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Effects of vegetation structure and landscape matrix on bird assemblages in secondary forests within the Biological Corridor La Gamba, Costa Rica

verfasst von / submitted by

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Abstract

Like in most other tropical regions, Costa Rica's biodiversity was threatened due to habitat loss by deforestation and resulting habitat fragmentation. While old-growth forest cover declined significantly, the cover of secondary forests expanded rapidly. As a result, secondary forest patches of various age, hence, different succession stage and, consequently, vegetation structure characterize today's landscape. The importance of secondary forest patches for birds can differ substantially. Therefore, we quantified to what extent understory bird species richness, species composition and the occurrence of vulnerable forest birds and Nearctic migrants in secondary forests within the Biological Corridor La Gamba (COBIGA) are influenced by vegetation structure and composition of the surrounding landscape matrix. For that reason, understory bird assemblages of 21 secondary forest patches and 9 old-growth forest sites as reference were assessed by mist-netting. Additionally, vegetation structure and landscape composition were evaluated for each study site. While vegetation structure and landscape matrix did not influence understory bird species richness, species composition changed substantially with progressing forest succession and increasing old-growth/old secondary forest cover as well as decreasing habitat diversity around the mist-netting sites. Understory bird assemblages were increasingly dominated by forest species as forest succession progresses, whereas Nearctic migrants were mainly found in younger secondary forests. Landscape matrix characteristics such as forest continuity and degree of habitat diversity played an important role for both, forest specialists and Nearctic migrants. Our results highlight the importance of secondary forest patches for bird assemblages within COBIGA as well as the necessity to protect old-growth forest for vulnerable forest bird species. Finally, there is evidence that forest specialists occupy secondary forest patches earlier than expected and that they may function as stepping stones for dispersal in the fragmented landscape.

Keywords: forest restoration, forest succession, bird conservation, forest specialists, Nearctic migrants, neotropics

German abstract in Appendix A

Eine deutsche Zusammenfassung befindet sich in Anhang A

Introduction

The "Golfo Dulce" region in the south of Costa Rica is known as an important biodiversity hotspot in Central America (Lobo & Bolaños 2005). Unfortunately, like in most other tropical regions, its biodiversity was threatened due to habitat loss by deforestation and resulting habitat fragmentation (Barnosky *et al.* 2011, Haddad *et al.* 2015). However, while old-growth forest cover declined significantly in practically all tropical regions, the cover of secondary forests expanded due to natural vegetational succession after abandonment of agricultural land and – to a minor extent – due to the implementation of reforestation measures (Aide *et al.* 2000, Rey Benayas 2000, Wright 2005). Therefore, secondary forest patches of various age and, hence, different succession stage and, consequently, vegetation structure are a prominent feature of modern tropical landscapes (Arroyo-Mora *et al.* 2005). Successional habitats can inhabit a valuable fraction of bird species (Blake & Loiselle 2001) and may alleviate habitat fragmentation by enhancing connectivity of forest patches (Stouffer & Bierregaard 1995a, b). Additionally, secondary forests can play an important role in climate change mitigation by biomass accumulation and carbon storage (Hall *et al.* 2022, Littleton *et al.* 2021, Chazdon *et al.* 2016).

For many resident bird species, especially forest specialists, secondary forests can potentially act as stepping stones for the dispersal through the fragmented landscape (Schulze *et al.* 2019) and probably function as a "safety net" for avian biodiversity in tropical rainforest ecosystems (Chazdon *et al.* 2009). Additionally, Nearctic migrants represent a significant fraction of the bird assemblages in Central American secondary forests during the northern winter (Hutto 1980, Martin 1985, Reid *et al.* 2008). Previous studies have shown that northern migrants are negatively affected by land cover change in their wintering grounds, but active forest restoration activities can mitigate such negative effects for migratory species (Lindell *et al*. 2012). Most northern migrants (e.g. new world warblers) are insectivorous during breading season but they change to a rather frugivorous diet in their wintering grounds, especially in the late dry season prior to migration (Blake & Loiselle 1992). Therefore, both resident and migratory species can be important seed dispersers, facilitating regrowth of secondary forests in early successional states (Galindo-González *et al.* 2000, Hutto 1980, Martin 1985, Medellín & Gaona 1999, Reid *et al.* 2008).

However, the importance of secondary forest patches for birds can differ substantially. Their structural complexity appears to be more important than their history (e.g. natural succession versus reforestation) (Schulze *et al.* 2019, Reid *et al.* 2012). Vegetation structure and food availability in secondary forests appear to act as environmental filters for understory birds (Betancurt-Grisales *et al.* 2021), consequently shaping functional and phylogenetic diversity (Batisteli *et al.* 2018, Acevedo-Charry & Aide 2019). Beside local habitat characteristics, landscape features such as the type of the surrounding non-forested matrix, forest cover and

forest fragment connectivity can affect species richness and species composition in secondary forest patches (Boyle & Sigel 2015, San-José *et al.* 2022, de Souza Leite *et al*. 2022, Reid *et al.* 2014).

In this study, we evaluate the importance of secondary forest patches for understory birds within the Biological Corridor La Gamba (COBGIA), Southwest Costa Rica. COBIGA is a project of the Tropical Research Station La Gamba that is intended to contribute to climate change mitigation by reducing the greenhouse gas CO_2 and preserve biodiversity of the Golfo Dulce region. Its aim is to connect the lowland rainforests of the Golfo Dulce region (e.g. Piedras Blancas National Park) with the adjacent mountain range Fila Cal by reforestation of agricultural fallow land with native tree species and protection of existing rainforest patches outside of the national park (Weissenhofer *et al.* 2008a).

We were particularly interested in identifying important vegetation and landscape features shaping understory bird assemblages of these secondary forest patches within the COBIGA. Therefore, we quantified to what extent species richness, species composition and the occurrence of vulnerable forest birds and Nearctic migrants in secondary forests are influenced by vegetation structure, forest age, and the composition of the surrounding landscape matrix.

We proposed the following hypothesis:

(1) Species richness is increasing rapidly, particularly in the early stages of succession, and species composition is increasingly dominated by forest specialists with progressing forest succession (Vargas-Daza *et al.* 2023, Acevedo-Charry & Aide 2019, Schulze *et al*. 2019).

(2) Since species richness and species composition in secondary forests might be affected by landscape matrix (San-José *et al.* 2022, Carrara *et al.* 2015, Reid *et al.* 2014) more fragmented secondary forest patches may show lower species richness (particularly of forest birds) than rather continuous forest patches (Carrara *et al.* 2015). Furthermore, species composition similarity to old-growth forest might increase with increasing forest cover in the surrounding of secondary forest patches (San-José *et al.* 2022, Reid *et al.* 2014).

(3) Forest specialists depend on vegetation structures such as large trees and dense canopy cover providing nesting and food resources and shelter against predators (Blake & Loiselle 2001, Schulze *et al.* 2019).

(4) Secondary forests may be characterized by higher relative abundances of northern migrants than old-growth forest sites (Hutto 1980, Martin 1985, Reid *et al.* 2008). In contrast to resident forest birds, for these more mobile migratory species only vegetation structures but not landscape composition of secondary forests represent important explanatory variables (Harris and Reed 2002).

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The results of this study were expected to shed light on the importance of the conservation of secondary forests and their management from an ornithological perspective, especially in secondary forests created by reforestation measures, such as in the La Gamba Biological Corridor.

Methods

Study area and study sites

The study was conducted in secondary and old-growth forests in vicinity of the Tropical Research Station La Gamba (N 8.7010° W -83.2015°) and its field station Finca Alexis (N 8.7648° W -83.1638°), located in the Golfo Dulce region of southwestern Costa Rica between the Piedras Blancas National Park and the Fila Gamba, a range of hills that separates the La Gamba valley and the Gulf of Golfito (Province Puntarenas). About 330 bird species, including several endemics, are recorded from the area (Tebb 2008).

All study sites are located in the lowlands between 26 m and 581 m above sea level. The selected sites cover the majority of secondary forests sites within the COBIGA that should provide a link between

Figure 1. Map indicating the 30 selected study sites and land cover in the vicinity of Tropical Research Station La Gamba and Finca Alexis. 14 young secondary forests (YSF), 7 old secondary forests (OSF) and 9 old-growth forests (OGF) were sampled.

lowland forests of the Golfo Dulce region and the inland mountain range Fila Cal (Weissenhofer *et al.* 2008a). A total of 21 different sites with secondary forests assigned to two different age classes were sampled: 14 young secondary forests (YSF, < 25 years, low canopy height) and 7 old secondary forests (OSF, > 25 years old, canopy higher than in YSF, more comparable to old-growth forests). Age of the forest patches was identified by date of reforestation if available or expertise of locals (Appendix B Table B1). Additionally, 9 old-growth forest sites were sampled as reference (Figure 1). Coordinates of sample sites were recorded by using a GPS device (GPSMAP 64s, Garmin). All study sites are at least about 200 m apart from each other.

Bird sampling

The assessment of understory bird assemblages in secondary and old-growth forests took place from 2 November 2021 – 22 January 2022 and 8 November 2022 – 13 January 2023. Data of the latter sampling period were provided by Kranl & Meisenzahl (unpublished). At each study site, birds were mist-netted for 1.5 days in both sampling periods with six nets (each 12 m long and 2.5 m high) from 05:30 am until 03:00 pm on the first day and from 05:30 am to 11:00 am on the second day, aiming to achieve a total of 15 trapping hours per site per year. However, in case of heavy rain or intense insolation, nets were closed due to the increased mortality risk for the birds.

During mist-netting, nets were controlled every 30 minutes. Trapped birds were identified (referring to Garrigues & Dean 2014) and, to avoid pseudoreplications, marked by aluminum or color rings. Only hummingbirds were marked by clipping one of the outer tail feathers. In addition, morphological measurements such as tarsus length, wing length and body weight were taken before the birds were released. In the second sampling period (Nov. 2022 – Jan. 2023) three study sites (VB01, WF1, FAl02) could not be accessed due to landslides and changes in river courses.

Assessment of vegetation and landscape characteristics

Canopy closure, structural complexity and the presence of large trees seem to be important factors for species richness and species composition in tropical secondary forests (Schulze *et al.* 2019, Blake & Loiselle 2001, Betancurt-Grisales *et al.* 2021, Acevedo Charry & Aide 2019). Therefore, the following eight explanatory variables were measured at each mist-netting site (Table 1):

(1) Understory density was quantified by using the mean of 10 random distance measures of a laser-based distance measuring device (DISTO^{TM} D2, Leica) orientated horizontally and right-angled to the mist-nets on each site of the mist-net, resulting in 10 distance measurements x 2 mist-net sites x 6 mist-nets = total of 120 distances. Lower mean values indicate a higher understory vegetation density.

(2) Canopy height was measured for each study site as the mean of 6 estimates of the height of the closed canopy above the center of each mist net by using a range finder (LASER 800 6 x 216, Nikon).

(3) Canopy cover was determined by photographs of the canopy, taken at the center of each mist net, that were converted into black & white pictures with the freeware program ImageJ, Version 1.53q (Wayne Rasband). Canopy cover was expressed as mean percentage of black pixels.

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(4) Standard deviation from the mean value of the six canopy cover measurements was then used as measure of canopy heterogeneity.

(5) Tree density was quantified by calculating the sum of the tree basal area (tba) for each study site. Therefore, the perimeter at breast height of all trees with a diameter at breast height > 10 cm within a buffer of 5 m towards both sites of the mist nets were measured (Schulze *et al.* 2019, Guariguata *et al.* 1997, Guariguata & Ostertag 2001).

Percentage of forest cover and landscape matrix composition can be highly relevant for understory bird assemblages (San-José *et al.* 2022, Carrara *et al.* 2015). Therefore, (6) percentage of young secondary forest (YSF) and (7) percentage of old secondary forest (OSF) and old-growth forest (OGF) in a buffer of 200 m around the center of study sites were calculated. Therefore, a land cover map (modified after Gallmetzer & Schulze 2015, Weissenhofer *et al.* 2008b, Figure 1) was edited in QGIS (Version 3.22.14) and percentages were calculated by the "buffer" and "statistics by categories" function.

(8) To determine habitat diversity in the surrounding of each study site the Shannon-Index (see formula below), considering 10 different habitat types according to an available land cover map (Weissenhofer *et al.* 2008b, modified after Gallmetzer & Schulze 2015; Figure 1) within the 200 m buffer around the study sites was calculated. Accounted habitat types were old secondary forest & old-growth forest, young secondary forest, shrubland, living fences, oil palm plantations, open land & open cultivated land, water bodies & gravel banks, settlements & gardens and roads.

$$Shannon\ Index = -\sum Pi * \ln Pi \qquad\qquad Pi = \text{percentage of habitat}$$

Table 1. Measured environmental predictors to describe vegetation structure and landscape composition of each study site. Canopy heterogeneity is described as the standard deviation of the mean canopy cover and habitat diversity is expressed as the Shannon index of surrounding habitat types. SD = Standard deviation, Min = minimum value, Max = maximum value, YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest.

Environmental predictor	Mean	SD	Min	Max
Understory density [m]	3.4	0.7	2.2	4.6
Canopy height [m]	22.7	7.0	4.1	38.8
Canopy cover [%]	89.6	7.2	55.7	94.7
Canopy heterogeneity	3.9	5.0	0.6	28.5
Basal tree area [cm²]	29402.8	19975.1	509.2	95424.2
Percentage YSF [%]	22.5	24.1	0.0	87.2
Percentage OSF & OGF [%]	45.6	39.5	0.0	100.0
Habitat diversity	0.9	0.5	0.0	1.6

Data analysis

Unless otherwise stated, all analyzes and graphs were carried out in R Statistical Software version 4.3.1 (R Core Team 2022).

Abundance and species richness of birds

Numbers of trapped bird individuals differed substantially between study sites (38 – 284 individuals). To account for substantial differences in sample size, species numbers were estimated for a shared sample size of 76 individuals by rarefaction (for sites with > 76 individuals) or extrapolation (< 76 individuals) using iNEXT Online (Chao *et al.* 2014, Hsieh *et al.* 2016). As basis for the sample size adjustment twice the smallest number of individuals that has been occurred, meaning 2 x 38 = 76 individuals, was used. All subsequent analyses dealing with species numbers were performed by using these species numbers estimated for each study site. Since we accounted for differences in sample size using this rarefaction/extrapolation approach, we also included the study sites VB01 (65 individuals), WF1 (99 individuals) and FAl02 (72 individuals), although they were only sampled in the first time mist-netting period.

Recaptures of the same sampling period were not included in the analyses whereas recaptures from previous study years and from other study sites were considered. Additionally, a total of 13 individuals of the genera *Euphonia* and *Manacus*, which could not be identified to species level, were not included in further analyses.

To test for differences in the number of mist-netted birds and the number of species estimated for a sample size of 76 individuals, one-way ANOVAs and subsequent Tukey's HSD tests were calculated.

Vegetation structure

To approximate normal distribution of environmental predictors, data transformation had to be carried out. Basal tree area was square root transformed whereas canopy cover, canopy heterogeneity (SD of canopy cover), percentage of YSF and percentage of OSF & OGF were normalized by arcsine transformation. All other data didn't show any significant deviation from a normal distribution.

To analyze the change of environmental predictors with increasing forest age Spearman's correlations were performed, because requirement of data normality was not completely fulfilled, even after transformation. As the basal tree area, canopy cover and canopy heterogeneity did not meet the requirements for normality of data and homogeneity of variance for one-way ANOVAs, Kruskal-Wallis rank sum tests were calculated to test for differences in vegetation variables between forest types. If significant effects were indicated, pairwise Wilcoxon tests were subsequently calculated.

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Due to the strong multicollinearity among environmental predictors (Figure 4) and the fact that 8 explanatory variables for a relatively small number of spatial replicates (30 mist-netting sites) can lead to overfitting, a Principal Component Analysis (PCA) and Varimax rotation with Kaiser normalization (Kaiser 1958) was applied (Table 2). Prior to that, all predictors were z-standardized. Standardization and PCA were performed in IBM SPSS Statistics version 27.0 (IBM Corporation). For the first three principal components (PC1 – 3), which show an Eigen-value greater than one, rotated loading factors were calculated (Table 2). Then, the scores of the first three principal components for each study site were extracted and used for the analysis of the effect of vegetation structure and landscape composition on species richness, species composition and the percentage of forest specialist as well as northern migrants.

