A temporal and spatial analysis of the frugivorous bird community in a cloud forest in Costa Rica

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5th of January 2026, Velp
Bachelor's degree Forest- and Nature Conservation

Colophon

Title:	A temporal and spatial analysis of the frugivorous bird community in a cloud forest in Costa Rica
Organization thesis:	Cloudbridge Nature Reserve
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Course code:	VBN4AVDNE
Date of submission:	16-03-26

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Preface

With pride, I present this thesis as the final component of the Forest and Nature Management program at Van Hall Larenstein University of Applied Sciences, completing my bachelor's degree. The topic of this research originated from my internship in Suriname during 2024–2025, where my interest in frugivorous bird species first developed. Through the guidance and enthusiasm of Serano Ramcharan, to whom I am deeply grateful, I learned a great deal about the avifauna of Suriname and became particularly interested in avian foraging guilds.

My motivation for this research derived from a broader interest in ecosystem services provided by birds, an area that is often overshadowed by most research focusing primarily on the role of large mammals. I became especially intrigued by the role of frugivorous birds in seed dispersal, a process that is critical in fragmented or deforested landscapes where large mammals are often absent. This thesis therefore aims to highlight the importance of frugivorous bird species and to emphasize the essential ecosystem services they provide.

I would like to express my sincere gratitude to Dr. Rens Brouwer for his excellent supervision throughout this research process. His guidance, particularly in statistical analysis, deepened my understanding of quantitative methods and strengthened the scientific quality of this thesis. His constructive feedback, critical questioning of methodology and hypotheses, and supportive attitude enabled me to grow academically while maintaining confidence in my own abilities.

I am also incredibly grateful to Steven Loebelt, whose support during the data collection period was invaluable. Without his help, especially during the early morning bird counts, the fieldwork would have been more demanding.

Furthermore, I would like to thank my sponsors, Frances Nijssen, Anna Timmermans, and Ilse Dijk. Without their financial support, I would not have been able to fulfil my wish to conduct this research abroad.
I am deeply thankful to my friends, family, and my partner for their emotional support throughout my time abroad, which contributed to making this experience meaningful and manageable.

Additionally, I would like to express my appreciation to Van Hall Larenstein University of Applied Sciences. The Tropical Forestry program has provided me with both valuable life experiences and a strong theoretical foundation, enabling me to conduct this research effectively. The facilities and support offered by the university made this thesis possible.

Finally, my sincere gratefulness goes to Blanca Cejalvo Insausti, Greillin Fallas-Rodriguez, and the Cloudbridge staff for making my stay at Cloudbridge both pleasant and enjoyable. Their assistance with weekly planning and logistical support ensured a comfortable and productive research environment.

Abstract

Tropical cloud forests are biodiversity hotspots that support a high diversity of frugivorous birds, which play a key role in forest regeneration through seed dispersal. Despite ongoing reforestation efforts, the temporal responses of frugivorous bird communities to natural regeneration and active planting remain poorly understood. It is unclear how species richness, specialization, species accumulation changes over time in restored forests, and how forest age, elevation, and edge distances shape these patterns. Understanding these dynamics is crucial to evaluate the effectiveness of restoration strategies and their capacity to restore ecosystem functions in fragmented cloud forest landscapes.

The aim of the study was to assess how frugivorous bird communities change over time in old-growth, naturally regenerated, and planted forests in a cloud forest in Costa Rica between 2016 and 2025. In specific, this study investigated spatial variables such as forest type, forest age, edge distance, and elevation influenced species richness, specialism, and species accumulation.

The study recorded 124 frugivorous bird species from 22 families. Naturally regenerated forests consistently supported highest species richness, followed by mixed planted/naturally regenerated forests, planted forests and finally old-growth forests. Species richness declined significantly over time in all forest types, with an average annual decrease of 7,6% between 2016 and 2025. The proportion of specialist frugivorous bird species also decreased significantly between 2016 and 2025. Distances from forest edges had a positive effect on species richness, whereas elevation and forest age showed no significant effects.
Species accumulation curves indicated that both naturally regenerated and planted forests have high potential to support relatively high species richness, whereas old-growth forests exhibited the lowest species accumulation.

