

MASTERARBEIT | MASTER'S THESIS

Titel | Title

Differences in recapture rates of tropical understory birds between primary and secondary rainforests
in the Golfe Dulce Region, Costa Rica

verfasst von | submitted by

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angestrebter akademischer Grad | in partial fulfilment of the requirements for the degree of

Master of Science (MSc)

Wien | Vienna, 2026

Studienkennzahl lt. Studienblatt |

Degree programme code as it appears on the student record
sheet:

UA 066 879

Studienrichtung lt. Studienblatt | Degree programme as it ap-
pears on the student record sheet:

Masterstudium Naturschutz und Biodiversitätsmanagement

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Abstract (Deutsch)

Habitat- und artspezifische Unterschiede in der Standorttreue von Vögeln können wichtige Erkenntnisse über die zeitliche Stabilität von Lebensräumen und die Fähigkeit von Arten mit sich verändernden Umweltbedingungen umzugehen, liefern. Diese Studie untersucht die Faktoren, die Einfluss auf die Wiederfangraten von Unterwuchs-Vogelarten in tropischen Regenwäldern der Golfo-Dulce-Region in Costa Rica haben. Ziel der Arbeit war es zu analysieren, ob Wiederfangraten mit dem Waldalter, der Waldstruktur sowie artspezifischen Merkmalen wie Nahrungsgilde, Körpergröße, Nischenbreite und Habitatpräferenz zusammenhängen. Die Datenerhebung erfolgte mittels Netzfang (mit Japannetzen, sogenannten Mistnets) und Beringung, sowie Artbestimmung in 27 Untersuchungsflächen, die in jungen Sekundärwald, alten Sekundärwald und Primärwald unterteilt wurden.

Die Ergebnisse zeigen, dass sich die Wiederfangraten nicht signifikant zwischen den Waldtypen unterscheiden. Weiters konnte kein signifikanter Zusammenhang zwischen Waldalter und Wiederfangraten festgestellt werden. Stattdessen stellte sich heraus, dass die Vegetationsstruktur, insbesondere die Dichte der Unterwuchsvegetation, einen stärkeren Zusammenhang mit den Wiederfangraten aufweist als das Alter der Waldflächen. Auf Artebene wurde festgestellt, dass Waldspezialisten signifikant höhere Wiederfangraten aufwiesen als Nicht-Waldspezialisten, was auf eine höhere Standorttreue dieser Arten hinweist. Weitere Modelle deuteten darauf hin, dass Wiederfangraten tendenziell mit zunehmender Körpergröße abnehmen und zwischen Nahrungsgilden variieren können, wobei Insektenfresser teilweise höhere Wiederfangraten aufweisen.

Die Ergebnisse legen nahe, dass nicht das Waldalter allein, sondern vor allem Habitatstruktur, die Fragmentierung der Landschaft und ökologische Spezialisierung wichtige Faktoren für Standorttreue und Bewegungsmuster tropischer Vogelarten sind. Sekundärwälder können einen wichtigen Beitrag zum Biodiversitätsschutz leisten, insbesondere wenn sie gut mit Primärwäldern vernetzt sind, können jedoch Primärwälder für spezialisierte Arten nicht vollständig ersetzen.

Schlagwörter: Tropischer Regenwald, Avifauna, Wiederfangraten, Vegetationsstruktur, Unterwuchsvögel, Waldstruktur, Sukzession, Costa Rica

Abstract (English)

Habitat and species-specific differences in site fidelity of animals can provide important information on the temporal stability of habitats and the capability of species to deal with changing environmental conditions. This study investigates the factors influencing site fidelity quantified as recapture rates of mist-netted understory bird species in tropical rainforests of the Golfo Dulce region in Costa Rica. The aim was to analyze whether recapture rates are related to forest age, forest structure, and species-specific traits such as feeding guild, body size, niche width, and habitat preference. Data were collected using mist-netting and bird banding across 27 study sites categorized into young secondary forest, old secondary forest, and old-growth forest.

The results show that recapture rates did not differ significantly between forest types, and no significant relationship between forest age and recapture rates was found. Instead, vegetation structure, particularly understory density, showed a stronger relationship with recapture rates. At the species level, forest specialists had significantly higher recapture rates than non-forest specialists, indicating higher site fidelity. Additional models suggested that recapture rates tend to decrease with increasing body size and may vary among feeding guilds, with insectivorous species sometimes showing higher recapture rates.

These findings suggest that forest age alone is not a sufficient predictor of site fidelity and movement patterns in tropical birds. Instead, habitat structure, landscape connectivity, and ecological specialization appear to be more important drivers. Secondary forests can contribute significantly to biodiversity conservation, particularly when well connected to primary forests, but they cannot fully replace old-growth forests for highly specialized species.

Keywords: Tropical rainforests, avifauna, recapture rate, vegetation structure, understory birds, site fidelity, forest structure, forest succession, Costa Rica

1 INTRODUCTION

Tropical rainforests represent some of the most biodiverse ecosystems on earth. However, extensive anthropogenic pressures (primarily deforestation) have led to a substantial decline in biodiversity across tropical regions. In Costa Rica, historical land use change, especially from the Spanish colonial period to the mid-20th century prioritized agricultural expansion and demographic growth at the expense of forest cover, resulting in one of the highest deforestation rates among nations with tropical rain forests (Sánchez-Azofeifa et al., 2003).

On a global scale, deforestation in the humid tropics accelerated by 62% between 1990 and 2010, causing an annual net loss of approximately 8 million hectares – a trend that continues today (Pollock et al., 2022). This widespread habitat destruction contributes significantly to the global biodiversity crisis. Loss of suitable habitats is recognized as one of the primary drivers of extinction events and loss of biodiversity, especially affecting species endemic to tropical forests (Dent & Wright, 2009). Forest fragmentation exacerbates these effects by creating isolated forest patches embedded in an agricultural or urban matrix, disrupting ecological connectivity and reducing population viability (Lopez-Gutierrez et al., 2019; Shaw et al., 2013). This increased forest fragmentation results in an increase of edge effects with well documented negative impacts on forest species (Lopez-Gutierrez et al., 2019). The decreasing connectivity of forest patches further contributes to the negative effects of deforestation on the composition of rainforest species assemblages, as documented for birds (Shaw et al., 2013). Stouffer et al. (2006) found that not only patch size, but also the composition of the surrounding landscape and the size and condition of adjacent forest patches is influencing the composition of forest bird assemblages.

Despite these negative trends, secondary forests (forests regrowing through succession after disturbances such as logging or agriculture) have become increasingly prominent across tropical landscapes. In Costa Rica, conservation efforts led to substantial reforestation, e.g. the current forest cover on the Osa Peninsula reaches approximately 80% and continues to grow (Lopez-Gutierrez et al., 2019). Secondary forests may help in mitigating biodiversity loss by restoring habitat structure, facilitating species dispersal and promoting ecosystem resilience. Secondary forests, particularly when adjacent to primary forest remnants, can

harbor significant avifaunal richness (Barlow et al., 2007; Dunn, 2004). Biological corridors composed of secondary forest patches, like those established in the *Corredor Biológico La Gamba* (COBIGA) project, cover 38% of Costa Rica's territory and enhance connectivity between forest fragments, thus supporting forest-dependent bird species (Beita et al., 2021; Schulze et al., 2019).

Although primary forests support the greatest number of forest specialists, secondary forests are increasingly recognized for their conservation value. Secondary forests often support distinct species assemblages, especially during intermediate successional stages, contributing to overall biodiversity (Casas et al., 2016). Functional diversity studies in Costa Rica have shown that various avian feeding guilds (such as seed dispersers, insectivores and nectarivores) occupy regenerating forest habitats depending on resource availability and vegetation complexity (Schulze & Riedl, 2008; Fleming, 1979). Additionally, the bird community and the composition of feeding guilds inhabiting secondary forests changes depending on the surrounding landscape. In more fragmented areas of Costa Rica, the predominant surrounding landscape of secondary forest consists of agricultural areas (Sánchez-Azofeifa et al., 2003). Although most bird species avoid agricultural areas, nearly a third of all species regularly uses such habitats. There they provide important ecosystem services like pest control, pollination and most importantly seed dispersal. The usage of agricultural areas as suitable habitats differs between feeding guilds. When compared to primary forests the species richness of large frugivorous birds declines in agroforests. The same results were shown for large insectivorous birds (especially terrestrial and understory species). In contrast, nectarivores, small-to-medium sized insectivores, omnivores, granivores and small frugivores frequently use agricultural landscapes. However, their occurrence in agricultural landscapes depends on the seasonal availability of resources (Sekercioglu, 2012; Fleming, 1979).

