity. Agroforestry Systems 85: 367–381.

Hughes, J.B., Daily, G.C. and Ehrlich, P.R. (2002): Conservation of tropical forest birds in countryside habitats. Ecology Letters 5: 121–129.

Johnson, M.D., Levy, N.J., Kellermann, J.L. and Robinson, D.E. (2011): Effects of shade and bird exclusion on arthropods and leaf damage on coffee farms in Jamaica's Blue Mountains. Agroforestry Systems 82(2): 139-148.

Johnson, R.J., Jedlicka, J.A., Quinn, J.E. and Brandle, J.R. (2011): Global perspectives on birds in agricultural landscapes. Pp. 55–140. In: Campbell, W.B. and López Ortíz, S. (eds.), Integrating Agriculture, Conservation and Ecotourism: Examples from the Field. Issues in Agroecology – Present Status and Future Prospectus 1, Springer Science+Business Media.

Kitazawa, M., Yamaura, Y., Senzaki, M., Kawamura, K., Hanioka, M. and Nakamura, F. (2019): An evaluation of five agricultural habitat types for openland birds: abandoned farmland can have comparative values to undisturbed wetland. Ornithological Science 18: 3–16.

Luck, G.W. and Daily, G.C. (2003): Tropical countryside bird assemblages: Richness, composition, and foraging differ by landscape context. Ecological Applications 13: 235–247.

Magurran, A.E. (2004): Measuring Biological Diversity. Blackwell.

Myers, N. Mittermeier, R.A., Mittermeier, C.G., Da Fonseca, G.A. and Kent, J. (2000): Biodiversity hotspots for conservation priorities. Nature 403: 853–858.

Schlaepfer, M.A., Runge, M. and Sherman, P.W. (2002): Ecological and evolutionary traps. Trends in Ecology & Evolution 17: 474–480.

Schulze, C.H., Waltert, M., Kessler, P.J.A., Pitopang, R., Shahabuddin, Veddeler, D., Steffan-Dewenter, I., Mühlenberg, M., Gradstein, S.R. and Tscharntke, T. (2004): Biodiversity indicator groups of tropical land-use systems: comparing plants, birds and insects. Ecological Applications 14: 1321–1333.

Seaman, B.S. and Schulze, C.H. (2010): The importance of gallery forests in the tropical lowlands of Costa Rica for understorey forest birds. Biological Conservation 143: 391–398.

Şekercioğlu, C.H., Loarie, S.R., Oviedo Brenes, F., Ehrlich, P.R.and Daily, G.C. (2007): Persistence of forest birds in the Costa Rican agricultural countryside. Conservation Biology 21(2): 482–494.

Şekercioğlu, Ç.H., Wenny, D.G., & Whelan, C.J. (2016): Why birds matter: Avian ecological function and ecosystem services. University of Chicago Press.

Şekercioğlu, Ç.H. Mendenhall, C.D., Oviedo-Brenes, F., Horns, J.J., Ehrlich, P.R. and Daily, G.C. (2019): Long-term declines in bird populations in tropical agricultural countryside. Proceedings of the National Academy of Sciences of the United States of America 116(20): 9903–9912.

Whelan, C.J., Şekercioğlu, Ç.H. and Wenny D.G. (2008): Why birds matter: From economic ornithology to ecosystem services. Journal of Ornithology 149(1): 161-168.

Weissenhofer, A. and Huber, W. (2008a): The climate of the Esquinas rainforest. Pp. 59–62. In: Weissenhofer, A., Huber, W., Mayer, V., Pamperl, S., Weber, A. and Aubrecht, G. (eds.), Natural and Cultural History of the Golfo Dulce Region, Costa Rica. Stapfia 88. Biologiezentrum des Oberösterreichischen Landesmuseums, Linz.