These results suggest that both naturally regenerated and planted forests can contribute to the recovery of frugivorous bird species richness in restored cloud forests. Naturally regenerated forests currently support the highest species richness, while planted forests show similar species accumulation patterns over time, indicating their potential to support diverse frugivorous bird communities in the future. However, the consistent decline in species richness and the decreasing proportion of specialist species suggest that the functional recovery of frugivorous bird communities may still be incomplete. The increasing dominance of generalist bird species may indicate that restored forests do not yet provide sufficient resources or habitat conditions required by specialist frugivores birds.

Long-term monitoring will therefore be essential to determine whether these forests continue to recover or whether current trends persist. Integrating bird monitoring with data on vegetation structure, fruit availability, and environmental conditions would further improve understanding of the drivers shaping frugivorous bird communities and help evaluate the long-term effectiveness of restoration strategies in Cloudbridge Nature Reserve.

Contents

1 Introduction

Tropical rainforests are estimated to host more than half of the world's vertebrates. Alarming deforestation rates threaten the future existence of these vertebrates. In 2023, 6.37 million hectares of forest were lost, estimated to be between 7.7–13.4 million football fields (Forest Declaration Assessment partners, 2024). The current leading driver of deforestation is agricultural expansion, accounting for 40% of deforestation rates (FAO & UNEP, 2020). The effects of forest cover loss alter climate regulation functions negatively, such as precipitation (Smith et al., 2023). Other ecosystem services such as carbon sequestration, intrinsic value, and biodiversity are also negatively impacted.

To counteract the negative effects of deforestation, the United Nations Climate Summit has declared to reforest ninety million hectares of deforested land by 2030 (Holl, 2017). Therefore, an increase in secondary forests (e.g., naturally regenerated and planted) is likely a future scenario. However, secondary forests typically support fewer undisturbed dependent taxa of organisms than old-growth forests (FAO & UNEP, 2020; Bruijnzeel et al., 2011), raising concerns about their capacity to conserve biodiversity effectively.

The conservation of biodiversity is a vital component for reforestation practices because biodiversity is closely related to ecosystem functionality. Essential ecosystem functions, such as plant-animal interactions contribute to the resilience of a forest, which in turn makes forests less susceptible to hazards, pests, or climate change. The regeneration of these ecosystem functions, apart from structural recovery of vegetation (e.g. canopy, biomass, tree height, and tree density), is decisive for long-term success of reforestation initiatives.

In the Neotropics, plant-animal interactions remain one of the most critical ecological processes for forest resilience. Birds, especially frugivorous birds, play a vital role in plant-animal interactions through seed dispersal networks. Over 50% of the 4,199 terrestrial bird species are predominantly frugivorous in the Neotropics, meaning that changes in the frugivorous bird community can have cascading effects on plant-animal interactions (Carlo et al., 2022). Frugivorous bird communities are composed of species that differ in dietary breadth and habitat specialization. By dispersing seeds across forests, frugivorous birds directly influence tree species composition, forest structure, and successional trajectories (Gomes et al., 2008; Emer et al., 2018). An incomplete recovery of the frugivorous bird community might therefore reflect an incomplete forest recovery over time. This particularly is revealed when the ratio of specialism within a frugivorous bird community is revealed. Generalist frugivorous bird species consume a wide variety of fruits and are often more tolerant of disturbed habitats. In early successional forests, these generalist frugivorous birds contribute to seed-rains and facilitating colonization by pioneer plant species (Carlo & Morales, 2016). Specialist frugivorous birds depend on specific fruit traits or plant species and are typically associated with structurally complex mature forests. Specialist species are often more sensitive to habitat disturbances, making the presence or absence of specialistic frugivory birds suitable as bio-indicators of ecosystem functioning (Caraballo-Ortiz et al., 2017; Carlo et al., 2022). Monitoring both frugivorous species richness and the specialization ratio therefore provides insight into forest recovery.