Effects of habitat and landscape variables on species richness and species composition

A multiple linear regression model was calculated to assess effects of PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density) as environmental predictors on species richness using the "lm()" function. For comparing species composition between sampling sites, a non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities was computed by using the "metaMDS" function in the "vegan" package version 2.6-4 (Oksanen *et al.* 2022). To test for differences in species composition between forest types a one-way analysis of similarities (ANOSIM) based on 999 permutations and Bray-Curtis dissimilarities was performed by using the "anosim" function in the "vegan" package version 2.6-4 (Oksanen *et al.* 2022). A post-hoc test for a pairwise comparison was carried out by using the function "pairwise.adonis2" in the "pairwiseAdonis" package version 0.4 (Martinez Arbizu 2020) including *p*-value adjustment by Bonferroni correction. Additionally, to analyze the impact of PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density) on species composition of study sites a permutation test based on 999 permutations by using the "envfit" function in the "vegan" package version 2.6-4 (Oksanen *et al.* 2022) was calculated.

Effects of habitat and landscape variables on forest specialist & northern migrants

To assess the impact of PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density) as environmental predictors on the percentage of forest specialists and northern migrants, again multiple linear regression models were calculated. In advance, relative species richness and abundance of both bird groups (in %) were calculated for each mist-netting site. Species were classified as forest specialists and northern migrants referring to Garrigues & Dean (2014) and Billerman *et al.* (2022) (see Appendix B Table B1). To test for differences in the proportion of forest specialists between forest types one-way ANOVAs were computed. Subsequently, for pairwise comparisons between forest types Tukey's HSD tests were applied. Data fulfilled the requirements of normality and variance homogeneity. Percentages of northern migrants did not show variance homogeneity. Therefore, Kruskal-

Wallis rank sum tests and pairwise Wilcoxon rank sum tests were calculated to assess the differences in the proportion of northern migrants between forest types. Bonferroni correction was used for p-value adjustment.

Results

Over the two sampling periods a total of 3578 birds, belonging to 134 species were trapped (Appendix B Table B1). Of these, 437 individuals (12% of total) were recaptured. Bird abundance and species richness differed between study sites (n = 30) and ranged from 38 to 284 individuals (Figure 2a,) and 21 to 41 species (estimated for shared sample size of 76 trapped individuals; Figure 2b). Abundances of understory birds were higher in young secondary forest (one-way ANOVA: $F_{(2, 27)}$ = 5.138, p = 0.0129), but only differed significantly from old-growth forest (Tukey's HSD test: p = 0.0113), but not from old secondary forest (p = 0.1928). In contrast, estimated species richness did not vary substantially between forest types (one-way ANOVA: $F_{(2, 27)}$ = 0.011, p = 0.250).
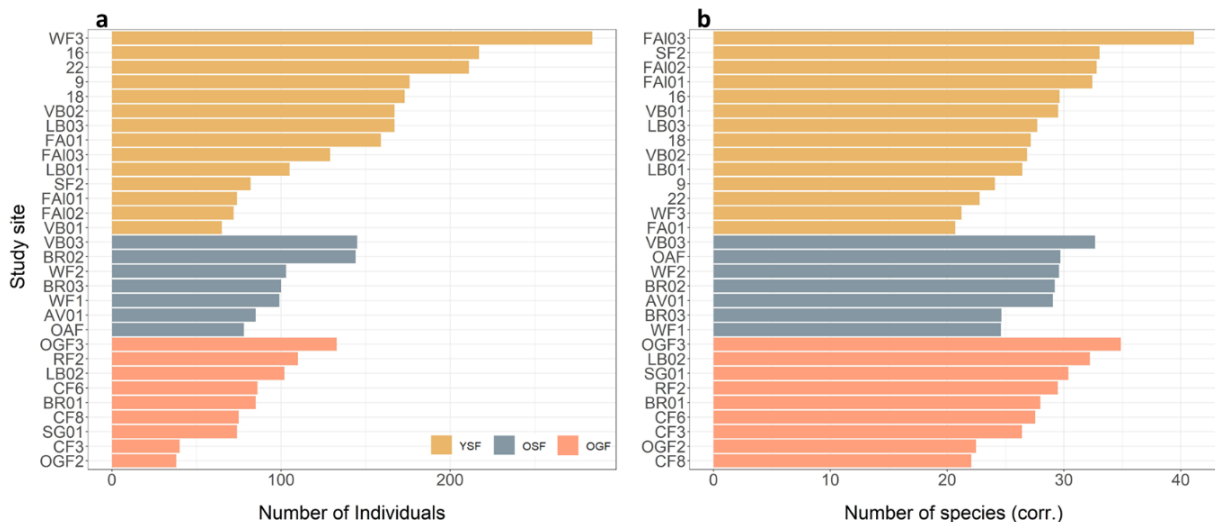
Figure 2. (a) Abundance and (b) species richness for each study site. Numbers of species are estimated for a common shared sample size of 76 individuals. Colours indicate forest type. YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest.

Vegetation structure and landscape composition

Spearman's rank correlations between vegetation structure and forest age of sampled young and old secondary forests (n = 21) showed a significant increase of canopy height (r_s = 0.560, p = 0.008) and basal tree area (r_s = 0.604, p = 0.004) with forest age, whereas canopy heterogeneity (SD canopy cover) decreased significantly with forest maturity (r_s = -0,515, p = 0.017). Understory density (r_s = 0.217, p = 0.345) and canopy cover (r_s = 0,377, p = 0.092) did not change significantly with forest age (Figure 3). While understory density was similar in all forest types (Kruskal-Wallis rank sum test: $H_{(2)}$ = 1.96, p = 0.375), all other vegetation variables differed significantly between forest types (canopy height: $H_{(2)}$ = 18.24, p < 0.001; canopy cover: $H_{(2)}$ = 8.90, p = 0.012; basal tree area: $H_{(2)}$ = 13.70, p = 0.001; canopy

heterogeneity: H$_{(2)}$ = 9.35, p = 0.009). Pairwise tests indicate that these results are predominately due to differences in vegetation structure between young secondary forest and old secondary forest (pairwise Wilcoxon tests; canopy height: p = 0.022; basal tree area: p = 0.007; canopy cover: p = 0.157; canopy heterogeneity: p = 0.037) and old-growth forest sites (canopy height: p < 0.001; canopy cover: p = 0.022; basal tree area: p = 0.003; canopy heterogeneity: p = 0.032), respectively. In contrast, no significant differences between old secondary and old-growth forest sites could be detected (canopy height: p = 0.165; all other variables: p = 1.000). Canopy height, basal tree area and canopy cover increased from young secondary forest towards old-growth forests, canopy heterogeneity declined (Figure 3).
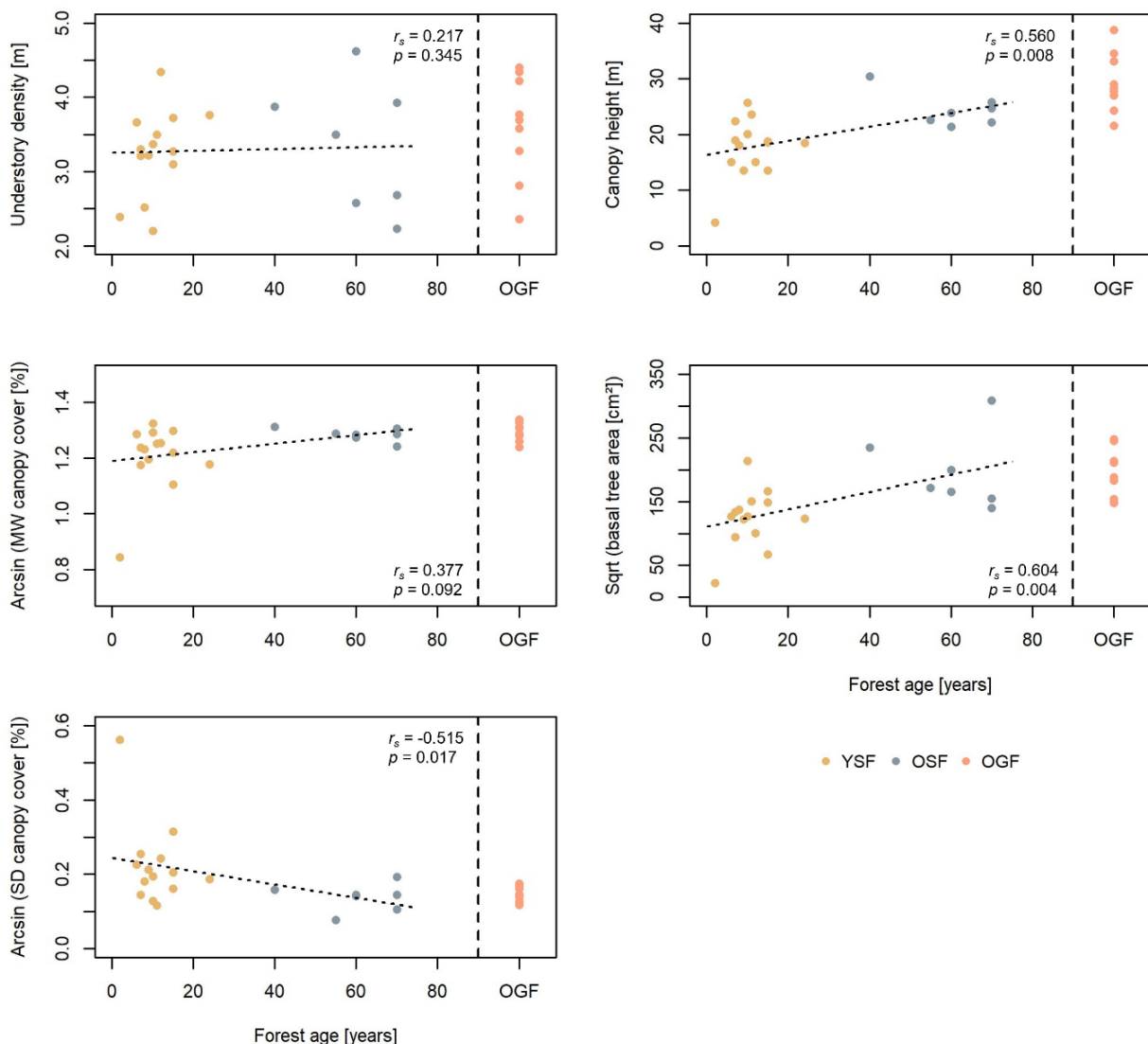
Figure 3. Relationships of vegetation structure and forest age of secondary forests in comparison to old-growth forest. Results of Spearman's rank correlations are shown for relationships between all vegetation variables and age of secondary forests (n = 21). YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest. Black dotted lines imply linear trend lines.

Due to the strong multicollinearity among of vegetation structure and landscape composition variables (Figure 4), a Principal Component Analyses (PCA) was applied. The first three Principal Components (PC1, PC2, PC3) do explain 85.5% of variance and were used for further analysis. PC1 is mainly loaded by variables explaining vegetation structure, PC2 is

primarily loaded by landscape composition variables and PC3 is almost merely loaded by understory density (Table 2). Hence, it allows to assume that PC1 indicates forest structure, PC2 describes landscape composition and PC3 represents understory density.
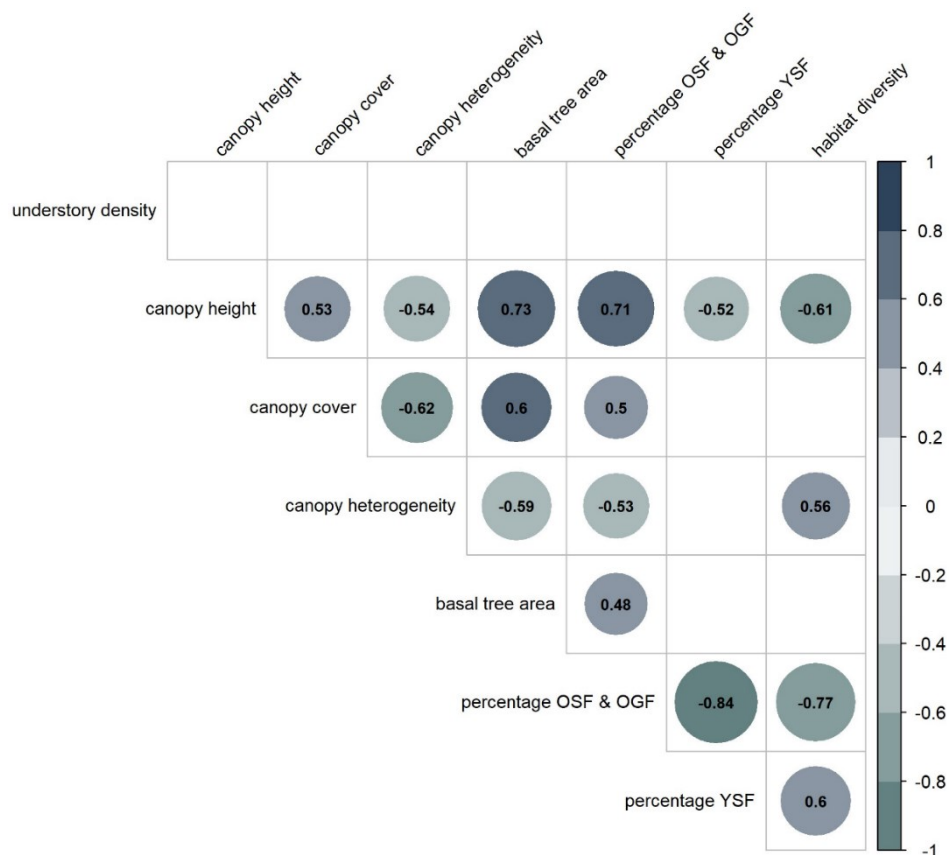
Figure 4. Correlation matrix of all environmental variables. Values represent correlation coefficients of calculated Spearman's rank correlations. Only significant ($p \leq 0.05$) correlations are shown (n = 30).

Table 2. Loading factors of environmental predictors on Principal Components 1, 2 and 3 computed by a Principal Component Analysis and Varimax rotation with Kaiser-Normalization. Colours indicate associations of predictors and principal components (factor loading > |0.6| implying PC1 ~ vegetation structure, PC2 ~ landscape composition and PC3 ~ understory density). YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest.

Predictors	Principal Component		
	1	2	3
Canopy height	0.675	0.571	-0.030
Canopy cover	0.911	0.124	0.248
Canopy heterogeneity	-0.902	-0.166	-0.203
Basal tree area	0.783	0.262	-0.344
Percentage OSF & OGF	0.323	0.912	0.081
Percentage YSF	-0.052	-0.886	-0.112
Habitat diversity	-0.223	-0.820	-0.014
Understory density	0.109	0.126	0.945
Eigenvalue	2.881	2.744	1.134
% variance explained	36.008	34.296	14.171
% cumulative variance explained	36.008	70.304	84.475

Species richness

A multiple linear regression model to analyze the effect of PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density) on understory species richness of study sites showed no statistically significant result ($F_{(3, 26)}$ = 1.419, p = 0.260, R^2 = 0.042). The differences of understory bird species richness among study sites cannot be explained by PC1 (~ forest structure, *Estimate* = 0.253, p = 0.759) or PC2 (~ landscape composition, *Estimate* = -0.355, p = 0.667, Figure 5, 6). The strongest effect on species richness shows PC3 (~ understory density, *Estimate* = 1.625, p = 0.057), hence understory species richness of the sampled sites probably tends to increase with decreasing understory density (Figure 5, 6).