Early stages of forest succession are characterized by rapid changes in vegetation structure and therefore resource availability, resulting in a higher turnover of both species and individuals. Different forest succession states play an important role in nature conservation as the habitat structure and habitat heterogeneity changes over time through succession (Peña-Claros, 2006). This includes providing different nutrient sources for a wide range of species,

especially forest birds. For example, secondary forests offer seasonally abundant fruit resources. Many factors that influence the habitat structure, such as the mean and maximum height of trees, the height variance between the different vegetation strata and the number of standing dead tree individuals change over the course of natural succession (Peña-Claros, 2006). But also, the number of species in each strata changes, with old secondary forests showing the highest habitat complexity regarding individual numbers in upper and intermediate strata, greater tree species richness and generally a greater variation in height. Canopy height and basal area can rapidly increase with forest succession. Hence, secondary forests can rapidly attain forest structures resembling those of old-growth forest. Furthermore, the diversity of tree species increases with ongoing forest successions (Peña-Claros, 2006). Because of these temporal changes in habitat composition and complexity the feeding guild composition differs between different succession stages. In early stages of succession nectarivores and insectivores usually have the highest abundance. This composition changes over time, with insectivores and omnivores being the most abundant feeding guilds in intermediate stages of forest succession (intermediate between young secondary forests and old-growth forests) because of the higher total food availability regarding arthropods and fruits in early to intermediate succession states (Casas et. al., 2016, Shankar Raman et al., 2002).

Birds are widely recognized as effective indicators of habitat quality and the state of the ecosystem due to their sensitivity to structural habitat changes and functional diversity across trophic levels. Functional diversity describes the range of functional roles played by species within a community. Birds provide a wide range of such functional roles in an ecosystem for example pollination, seed dispersal and removal of carrion (Sayer et. al., 2017). In this context, mist netting and mark-recapture techniques can provide valuable insights into bird community dynamics in regenerating forests. Capture and recapture rates of understorey birds can vary significantly depending on forest age, structure and edge effects. For example, insectivorous birds show higher recapture rates in forest interiors compared to edges, indicating their preference for undisturbed microhabitats. In contrast, nectarivores and some omnivores may be more prevalent at forest edges, reflecting their resource use strategies and greater tolerance for disturbance (Restrepo & Gómez, 1998; Jones et al., 2021). Recapture rates and site fidelity among different bird species are strongly influenced

by ecological and life-history traits such as body size, habitat specialization, dispersal ability and feeding guild affiliation. Gray et al. (2006) showed that granivores tend to increase in abundance after forest disturbance, while insectivores and frugivores typically decline. Moreover, species with small geographic ranges and narrow habitat requirements are more adversely affected by habitat modification than widespread generalists (Maas et al., 2009).

The degree to which bird communities recover following disturbance and succession also depends on species identity. While some feeding guilds exhibit relatively rapid recovery (<13 years), others – particularly understorey insectivores – may require 30 years or more for their population to reach pre-disturbance levels (Powell et al., 2013; Schulze et al., 2019).

Comparing recapture rates across secondary forests of different successional stages allows for an assessment of habitat suitability, population stability and movement patterns, which all are critical factors for evaluating the conservation potential of secondary forests (Powell et al., 2013). However, data on recaptures must be interpreted not only in the context of forest age and structural complexity but also with regard to the ecological characteristics and functional roles of individual species (Reid et al., 2018; Castaño-Villa et al., 2014). Only by including these factors we can accurately assess the long-term conservation value of secondary forests in tropical biodiversity hotspots such as the Golfo Dulce Region of Costa Rica.

In this study, we investigate whether recapture rates of birds are related to forest age and if differences of overall recapture rates between species are related to their biological traits. In particular, we addressed the two following hypotheses:

(1) *Younger forests are characterized by lower overall recapture rates.* Since in the first years of forest succession vegetation structure and therefore the habitat conditions for birds are changing more rapidly, younger forests may be characterized by species showing a higher spatial mobility/dispersal since they must respond to the changing habitat conditions. As result, species of younger secondary forests may show a lower site fidelity resulting in lower recapture rates.

(2) *Recapture rates are affected by vegetation structure.* However, lower recapture rates in secondary forests may be more directly related to changing vegetation structure. Since vegetation structure of sites may not only be related to forest age but also to the landscape setting, disturbance history and the succession history (e.g. natural succession vs. reforestation measures), factors like tree cover and understory density may be better predictors for differences in recapture rates than forest age. (3) *Recapture rates of species are affected by biological traits such as feeding guild affiliation, niche width, body size and habitat specialisation.* As stated before, insectivorous and frugivorous birds proved being more sensitive against habitat changes than e.g., granivores. Hence, we expect that there will be differences in recapture rates between feeding guilds, particularly in younger secondary forest. In general, species which larger niche width should be more robust against habitat changes and, therefore, should show higher site fidelity resulting in higher recapture rates than species occupying smaller niches. Additionally, recapture rates could be related to species' body size with larger species typically requiring larger home ranges thereby reducing the likelihood of recaptures. Finally, forest specialist occurring in more stable habitats and having higher difficulties dispersing to new sites should show higher site fidelity.

2 MATERIAL AND METHODS

2.1 Study area and study sites

The study was carried out in the Golfo-Dulce Region of southwestern Costa Rica in vicinity of the Tropical Research Station La Gamba (N 8.701896, W 83.202009; 70 m a.s.l.), located at the eastern border of the Piedras Blancas National Park, and the Finca Alexis (N 8.7648° W 83.1638°; 375 m a.s.l.) which serves as a field station at a higher elevation north of the tropical research station. The annual precipitation in at the Tropical Research Station La Gamba is 5836 mm, while the number of days with rain ranges between 246 and 302 days over 9 years. The average annual temperature ranges between 27.3 and 29.1°C

(Weissenhofer & Huber 2008). Fieldwork for this study took place between November and January, therefore covering the transition from the rainy to the dry season.

The 27 study sites were located at elevations between 26 m and 581 m above sea level. Sites were categorised as young secondary forests (YSF; N = 11 sites), old secondary forests (OSF; 7 sites) and old-growth forests (OGF; 9 sites) (see Figure 1).