The frugivorous bird community remain a complex but valuable indicator of reforestation success. These communities are shaped and influenced by different spatial variables. Understanding the effects of the spatial variables are necessary to effectively restore forests. This is particularly challenging in tropical cloud forests. Tropical cloud forests only persevere on mountain ranges, where restricted elevational ranges are created by persistent cloud immersion. These mountain ranges create naturally fragmented landscapes through steep cliffs and hills, making local circumstances quickly different. Optimal hydrologic circumstances are linked to cloud immersion patterns, creating long elevational ranged bands of tropical cloud forests (Merlin & Juvik, 1995; Bruijnzeel et al., 2011). Through these spatial characteristics, the tropical cloud forests are a complex ecosystem that needs to be carefully studied to assess reforestation success.

Elevation is one of the spatial variables that serves as an environmental filter for the perseverance of frugivorous birds. From 1500 meters, increased elevation is associated with lower temperatures and changes in vegetation composition. Environmental filtering at higher elevations constrains the distribution of both plant and bird species, excluding taxa lacking physiological or ecological adaptations to harsher abiotic conditions. This filtering decreases species richness patterns and increases the specialization of frugivorous bird communities with increasing elevation (Rabhek, 1997; Quintero & Jetz, 2018; Dehling et al., 2014).

Forest type (e.g., planted, naturally regenerated and old-growth forests) strongly influences vegetation structure, tree species composition, and fruit availability. Old-growth forests generally exhibit high structural complexity, vertical stratification, and diverse fruit assemblages, supporting a wide range of ecological niches (Gomes et al., 2008;

Bregman et al., 2016). Naturally regenerated forests develop through divers seed dispersal, variable site conditions, and unassisted successional dynamics. This often results in a heterogeneous vegetation structure. Planted forests, in contrast, frequently originate from active restoration schemes that prioritize a limited number of tree species, leading to a more homogeneous stand structure, particularly during early development. These structural differences can influence niche availability and resource diversity for frugivorous birds, but knowledge of long-term faunal recovery is still lacking (Bruijnzeel et al., 2011; Staples et al., 2019).

Forest age further mediates these patterns. As forests mature, structural complexity increases through canopy closure, vertical stratification, and diversification of fruiting plant communities. Early successional stages are typically dominated by small and abundant fruits, whereas later stages increasingly include large-seeded and fleshy-fruited species. Such temporal shifts in resource availability can alter which frugivorous bird species are able to persist. This can potentially promote greater niche differentiation and specialization over time (Vargas-Daza et al., 2023).

Landscape configuration, particularly the distance to forest edges, also influences frugivorous bird communities. Forest edges experience altered microclimatic conditions, increased light penetration, and different vegetation structures compared with forest interiors. According to the Intermediate Disturbance Hypothesis, species richness may peak at intermediate disturbance levels. Where competitive exclusion is reduced, and environmental stress remains tolerable, the frugivorous bird species richness increases (Moi et al., 2020; Terraube et al., 2016). Forest edges represent these intermediate conditions, potentially allowing the coexistence of interior forest bird species and edge-associated bird species (Vallejos et al., 2024).

To assess reforestation success comprehensively, it is necessary to evaluate not only frugivorous bird species richness and specialism, but also frugivorous species accumulation trajectories. Species accumulation trajectories describe how community diversity builds over time. Rapid initial increases reflect early colonization by generalist frugivorous bird species, whereas gradual long-term increases can indicate ongoing replacement of specialist frugivorous bird species and increasing niche differentiation. Comparisons of these trajectories among old-growth, naturally regenerated, and planted forests can reveal differences in restoration potential and successional dynamics.