Figure 5. Estimates (± 95% confidence interval) of predictors computed by a multiple regression model analysing the effect of PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density) on understory species richness of the study sites (n = 30). PC = Principal Component.
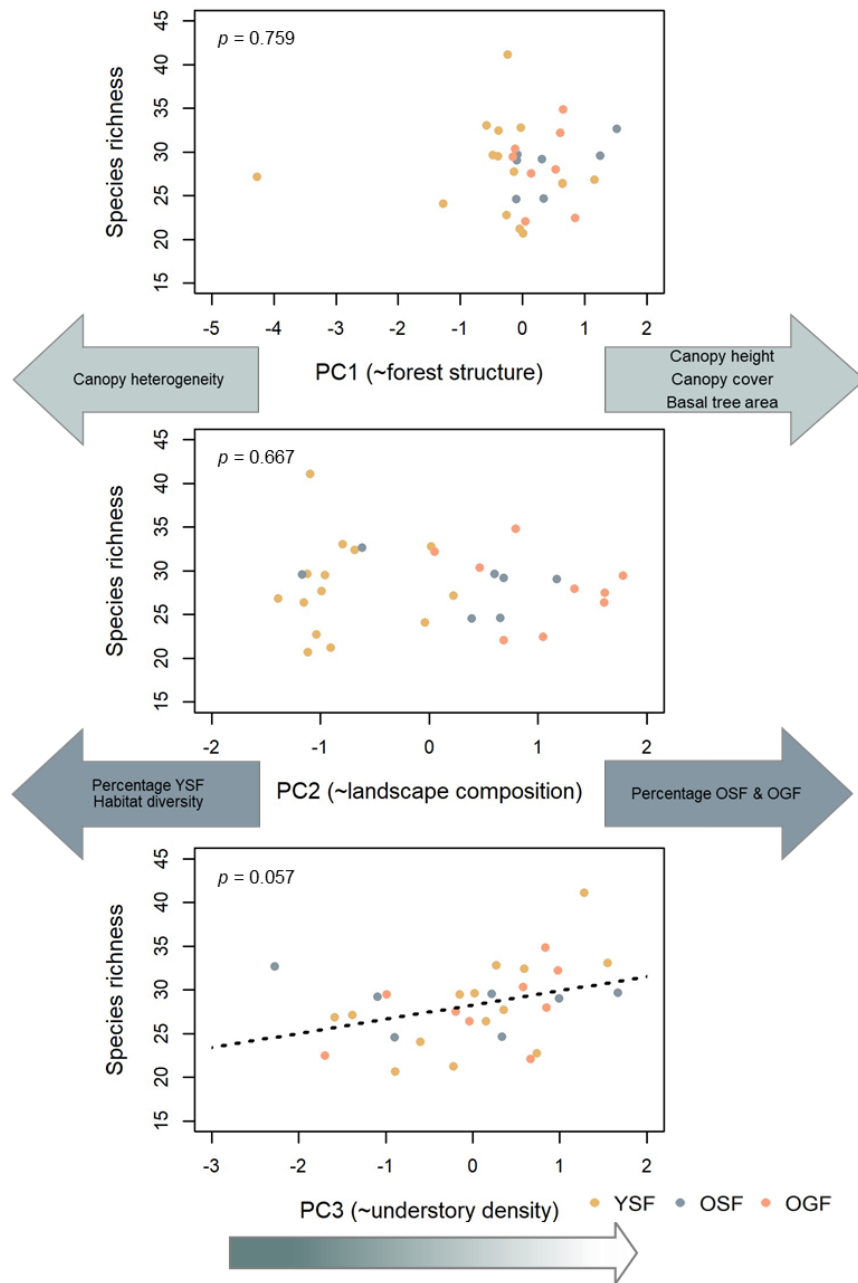
Figure 6. Relationships between understory species richness and PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density). The *p*-values were calculated by a multiple regression model (n = 30). Dotted line in the lower graph represents linear regression line visualizing the weak relationship between species richness and understorey density. YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest. PC = Principal Component. Directions of arrows below the graphs indicate important factor loadings of habitat variables on the respective PCs (note that a positive factor loading of understory density on PC3 indicates a decreasing understory density!).

Species composition

A NMDS-Ordination based on Bray-Curtis dissimilarities shows fundamental differences in species composition between the three forest types (n = 30 study sites; Figure 7). The distribution of study sites in respect to their species composition clearly shows that the three forest types segregate roughly into three distinct clusters (Figure 7). Differences in species composition between forest types are statistically confirmed by one-way ANOSIM (*R* = 0.318, *p* = 0.002). Pairwise comparisons reveal statistically significant differences in species

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composition between all pairwise combinations of forest types (YSF vs. OSF: R^2 = 0.157, p = 0.005; YSF vs. OGF: R^2 = 0.222, p = 0.001; OSF vs. OGF: R^2 = 0.127, p = 0.019). Additionally, variance of species composition is rather high in YSF study sites and decline with forest age (Figure 7). This allows to assume that species turnover is higher in YSF and species composition becomes more stable in OSF and OGF study sites.

A permutation test analyzing the impact of environmental predictors (PC1, PC2, PC3) on species composition of study sites implies that differences in species composition are significantly driven by PC1 (~ forest structure, R^2 = 0.338, p = 0.006) and PC2 (~ landscape composition, R^2 = 0.470, p = 0.001, Figure 7). Hence, species composition tends to change with increasing canopy height, canopy cover, basal tree area and decreasing canopy heterogeneity on the one hand, and increasing amount of OSF and OGF around the study site and declining habitat diversity on the other hand. PC3 (~ understory density, R^2 = 0.144, p = 0.131, Figure 7) does not show a significant impact on changes in species composition.
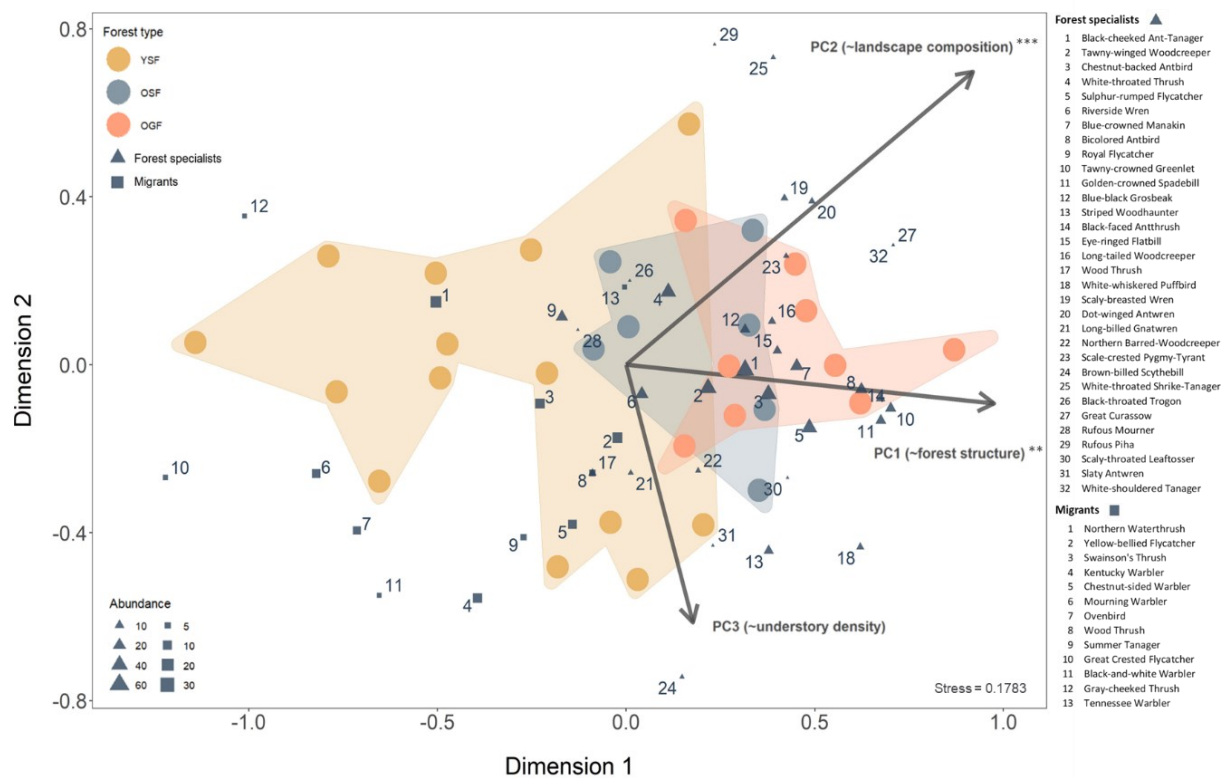
Figure 7. NMDS-Ordination based on Bray-Curtis dissimilarities in species composition between study sites. Grey arrows explain changes in species composition caused by PC1 (~ forest structure), PC2 (~ landscape composition) and PC 3 (~ understory density). Triangles and squares show forest specialists and Nearctic migrants, respectively. YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest. Indicated p values were calculated by a permutation test based on 999 permutations (** = p < 0.01, *** = p < 0.001). PC = Principal Component.

Forest specialists

Of the 134 bird species, 32 species (509 individuals) were identified as forest specialists (Figure 8). Forest specialists were captured on each study site, ranging from 2.6% to 48.3% of species and 0.6% to 38.8% of individuals per site. A total of 16 species were found in all forest types (YSF, OSF, OGF), 4 species only in OSF and OGF, 4 species only in YSF and OGF, 1 species only in YSF and OGF, 2 species only in OSF and 5 species only in OGF (Figure 8).
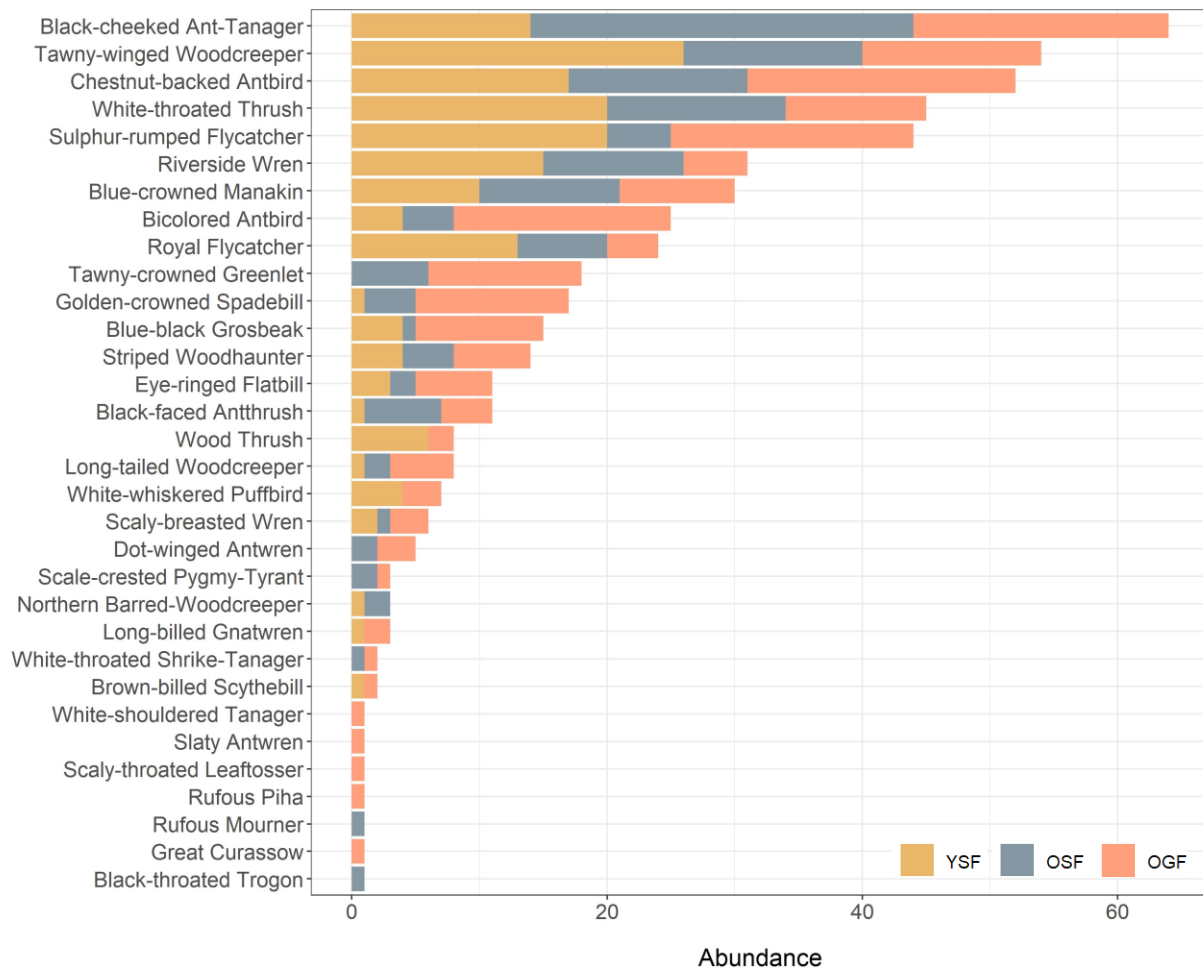
Figure 8. Abundance of forest specialists. YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest.

A multiple linear regression model to analyse the relationships between percentage of forest specialists and environmental predictors revealed highly significant results (species: $F_{(3, 26)}$ = 22.42, $p < 0.001$, R^2 = 0.689; individuals: $F_{(3, 26)}$ = 15.68, $p < 0.001$, R^2 = 0.603). The percentage of forest specialists (species and individuals) increases significantly with increasing PC1 (~ forest structure; species: *Estimate* = 7.449, $p < 0.001$; individuals: *Estimate* = 4.830, $p < 0.001$) and PC2 (~ landscape composition; species: *Estimate* = 8.976, $p < 0.001$; individuals: *Estimate* = 5.808, $p < 0.001$), with the latter showing the strongest relationship (Figure 9, 10). Hence the amount of forest specialists of the study sites tends to increase with