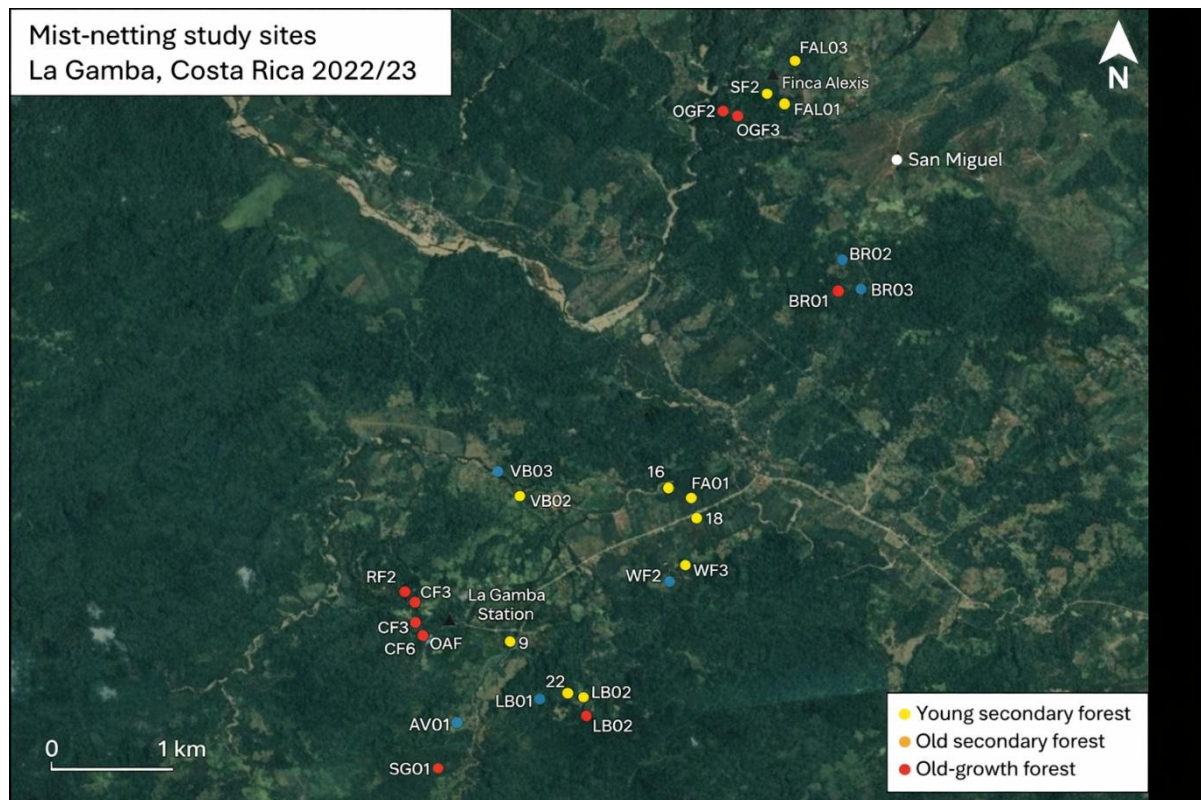


Figure 1. Study area and study sites at La Gamba and Finca Alexis, Province Puntarenas.

2.2 Sampling method

The study was carried out from 2nd November 2021 – 22nd January 2022 and 1st November 2022 – 19th January 2023. In both fieldwork periods, mist netting was used to capture understorey birds at each study site for 1.5 days with six nets (12 m x 2.5 m, 16 mm mesh size). On the first day sampling took place from 5:30 till 15:00 and from 5:30 till 11:00 on the second day. The nets were checked for birds every 30 mins. Captured individuals were

taken to the nearby temporary working area. At first the birds were identified referring to Garrigues & Dean (2014). Subsequently, several morphological measurements (such as wing length, weight, tarsus length...) were taken. For individual identification, birds were ringed with color and/or aluminium rings (with an ID number), with the exception of hummingbirds. In the later, the tip of single tail feathers was clipped to recognize recaptured birds and therefore assure no pseudo-replication during the same mist-netting periods. However, since this does not allow the identification of recaptured birds in subsequent years, hummingbirds were not further considered in this study.

2.3 Species traits

Feeding niche width was calculated using data on the relative use of different types of food sources from Wilman et. al. (2014). The niche width of every species was calculated using the following formula:

$$\frac{1}{\sum_{i=1}^{i=m} P_i^2}$$

Where P_i is the relative resource use of resource class i out of a total of m classes (Nentwig et al. 2007).

Also, data on species' body weight and feeding guild affiliation were extracted from Wilman et. al. (2014). The following five feeding guild were used: frugivores/granivores and insectivores (predominantly feeding on invertebrates).

2.4 Data analysis

To test for differences in total recapture rates between OGF, OSF and YSF sites a one-way ANOVA was calculated.

To approach normal distribution of data, variables potentially being related to recapture rates were arcsin-transformed (proportion of OGF+OSF cover, proportion of YSF cover, proportion of forest cover) or log-transformed (basal area). To test for intercorrelations between assessed landscape (percentage of OGF+OSF cover, percentage of YSF cover) and vegetation variables (understory density, tree basal area, canopy height, canopy cover), Spearman rank correlations were used. Since several variables proved to be highly correlated, a principal component analysis (PCA) with Varimax rotation and Kaiser normalization was applied. Using a model selection approach, it was evaluated to what extent the three first principal components (PCs), which explained more than 88% of the total variance, can explain differences in site-specific recapture rates. Calculated generalized linear models (GLMs) were ranked using Akaike's information criterion corrected for small-sample sizes (AICc). Subsequently, we only considered models that had an AICc difference from the best ranked model of <2. To avoid over-parametrization of models, all candidate models did not include more than two variables (PCs). The site Fal01 was excluded from these analyses due to the extremely low number of individuals ringed there during the first mist-netting period.

We also used a model selection approach to identify effects of predictor variables for secondary forest only, additionally including their age (log-transformed). Since Spearman rank correlations again identified several pairs of highly correlated predictor variables, we again calculated a PCA with Varimax rotation and Kaiser normalization. However, this did not result in a meaningful reduction of habitat variables. Therefore, and due to the relatively small sample size of only 16 secondary forest mist-netting sites not allowing for more complex models, we calculated univariate Spearman rank correlations to evaluate relationships between recapture rates and predictor variables.

A t-test was calculated to test for differences in recapture rates between forest specialists and non-forest specialists.

A model selection approach was also used to evaluate effects of feeding niche width, body weight, feeding guild affiliation and habitat preference on recapture rates of species. Calculated generalized linear models (GLMs) were again ranked using AICc values, subsequently only considered models with an AICc difference from the best ranked model of <2 . In this analysis, only species with a total number of at least 10 individuals banded in both mist-netting periods combined were taken into account. This resulted in 26 different species. Migrants were not considered in this analysis. To evaluate if predictor have a significant effect in the respective models, Wald statistics were used.

3 RESULTS

3.1 Effects of forest type on recapture rates

Mean recapture rates ($\pm$ Std.dev) ranged between 10.39 % ($\pm$ 6.11 %) for OSF sites and 11.19 % ($\pm$ 4.19 %) for OGF sites (see Figure). These small differences were not significant (one-way ANOVA: $F_2 = 0.059$, $p = 0.9528$).

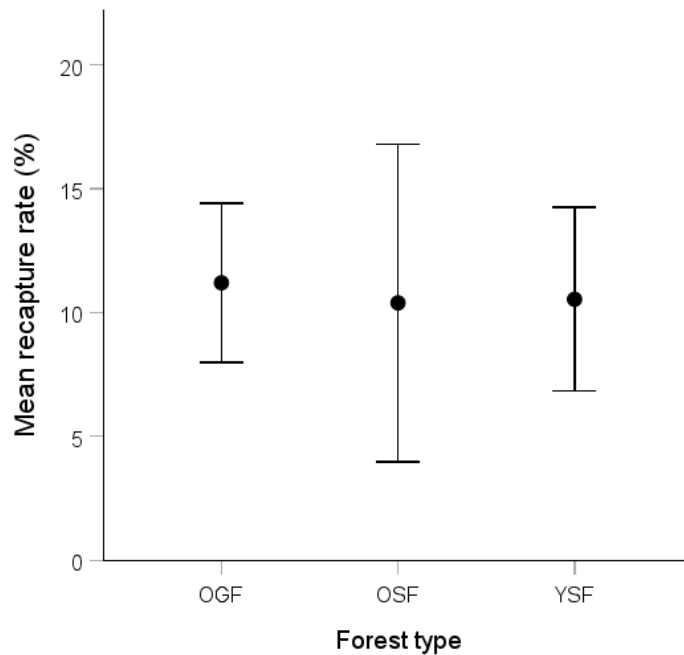


Figure 2. Mean recapture rates ($\pm$ Std.dev.) for old-growth forest (OGF), old secondary forest (OSF) and young secondary forest (YSF).

3.2 Effects of landscape composition, vegetation variables and forest age on recapture rates

When considering all mist-netting sites, Spearman rank correlations identified five pairs of highly correlated ($r > 0.5$) predictor variables (see Table 1). Hence, a PCA was used to reduce the number of variables to three PCs, which explained 88.30% of the variance (see Table 2). The PC1 had high positive factor loadings of the vegetation variables canopy height, basal area and canopy cover. The cover of the two forest cover types is highly positive (cover YSF) and negative (cover OGF + OSF) correlated with the PC2 values, respectively. PC3 predominately represents the variable understory density as indicated by its high factor loading (see Table 3).

Table 1. Results of Spearman rank correlations testing for multicollinearity of predictor variables evaluating effects of landscape and vegetation variables.