Despite growing research on tropical forest restoration, a limited understanding exists regarding how frugivorous bird communities respond temporally and spatially across different reforestation strategies in tropical cloud forests. In particular, it remains unclear whether planted and naturally regenerated forests converge toward the old-growth community structure over time, and how the spatial variables (e.g., elevation, edge distance, forest age, and forest type) modulate these trajectories (Bruijnzeel et al., 2011).

This study investigates temporal and spatial changes in frugivorous bird communities across planted, naturally regenerated, and old-growth tropical cloud forests in Costa Rica between 2016-2025. By examining frugivorous bird species richness, specialism, and species accumulation trajectories in relation to forest type, forest age, elevation, and edge distance, this study aims to clarify how spatial variables shape the ecological recovery of seed dispersal networks and contribute to reforestation success.

2 Problem description

Cloudbridge Nature Reserve actively engages in the reforestation and conservation of cloud forests in Costa Rica. Since its establishment, previously degraded agricultural lands have been restored through various reforestation strategies, including naturally regenerated and planted forests. In addition, old-growth forests remnants are present within the reserve. As a result, the landscape consists of a mosaic of forest types representing various restoration strategies and successional stages (Cloudbridge Nature Reserve, 2025a).

Since 2016, systematic bird monitoring has been conducted through the establishment of permanent point-count locations (Cloudbridge Nature Reserve, 2025a). However, despite nearly a decade of monitoring, temporal changes in frugivorous bird communities have not been evaluated. Spatial differences among forest types and recovery methods, as well as the development over time, remain unclear. Providing insight into these unknown subjects could help evaluate past reforestation methods. The knowledge gained could therefore be implemented in future reforestation projects initiated by Cloudbridge Nature Reserve.

Frugivorous birds play a central role in forest recovery because of seed dispersal, enhance plant recruitment, and contribute to maintaining plant species diversity and forest structure (Carlo et al., 2022; Palacio et al., 2019). Through seed dispersal, frugivorous birds influence patterns of natural regeneration and vegetation composition. When frugivorous bird diversity is low, or specialist species are absent, seed dispersal networks may become simplified, potentially slowing forest recovery and reducing ecosystem resilience (Gray et al., 2006; Emer et al., 2018). In contrast, increases in frugivorous bird species richness and specialism may indicate increasing structural complexity, fruit availability, and ecological functioning.

Changes in frugivorous bird species richness, community specialism and species accumulation can therefore serve as ecological indicators of forest development and restoration success. However, these community dynamics are shaped by multiple spatial variables, including forest type, forest age, elevation, and edge distance (Carlo et al., 2022). Understanding how these spatial and temporal factors influence frugivorous bird communities is essential to evaluate whether different reforestation strategies effectively promote ecological recovery.
Currently, the temporal trajectories of frugivorous bird communities within Cloudbridge Nature Reserve remain unknown. This knowledge gap limits the organization’s ability to assess whether naturally regenerated, planted, and old-growth forests differ in their capacity to support diverse and specialized frugivorous bird communities over time.

Furthermore, Cloudbridge Nature Reserve is considering future land acquisition for reforestation. To design effective restoration strategies, it is important to identify which spatial characteristics most strongly influence the recovery of frugivorous bird communities and, by extension, ecosystem functioning, and forest resilience. Evaluating spatial and temporal patterns in species richness, community specialism, and species accumulation will therefore provide Cloudbridge Nature Reserve with practical guidance for future reforestation planning and long-term conservation management. In doing so, the study contributes directly to sustainability by identifying restoration and landscape conditions that enhance biodiversity recovery, strengthen seed dispersal networks, support long-term forest regeneration, and ecosystem resilience.

3 Goal & sustainability

The goal of this study is to provide scientific and practical insight into how different reforestation strategies influence the recovery of frugivorous bird communities over time. By identifying spatial and temporal differences in species richness, community specialism, and species accumulation, this research supports evidence-based decision-making within Cloudbridge Nature Reserve.