Weissenhofer, A., Barquero, M., Huber, W., Mayer, V.E. and Umana, J.N. (2008b): The Biological Corridor Project in the Piedras Blancas National Park, Costa Rica. A project to preserve the biodiversity by reforestation and alternative culture, with support of the community La Gamba by new marketing strategies. Pp. 715–723.

In: Weissenhofer, A., Huber, W., Mayer, V., Pamperl, S., Weber, A. & Aubrecht, G. (eds.), Natural and Cultural History of the Golfo Dulce Region, Costa Rica. Stapfia 88. Biologiezentrum des Oberösterreichischen Landesmuseums, Linz.

Zahawi, R.A., Duran, G. and Kormann, U. (2015): Sixty-Seven Years of Land-Use Change in Southern Costa Rica. PLoS ONE 10(11): e0143554.

APPENDIX

Table A1. List of recorded species.

Common Name	Latin Name	Bird Family
American Pygmy Kingfisher	Chloroceryle aenea	Alcedinidae
American White Ibis	Eudocimus albus	Threskiornithidae
American Yellow Warbler	Setophaga petechia	Parulidae
Baltimore Oriole	Icterus galbula	Icteridae
Bananaquit	Coereba flaveola	Thraupidae
Bare-throated Tiger-Heron	Tigrisoma mexicanum	Ardeidae
Barn Swallow	Hirundo rustica	Hirundinidae
Bay-headed Tanager	Tangara gyrola	Thraupidae
Black Vulture	Coragyps atratus	Cathartidae
Black-bellied Whistling Duck	Dendrocygna autumnalis	Anatidae
Black-crowned Tityra	Tityra inquisitor	Tityridae
Black-mandibled Toucan	Ramphastos ambiguus	Ramphastidae
Black-striped Sparrow	Arremonops conirostris	Passerellidae
Blue Dacnis	Dacnis cayana	Thraupidae
Blue Ground-Dove	Claravis pretiosa	Columbidae
Blue-black Grassquit	Volatinia jacarina	Thraupidae
Blue-gray Tanager	Thraupis episcopus	Thraupidae
Blue-headed Parrot	Pionus menstruus	Psittacidae
Boat-billed Flycatcher	Megarynchus pitangua	Tyrannidae
Bright-rumped Attila	Attila spadiceus	Tyrannidae
Bronzed Cowbird	Molothrus aeneus	Icteridae
Buff-throated Saltator	Saltator maximus	Thraupidae
Cherrie's Tanager	Ramphocelus costaricensis	Thraupidae
Chestnut-sided Warbler	Setophaga pensylvanica	Parulidae
Clay-colored Thrush	Turdus grayi	Turdidae
Cocoa Woodcreeper	Xiphorhynchus susurrans	Furnariidae
Common Tody-Flycatcher	Todirostrum cinereum	Tyrannidae
Costa Rican Swift	Chaetura fumosa	Apodidae
Crested Caracara	Caracara plancus	Falconidae
Crimson-fronted Parakeet	Psittacara finschi	Psittacidae
Dusky-capped Flycatcher	Myiarchus tuberculifer	Tyrannidae
Eastern Meadowlark	Sturnella magna	Icteridae
Eastern Wood-Pewee	Contopus virens	Tyrannidae
Fiery-billed Aracari	Pteroglossus frantzii	Ramphastidae
Fork-tailed Flycatcher	Tyrannus savana	Tyrannidae
Gartered Trogon	Trogon caligatus	Trogonidae
Golden-hooded Tanager	Tangara larvata	Thraupidae
Golden-naped Woodpecker	Melanerpes chrysauchen	Picidae
Gray-breasted Crake	Laterallus exilis	Rallidae
Gray-breasted Martin	Progne chalybea	Hirundinidae
Gray-capped Flycatcher	Myiozetetes granadensis	Tyrannidae
Gray-chested Dove	Leptotila cassinii	Columbidae
Gray-headed Chachalaca	Ortalis cinereiceps	Cracidae
Gray-necked Wood-Rail	Aramides cajaneus	Rallidae
Great Blue Heron	Ardea herodias	Ardeidae
Great Crested Flycatcher	Myiarchus crinitus	Tyrannidae
Great Egret	Ardea alba	Ardeidae
Great Kiskadee	Pitangus sulphuratus	Tyrannidae
Great-tailed Grackle	Quiscalus mexicanus	Icteridae
Green Heron	Butorides virescens	Ardeidae
Green Honeycreeper	Chlorophanes spiza	Thraupidae
Green Ibis	Mesembrinibis cayennensis	Threskiornithidae
House Wren	Troglodytes aedon	Troglodytidae
Laughing Falcon	Herpetotheres cachinnans	Falconidae
Lesser Elaenia	Elaenia chiriquensis	Tyrannidae
Lineated Woodpecker	Dryocopus lineatus	Picidae
Little Blue Heron	Egretta caerulea	Ardeidae
Little Tinamou	Crypturellus soui	Tinamidae