Predictor variables	OGF + OSF cover	YSF cover	Understory density	Canopy height	Basal area
YSF cover	$r = -0.866$ $p < 0.0001$				
Understory density	$r = -0.173$ $p = 0.4074$	$r = 0.140$ $p = 0.5034$			
Canopy height	$r = 0.133$ $p = 0.5247$	$r = -0.117$ $p = 0.5762$	$r = 0.2119$ $p = 0.3093$		
Basal area	$r = 0.3739$ $p = 0.0656$	$r = -0.273$ $p = 0.1875$	$r = -0.0477$ $p = 0.8208$	$r = 0.721$ $p < 0.0001$	
Canopy cover	$r = 0.2525$ $p = 0.2233$	$r = -0.215$ $p = 0.3022$	$r = 0.2384$ $p = 0.2510$	$r = 0.598$ $p = 0.0016$	$r = 0.698$ $p = 0.0001$

Table 2. Results of the principal component analysis on the two landscape and four vegetation variables.

Principal components	Eigenvalues	% of Variance	Cumulative %
PC1	2.58	42.95	42.95
PC2	1.85	30.78	73.74
PC3	0.87	14.56	88.30
PC4	0.40	6.64	94.94
PC5	0.20	3.33	98.27
PC6	0.10	1.73	100.00

Table 3. Factor loadings of two landscape and four vegetation variables.

Variable category	Variables	PC1	PC2	PC3
Landscape	Cover OGF + OSF	0.03	-0.94	-0.10
	Cover YSF	0.03	0.95	0.04
Vegetation	Understory density	0.14	0.11	0.98
	Canopy height	0.85	-0.04	0.13
	Basal area	0.96	-0.02	-0.05
	Canopy cover	0.90	0.06	0.19

The three best models of the model selection evaluating effects of the three principal components on recapture rates all included PC3. The model only including PC3 was even

ranked as overall best model. Although, two models including PC1 and PC2, respectively, belonged to the group of best models ($\Delta i < 2$), in both models only PC3 contributed significantly to the explanation of differences in recapture rates according to the Wald statistics (see Table 4). The β coefficient indicates a positive relationship between PC3 (with a high factor loading of the variable understory density) and the recapture rate. Hence, it is not surprising that there is a significant positive relationship between recapture rates and the variable understory density (see Figure 3). Since larger understory density values indicate a lower vegetation density, in fact recapture rates decrease with increasing vegetation density of the understory layer.

Table 4. Best ranked models ($\Delta i < 2$) evaluating the relationships between recapture rates and the three PCs (Tab. 3). For all included PCs, the β coefficients, the number of estimable parameters (K), the AICc values, and the differences between each model's AICc values and the AICc value of the model with the lowest AICc value (Δi) are provided. Gray marked cells indicate a significant effect of variables in the respective models according to Wald statistics.

		Model 1	Model 2	Model 3
Included variable	PC1			1.254
	PC2		-1.253	
	PC3	1.843	1.843	1.843
Model summary	K	2	3	3
	AICc	152.49	153.34	153.34
	Δi	0	0.853	0.854

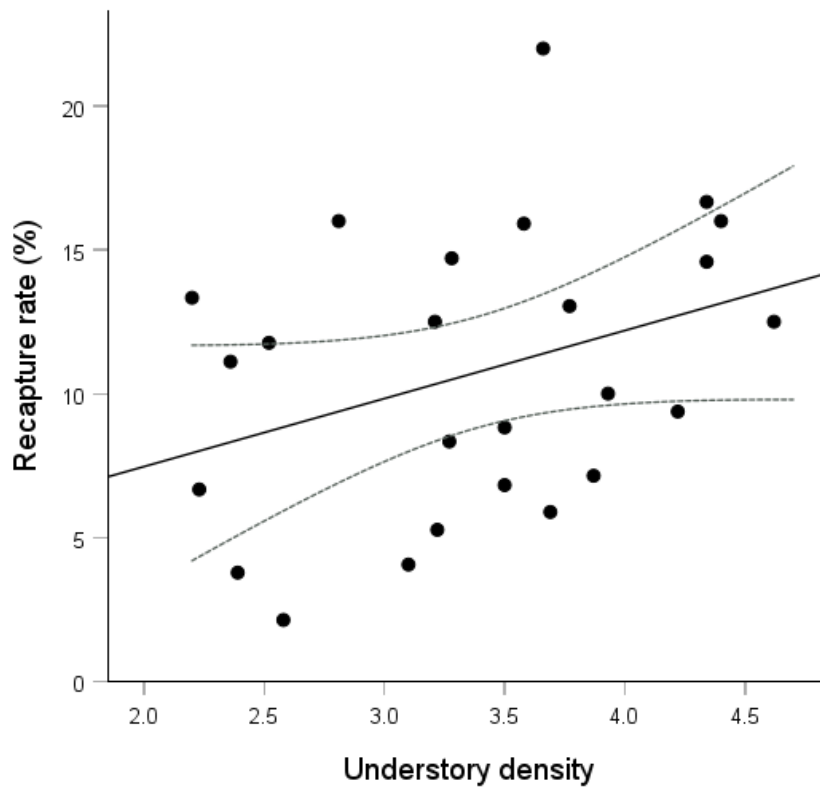


Figure 3. Relationship between recapture rate and understory density of mist-netting sites visualized by a linear regression curve ($\pm$ 95% CI).

To identify effects of our set of predictor variables for secondary forest only, additionally including their age (log-transformed), again a model selection approach was used. Variables that were not normally distributed were again log-transformed (forest age) or arcsin-transformed (proportion of OGF+OSF cover, proportion of YSF cover, proportion of forest cover). Subsequently, again Spearman rank correlations were calculated to identify pairs of highly correlated ($r > 0.5$) predictor variables (see Table).

Table 5. Results of Spearman rank correlations testing for multicollinearity of predictor variables evaluating effects of forest age, landscape and vegetation variables.

Predictor variables	Forest age	OGF + OSF cover	YSF cover	Understory density	Canopy height	Basal area
OGF + OSF cover	$r_s = 0.787$ $p = 0.0003$					
YSF cover	$r_s = -0.424$ $p = 0.1018$	$r_s = -0.728$ $p = 0.0014$				
Understory density	$r_s = 0.449$ $p = 0.0813$	$r_s = 0.305$ $p = 0.2508$	$r_s = -0.266$ $p = 0.3201$			
Canopy height	$r_s = 0.124$ $p = 0.6476$	$r_s = 0.102$ $p = 0.7082$	$r_s = -0.085$ $p = 0.7536$	$r_s = 0.123$ $p = 0.6498$		
Basal area	$r_s = 0.3213$ $p = 0.2250$	$r_s = 0.206$ $p = 0.4440$	$r_s = 0.015$ $p = 0.9566$	$r_s = 0.186$ $p = 0.4914$	$r_s = 0.765$ $p = 0.0006$	
Canopy cover	$r_s = 0.4893$ $p = 0.0544$	$r_s = 0.356$ $p = 0.1762$	$r_s = -0.289$ $p = 0.2784$	$r_s = 0.435$ $p = 0.0921$	$r_s = 0.552$ $p = 0.0266$	$r_s = 0.655$ $p = 0.0059$

Since a calculated PCA did not result in a meaningful reduction of habitat variables and due to the relatively small sample size of only 16 secondary forest mist-netting sites not allowing for more complex models, univariate Spearman rank correlations were used to evaluate relationships between recapture rates and predictor variables. Only understory density at least nearly approached a significant effect indicating a weak increase of recapture rates with decreasing understory density (see Table & Figure).