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increasing canopy height, canopy cover, basal tree area and decreasing canopy heterogeneity on one hand and increasing amount of OSF and OGF around the study site and declining habitat diversity on the other hand. In addition, the abundance of forest specialists is also significantly affected by PC3 (~ understory density; *Estimate* = 3.978, *p* = 0.004). Study sites with less dense understory seems to inhabit higher abundances of forest specialists (Figure 9, 10).
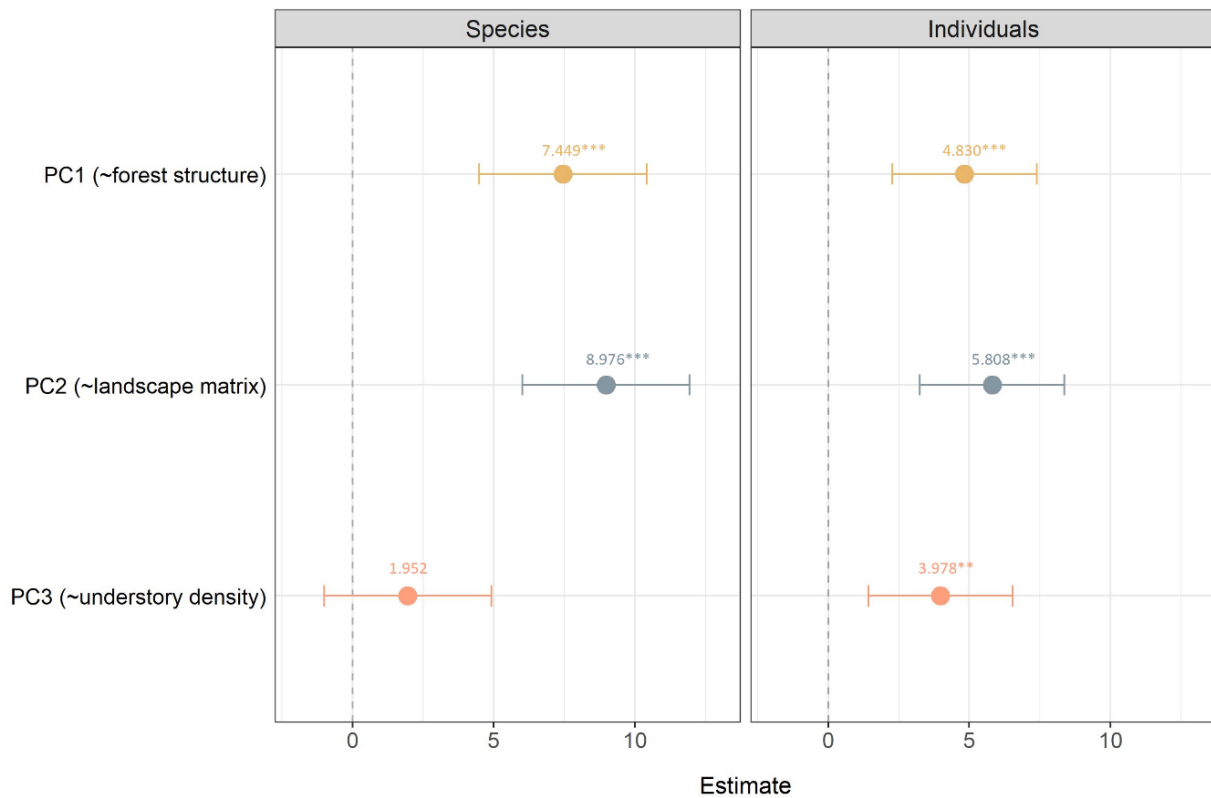
Figure 9. Estimates (± 95% Confidence Interval) of predictors computed by a multiple regression model analysing the effect of PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density) on percentage of forest specialists (species and individuals: n = 30 mist-netting sites). Indicated *p*-values are calculated by F-statistics (** = *p* < 0.01, *** = *p* < 0.001). PC = Principal Component.
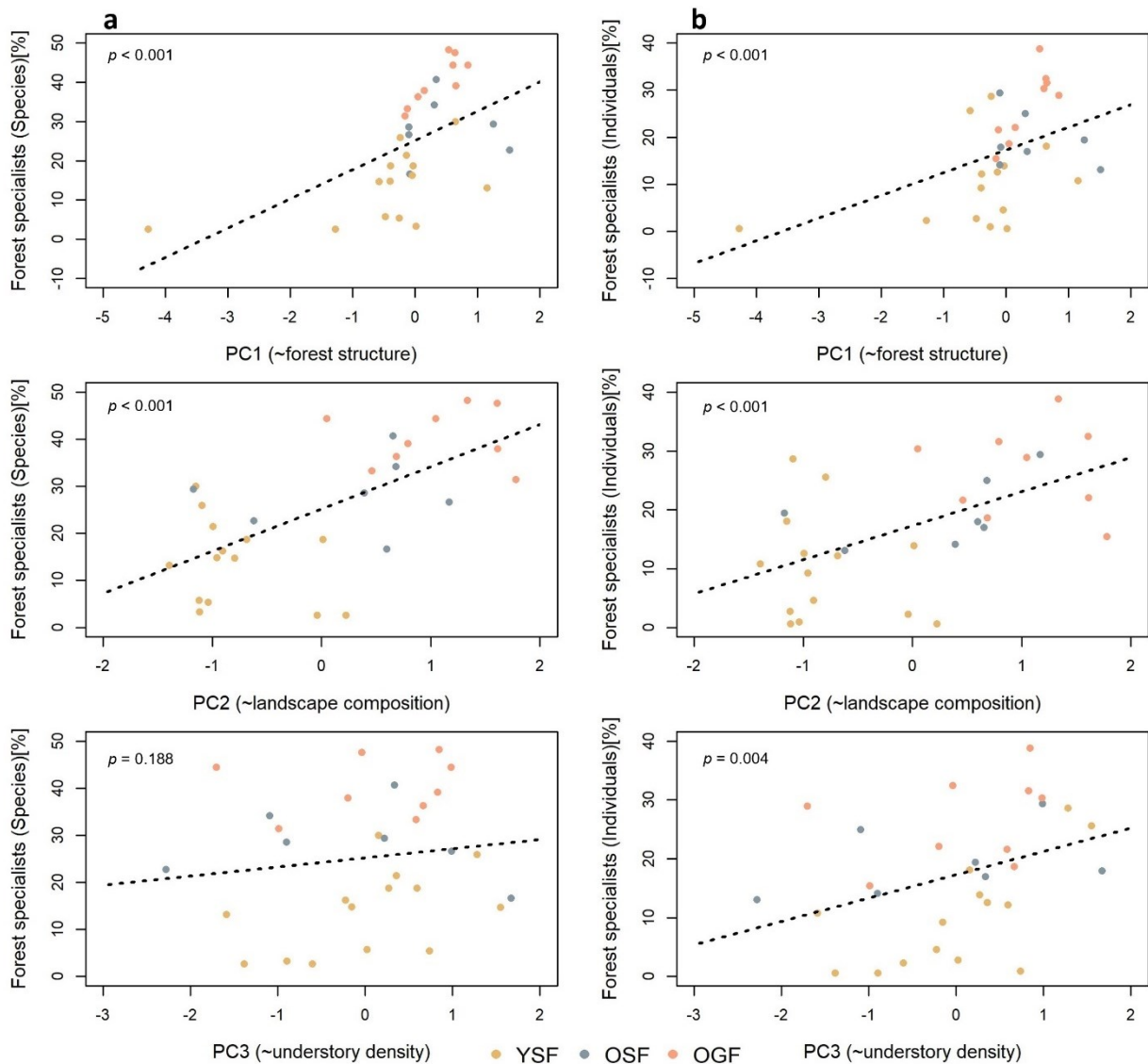
Figure 10. Relationships between percentage of forest specialists (a: species; b: individuals) and PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density). The *p*-values are calculated by a multiple regression model (n = 30 mist-netting sites). Dotted lines represent linear regression lines. YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest. PC = Principal Component.

A one-way ANOVA showed highly significant differences in percentage of forest specialists in YSF, OSF and OGF (species: $F_{(2, 27)}$ = 31.69, $p < 0.001$; individuals: $F_{(2, 27)}$ = 11.77, $p < 0.001$; Figure 11). Tukey's HSD tests indicate that the percentage of forest species was significantly higher in OGF (n = 9, median = 39.1%, IQR = 8.1%) and OSF (n = 7, median = 28.6%, IQR = 7.1%) than in YSF (n = 14, median = 13.8%, IQR = 13.3%; YSF vs. OSF: $p = 0.001$; YSF vs. OGF: $p < 0.001$; OSF vs. OGF: $p = 0.016$; Figure 11). The abundance of forest specialists only differs significantly between YSF and OGF (YSF vs. OSF: $p = 0.050$; YSF vs. OGF: $p < 0.001$; OSF vs. OGF: $p = 0.194$). OGF study sites (median = 28.9%, IQR = 10.0%) seem to have significant higher abundances of forest specialists than YSF sites (median = 10.0%, IQR = 11.2%; Figure 11).
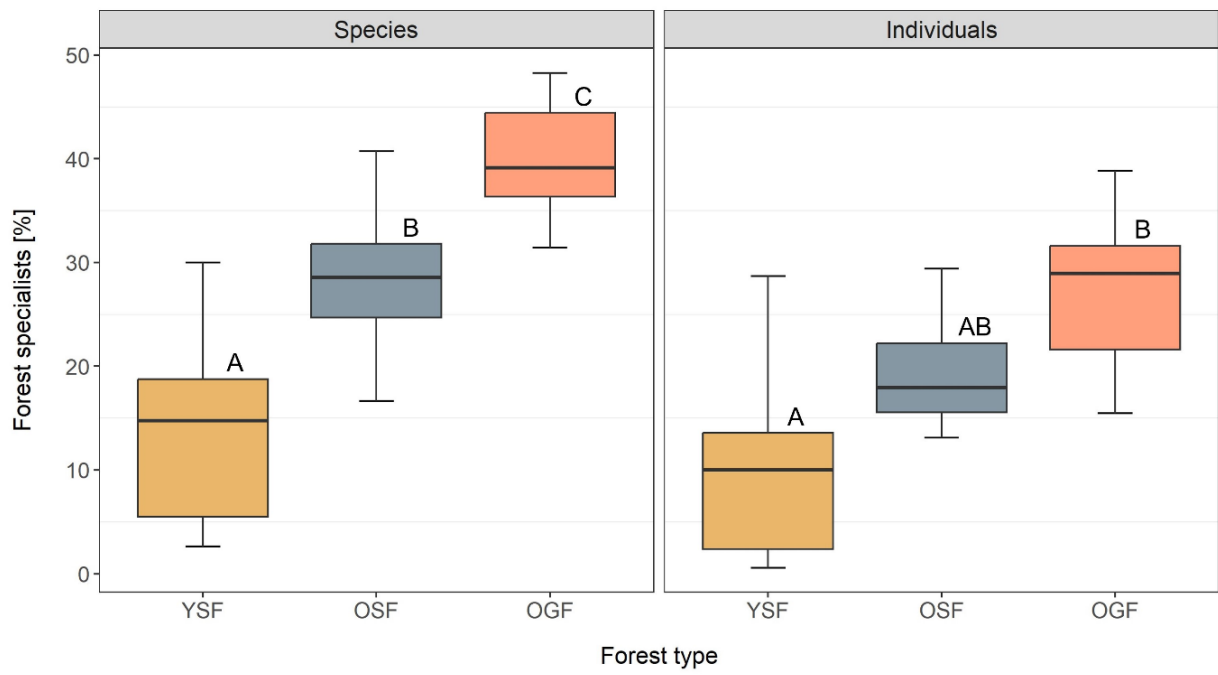
Figure 11. Median percentage of forest specialists (species and individuals) in YSF (young secondary forest, n = 14), OSF (old secondary forest, n = 7) and OGF (old-growth forest, n = 9). Boxes represent the interquartile range, whiskers display 1.5 x interquartile range. Different capital letters indicate significant differences between forest types (Tukey's HSD tests).

Nearctic migrants

Twenty species (205 individuals) of 134 species in total have been identified as Nearctic migrants (Figure 12). Nearctic migrants were captured at each study site, except BR01 (OGF), BR03 (OSF), FAI02 (YSF), OGF2 (OGF), SG01 (OGF), with up to 33.3% of species and 20.7% of individuals per site.
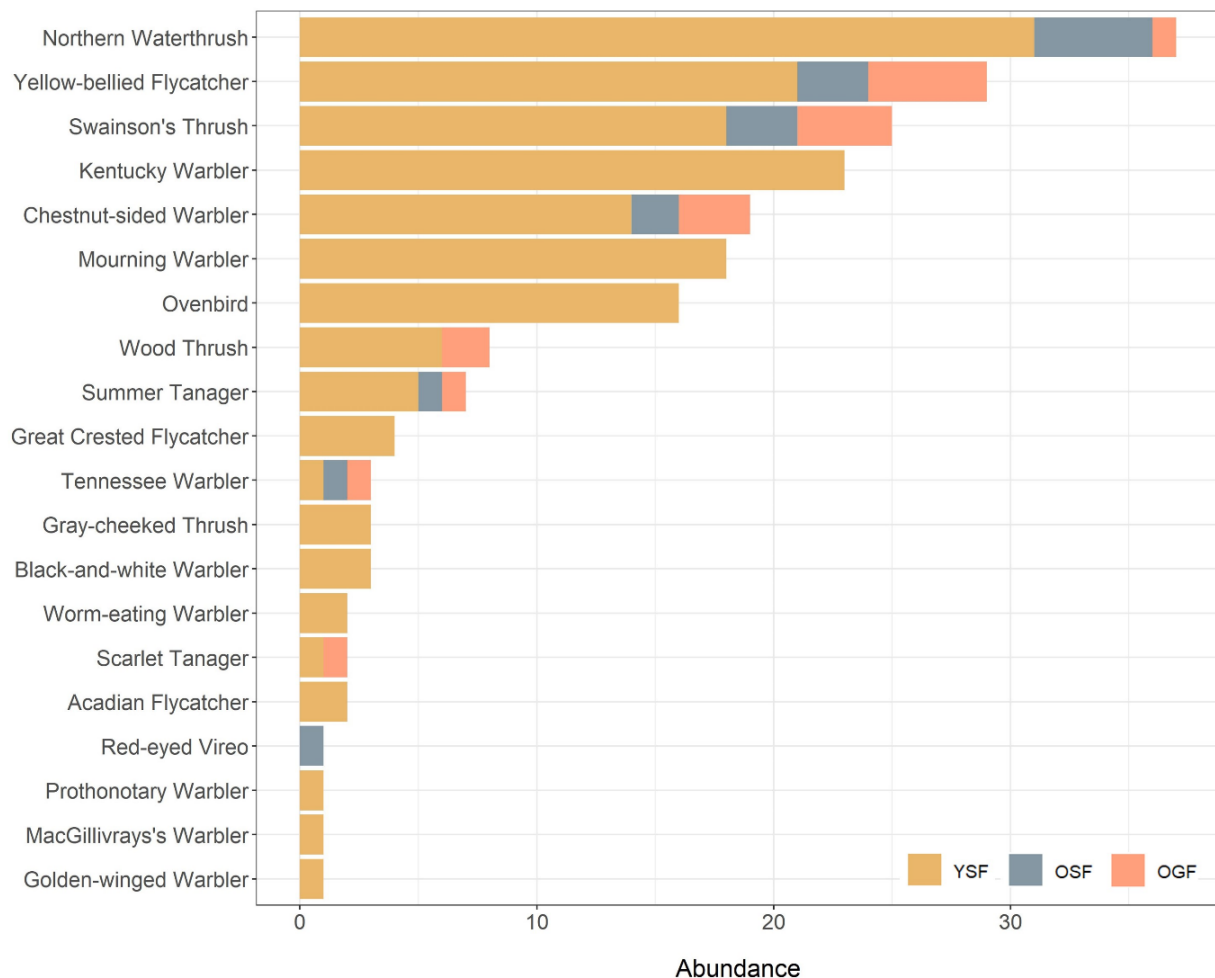
Figure 12. Abundance of Nearctic migratory species in the three different forest types. YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest.

A multiple linear regression model to analyse the effect of environmental predictors on the percentage of Nearctic migrants of the study sites (n = 30) revealed significant results (species: $F_{(3, 26)}$ = 5.59, p = 0.004, R^2 = 0.322; individuals: $F_{(3, 26)}$ = 5.21, p = 0.006, R^2 = 0.303; Figure 13, 14). The percentage of Nearctic migrants decreased significantly with increasing PC1 (~ forest structure; species: *Estimate* = -2.986, p = 0.027; individuals: *Estimate* = -1.640, p = 0.050) and PC2 (~ landscape composition; species: *Estimate* = -4.269, p = 0.003; individuals: *Estimate* = -2.557, p = 0.004), with the latter showing the strongest relationship (Figure 13, 14). Hence, the relative abundance of Nearctic migrants in the understory of the study sites seemed to increase with decreasing canopy height, canopy cover, basal tree area and increasing canopy heterogeneity on the one hand and with the increasing cover of YSF