Long-billed Hermit	Phaethornis longirostris	Trochilidae
Masked Tityra	Tityra semifasciata	Tityridae
Mealy Parrot	Amazona farinosa	Psittacidae
Muscovy Duck	Cairina moschata	Anatidae
Northern Jacana	Jacana spinosa	Jacanidae
Northern Waterthrush	Parkesia noveboracensis	Parulidae
Ochre-bellied Flycatcher	Mionectes oleagineus	Tyrannidae
Orange-chinned Parakeet	Brotogeris jugularis	Psittacidae
Osprey	Pandion haliaetus	Pandionidae
Pale-breasted Spinetail	Synallaxis albescens	Furnariidae
Pale-vented Pigeon	Patagioenas cayennensis	Columbidae
Palm Tanager	Thraupis palmarum	Thraupidae
Paltry Tyrannulet	Zimmerius vilissimus	Tyrannidae
Philadelphia Vireo	Vireo philadelphicus	Vireonidae
Plain Wren	Cantorchilus modestus	Troglodytidae
Plain-breasted Ground-Dove	Columbina minuta	Columbidae
Prothonotary Warbler	Protonotaria citrea	Parulidae
Purple Gallinule	Porphyrio martinicus	Rallidae
Red-breasted Blackbird	Leistes militaris	Icteridae
Red-capped Manakin	Ceratopipra mentalis	Pipridae
Red-crowned Woodpecker	Melanerpes rubricapillus	Picidae
Red-lored Parrot	Amazona autumnalis	Psittacidae
Red-rumped Woodpecker	Dryobates kirkii	Picidae
Ringed Kingfisher	Megaceryle torquata	Alcedinidae
Riverside Wren	Cantorchilus semibadius	Troglodytidae
Roadside Hawk	Rupornis magnirostris	Accipitridae
Rose-throated Becard	Pachyramphus aglaiae	Tityridae
Ruddy Ground-Dove	Columbina talpacoti	Columbidae
Ruddy Quail-Dove	Geotrygon montana	Columbidae
Ruddy-breasted Seedeater	Sporophila minuta	Thraupidae
Rufous-tailed Hummingbird	Amazilia tzacatl	Trochilidae
Rufous-winged Woodpecker	Piculus simplex	Picidae
Rusty-margined Flycatcher	Myiozetetes cayanensis	Tyrannidae
Scarlet Tanager	Piranga olivacea	Cardinalidae
Scarlet-rumped Cacique	Cacicus uropygialis	Icteridae
Scrub Greenlet	Hylophilus flavipes	Vireonidae
Short-billed Pigeon	Patagioenas nigrirostris	Columbidae
Smooth-billed Ani	Crotophaga ani	Cuculidae
Snowy Egret	Egretta thula	Ardeidae
Social Flycatcher	Myiozetetes similis	Tyrannidae
Solitary Sandpiper	Tringa solitaria	Scolopacidae
Southern Lapwing	Vanellus chilensis	Charadriidae
Southern Rough-winged Swallow	Stelgidopteryx ruficollis	Hirundinidae
Spot-crowned Euphonia	Euphonia imitans	Fringillidae
Spotted Sandpiper	Actitis macularius	Scolopacidae
Squirrel Cuckoo	Piaya cayana	Cuculidae
Streak-headed Woodcreeper	Lepidocolaptes souleyetii	Furnariidae
Streaked Flycatcher	Myiodynastes maculatus	Tyrannidae
Streaked Saltator	Saltator striatipectus	Thraupidae
Stripe-throated Hermit	Phaethornis striigularis	Trochilidae
Striped Cuckoo	Tapera naevia	Cuculidae
Summer Tanager	Piranga rubra	Cardinalidae
Swainson's Thrush	Catharus ustulatus	Turdidae
Tennessee Warbler	Leiothlypis peregrina	Parulidae
Thick-billed Euphonia	Euphonia laniirostris	Fringillidae
Thick-billed Seed-Finch	Sporophila funerea	Thraupidae
Tropical Kingbird	Tyrannus melancholicus	Tyrannidae
Tropical Mockingbird	Mimus gilvus	Mimidae
Turkey Vulture	Cathartes aura	Cathartidae
Variable Seedeater	Sporophila corvina	Thraupidae
Western Cattle Egret	Bubulcus ibis	Ardeidae
Western Wood-Pewee	Contopus sordidulus	Tyrannidae
White-throated Crake	Laterallus albigularis	Rallidae
White-tipped Dove	Leptotila verreauxi	Columbidae
Wilson's Snipe	Gallinago delicata	Scolopacidae
Wood Stork	Mycteria americana	Ciconiidae
Yellow-bellied Elaenia	Elaenia flavogaster	Tyrannidae
Yellow-bellied Flycatcher	Empidonax flaviventris	Tyrannidae
Yellow-billed Cuckoo	Coccyzus americanus	Cuculidae
Yellow-crowned Euphonia	Euphonia luteicapilla	Fringillidae
Yellow-headed Caracara	Milvago chimachima	Falconidae
Mistletoe Tyrannulet	Zimmerius parvus	Tyrannidae