Table 6. Results of Spearman rank correlations between recapture rates and age, landscape composition and vegetation variables

Variables	Spearman rank correlation
Forest age	$r = 0.131, p = 0.6282$
OGF + OSF cover	$r = 0.305, p = 0.2515$
YSF cover	$r = -0.375, p = 0.1526$
Understory density	$r = 0.467, p = 0.0683$
Canopy height	$r = 0.072, p = 0.7907$
Basal area	$r = -0.206, p = 0.4443$

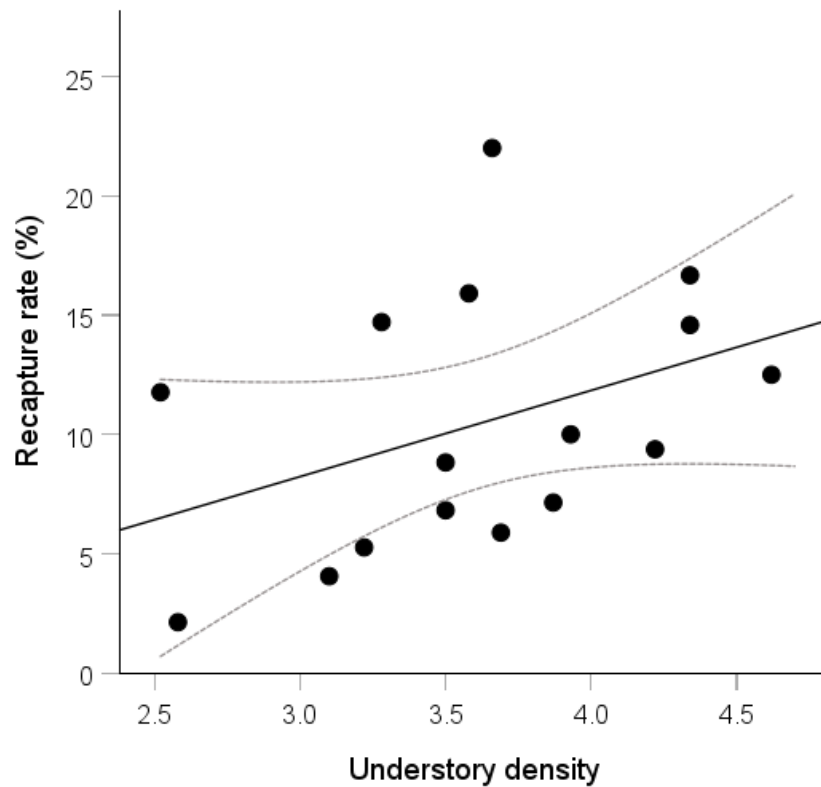


Figure 4. Relationship between recapture rate and understory density of mist-netting sites visualized by a linear regression curve ($\pm$ 95% CI), only considering secondary forest sites.

3.3 Effects of species traits on recapture rates

Recapture rates differed substantially between species (see Figure). Highest recapture rates were recorded for the Riverside Wren (23.1 %), Tropical Royal Flycatcher (20.0 %) and Black-cheeked Ant-Tanager (18.8 %). In contrast, several species were not recaptured at all (White-ruffed Manakin, Thick-billed Euphonia, Clay-colored Thrush, Buff-throated Saltator, Blue-gray Tanager).

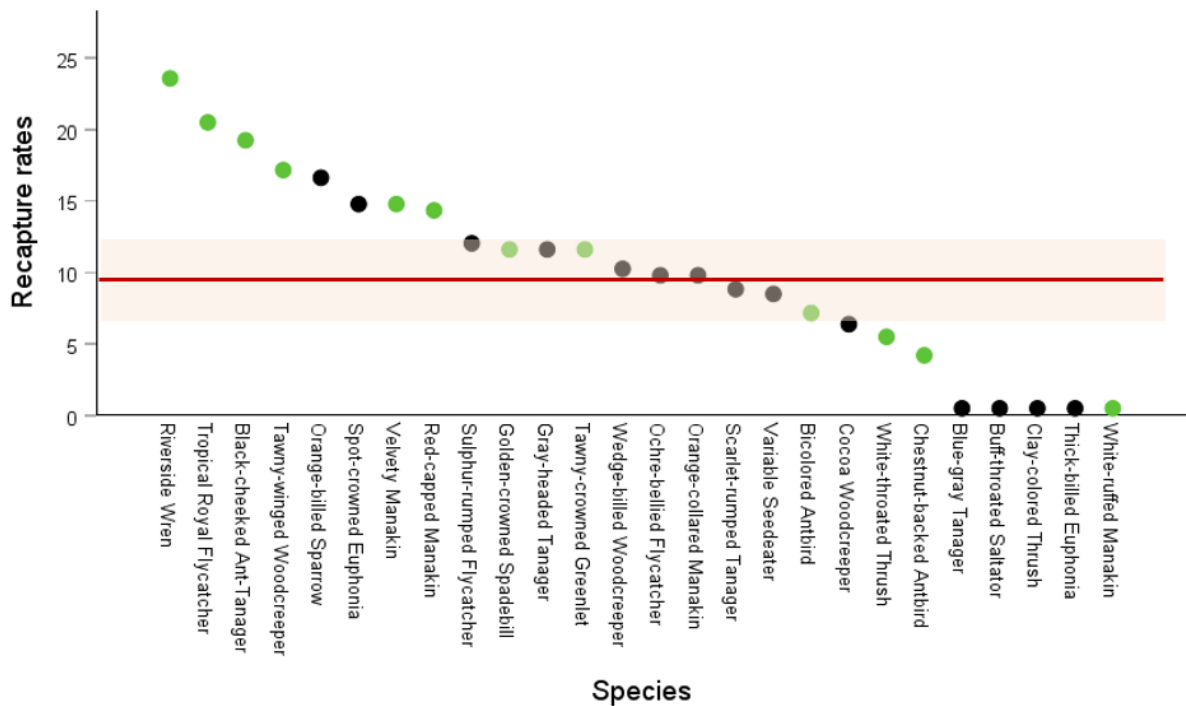


Figure 5. Recapture rates of all analysed species with at least 10 individuals individually marked in 2020/2021 (N = 26 species). Additionally, the mean recapture rate $\pm$ 95% confidence interval of the considered species is indicated. Green dots indicate species classified as forest specialists

The mean recapture rate ($\pm$ std.dev.) of forest specialists ($12.01\% \pm 7.10\%$) was significantly higher than the mean recapture rate of non-forest specialists ($7.40\% \pm 5.48\%$) (t-Test: $t = 1.87$, $df = 24$, $p = 0.0368$). The four species with highest recapture rates were all forest specialists (Riverside Wren, Tropical Royal Flycatcher, Black-cheeked Ant-Tanager, Tawny-winged Woodcreeper) (see Figure). Whether species were classified as forest specialist or not was also the only variable which was included in the best ranked model in our model selection testing for effects of forest specialization, feeding guild affiliation, body weight and niche width on recapture rates (see Table).

Table 7. Best ranked models ($\Delta i < 2$) evaluating the relationships between recapture rates and the three PCs (Tab. 3). For all included PCs, the β coefficients are provided, the number of estimable parameters (K), the AICc values), the differences between each model's AICc values and the AICc value of the model with the lowest AICc value (Δi), and the Akaike weights (w_i) are provided. Gray marked cells indicate a significant effect of variables in the respective models according to Wald statistics.

		Model 1	Model 2	Model 3	Model 4
Included variable	Forest specialist	-4.615			
	Feeding guild		-4.490	-3.236	
	Niche width				
	Body weight		-8.335		-5.996
Model summary	K	2	3	2	2
	AICc	174.28	175.69	176.14	176.15
	Δi	0	1.41	1.86	1.87

Mean recapture rate predicted by model 2 (compare Table) was estimated to be slightly larger in insectivorous bird species than in frugivorous & granivorous species (see Figure). Further, recapture rate decreased with increasing body size of understory bird species (see Figure).