The findings contribute to reducing uncertainty in future land acquisition and restoration planning. By understanding which forest characteristics promote diverse and specialized frugivorous bird communities, restoration efforts can be designed to enhance biodiversity and ecosystem functioning more effectively.

Frugivorous birds are closely linked to seed dispersal and natural regeneration processes. Supporting their recovery contributes to long-term forest resilience and structural development. Therefore, improving knowledge of how forest type and forest development influences frugivorous bird communities promotes more sustainable reforestation practices.

Beyond the local scale, this study contributes to a broader understanding of forest recovery trajectories in tropical cloud forests. The insights gained can support policymakers and conservation practitioners in selecting restoration strategies that strengthen biodiversity conservation and ecosystem resilience in restoration initiatives.

4 Research questions

How does the frugivorous bird community change in naturally regenerated, planted, and old-growth Cloud forest in Costa Rica between 2016 and 2025?

4.1 Supportive questions

1. *How does the species richness of the frugivorous bird community differ between naturally regenerated, planted, and old-growth forests in 2025?*

2. *How does species richness in the frugivorous bird community change in naturally regenerated, planted, old-growth forest between 2016 and 2025?*

3. *How does frugivorous bird community specialism change in naturally regenerated, planted, and old-growth forest between 2016 and 2025?*

4. *How does species accumulation differ among naturally regenerated, planted, and old-growth forest between 2016 and 2025?*

4.2 Hypotheses

The hypotheses are derived from existing literature on how temporal and spatial variables (forest type, forest age, elevation, and edge effects) shape frugivorous bird communities, which are characterized by species richness, specialism, and species accumulation trajectories. Appendix A contains a table describing the proposed hypotheses for each spatial variable's effect on frugivorous bird species richness and specialism.

4.2.1 Species richness

Frugivorous bird species richness, hereafter referred to as species richness, is expected to vary among forest types due to differences in structural complexity and tree species composition, which influence resource availability and the diversity of ecological niches available to birds. Species richness is hypothesized to be highest in old-growth forests, followed by naturally regenerated forests, and lowest in planted forests (Bregman et al., 2016).

Independently of forest type, species richness is expected to increase with forest age, as structural complexity and fruit resource diversity develop over time (Bu et al., 2014).

Species richness is expected to increase with elevation up to approximately 1500 m above sea level. Species richness is expected to decline at higher elevations, as environmental conditions become more restrictive and fewer species are able to persist (Quintero & Jetz, 2018; Rabhek, 1997).

Species richness is expected to be higher closer to forest edges, where moderate levels of disturbance allow both forest-interior and edge-associated species to occur together. According to the intermediate disturbance hypothesis, such conditions can increase species richness by preventing competitive exclusion while still maintaining suitable habitat for a wide range of species (Connell, 1978; Moi et al., 2020; Terraube et al., 2016).

4.2.2 Frugivorous specialism

Old-growth forests are expected to show the highest levels of frugivorous bird specialism, hereafter referred to as specialism. Naturally regenerated forests are expected to show higher specialism than planted forests due to greater long-term structural heterogeneity (Falconí-López et al., 2024; Vargas-Daza et al., 2023).

Specialism is expected to increase with forest age, as increasing structural complexity promote niche differentiation and resource partitioning (Vargaz-Daza et al., 2023).

Specialism is expected to increase with greater distance from forest edges, as specialist species are more restricted to stable forest interiors and specific niches (Vallejos et al., 2024).

With increasing elevation, specialism is expected to increase due to environmental filtering that only allows well-adapted species (Dehling et al., 2014).

4.2.3 Species accumulation trajectories

Species accumulation trajectories are expected to reflect differences in structural complexity and successional development among forest types.

Old-growth forests are expected to show high and relatively saturated accumulation curves.

Planted forests are expected to show relatively rapid initial increases in species accumulation, because structural restoration of trees occurs relatively quickly compared to naturally regenerated forests.