around the study site and habitat diversity on the other hand. PC3 (~ understory density) did not show any effect on the percentage of Nearctic migrants (species: *Estimate* = 0.429, p = 0.739; individuals: *Estimate* = 0.824, p = 0.310; Figure 13, 14).
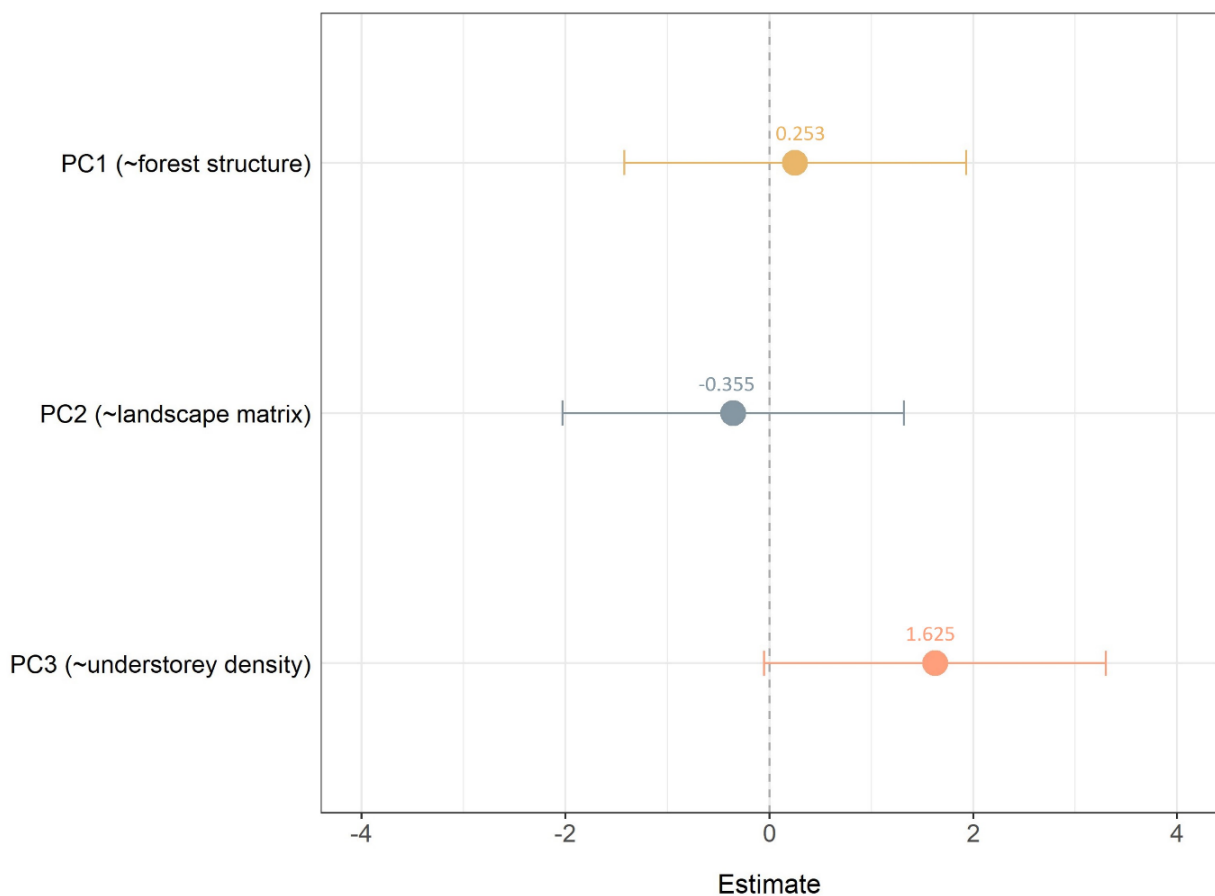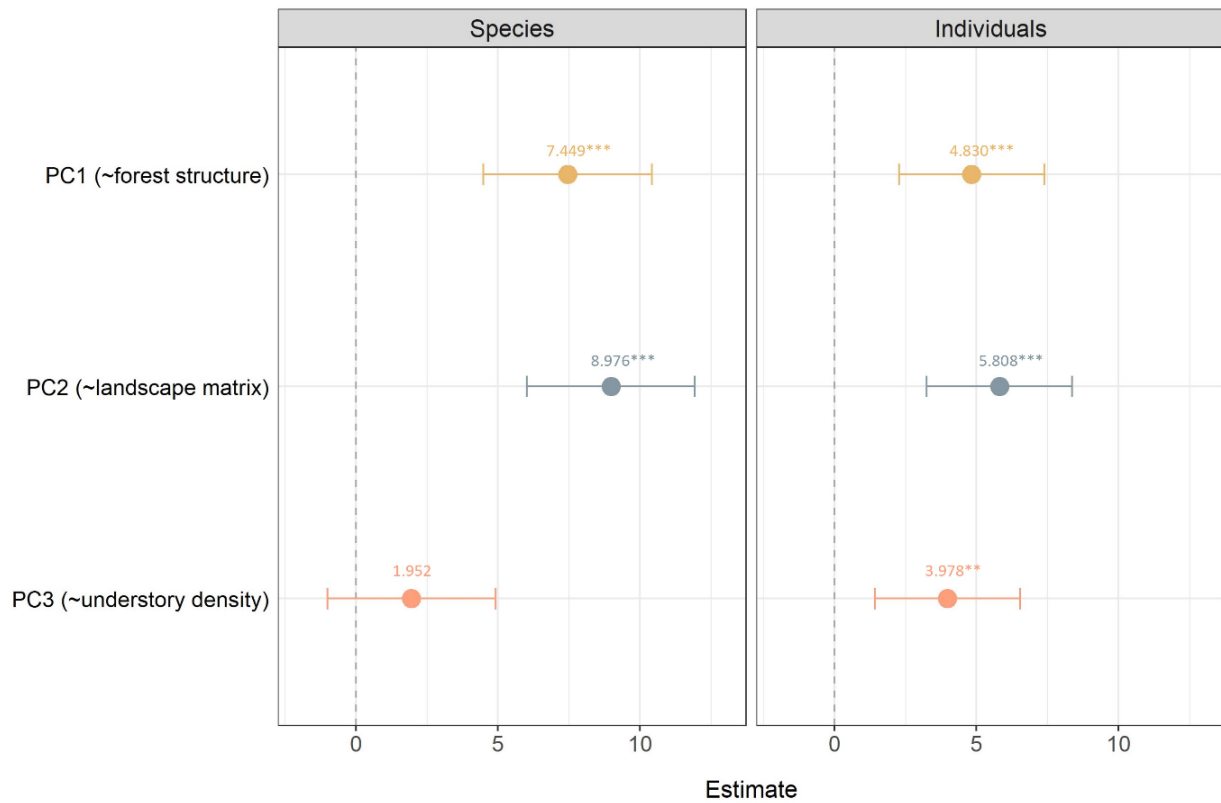

Figure 13. Estimates (± 95% Confidence Interval) of predictors computed by a multiple regression model analysing the effect of PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density) on percentage of Nearctic migrants (species and individuals: n = 30 mist-netting sites). Indicated *p*-values are calculated by *F*-statistics (** = p < 0.01; *** = p < 0.001). PC = Principal Component.
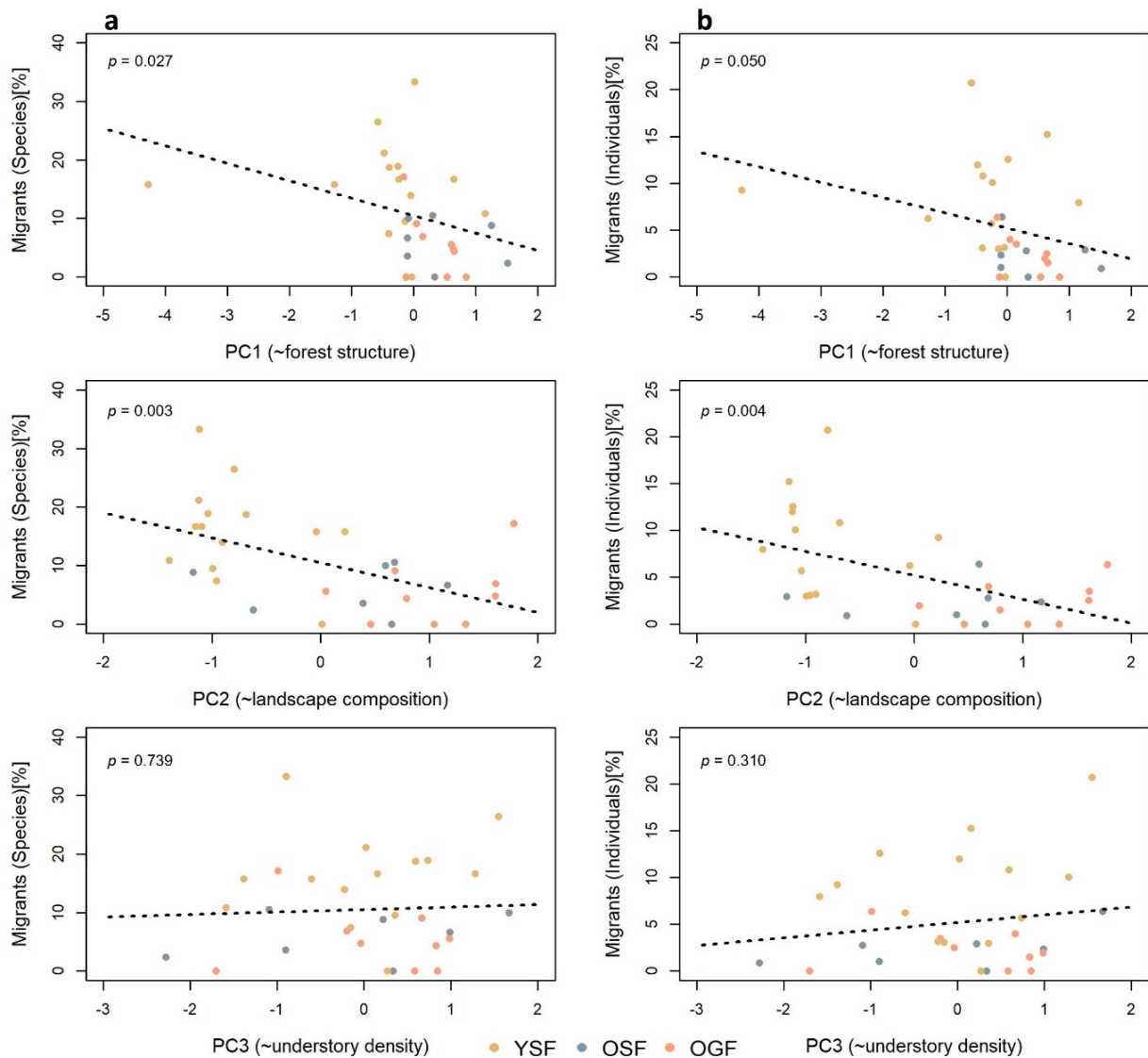
Figure 14. Relationships between percentage of Nearctic migrants (a. species. b. individuals) and PC1 (~ forest structure), PC2 (~ landscape composition) and PC3 (~ understory density). Shown *p*-values were calculated by a multiple regression model (n = 30 mist-netting sites). Dotted lines indicate linear regression lines. YSF = young secondary forest, OSF = old secondary forest, OGF = old-growth forest. PC = Principal Component.

A Kruskal-Wallis rank sum test showed significant differences in percentage of Nearctic migrants between forest types (species: $H_{(2)}$ = 12.31, *p* = 0.002; individuals: $H_{(2)}$ = 11.67, *p* = 0.003; Figure 15). The percentage of species as well as individuals are significantly higher in YSF (n = 14; species: median = 16.2%, IQR = 7.2%; Individuals: median: 8.6%, IQR = 7.9%) than in OSF (n = 7; species: median = 6.7%, IQR = 6.4%; individuals: median = 2.4%, IQR = 1.9%) and OGF (n = 9; species: median = 4.8%, IQR = 6.9%; individuals: median = 2.0%, IQR = 3.5%; species: YSF vs. OSF: *p* = 0.017, YSF vs. OGF: *p* = 0.011; individuals: YSF vs. OSF: *p* = 0.017, YSF vs. OGF: *p* = 0.016). There is no significant difference in percentage of species and individuals of migratory birds between OSF and OGF (species and individuals: both *p* = 1.000).
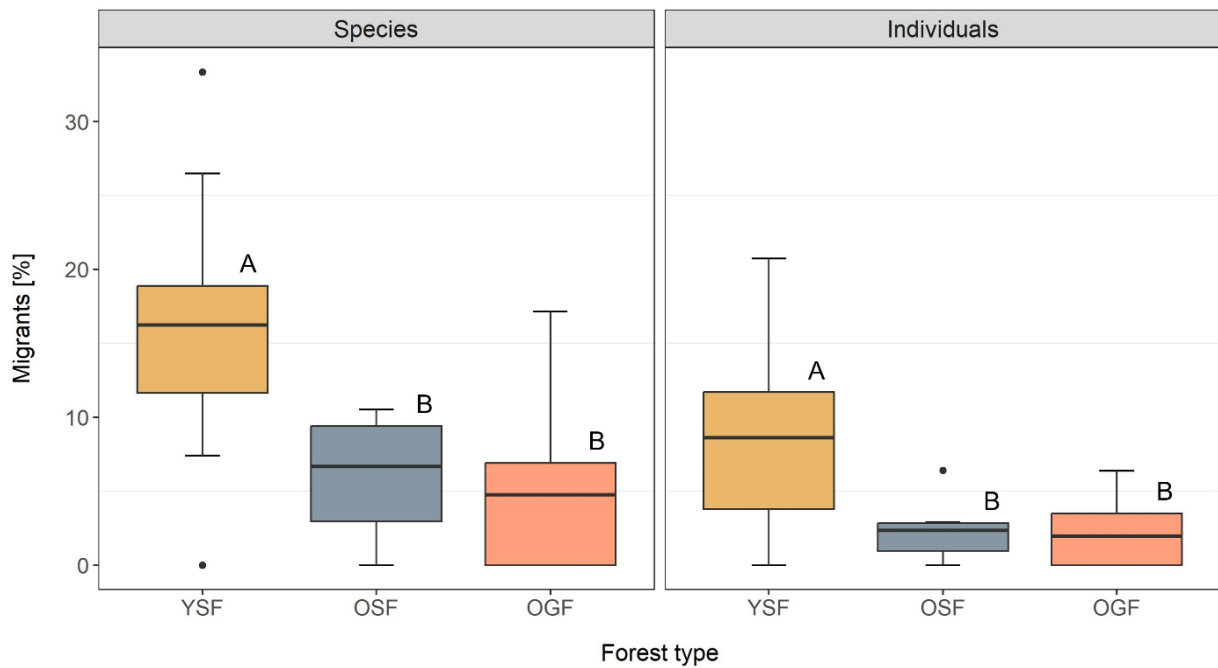
Figure 15. Median percentage of Nearctic migrants (species and individuals) in YSF (young secondary forest, n = 14), OSF (old secondary forest, n = 7) and OGF (old-growth forest, n = 9). Boxes represent the interquartile range, whiskers display 1.5 x interquartile range. Different capital letters indicate significant differences between forest types (pairwise Wilcoxon tests).

Discussion

Species richness

Although species richness differed substantially between study sites, contrary to our expectations, species richness was not increasing with progressing forest succession. Similar results were found by Schulze *et al.* (2019) where some of the same study sites were sampled. A comparable study was carried out in La Selva, Costa Rica where young secondary forests showed higher species richness than old-growth forest (Blake & Loiselle 2001). This result is not only in contrast to our study, but also to a meta-analysis, which reports that species richness of fauna increases rapidly with increasing forest age, especially in young successional stages (0-15 years after abandonment) (Acevedo-Charry & Aide 2019).

From a landscape perspective, species richness tends to be higher in rather undisturbed and continuous forest patches (Carrara *et al.* 2015). This cannot be supported by our results since surrounding landscape characteristics such as percentage of forest cover or habitat diversity did not affect species richness of our study sites. Interestingly, there is evidence that species richness tended to be higher in study sites with less dense understory. Since there is no relationship between understory density and forest age, age does not explain this effect. Rodewald & Smith (1998) observed that some canopy- and forest edge-nesting bird species may take advantage of forest areas with less dense understory potentially due to better foraging possibilities but further reasons are still unknown.

However, there are various other ecological and methodological aspects that might influence numbers of recorded species (Blake & Loiselle 2001). Firstly, our study period (November – January) took place during the northern winter. Ten of the 20 assessed Nearctic migrant species were exclusively trapped in YSF sites. Therefore, there is a seasonal effect on species richness in YSF sites. Secondly, bird data are highly influenced by sampling method (Blake & Loiselle 2001, Mallory *et al.* 2004). By mist-netting only understory birds are supposed to be assessed. Including point counts would detect also birds foraging in the canopy which represent an important fraction of bird species assemblages, particularly in older forests with higher canopy (Blake & Loiselle 2001, Schulze *et al.* 2019). Underestimation of species numbers in old secondary forests (OSF) and old-growth forests (OGF) could be a consequence. Thirdly, secondary forests might attract birds by their high productivity and consequently high abundance of flowers, fruits and foliage (Blake & Loiselle 1991, Martin 1985). Since many of the YSF sites are surrounded by OSF and OGF, birds of the adjacent older forests might use YSF for foraging and hence contribute to the high bird diversity of YSF sites (Blake & Loiselle 2001). Finally, species richness might be influenced by species turnover, especially in young succession states. Accumulation of species in a certain succession state can also contribute to high species numbers in young secondary forest sites (Blake & Loiselle 2001).