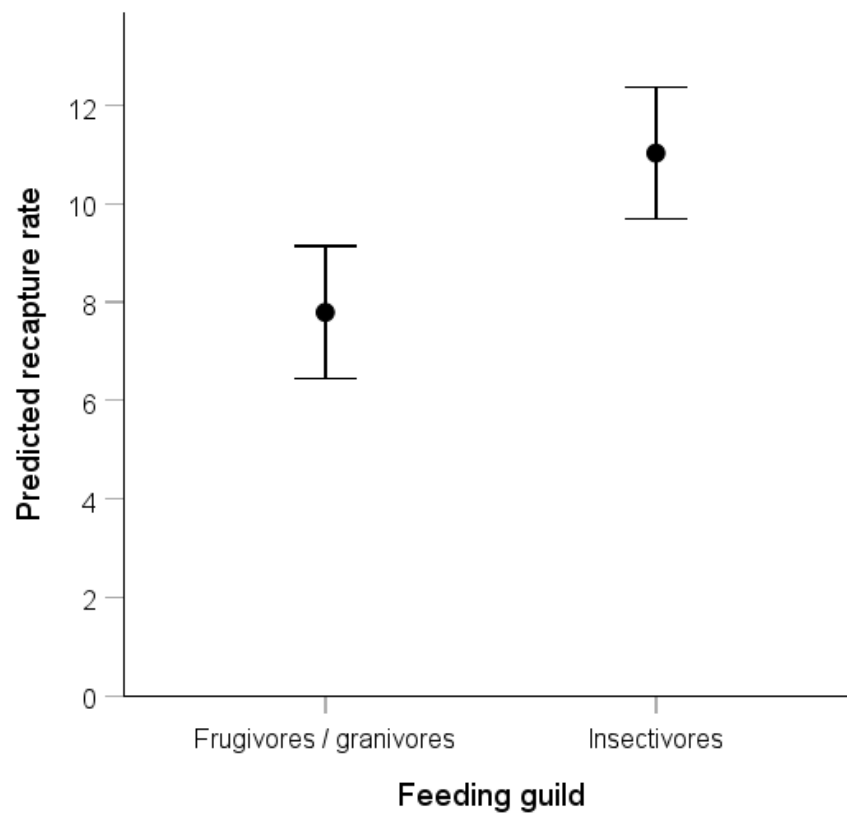


Figure 6. Mean recapture rate $\pm$ 95 % CI predicted by a GLMM (model 2; compare Tab. 7) for frugivorous /granivorous and insectivorous bird species.

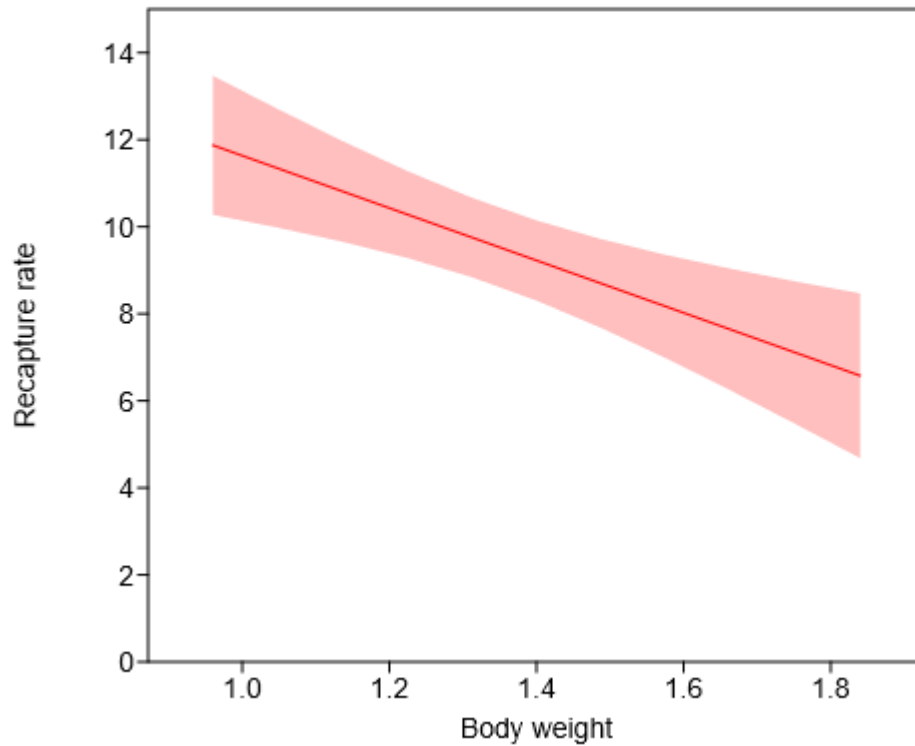


Figure 7: Relationship (linear regression $\pm$ 95 % CI) between recapture rate and log-transformed body weight (g) predicted by a GLMM (model 2; compare Tab. 7).

4 DISCUSSION

The results of this study show that there are no prominent differences in recapture rates between forest types, indicating that forest type alone (old-growth forest, old secondary forest & young secondary forest) does not significantly influence the recapture rates of tropical bird assemblages. Furthermore, no detectable effect of secondary forest age on recapture rates was found. Most likely, other parameters like connectivity of rain forest patches (of

different ages and succession states), levels of disturbance and the resulting fragmentation of habitats (with increasing edge effects), food availability and forest structure, are more important for shaping patterns of site fidelity of bird species in tropical forests. For example, studies conducted in secondary rainforests (of varying degree of connectivity to primary forests) in central Panama suggest connectivity is a more important determinant of overall species richness and community structure, than forest age (Mayhew et al., 2019).

,In contrast to this study, the age of rain forest patches influenced the occurrence, abundance and distribution of understorey bird species in other studies. Without ongoing disturbance, secondary forests gradually become structurally similar to primary forests over time, although this process may take several decades (>30 years). These structural changes affect habitat suitability for different feeding guilds inhabiting the forest (Powell et. al., 2013). The recapturing rates can increase across all feeding guilds with increasing forest age except for non-forest species. The recovery time differs between feeding guilds but shows a clear pattern. Most of the studied feeding guilds (9 out of 10 feeding guilds) recovered fast (within <13 years) after the disturbance, while insectivores need 13 to 34 years to recover to pre-disturbance-levels, with 6 out of 12 species never being caught in the secondary forest patches again (Powell et. al., 2013; Schulze et. al., 2019). While the speed of natural forest recovery is highly variable, a global meta-analysis found that species abundance, diversity and the adequate functioning of ecosystems require decades to recover to predisturbance conditions (Reid et. al., 2018; Castaño-Villa et.al., 2014). For example, regenerating tropical forests take about 50 years to recover tree species richness to predisturbance levels (Reid et. al., 2018; Castaño-Villa et.al., 2014). These long recovery times indicate that structural differences between forest patches of different ages may influence movement behaviour and site fidelity of bird species.

Human disturbance is one of the most significant drivers of habitat change in tropical forests, primarily through alterations in forest structure. The use and the subsequent abandonment of (mainly agricultural) areas start the process of natural succession resulting in heterogeneous landscapes consisting of secondary forest in different stages of succession and patches of old-growth forest (Leyequién et. al., 2014). Casas et. al. (2016) investigated the effects of forest succession on not only species composition but also feeding guild

composition in an area resembling the one of this study: a mosaic of successional forests connected through secondary rain forest patches at different successional stages. The different forest succession states play an important role in nature conservation as the habitat structure and habitat heterogeneity changes over time through succession. This includes providing different food sources for a wide range of species, especially forest birds. For example, secondary forests may provide seasonally abundant fruit resources. Many factors that influence the habitat structure, such as the mean and maximum height of trees, the height variance between the different strata and the number of standing dead tree individuals change over the course of natural succession. But also, the number of species in each strata changes, with old secondary forests showing the highest habitat complexity regarding individual numbers in upper and intermediate strata, greater tree species richness and generally a greater variation in height. Canopy height and basal area increased with forest succession, indicating that secondary forests rapidly attain forest structures similar to old-growth forest. Furthermore, the diversity of tree species increases with ongoing forest successions, showing a clear variation of diversity between the different strata, with the lowest diversity being in the canopy strata (Peña-Claros, 2006). These changes influence the availability of ecological niches and therefore the composition of feeding guilds. In early stages of succession nectarivores and insectivores often show high abundance. This composition changes over time, with insectivores and omnivores being the most abundant feeding guilds in intermediate forest stages (intermediate between young secondary forests and old-growth forests) because of the higher total food availability regarding arthropods and fruits in early to intermediate succession states (Casas et. al., 2016). In contrast, old secondary forests show higher habitat complexity and greater variation in vegetation structure, which may favour forest specialists. Because these structural and resource-related changes occur gradually over time, forest age alone may not be sufficient to explain differences in recapture rates. Instead, the interaction between vegetation structure, resource availability and landscape composition likely determine movement patterns and site fidelity of tropical bird species.