Table A2. List of species only recorded in one of the three surveyed openland habitat types.

Open	Semi-open	Wetland
Black Vulture	American Pygmy Kingfisher	Gartered Trogon
Gray-headed Chachalaca	Bay-headed Tanager	Great Blue Heron
Green Ibis	Boat-billed Flycatcher	Muscovy Duck
Long-billed Hermit	Bright-rumped Attila	Scarlet-rumped Cacique
	Buff-throated Saltator	Wood Stork
	Chestnut-sided Warbler	
	Clay-colored Thrush	
	Cocoa Woodcreeper	
	Costa Rican Swift	
	Dusky-capped Flycatcher	
	Fiery-billed Aracari	
	Gray-breasted Crake	
	Great Crested Flycatcher	
	Lesser Elaenia	
	Little Tinamou	
	Masked Tityra	
	Mealy Parrot	
	Misteltoe Tyrannulet	
	Ochre-bellied Flycatcher	
	Osprey	
	Palm Tanager	
	Philadelphia Vireo	
	Purple Gallinule	
	Red-capped Manakin	
	Red-lored Parrot	
	Red-rumped Woodpecker	
	Riverside Wren	
	Ruddy Quail-Dove	
	Ruddy-breasted Seedeater	
	Rufous-winged Woodpecker	
	Scarlet Tanager	
	Scrub Greenlet	
	Solitary Sandpiper	
	Spot-crowned Euphonia	
	Squirrel Cuckoo	
	Streak-headed Woodcreeper	
	Streaked Flycatcher	
	Streaked Saltator	
	Stripe-throated Hermit	
	Striped Cuckoo	
	Swainson's Thrush	
	Thick-billed Euphonia	
	Yellow-billed Cuckoo	
	Yellow-crowned Euphonia	