Species composition

Our results revealed fundamental changes in species composition with increasing forest age. As we hypothesized, species composition of our study sites is increasingly dominated by forest specialists with progressing forest succession. These results are consistent with the majority of previous studies dealing with changes in bird species composition during forest succession in the neotropics (Vargas-Daza *et al.* 2023, Acevedo-Charry & Aide 2019, Schulze *et al*. 2019, Blake & Loiselle 2001). Additionally, as expected, species composition of secondary forest patches is highly affected by the surrounding landscape. The similarity of the species composition of young secondary forests with old-growth forests increases with increasing OSF and OGF cover and declining habitat diversity in the surrounding area. Our results are coherent with former studies investigating the impact of landscape composition on bird assemblages in tropical forests in southern Costa Rica (San-José *et al.* 2022, Reid *et al.* 2014).

Furthermore, our results clearly showed that species turnover is extremely high in young secondary forests und species composition becomes rather stable in later forest succession. Rapid changes in vegetation structure during succession, especially in early succession states, reassemble bird communities since they depend on certain vegetation structures (Blake & Loiselle 2001, Borges 2007). Bird species from early successional stages that tolerate degraded and open habitats are replaced by species that use forest edges or young

successional stages, which are then gradually replaced by forest species as succession progresses (Acevedo-Charry & Aide 2019).

From a botanical view, the recovery of tropical forests has been well studied and it has been shown that in term of vegetation structure and plant species richness tropical forest can recover within 25 to 60 years on abandoned land (Poorter *et al.* 2021, Aide *et al.* 2000). In contrast, the recovery of bird assemblages comparable to old-growth forest bird communities can take considerably longer, particularly because of the delayed appearance of forest specialists due to their dependency on certain microhabitats such as tree cavities for nesting (Stratford & Stouffer 2015). While forest attributes can reach 78% of their old-growth forest values after 20 years of secondary succession (Poorter *et al.* 2021), the recovery of forest bird specialists in secondary forests might take more than 100 years (Sayer *et al.* 2017). Surprisingly, even though species composition differs significantly between YSF, OSF and OGF sites, four of seven OSF sites (55 – 70 years old) show species composition comparable to OGF sites. Even a few YSF sites, in particular LB01 (11 years) and FAI02 (10 years), which are both embedded in or adjacent to OGF, already show a rather high similarity in species composition with OGF sites. Since the changes in species composition as forest succession progresses are due to the colonization of forest specialists, this suggests that forest specialists may appear, at least temporarily, earlier in secondary forests than is commonly assumed, underlining the importance of secondary forests within the Biological Corridor La Gamba (COBIGA).

Forest specialists

Of the 134 trapped bird species 32 species (~ 24%) were classified as forest specialists. As expected, our results show that forest specialists clearly depend on OGF-like vegetation structure such as high canopy, dense canopy cover and a high number of larger trees providing nesting sites, food sources and shelter against predators. The percentage of forest specialists is rapidly increasing with progressing forest succession and – as expected – show highest values at OGF sites. Additionally, as hypothesized, percentage of forest specialists is highly influenced by landscape matrix. Forest specialists are more likely to be found in continuous forest sites with low degree of disturbance. These results are consistent with former studies (Blake & Loiselle 2001, Schulze *et al.* 2019, Carrara *et al.* 2015) and support the idea that forest specialists require large forest remnants to persist due to their higher sensitivity to edge effects and forest fragmentation (San-José *et al.* 2022, Şekercioğlu *et al.* 2015, Fahrig 2003). Hence, our study highlights the importance of undisturbed continuous old-growth forests for COBIGA.

Surprisingly, some forest specialists, especially the most abundant ones within our study area, e.g. Black-cheeked Ant-Tanger (*Habia atrimaxillaris*), a species endemic to the Golfo Dulce Region (Tebb 2008), or Tawny-winged Woodcreeper (*Dendrocincla anabatina*), White-throated Thrush (*Turdus assimilis*), Sulphur-rumped Flycatcher (*Myiobius sulphureipygius*)

and the army-ant-following Chestnut-backed Antbird (*Myrmeciza exsul*) could be recorded in YSF patches. Although forest specialists may not use young secondary forests as breeding habitat (Schulze *et al.* 2019, MacArthur & MacArthur 1961, Bowen *et al.* 2007), it seems at least some of them may occasionally take advantage of various resources of this forest type as it was shown for Blue-crowned Manakin (*Lepidothrix coronata*), a forest-dependent frugivorous understory bird species (Şekercioğlu *et al.* 2015). Our results might also provide evidence that some forest specialists may use the YSF patches as stepping stones to access older forests that potentially provide more suitable breeding habitats (Schulze *et al.* 2019), highlighting again the importance of young secondary forests for forest specialists.

Interestingly, within our study area rather rare forest specialists like Brown-billed Scythebill (*Campylorhamphus pusillus*), White-shouldered Tanager (*Tachyphonus luctuosus*), Slaty Antwren (*Myrmotherula schisticolor*), Scaly-throated Leaftosser (*Sclerurus guatemalensis*) or Rufous Piha (*Lipaugus unirufus*) were only found in continuous old-growth forests. Dispersal ability varies enormously between forest bird species. Although bird movements can occur over long distances across open land (Ramos *et al.* 2020, Marini 2010), many forest restricted bird species are reluctant to cross forest edges and adjacent open areas (Harris and Reed 2002, Ibarra-Macias *et. al.* 2011, Moore *et al.* 2008). However, there is already a high degree of landscape connectivity in our study area facilitated by strips of gallery forests, living fences and various secondary forest patches created by the COBIGA project as part of reforestation measures. Therefore, at least theoretically, it would be possible to reach most of the secondary forest patches within our study region without crossing larger areas of open land. However, since some forest restricted bird species might be highly sensitive to forest edges it seems they rather tend to remain in the forest interior than using smaller YSF patches with a potentially higher degree of edge effects for foraging or dispersal (San-José *et al.* 2022). This is underlining again that a landscape matrix with a high extent of remaining forest cover plays an important role for many forest specialized understory bird species.

Nearctic migrants

A total of 20 species (~ 15% of all mist-netted species) were Nearctic migrants. As hypothesized, secondary forests, especially young secondary forest (3 – 25 years old) are characterized by higher relative abundances of northern migrants than old-growth forest sites. Similar results were found in former studies (Hutto 1980, Martin 1985, Reid *et al.* 2008). Contrary to our expectations, also landscape features such as increasing cover of YSF and increasing habitat diversity in the surroundings positively affected species richness and abundance of Nearctic migrants. Most Nearctic migrant species breed in shrubby and woody habitats that are comparable to the mosaic of young secondary forests in our study area (Billerman *et al.* 2022). This indicates that Nearctic migrants tend to use similar habitats in their wintering grounds. Furthermore, most northern migrants (e.g. New World warblers) are

insectivorous during breading season but they change to a rather frugivorous diet in their wintering grounds, especially in the late dry season prior to migration (Blake & Loiselle 1992). Since secondary forests are characterized by high productivity and consequently high abundance of fruits (Blake & Loiselle 1991, Martin 1985) they may attract resident bird species as well as Nearctic migrants. Therefore, both resident and migratory species can act as important seed dispersers, a limiting factor in reforestation that facilitates the regrowth of secondary forests in early successional stages (Galindo-González *et al.* 2000, Hutto 1980, Martin 1985, Medellín & Gaona 1999, Reid *et al.* 2008).

However, many populations of Nearctic migrant species such as Golden-winged Warbler (*Vermivora chrysoptera*) tend to decline, due to habitat loss in their wintering grounds as one reason (BirdLife International 2023). As many studies before, our results clearly underline the importance of second growth for Nearctic migrants as wintering grounds and, hence, highlights the need of conservation measures to maintain second growth patches to protect already threatened Nearctic migrant species (Hutto 1980, Martin 1985, Reid *et al.* 2008, Lindell *et al.* 2012).

There is potentially a slight overestimation of the importance of YSF forest patches for Nearctic migrants because some New World warblers, e.g. Chestnut-sided Warbler (*Setophaga pensylvanica)* were also observed foraging in the canopy of OSF or OGF as part of mixed species flocks. However, only about 9% of all trapped Nearctic migrants were Chestnut-sided Warblers, the majority were true understory birds, like e.g. Mourning Warbler (*Geothlypis philadelphia*), Kentucky Warbler (*Geothlypis formosa*), Northern Waterthrush (*Parkesia noveboracensis*) or Ovenbird (*Seiurus aurocapilla*), underlining the importance of YSF patches as wintering habitats for Nearctic migrants. This is further emphasized by the fact that few marked individuals were even recaptured in the same secondary forest patches in consecutive years. Such high wintering site fidelity may indicate suitable habitat conditions for those Nearctic migrants.

Conclusion

While vegetation structure and landscape matrix did not influence understory bird species richness in our study area, species composition changed substantially with increasing vegetational succession of secondary forests and increasing old-growth/old secondary forest area and decreasing habitat diversity in the surrounding landscape. Understory bird communities were increasingly dominated by forest species as forest succession progresses. Landscape matrix characteristics such as forest continuity and low degree of disturbance play an important role for forest specialists, particularly for rather rare species. Our study as well as many others have shown that forest dependent bird species that are very sensitive to disturbance and fragmentation are mainly restricted to old-growth forests (Vargas-Daza *et al.* 2023, San-José *et al.* 2022). Ongoing deforestation and fragmentation of forests can therefore

lead to the local extinction of these highly specialized bird species, as their dispersal abilities are limited (Moore *et al.* 2008). Our results therefore underline how important it is to keep existing old-growth forests in good condition as far as possible.

However, secondary forest patches in our study areas inhabited high abundances of understory birds and remarkable species numbers comparable to old-growth forest sites. Surprisingly, some young secondary forests already have attracted high proportions of forest specialists (especially common species). This may indicate that YSF patches in our study area at least already function as stepping stones for the dispersal of forest specialists in the fragmented landscape or are used as foraging habitat. To what extent they are utilized as breeding habitats still has to be assessed by further studies. Additionally, it was shown that Nearctic migrants mainly use young secondary forests as wintering habitat and habitat diversity on a landscape level proved to positively affect their abundance. Without these structures already declining Nearctic migrant species would become more and more threatened (Reid *et al.* 2008, Lindell *et al.* 2012).

We conclude that for the conservation of understory bird diversity it is crucial to maintain a mosaic of different forest types. However, the preservation of contiguous blocks of old-growth forests is still absolutely necessary in order to protect highly specialized forest species (Vargas-Daza *et al.* 2023, Reid *et al.* 2014). On the other hand, secondary forest patches in the surroundings might function as important safety net or stepping stones for forest specialists (Schulze *et al.* 2019, Chazdon *et al.* 2009) and provide essential wintering habitats for Nearctic migrants (Hutto 1980, Martin 1985, Reid *et al.* 2008). Since the loss of forest connectivity outside of large forest reserves may lead to biodiversity loss even within reserves (Pollock et al. 2022) it is crucial to keep connective structures such as gallery forests or small second-growth patches intact or improve connectivity by further reforestation measures.

References

Acevedo-Charry, O., & Aide, T. M. (2019). Recovery of amphibian, reptile, bird and mammal diversity during secondary forest succession in the tropics. Oikos, 128(8), 1065-1078.

Aide, T. M., Zimmerman, J. K., Pascarella, J. B., Rivera, L., & Marcano-Vega, H. (2000). Forest regeneration in a chronosequence of tropical abandoned pastures: implications for restoration ecology. Restoration Ecology, 8(4), 328-338.

Arroyo-Mora, J. P., Sánchez-Azofeifa, G. A., Rivard, B., Calvo, J. C., & Janzen, D. H. (2005). Dynamics in landscape structure and composition for the Chorotega region, Costa Rica from 1960 to 2000. Agriculture, Ecosystems & Environment, 106(1), 27-39.

Barnosky, A. D., Matzke, N., Tomiya, S., Wogan, G. O., Swartz, B., Quental, T. B., ... & Ferrer, E. A. (2011). Has the Earth's sixth mass extinction already arrived? Nature, 471(7336), 51-57.

Batisteli, A. F., Tanaka, M. O., & Souza, A. L. (2018). Bird functional traits respond to forest structure in riparian areas undergoing active restoration. Diversity, 10(3), 90.

Betancurt-Grisales, J. F., Vargas-Daza, A. M., Castaño-Villa, G. J., & Ospina-Bautista, F. (2021). Bird functional diversity in restored and secondary forests of the Colombian Andes. Restoration Ecology, 29(3), e13315.

Billerman, S. M., Keeney, B. K., Rodewald, P. G., & Schulenberg, T. S. (2022). Birds of the World. Cornell Laboratory of Ornithology, Ithaca, NY, USA. Downloaded from https://birdsoftheworld.org/bow/home on 30/11/2023.

BirdLife International (2023). IUCN Red List for birds. Downloaded from http://datazone.birdlife.org on 21/11/2023.

Blake, J. G., & Loiselle, B. A. (1991). Variation in resource abundance affects capture rates of birds in three lowland habitats in Costa Rica. The Auk, 108(1), 114-130.

Blake, J. G., & Loiselle, B. A. (1992). Fruits in the diets of Neotropical migrant birds in Costa Rica. Biotropica, 24(2), 200-210.

Blake, J. G., & Loiselle, B. A. (2001). Bird assemblages in second-growth and old-growth forests, Costa Rica: perspectives from mist nets and point counts. The Auk, 118(2), 304-326.

Borges, S. H. (2007). Bird assemblages in secondary forests developing after slash-and-burn agriculture in the Brazilian Amazon. Journal of Tropical Ecology, 23(4), 469-477.

Bowen, M. E., McAlpine, C. A., House, A. P., & Smith, G. C. (2007). Regrowth forests on abandoned agricultural land: a review of their habitat values for recovering forest fauna. Biological Conservation, 140(3-4), 273-296.

Boyle, W. A., & Sigel, B. J. (2015). Ongoing changes in the avifauna of La Selva Biological Station, Costa Rica: twenty-three years of Christmas bird counts. Biological Conservation, 188, 11-21.

Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J.H., Schondube, J.E., de Freitas, S. M., & Fahrig, L. (2015). Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. Biological Conservation, 184, 117-126.

Chao, A., Gotelli, N. J., Hsieh, T. C., Sander, E. L., Ma, K. H., Colwell, R. K., & Ellison, A. M. (2014). Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecological Monographs, 84(1), 45-67.

Chazdon, R. L., Broadbent, E. N., Rozendaal, D. M., Bongers, F., Zambrano, A. M. A., Aide, T. M., ... & Poorter, L. (2016). Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. Science Advances, 2(5), e1501639.

Chazdon, R. L., Peres, C. A., Dent, D., Sheil, D., Lugo, A. E., Lamb, D., ... & Miller, S. E. (2009). The potential for species conservation in tropical secondary forests. Conservation Biology, 23(6), 1406-1417.

de Souza Leite, M., Boesing, A. L., Metzger, J. P., & Prado, P. I. (2022). Matrix quality determines the strength of habitat loss filtering on bird communities at the landscape scale. Journal of Applied Ecology, 59(11), 2790-2802.

Fahrig, L. (2003). Effects of habitat fragmentation on biodiversity. Annual Review of Ecology, Evolution, and Systematics, 34(1), 487-515.

Galindo-González, J., Guevara, S., & Sosa, V. J. (2000). Bat-and bird-generated seed rains at isolated trees in pastures in a tropical rainforest. Conservation Biology, 14(6), 1693-1703.

Gallmetzer, N., & Schulze, C. H. (2015). Impact of oil palm agriculture on understory amphibians and reptiles: A Mesoamerican perspective. Global Ecology and Conservation, 4, 95-109.

Garrigues, R., & Dean, R. (2014). The Birds of Costa Rica: A Field Guide. Cornell University Press, New York.

Guariguata, M. R., & Ostertag, R. (2001). Neotropical secondary forest succession: changes in structural and functional characteristics. Forest Ecology and Management, 148(1-3), 185-206.

Guariguata, M. R., Chazdon, R. L., Denslow, J. S., Dupuy, J. M., & Anderson, L. (1997). Structure and floristics of secondary and old-growth forest stands in lowland Costa Rica. Plant Ecology, 132, 107-120.

Haddad, N. M., Brudvig, L. A., Clobert, J., Davies, K. F., Gonzalez, A., Holt, R. D., ... & Townshend, J. R. (2015). Habitat fragmentation and its lasting impact on Earth's ecosystems. Science Advances, 1(2), e1500052.