Human land use and the resulting fragmentation of tropical forests further influence the composition of bird communities. The conversion of forest into agricultural land reduces connectivity between forest patches and increases edge effects, which are known to

negatively affect forest-dependent species (Lopez-Gutierrez et. al., 2019). Reduced connectivity contributes to changes in species assemblages, as documented for tropical birds (Shaw et. al., 2013). Not only patch size, but also the composition of the surrounding landscape and the condition of adjacent forest patches influence the occurrence of bird species. Stouffer et al. (2006) showed that forest fragments surrounded by open pasture experienced strong declines in certain feeding guilds, especially insectivorous birds, with reductions of more than 95% compared to better-connected forest sites. Increased isolation also leads to higher species turnover, indicating that connectivity plays a crucial role in maintain stable bird communities, and thus influencing recapture rates (because of reduced site fidelity of bird species).

Habitat fragmentation is often accompanied by changes in vegetation structure and habitat heterogeneity, which may alter resource availability. Disturbance events such as selective logging or agricultural use can change forest structure and therefore affect bird assemblages differently depending on their ecological traits. A meta-analysis by Gray et al. (2006), including data from 56 studies covering 1214 bird species in Asia and the Neotropics, demonstrated that feeding guilds respond differently to moderate disturbance. Granivorous species often increase in abundance following disturbance, whereas insectivorous and frugivorous birds tend to decline. The response of species to disturbance is also influenced by ecological traits such as body size, geographic range and local population size (Gray et al., 2006). These differences in disturbance sensitivity may contribute to variation in recapture rates among species and forest types.

As mentioned above, the bird community and the composition of feeding guilds inhabiting secondary forests changes depending on the surrounding landscape. In more fragmented areas of Costa Rica, the predominant landscape component surrounding secondary forests are agricultural areas (Sánchez-Azofeifa et.al., 2003). Although most bird species avoid agricultural areas, nearly a third of all birds regularly uses such habitats. There they provide important ecosystem services like pest control, pollination and most importantly seed dispersal. The usage of agricultural areas as suitable habitats differs between feeding guilds. When compared to primary forests the species richness of large frugivorous birds declines in agroforests. The same results were shown for large insectivorous birds (especially

terrestrial and understorey species). In contrast, nectarivores, small-to-medium insectivorous, omnivores, granivores and small frugivores respond more frequently use agricultural landscapes. This usage is dependent on the seasonal availability of resources (Sekercioglu, 2012; Fleming, 1979). These differences highlight the importance of landscape context when interpreting patterns of species movement and recapture rates.

Comparative studies of primary forest, secondary forest, and agricultural land further demonstrate that secondary forests can support relatively high species richness, especially when located close to primary forest habitats (Dunn, 2004; Barlow et al., 2007). However, similarities in species richness between primary and secondary forest are often influenced by the proximity of undisturbed forest, which allows recolonization of secondary habitats (Barlow et al., 2007; Gardner et al., 2007). In more isolated secondary forests, species richness may be considerably lower. Highly specialized primary forest species, such as canopy frugivores or seed predators, often depend on specific resources that may not be available in secondary forests, particularly due to seasonal or reduced fruit availability (Barlow et al., 2007; Fleming, 1979). These findings indicate that forest age alone does not determine habitat quality, but must be considered together with connectivity, landscape structure, and resource availability.

Another factor that may explain the absence of a clear relationship between forest age and recapture rates is the temporal variation in food availability. In tropical forests, the availability of fruits, insects, and other resources often fluctuates seasonally, which can influence movement patterns of birds. The availability of fruit resources differs between forest types and succession stages and may vary considerably throughout the year. Plants show different strategies of fruit production, ranging from short periods with high fruit abundance to prolonged periods with low but continuous availability. Studies conducted in lowland tropical forests of Costa Rica showed strong seasonality in fruit production, with clear peaks in fruit availability during specific periods of the year (Fleming, 1979; Frankie et al., 1974). Such seasonal variation may force birds to move between habitat patches in search of resources, resulting in lower recapture rates even in structurally suitable habitats. Seasonal fluctuations in food availability may therefore mask potential effects of forest succession on site fidelity. Even if older forests provide more complex vegetation structures, temporary shortages of

food resources may cause individuals to leave a site and return later, reducing the probability of recapture. This may explain why no significant relationship between forest age, feeding guild, and recapture rates was detected in the present study, despite structural differences between forest types. Vegetation parameters such as canopy cover, canopy height, basal area, or understory density may therefore be more relevant for site fidelity than forest age alone.

The results of this study further indicate that forest specialists show higher recapture rates than non-forest specialists. This pattern is consistent with previous studies demonstrating that habitat loss and fragmentation are major drivers of species decline in tropical ecosystems (Blandón et al., 2016). Forest specialist species often depend on specific structural features of mature forests and therefore show limited movement between habitat patches. Studies on movement patterns of tropical forest birds in forest patches of different ages have shown that specialists tend to remain within intact forest habitats and rarely enter degraded or open areas (Habel et al., 2015). Some species even return to their original forest patch after experimental translocation to habitats of lower quality, indicating strong site fidelity. In contrast, generalist species usually show greater flexibility in habitat use and larger home ranges, which may result in lower recapture rates.

Differences between primary and secondary forests may also contribute to these patterns. Studies conducted in Amazonian rainforests showed that some forest specialists exhibit higher site fidelity in primary forests than in secondary forests, suggesting that secondary habitats may not always provide the necessary structural complexity or resource availability for highly specialized species (Powell et al., 2015). This supports the assumption that habitat quality, rather than forest age alone, determines the behaviour of tropical birds.

As predicted, recapture rates decreased with body size. However, this does not necessarily have to be caused by larger home ranges since the likelihood of recaptures of larger species can be also affected by decreasing mesh sizes (Leidinger 2021).

Overall, the results of this study highlight, that bird community composition in tropical forests is influenced by multiple interacting factors, including forest structure, disturbance history,

connectivity between forest patches, and seasonal variation in resource availability. These factors may affect species differently depending on their ecological requirements. Specialist species often depend on structurally complex and well-connected forest habitats, whereas generalist species may benefit from heterogeneous landscapes containing secondary forest and disturbed areas. Consequently, conservation strategies must consider the trade-off between maintaining high overall species richness and preserving habitat conditions required by specialized forest species. Secondary forests can contribute substantially to biodiversity conservation, particularly when they are well connected to primary forest habitats, but they may not fully replace old-growth forest for highly specialized species. Maintaining connected forest landscapes with patches of different successional stages may therefore be essential for preserving both species richness and functional diversity in tropical bird communities.

5 REFERENCES

- Barlow, J.; Mestre, L. A. M.; Gardner, T. A.; Peres, C. A. (2007): The value of primary, secondary and plantation forests for Amazonian birds. *Biological Conservation* 136: 212-231
- Beita, C. M.; Murillo, L. F. S.; Alvarado, L. D. A. (2021): Ecological corridors in Costa Rica: An evaluation applying landscape structure, fragmentation-connectivity process, and climate adaptation. *Conservation Science and Practice* 3: e475
- Blandon, A. C.; Perelman, S.; Ramirez, M.; López, A.; Javier, O.; Robbins, C. S. (2016): Temporal bird community dynamics are strongly affected by landscape fragmentation in a Central American tropical forest region. *Biodiversity and Conservation* 25: 311-330
- Casas, G.; Darski, B.; Müller, S. C. (2016): Habitat structure influences the diversity, richness and composition of bird assemblages in successional Atlantic rain forests. *Tropical Conservation Science* 9: 503-524
- Castaño-Villa, G. J.; Ramos-Valencia, S. A.; Fontúrbel, F. E. (2014): Fine-scale habitat structure complexity determines insectivorous bird diversity in a tropical forest. *Acta Oecologica* 61: 19-23