Naturally regenerated forests are expected to show a slower increase in species accumulation compared to planted forests, as structural complexity develops more slowly through competition of weeds and grasses (Chazdon & Guariguata, 2016).

5 Methodology

In this chapter, the methodology used to study frugivorous bird communities at Cloudbridge Nature Reserve is described, including site characteristics, forest types, bird classification, and data collection. The chapter outlines data collection protocols, spatial variables, and statistical procedures employed to analyze species richness, community specialization, and species accumulation over time. Detailed methods ensure that analyses are reproducible and directly address the main research question and sub-questions concerning changes in frugivorous bird communities across different forest types between 2016 and 2025.

5.1 Site description

The research was conducted at Cloudbridge Nature Reserve, located in the Talamanca Mountains and bordering the Chirripó National Park, which is the largest national park of Costa Rica. Cloudbridge has established reforestation projects since its origination in 2002, which resulted in an ecological corridor for different mammals, birds, and various organisms (Cloudbridge Nature Reserve, 2025a). Cloud forests are home to a variety of species, and the forests at Cloudbridge are no exception. An extensive bird list, gathered by previous researchers, has accumulated 360 bird species over the years (Cloudbridge Nature Reserve, 2025b).
Annual rainfall is estimated at 4000 mm, with an average temperature between 21-25 degrees Celsius (Giddy, 2006). Lastly, the elevation ranges between 1500 and roughly 2300 meters in the reserve (Cloudbridge Nature Reserve, 2025b).

5.2 Forest type descriptions

Cloudbridge is a transitional cloud forest, which has undergone extensive natural and assisted regeneration since its establishment in 2002. Historically, the landscape consisted of pasture and agricultural lands, interspersed with remnant patches of old-growth forests. In 2025, the reserve has identified three main forest types: old-growth (OG), naturally regenerated (NR), and planted (P) forest (see figure 1). An additional forest type is added in this research: planted/naturally regenerated (P/NR). The mixed forest type was added because data collection of birds in previous years was on the edge of P/NR.