Hall, J. S., Plisinski, J. S., Mladinich, S. K., van Breugel, M., Lai, H. R., Asner, G. P., ... & Thompson, J. R. (2022). Deforestation scenarios show the importance of secondary forest for meeting Panama's carbon goals. Landscape Ecology, 37(3), 673-694.

Harris, R. J., & Reed, J. M. (2002). Behavioral barriers to non-migratory movements of birds. Annales Zoologici Fennici, 39, 275-290.

Hsieh, T. C., Ma, K. H., & Chao, A. (2016). iNEXT: an R package for rarefaction and extrapolation of species diversity (H ill numbers). Methods in Ecology and Evolution, 7(12), 1451-1456.

Hutto, R. L. (1980). Winter habitat distribution of migratory land birds in western Mexico, with special reference to small, foliage-gleaning insectivores. In Keast, A., & Morton, E. S. (eds.): Migrant birds in the Neotropics: ecology, behavior, distribution and conservation. Smithsonian Institution Press, Washington, DC, 181-203.

Ibarra-Macias, A., Robinson, W. D., & Gaines, M. S. (2011). Experimental evaluation of bird movements in a fragmented Neotropical landscape. Biological Conservation, 144(2), 703-712.

Kaiser, H. F. (1958). The varimax criterion for analytic rotation in factor analysis. Psychometrika, 23(3), 187-200.

Lindell, C. A., Cole, R. J., Holl, K. D., & Zahawi, R. A. (2012). Migratory bird species in young tropical forest restoration sites: effects of vegetation height, planting design, and season. Bird Conservation International, 22(1), 94-105.

Littleton, E. W., Dooley, K., Webb, G., Harper, A. B., Powell, T., Nicholls, Z., ... & Lenton, T. M. (2021). Dynamic modelling shows substantial contribution of ecosystem restoration to climate change mitigation. Environmental Research Letters, 16(12), 124061.

Lobo, J., & Bolaños, F. (2005). Historia natural de Golfito. Heredia, Costa Rica. Instituto Nacional de Biodiversidad.

Mallory, E. P., Brokaw, N. V., & Hess, S. C. (2004). Coping with capture rate bias: canopy height and several extrinsic factors. Studies in Avian Biology, 29, 151-160.

Marini, M. Â (2010). Bird movement in a fragmented Atlantic Forest landscape. Studies on Neotropical Fauna and Environment, 45(1), 1-10.

Martin, T. E. (1985). Selection of second-growth woodlands by frugivorous migrating birds in Panama: an effect of fruit size and plant density? Journal of Tropical Ecology, 1(2), 157-170.

Martinez Arbizu, P. (2020). pairwiseAdonis: Pairwise multilevel comparison using adonis. R package version 0.4, 1.

MacArthur, R. H., & MacArthur, J. W. (1961). On bird species diversity. Ecology, 42(3), 594-598.

Medellín, R. A., & Gaona, O. (1999). Seed dispersal by bats and birds in forest and disturbed habitats of Chiapas, Mexico 1. Biotropica, 31(3), 478-485.

Moore, R. P., Robinson, W. D., Lovette, I. J., & Robinson, T. R. (2008). Experimental evidence for extreme dispersal limitation in tropical forest birds. Ecology Letters, 11(9), 960-968.

Oksanen, J., Simpson, G., Blanchet, F., Kindt, R., Legendre, P., Minchin, P., ... & Weedon, J. (2022). Vegan: Community Ecology Package, R Package Version 2.6-4.

Poorter, L., Craven, D., Jakovac, C. C., Van Der Sande, M. T., Amissah, L., Bongers, F., ... & Hérault, B. (2021). Multidimensional tropical forest recovery. Science, 374(6573), 1370-1376.

R Core Team (2022). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Ramos, D. L., Pizo, M. A., Ribeiro, M. C., Cruz, R. S., Morales, J. M., & Ovaskainen, O. (2020). Forest and connectivity loss drive changes in movement behavior of bird species. Ecography, 43(8), 1203-1214.

Reid, J. L., Harris, J. B. C., & Zahawi, R. A. (2012). Avian habitat preference in tropical forest restoration in southern Costa Rica. Biotropica, 44(3), 350-359.

Reid, J. L., Harris, J. B. C., Martin, L. J., Barnett, J. R., & Zahawi, R. A. (2008). Distribution and abundance of nearctic–neotropical songbird migrants in a forest restoration site in southern Costa Rica. Journal of Tropical Ecology, 24(6), 685-688.

Reid, J. L., Mendenhall, C. D., Rosales, J. A., Zahawi, R. A., & Holl, K. D. (2014). Landscape context mediates avian habitat choice in tropical forest restoration. PLoS ONE, 9(3), e90573.

Rey Benayas J. M. (2000). Restoring forests after land abandonment. In: Mansourian S., Vallauri D., & Dudley N. (eds.): Forest restoration in landscapes: beyond planting trees. Springer, New York, 356-360

Rodewald, P. G., & Smith, K. G. (1998). Short-term effects of understory and overstory management on breeding birds in Arkansas oak-hickory forests. The Journal of Wildlife Management, 62(4), 1411-1417.

San-José, M., Werden, L. K., Joyce, F. H., Reid, J. L., Holl, K. D., & Zahawi, R. A. (2022). Effects of landscape structure on restoration success in tropical premontane forest. Scientific Reports, 12(1), 13452.

Sayer, C. A., Bullock, J. M., & Martin, P. A. (2017). Dynamics of avian species and functional diversity in secondary tropical forests. Biological Conservation, 211, 1-9.

Schulze, C. H., Leidinger, P., Paces, B., & Páez, A. F. R. (2019). The importance of reforested and naturally regenerating young forest patches as secondary habitats for forest birds in the Biological Corridor La Gamba, Costa Rica. Acta ZooBot Austria, 156, 79-98.

Şekercioğlu, Ç. H., Loarie, S. R., Oviedo-Brenes, F., Mendenhall, C. D., Daily, G. C., & Ehrlich, P. R. (2015). Tropical countryside riparian corridors provide critical habitat and connectivity for seed-dispersing forest birds in a fragmented landscape. Journal of Ornithology, 156(Suppl 1), 343-353.

Stouffer, P. C., & Bierregaard Jr, R. O. (1995a). Use of Amazonian forest fragments by understory insectivorous birds. Ecology, 76(8), 2429-2445.

Stouffer, P. C., & Bierregaard Jr, R. O. (1995b). Effects of forest fragmentation on understory hummingbirds in Amazonian Brazil. Conservation Biology, 9(5), 1085-1094.

Stratford, J. A., & Stouffer, P. C. (2015). Forest fragmentation alters microhabitat availability for Neotropical terrestrial insectivorous birds. Biological Conservation, 188, 109-115.

Tebb, G. (2008). The birds of La Gamba. Stapfia, 88, 353–380.

Vargas-Daza, A. M., Betancurt-Grisales, J. F., Castaño-Villa, G. J., & Fontúrbel, F. E. (2023). The importance of old secondary forests for understory birds in the tropical Andes. Global Ecology and Conservation, 47, e02658.

Weissenhofer, A., Barquero, M., Huber, W., Mayer, V., & N'ajera Umana, J. (2008). 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. Stapfia, 88, 715-723.

Weissenhofer, A., Huber, W., Koukal, T., Immitzer, M., Schembera, E., Sontag, S., Zamora, N., & Weber, A. (2008). Ecosystem diversity in the Piedras Blancas National Park and adjacent areas (Costa Rica), with the first vegetation map of the area. Stapfia, 88, 65–96.

Wright, S. J. (2005). Tropical forests in a changing environment. Trends in Ecology & Evolution, 20(10), 553-560.

Appendix A

Zusammenfassung

Costa Ricas Biodiversität war, wie in den meisten anderen tropischen Regionen, durch den Verlust von Lebensräumen aufgrund großflächiger Entwaldung bedroht. Während der Anteil an Altwäldern deutlich abgenommen hat, vergrößert sich die Fläche an Sekundärwäldern in vielen tropischen Regionen, darunter auch in Costa Rica, kontinuierlich. Daher prägen zunehmend Sekundärwälder unterschiedlichen Alters, somit unterschiedlichen Sukzessionsstadiums und folglich variierender Vegetationsstruktur die heutige Kulturlandschaft. Die Bedeutung von Sekundärwaldflächen kann für Vogelgemeinschaften sehr unterschiedlich sein. Ziel dieser Studie war daher zu quantifizieren, inwieweit Vegetationsstruktur und Zusammensetzung der umgebenden Landschaftsmatrix den Artenreichtum und die Artenzusammensetzung von Unterwuchsvögel und das Vorkommen gefährdeter Waldvögel und nearktischer Zugvögel in Sekundärwäldern innerhalb des Biologischen Korridors von La Gamba (COBIGA) im Südwesten von Costa Rica beeinflussen. Dazu wurden an 21 verschiedenen Sekundärwald-Standorten und 9 Altwald-Standorten, die als Referenz dienten, in der Umgebung der Tropenstation La Gamba Unterwuchsvögel mit Japannetzen gefangen. Darüber hinaus wurden die Vegetationsstruktur und die Zusammensetzung der umgebenden Landschaftsmatrix für jeden Untersuchungsstandort erfasst. Während Vegetationsstruktur und Landschaftsmatrix keinen Einfluss auf den Artenreichtum hatten, änderte sich die Artenzusammensetzung mit zunehmender Waldsukzession und zunehmender Fläche von alten Sekundärwäldern/Altwäldern, sowie mit abnehmender Habitatdiversität in der umgebenden Landschaft erheblich. Mit fortschreitender Waldsukzession wurden Vogelgemeinschaften zunehmend von Waldarten dominiert, während nearktische Zugvögel vor allem in jüngeren Sekundärwäldern zu finden waren. Charakteristika der Landschaftsmatrix, wie zusammenhängende Waldbedeckung und Habitatdiversität spielten sowohl für Waldspezialisten als auch für nearktische Zugvögel eine wichtige Rolle. Unsere Ergebnisse unterstreichen die Bedeutung von Sekundärwaldflächen für die Vogelwelt im Biologischen Korridor von La Gamba sowie die Wichtigkeit von Altwald für gefährdete Waldvogelarten. Vor allem gibt es Hinweise darauf, dass Waldspezialisten Sekundärwald-flächen früher als erwartet nutzen und diese als Trittsteine in der fragmentierten Landschaft fungieren.

Schlagwörter: Wiederbewaldung, Waldsukzession, Vogelschutz, Waldspezialisten, Nearktische Zugvögel, Neotropen

Appendix B

Table B1. Overview of species captured at each study site, including total abundances of species and percentages of forest specialists and Nearctic migrants. FS = forest specialist, NM = Nearctic migrant.

Species		FS	NM	9	16	18	22	AV01	BR01	BR02	BR03	CF3	CF6	CF8	FA01	FAI01	FAI02	FAI03	LB01	LB02	LB03	OAF	OGF2	OGF3	RF2	SF2	SG01	VB01	VB02	VB03	WF1	WF2	WF3	Total
Acadian Flycatcher	*Empidonax virescens*		x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**2**
American Pygmy Kingfisher	*Chloroceryle aenea*			-	-	-	1	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	**5**
Bananaquit	*Coereba flaveola*			17	4	2	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	-	1	-	-	-	-	1	6	1	-	1	4	**40**
Band-tailed Barbthroat	*Threnetes ruckeri*			6	13	11	11	6	3	3	8	2	3	3	11	6	5	5	4	8	12	8	-	3	6	2	6	7	10	16	13	8	18	**217**
Bare-crowned Antbird	*Gymnocichla nudiceps*			-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**2**
Bay-headed Tanager	*Tangara gyrola*			-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	**3**
Bicolored Antbird	*Gymnopithys leucaspis*	x		-	-	-	-	-	2	4	-	3	3	-	-	-	2	-	1	-	-	-	1	6	-	1	2	-	-	-	-	-	-	**25**
Black-and-white Warbler	*Mniotilta varia*		x	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	**3**
Black-bellied Wren	*Pheugopedius fasciatoventris*			1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	**2**
Black-cheeked Ant-Tanager	*Habia atrimaxillaris*	x		-	-	-	-	7	2	6	2	1	5	-	-	-	1	2	-	4	3	5	-	4	3	8	1	-	-	4	4	2	-	**64**
Black-faced Antthrush	*Formicarius analis*	x		-	-	-	-	2	-	2	1	1	-	1	-	-	-	-	1	-	1	-	-	-	1	-	-	-	-	-	-	1	-	**11**
Black-hooded Antshrike	*Thamnophilus bridgesi*			-	-	-	-	-	-	-	-	-	-	-	-	1	1	-	1	1	-	-	-	1	1	-	-	1	1	1	-	-	-	**9**
Black-striped Sparrow	*Arremonops conirostris*			1	2	5	3	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	1	3	**18**
Black-throated Trogon	*Trogon rufus*	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	**1**
Blue Ground-Dove	*Claravis pretiosa*			1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	**2**
Blue-black Grassquit	*Volatinia jacarina*			-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**2**
Blue-black Grosbeak	*Cyanoloxia cyanoides*	x		-	-	-	-	-	2	-	1	-	1	2	-	1	-	1	-	-	-	-	-	3	2	-	-	-	-	1	-	-	1	**15**
Blue-crowned Manakin	*Lepidothrix coronata*	x		-	-	-	-	-	2	8	1	-	-	-	-	2	3	3	-	1	-	-	-	1	3	1	2	-	-	-	2	-	-	**30**
Blue-crowned Motmot	*Momotus coeruliceps*			-	-	-	-	2	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	**5**
Blue-gray Tanager	*Thraupis episcopus*			1	2	9	-	-	-	-	-	-	-	-	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	**17**
Blue-throated Goldentail	*Hylocharis eliciae*			-	-	-	-	2	4	-	1	-	-	-	-	-	1	-	1	2	1	-	-	-	2	-	-	1	-	-	4	-	2	**21**
Bran-colored Flycatcher	*Myiophobus fasciatus*			-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**
Bright-rumped Attila	*Attila spadiceus*			-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	2	1	-	-	-	2	-	1	-	-	-	-	1	1	**11**
Bronzy Hermit	*Glaucis aeneus*			-	1	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	2	-	-	-	-	**6**
Brown-billed Scythebill	*Campylorhamphus pusillus*	x		-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	**2**
Buff-rumped Warbler	*Myiothlypis fulvicauda*			-	-	-	-	3	-	-	-	-	-	-	-	-	-	-	2	2	1	-	-	1	-	-	1	-	-	-	-	-	-	**10**
Buff-throated Saltator	*Saltator maximus*			3	4	6	1	-	-	-	-	-	-	-	-	-	-	-	3	2	-	-	2	2	1	-	1	1	1	5	3	1	2	**38**
Charming Hummingbird	*Amazilia decora*			1	1	-	11	4	4	2	10	-	2	2	-	2	1	5	1	2	12	4	-	1	10	1	3	3	-	9	7	3	1	**102**
Cherrie's Tanager	*Ramphocelus costaricensis*			19	17	22	21	-	-	-	-	-	-	10	-	-	-	-	-	-	-	-	-	3	-	-	-	5	12	-	-	-	22	**131**
Chestnut-backed Antbird	*Myrmeciza exsul*	x		-	3	-	-	5	4	2	2	1	2	3	1	1	-	4	5	4	1	-	2	2	2	-	1	1	-	3	2	-	1	**52**
Chestnut-sided Warbler	*Setophaga pensylvanica*		x	1	2	-	-	-	-	1	-	-	-	1	2	1	-	-	1	3	1	-	-	-	1	1	3	-	-	-	1	-	-	**19**
Chiriqui Foliage-gleaner	*Automolus exsertus*			-	-	-	-	-	1	1	3	-	-	-	-	2	-	1	3	3	2	-	-	-	-	-	2	-	2	-	-	-	-	**20**
Clay-colored Thrush	*Turdus grayi*			-	2	-	5	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	6	-	-	1	3	4	-	-	2	2	**26**
Cocoa Woodcreeper	*Xiphorhynchus susurrans*			1	2	-	2	1	-	4	2	1	-	-	1	1	1	2	-	1	2	-	1	1	1	-	1	2	2	-	1	-	5	**35**
Common Pauraque	*Nyctidromus albicollis*			-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**
Common Tody-Flycatcher	*Todirostrum cinereum*			-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**
Crowned Woodnymph	*Thalurania colombica*			-	-	-	1	-	4	5	12	3	6	6	-	-	5	6	2	5	1	4	4	3	15	-	3	-	-	-	8	15	2	**110**
Dot-winged Antwren	*Microrhopias quixensis*	x		-	-	-	-	-	-	1	1	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	**5**
Dusky Antbird	*Cercomacroides tyrannina*			-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**1**
Dusky-capped Flycatcher	*Myiarchus tuberculifer*			1	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	**3**