- Chazdon, R. L.; Broadbent, E. N.; Rozendaal, D. M. A.; Bongers, F.; Poorter, L. (2016): Carbon sequestration potential of second-growth forest regeneration in the Latin American tropics. *Science Advances* 2: e1501639
- Dent, D. H.; Wright, J. S. (2009) The future of tropical species in secondary forests: A quantitative review. *Biological Conservation* 142: 2833-2843
- Dunn, R. R. (2004): Recovery of faunal communities during tropical forest regeneration. *Conservation Biology* 18: 302-309
- Dario, F. R. (2017): Diversity of frugivorous and omnivorous birds in different stages of ecological succession in Amazon rainforest fragments. *World News of Natural Sciences* 15: 37-48
- Fleming, T.H. (1979): Do tropical frugivores compete for food? *American Zoologist* 19:1157-1172
- Frankie, G.W.; Baker, H.G.; Opler, P.A. (1974): Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *Journal of Ecology* 62: 881-919
- Gardner, T. A.; Barlow, J.; Parry, L. W.; Peres, C. P. (2007): Predicting the uncertain future of tropical forest species in a data vacuum. *Biotropica* 39: 25-30
- Gray, M.A.; Baldauf, S. L.; Mahew, P. J.; Hill, J.K. (2006): The response of avian feeding guilds to tropical forest disturbance. *Conservation Biology* 21: 133-141
- Habel, J., Hillen, J., Schmitt, T., & Fischer, C. (2015). Restricted movements and high site fidelity in three East African cloud-forest birds. *Journal of Tropical Ecology*, 32, 83-87.
- Herrera, W (2016): Climate of Costa Rica, Costa Rican Ecosystems. University of Chicago Press: 24-25
- Huber, W.; Weissenhofer, A.; Aubrecht, G. (2008): First observations of nest and nestling of the Black-cheeked Ant-Tanager *Habia atrimaxillaris*, endemic to the Golfo Dulce rainforests, Costa Rica. *Brenesia* 70: 53-56
- Jones, H. H.; Barreto, E.; Murillo, O.; Robinson, S. K. (2021): Turnover-driven loss of forest-dependent species changes avian species richness, functional diversity, and community composition in Andean forest fragments. *Global Ecology and Conservation* 32: e01922

- Kemppinen, K. M. S.; Collins, P. M.; Hole, D. G.; Wolf, C.; Ripple, W. J.; Gerber, L. R. (2020): Global reforestation and biodiversity conservation. *Conservation Biology* 34: 1221-1228
- Leidinger, P. (2021): Effects of different mesh sizes of mist nets on trapping efficiency of tropical understorey birds and implications for avian biodiversity studies. Master thesis, University of Vienna, Austria.
- Leyequién, E.; Hernández-Stefanoni, J. L.; Santamaría-Rivero, W.; Dupuy-Rada, J.M.; Chable-Santos, J.B. (2014). Effects of tropical successional forests on bird feeding guilds. Pp. 177-202. In: Nakagoshi, N.; Mabuhay, J. A. (eds), *Designing Low Carbon Societies in Landscapes. Ecological Research Monographs*. Springer, Tokyo.
- Lohbeck, M.; Poorter, L.; Martínez-Ramos, M.; Bongers, F. (2015): Biomass is the main driver of changes in ecosystem process rates during tropical forest succession. *Ecology* 96: 1242-1252
- Lopez Gutierrez, B.; Almeyda Zambrano, A. M.; Almeyda Zambrano, S. L.; Quispe Gil, C. A.; Bohlman, S.; Avellan Arias, E.; Mulder, G.; Ols, C.; Dirzo, R.; DeLuycker, A. M.; Lewis, K.; Broadbent, E. N. (2019): An island of wildlife in a human-dominated landscape: The last fragment of primary forest on the Osa Peninsula's Golfo Dulce coastline, Costa Rica. *PLoS ONE* 14: e0214390
- Maas, B.; Putra, D. D.; Waltert, M.; Clough, Y.; Tschardtke, T.; Schulze, C. H. (2009): Six years of habitat modification in a tropical rainforest margin of Indonesia do not affect bird diversity but endemic forest species. *Biological Conservation* 142: 2665-2671
- Marín-Spiotta, E.; Sharma, S. (2012): Carbon storage in successional and plantation forest soils: a tropical analysis. *Global Ecology and Biogeography* 22: 105-117
- Mayhew, R., J.; Tobias, J.; Bunnefeld, L.; Dent, D. (2019): Connectivity with primary forest determines the value of secondary tropical forests for bird conservation. *Biotropica* 51: 219-233
- Peña-Claros, M. (2006): Changes in forest structure and species composition during secondary forest succession in the Bolivian Amazon. *Biotropica* 35: 450-461
- Pollock, H. S.; Toms, J. D.; Tarwater, C. E.; Benson, T. J.; Karr, J. R.; Brawn, J. D. (2022): Long-term monitoring reveals widespread and severe declines of understory birds in

- a protected Neotropical forest. *Proceedings of the National Academy of Sciences* 119: e2108731119
- Powell, L.; Stouffer, P. C.; Johnson, E. I. (2013): Recovery of understory bird movement across the interface of primary and secondary Amazon rainforest. *The Auk* 130: 459-468
- Powell, L.; Wolfe, J. D.; Johnson, E. I.; Hines, J. E.; Nichols, J. D.; Stouffer, P. C. (2015): Heterogeneous movement of insectivorous Amazonian birds through primary and secondary forest: A case study using multistate models with radiotelemetry data. *Biological Conservation* 188: 100-108
- Powers, J. S.; Marín-Spiotta, E. (2017): Ecosystem processes and biogeochemical cycles in secondary tropical forest succession. *Annual Review of Ecology, Evolution, and Systematics* 48: 497-519
- Reid, J. L.; Fagan, M. E.; Lucas, J.; Slaughter, J.; Zahawi, R. A. (2018): The ephemerality of secondary forests in southern Costa Rica. *Conservation Letters* 12: e12607
- Restrepo, C.; Gómez, N. (1998): Responses of understory birds to anthropogenic edges in a neotropical montane forest. *Ecological Applications* 8: 170-183
- Sánchez-Azofeifa, G. A.; Daily, G. C.; Pfaff, A. S. P.; Busch, C. (2003): Integrity and isolation of Costa Rica's national parks and biological reserves: examining the dynamics of land-cover change. *Biological Conservation* 109: 123-125
- Sayer, C. A.; Bullock, J. M.; Martin, P. A. (2017): Dynamics of avian species and functional diversity in tropical forests. *Biological Conservation* 211: 1-9
- Schulze, C. H.; Leidinger, P.; Paces, B.; Reyes P., Andrés F. (2019): The importance of reforested and naturally regenerating young forest patches as secondary habitats of forest birds in the Biological Corridor La Gamba, Costa Rica. *Acta ZooBot Austria* 156: 79-98.
- Schulze, C. H.; Riedl, I. (2008): Bird assemblages of forested and human-modified countryside habitats in the Pacific lowlands of southern Costa Rica. *Stapfia* 88: 395-408
- Seaman, B. S.; Schulze, C. H. (2010): The importance of gallery forest in the tropical lowlands of Costa Rica for understory forest birds. *Biological Conservation* 143: 391-398

- Sekercioglu, C. H. (2012): Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *Journal of Ornithology* 153: 153-161
- Shankar Raman, T. R.; Rawat, G. S.; Johnsingh, A. J. T. (2002): Recovery of tropical rainforest avifauna in relation to vegetation succession following shifting cultivation in Mizoram, north-east India. *Journal of Applied Ecology* 35: 214-231
- Shaw, D. W.; Escalante, P.; Rappole, J.H.; Ramos, M. A.; Oehlenschläger, R. J.; Warner, D. W.; Winker, K. (2013): Decadal changes and delayed avian species losses due to deforestation in the northern Neotropics. *PeerJ* 1: e179
- Stouffer, P. C.; Bierregaard Jr., R.O.; Strong, C.; Lovejoy, T. E. (2006): Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20: 1212-1223
- Weissenhofer, A.; Huber, W. (2008). The climate of the Esquinas rainforest. *Stapfia* 88: 59-62.
- Wilman, H.; Belmaker, J.; Simpson, J.; De la Rosa, C. (2014): Species-level foraging attributes of the world's birds and mammals. *Ecology* 95: 2027-2027
- Wilson, S.; Wilson, A. G. (2011): Community composition and annual survival of lowland tropical forest birds on the Osa Peninsula, Costa Rica. *Ornitologia Neotropical* 22: 421-436.