Species		FS	NM	9	16	18	22	AV01	BR01	BR02	BR03	CF3	CF6	CF8	FA01	FAI01	FAI02	FAI03	LB01	LB02	LB03	OAF	OGF2	OGF3	RF2	SF2	SG01	VB01	VB02	VB03	WF1	WF2	WF3	Total
Eye-ringed Flatbill	*Rhynchocyclus brevirostris*	x	-	-	-	-	-	-	1	-	-	1	-	-	-	-	1	2	-	2	-	1	-	1	-	-	1	-	-	-	-	1	-	11
Fiery-billed Aracari	*Pteroglossus frantzii*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Golden-crowned Spadebill	*Platyrinchus coronatus*	x	-	-	-	-	-	2	4	-	-	1	2	-	-	-	-	1	-	-	-	-	1	3	-	-	1	-	-	2	-	-	-	17
Golden-hooded Tanager	*Tangara larvata*	-	-	-	-	7	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	8
Golden-winged Warbler	*Vermivora chrysoptera*	-	x	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Gray-cheeked Thrush	*Catharus minimus*	-	x	1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3
Gray-chested Dove	*Leptotila cassini*	-	-	1	1	-	3	-	-	2	-	-	1	-	-	-	-	1	-	2	1	2	-	1	-	2	3	-	2	-	-	3	6	31
Gray-headed Tanager	*Eucometis penicillata*	-	-	-	-	-	-	3	3	-	-	-	-	-	-	1	-	3	1	4	-	1	2	10	1	2	2	-	-	2	-	3	-	38
Great Antshrike	*Taraba major*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Great Crested Flycatcher	*Myiarchus crinitus*	-	x	-	2	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Great Curassow	*Crax rubra*	x	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Green Hermit	*Phaethornis guy*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	1	-	-	-	2	-	-	-	-	-	-	-	-	-	-	5
Green Kingfisher	*Chloroceryle americana*	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	1	-	-	-	-	-	3	-	-	-	-	1	-	7
House Wren	*Troglodytes aedon*	-	-	3	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
Isthmian Wren	*Cantorchilus elutus*	-	-	-	2	4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	7
Kentucky Warbler	*Geothlypis formosa*	-	x	-	1	-	5	-	-	-	-	-	-	2	1	-	-	4	2	-	1	-	-	-	-	-	4	-	-	-	-	3	-	23
Long-billed Gnatwren	*Ramphocaenus melanurus*	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	-	-	1	-	3
Long-billed Hermit	*Phaethornis longirostris*	-	-	2	3	1	10	2	9	21	7	4	7	3	-	8	4	4	3	3	12	5	2	2	10	2	3	4	2	3	3	1	1	141
Long-tailed Woodcreeper	*Deconychura longicauda*	x	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	2	-	-	-	-	-	2	-	-	-	-	1	1	-	8
MacGillivrays's Warbler	*Geothlypis tolmiei*	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1
Mourning Warbler	*Geothlypis philadelphia*	-	x	1	6	5	1	-	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	1	-	-	-	-	-	2	-	18
Northern Barred-Woodcreeper	*Dendrocolaptes sanctithomae*	x	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	1	-	3
Northern Bentbill	*Oncostoma cinereigulare*	-	-	-	-	-	-	-	1	2	-	-	-	-	-	2	1	-	2	1	1	-	-	-	-	2	-	-	-	-	-	-	-	12
Northern Waterthrush	*Parkesia noveboracensis*	-	x	6	5	-	2	1	-	-	-	-	-	3	-	-	1	-	-	2	3	-	-	1	-	-	1	-	10	-	-	1	1	37
Ochre-bellied Flycatcher	*Mionectes oleagineus*	-	-	39	77	21	65	3	3	5	10	3	7	18	70	4	8	3	15	11	46	7	5	16	7	8	9	4	28	9	7	13	39	560
Olivaceous Piculet	*Picumnus olivaceus*	-	-	1	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	4
Orange-billed Sparrow	*Arremon aurantiirostris*	-	-	2	7	-	2	8	4	3	7	2	5	2	8	3	4	5	2	3	6	1	5	2	2	-	5	3	11	4	1	11	10	128
Orange-collared Manakin	*Manacus aurantiacus*	-	-	6	11	9	9	2	-	3	2	-	6	5	9	6	3	6	10	2	8	3	-	7	-	4	-	8	15	5	2	9	111	261
Ovenbird	*Seiurus aurocapilla*	-	x	-	3	4	1	-	-	-	-	-	-	-	1	2	-	1	-	-	-	-	-	-	-	2	-	-	1	-	-	-	1	16
Pale-breasted Spinetail	*Synallaxis albescens*	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Paltry Tyrannulet	*Zimmerius vilissimus*	-	-	1	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	1	-	-	-	1	6
Plain Xenops	*Xenops minutus*	-	-	-	-	1	1	-	-	-	-	-	-	-	-	1	-	2	-	-	-	1	-	2	-	-	-	-	-	-	1	1	-	10
Prothonotary Warbler	*Protonotaria citrea*	-	x	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Purple-crowned Fairy	*Heliothryx barroti*	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4	-	-	-	6
Red-capped Manakin	*Ceratopipra mentalis*	-	-	2	-	-	2	1	11	16	4	5	11	4	2	2	1	-	-	5	-	2	3	10	12	-	4	1	1	6	17	5	9	136
Red-eyed Vireo	*Vireo olivaceus*	-	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	1
Red-legged Honeycreeper	*Cyanerpes cyaneus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Red-rumped Woodpecker	*Veniliornis kirkii*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2
Riverside Wren	*Cantorchilus semibadius*	x	-	-	-	-	-	3	-	-	-	-	1	-	-	3	-	-	-	1	1	5	5	-	-	-	3	-	5	1	-	2	1	31
Rose-throated Becard	*Pachyramphus aglaiae*	-	-	-	2	2	-	-	-	-	-	-	-	-	-	1	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	1	-	8
Royal Flycatcher	*Onychorhynchus coronatus*	x	-	4	2	1	1	-	-	1	1	-	-	-	2	-	1	-	1	-	1	1	-	-	1	-	-	1	1	1	-	4	-	24
Ruddy Foliage-gleaner	*Automolus rubiginosus*	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Ruddy Quail-Dove	*Geotrygon montana*	-	-	1	1	-	1	2	-	-	-	-	-	-	-	-	1	-	-	2	3	-	-	1	-	-	-	-	4	1	1	1	4	23
Ruddy-tailed Flycatcher	*Terenotriccus erythrurus*	-	-	-	-	-	-	2	-	-	-	-	2	-	-	1	1	2	-	-	-	-	-	-	3	3	2	-	-	-	-	-	-	16
Rufous Mourner	*Rhytipterna holerythra*	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Rufous Piha	*Lipaugus unirufus*	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1

Species		FS	NM	Study site																														Total
				9	16	18	22	AV01	BR01	BR02	BR03	CF3	CF6	CF8	FA01	FAI01	FAI02	FAI03	LB01	LB02	LB03	OAF	OGF2	OGF3	RF2	SF2	SG01	VB01	VB02	VB03	WF1	WF2	WF3	
Rufous-tailed Hummingbird	*Amazilia tzacatl*			4	2	1	16	1	-	3	3	-	-	-	3	1	-	4	2	-	9	3	-	1	-	1	1	4	3	8	1	3	6	80
Rufous-tailed Jacamar	*Galbula ruficauda*			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	1
Scale-crested Pygmy-Tyrant	*Lophotriccus pileatus*	x		-	-	-	-	-	-	1	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	3
Scaly-breasted Hummingbird	*Phaeochroa cuvierii*			1	-	-	1	-	-	-	-	-	-	-	-	-	2	1	-	-	-	-	-	-	-	-	-	-	-	-	1	1	1	8
Scaly-breasted Wren	*Microcerculus marginatus*	x		-	-	-	-	-	1	-	-	1	-	-	-	-	2	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	-	6
Scaly-throated Leaftosser	*Sclerurus guatemalensis*	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1
Scarlet Tanager	*Piranga olivacea*		x	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	2
Scrub Greenlet	*Hylophilus flavipes*			-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	3
Shining Honeycreeper	*Cyanerpes lucidus*			-	-	-	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	3
Silver-throated Tanager	*Tangara icterocephala*			-	-	1	-	-	-	-	-	-	-	-	-	1	-	4	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	8
Slate-headed Tody-Flycatcher	*Poecilotriccus sylvia*			-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	2
Slaty Antwren	*Myrmotherula schisticolor*	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	1
Slaty Spinetail	*Synallaxis brachyura*			-	1	6	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	7
Social Flycatcher	*Myiozetetes similis*			1	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Spot-crowned Euphonia	*Euphonia imitans*			1	2	7	2	-	1	-	-	-	4	2	2	-	1	-	1	-	-	1	2	3	3	-	-	-	-	-	1	2	1	36
Streaked Flycatcher	*Myiodynastes maculatus*			-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Streaked Saltator	*Saltator striatipectus*			-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	1	3
Streak-headed Woodcreeper	*Lepidocolaptes souleyetii*			-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	2
Striped Woodhaunter	*Hyloctistes subulatus*	x		-	-	-	-	2	1	2	-	-	-	-	-	-	-	-	2	1	4	1	-	-	1	-	-	-	-	-	-	-	-	14
Stripe-throated Hermit	*Phaethornis striigularis*			-	3	-	1	3	-	1	1	2	4	3	1	8	-	6	2	-	3	3	-	2	2	2	1	1	3	1	2	2	1	58
Sulphur-rumped Flycatcher	*Myiobius sulphureipygius*	x		-	-	-	-	3	-	-	-	-	1	1	3	-	-	1	8	5	3	3	-	3	6	-	3	2	-	-	1	1	-	44
Summer Tanager	*Piranga rubra*		x	1	-	-	-	1	-	-	-	-	-	-	-	1	-	-	1	-	-	-	-	-	-	1	2	-	-	-	-	-	-	7
Swainson's Thrush	*Catharus ustulatus*		x	-	3	3	1	-	-	1	-	-	2	6	-	-	-	1	2	-	-	-	-	-	2	1	-	-	-	-	1	1	1	25
Tawny-crowned Greenlet	*Tunchiornis ochraceiceps*	x		-	-	-	-	1	3	2	3	2	-	-	-	-	-	-	-	1	-	-	1	2	-	-	3	-	-	-	-	-	-	18
Tawny-winged Woodcreeper	*Dendrocincla anabatina*	x		-	1	-	1	-	4	4	2	1	-	1	-	1	-	7	-	2	3	2	1	3	1	7	1	1	-	2	1	3	5	54
Tennessee Warbler	*Oreothlypis peregrina*		x	-	1	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	3
Thick-billed Euphonia	*Euphonia laniirostris*			-	1	18	1	-	-	-	-	-	-	-	-	-	2	-	-	-	-	-	-	1	-	-	-	-	-	-	-	1	-	24
Thick-billed Seed-Finch	*Oryzoborus funereus*			4	4	3	6	-	-	-	-	-	-	-	1	-	1	-	-	-	-	-	-	-	3	1	-	2	-	-	-	-	-	25
Variable Seedeater	*Sporophila corvina*			32	3	5	11	1	-	-	-	-	-	-	-	1	2	-	1	-	-	-	-	-	3	-	-	1	2	2	-	-	-	64
Violet Sabrewing	*Campylopterus hemileucurus*			-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
Violet-headed Hummingbird	*Klais guimeti*			-	-	-	-	3	-	1	-	-	-	-	-	1	1	1	-	-	-	-	-	-	-	2	-	-	-	-	-	1	-	10
Wedge-billed Woodcreeper	*Glyphorynchus spirurus*			2	2	1	6	8	1	15	7	2	3	9	9	-	-	2	20	10	1	3	1	4	4	5	7	4	11	13	6	7	5	168
White-lined Tanager	*Tachyphonus rufus*			-	2	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	4
White-necked Jacobin	*Florisuga mellivora*			-	-	-	-	-	-	2	-	-	-	-	-	-	-	-	1	1	-	-	2	-	-	-	2	2	4	1	-	-	-	15
White-ruffed Manakin	*Corapipo altera*			1	-	-	-	-	1	9	4	-	-	-	-	-	4	6	3	1	2	-	-	9	-	2	1	-	1	6	-	-	2	52
White-shouldered Tanager	*Tachyphonus luctuosus*	x		-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1
White-throated Shrike-Tanager	*Lanio leucothorax*	x		-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	1	-	2
White-throated Thrush	*Turdus assimilis*	x		-	-	-	-	-	4	2	2	-	-	1	-	-	-	-	2	2	3	1	-	2	1	-	1	3	9	3	2	4	3	45
White-tipped Dove	*Leptotila verreauxi*			2	2	1	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	1	-	-	-	-	-	1	8
White-tipped Sicklebill	*Eutoxeres aquila*			-	-	-	-	-	2	4	2	-	1	-	-	-	2	-	-	-	3	-	-	-	1	-	1	1	-	-	-	2	-	19
White-whiskered Puffbird	*Malacoptila panamensis*	x		-	-	-	-	-	2	-	-	1	-	-	-	-	-	-	3	1	-	-	-	-	-	-	-	-	-	-	-	-	-	7
Wood Thrush	*Hylocichla mustelina*	x	x	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2	1	1	-	-	-	1	-	-	-	2	-	-	-	1	8
Worm-eating Warbler	*Helmitheros vermivorum*		x	-	1	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Yellow Tyrannulet	*Capsiempis flaveola*			-	-	2	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Yellow-bellied Elaenia	*Elaenia flavogaster*			3	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	4
Yellow-bellied Flycatcher	*Empidonax flaviventris*		x	-	1	2	1	-	-	1	-	1	2	1	2	2	-	1	7	1	-	1	-	-	-	2	-	1	2	-	-	1	-	29

Species	Species	FS	NM	9	16	18	22	AV01	BR01	BR02	BR03	CF3	CF6	CF8	FA01	FAI01	FAI02	FAI03	LB01	LB02	LB03	OAF	OGF2	OGF3	RF2	SF2	SG01	VB01	VB02	VB03	WF1	WF2	WF3	Total
																													Study site						
Yellow-billed Cacique	*Amblycercus holosericeus*	-	-	-	1	-	-	-	-	-	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	2
Yellow-olive Flycatcher	*Tolmomyias sulphurescens*	-	-	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1	-	-	-	-	2
	Total			176	217	173	211	85	85	144	100	40	86	75	159	74	72	129	105	102	167	78	38	133	110	82	74	65	167	145	99	103	284	3578
	% Forest specialists			2.3	2.8	0.6	0.9	29.4	38.8	25.0	17.0	32.5	22.1	18.7	0.6	12.2	13.9	28.7	18.1	30.4	12.6	17.9	28.9	31.6	15.5	25.6	21.6	9.2	10.8	13.1	14.1	19.4	4.6	14.2
	% Northern Migrants			6.3	12.0	9.2	5.7	2.4	0.0	2.8	0.0	2.5	3.5	4.0	12.6	10.8	0.0	10.1	15.2	2.0	3.0	6.4	0.0	1.5	6.4	20.7	0.0	3.1	8.0	0.9	1.0	2.9	3.2	5.7
	Forest type			YSF	YSF	YSF	YSF	OSF	OGF	OSF	OSF	OGF	OGF	OGF	YSF	YSF	YSF	YSF	YSF	OGF	YSF	OSF	OGF	OGF	OGF	YSF	OGF	YSF	YSF	OSF	OSF	OSF	YSF	
	Forest age [years]			15	9	2	6	70	-	60	55	-	-	-	8	24	10	15	11	-	7	60	-	-	-	12	-	7	10	70	70	40	15	