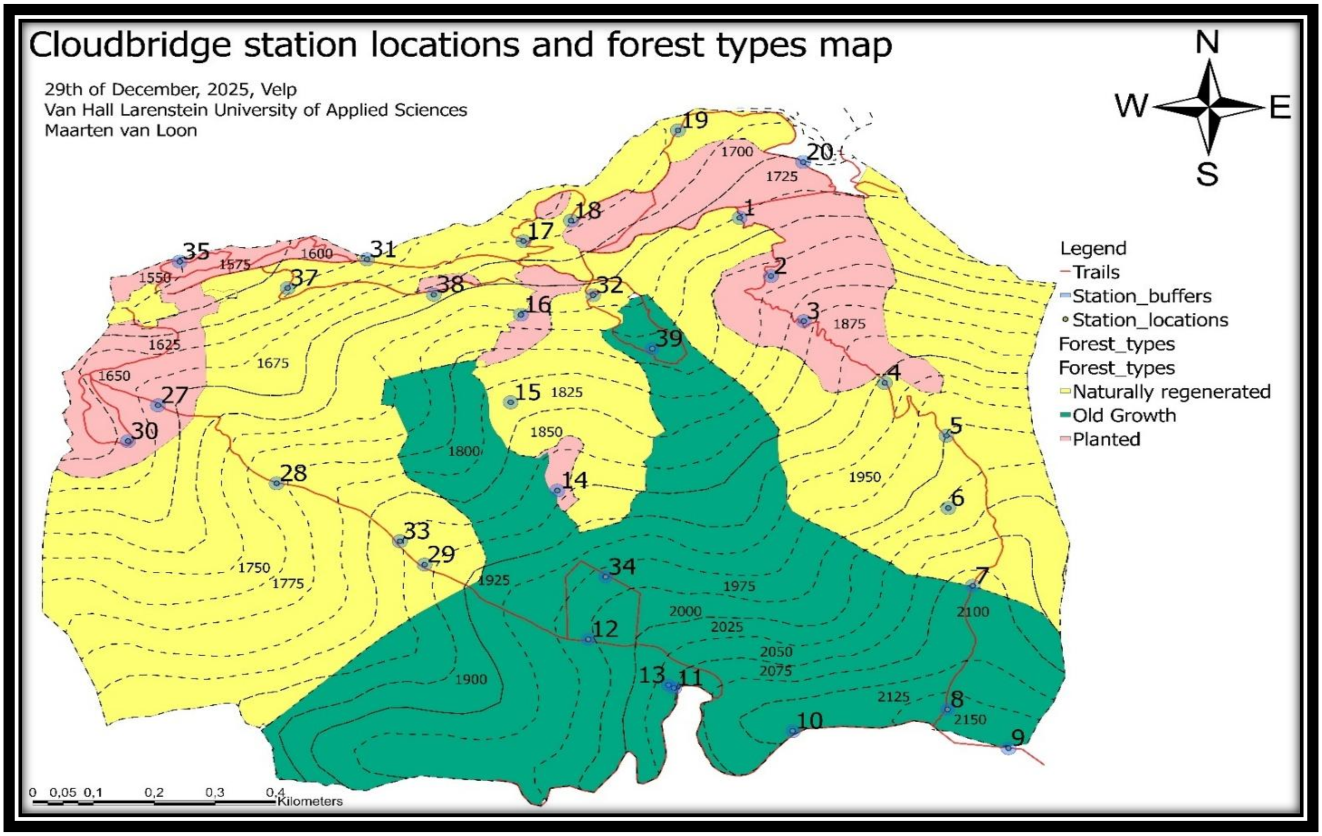

Figure 1: Station locations with forest types in Cloudbridge Nature Reserve

The forest types differ in structure, elevational range, and forest age. As the reserve is dependent on interns and graduates for the data collection, information on these subjects remains limited and understudied (G. Fallas-

Rodríguez, personal communications, 14th of October 2025). The forest structure differed significantly across the forest types in mean diameter at breast height (DBH), mean tree height in meters (m), and mean basal area (m2) (Fleer, 2017). The differences between the forest types are shown in table 1.

Table 1 Structural differences between the forest types (Fleer, 2017)

Forest type	Mean basal area in square meters	Mean DBH in cm (trees > 10 cm)	Mean tree height in meters
Old-growth	6,6 m^2	23.8 cm	14,76 m
Naturally regenerated	3.3 m^2	20.3 cm	10.55 m
Planted	2.5 m^2	21.1 cm	10,33 m

5.2.1 Old-growth forest

The old-growth (OG) forests are estimated to be over 70 years old and cover approximately 70 hectares (Cloudbridge, 2025b). Access into the OG forests is done through the trails: Jilguero, Montana, Sentinel, and Chirripó. OG forests have the highest mean of DBH (23.8 cm), the largest basal area (6.6 m^2), and the greatest mean tree height (14.76 m), indicating a late-successional forest (Fleer, 2017).

The OG forests differ in tree composition across the elevational gradient. Above 2000 m, these OG forests should resemble oak-dominated forests with bamboo understory, typical of upper montane conditions (Ibbotson & Cloudbridge Reserve, 2017). Below 2000 m, the vegetation is characterized by dense palm and fern understory of lower montane cloud forests. The forest structure and tree diversity at these lower elevations closely resemble mature cloud forest ecosystems (Ibbotson & Cloudbridge Reserve, 2017).

Fruit resources for frugivorous bird species are unknown in Cloudbridge Nature Reserve. According to literature, the family of *Lauraceae* should be present and are important fruit-providing trees for specialists such as the Resplendent Quetzal (*Pharomachrus mocinno*), Northern Emerald Toucanet (*Aulacorhynchus prasinus*), and Black Guan (*Chamaepetes unicolor*), which should be present in mature cloud forests (Wenny, 2000).

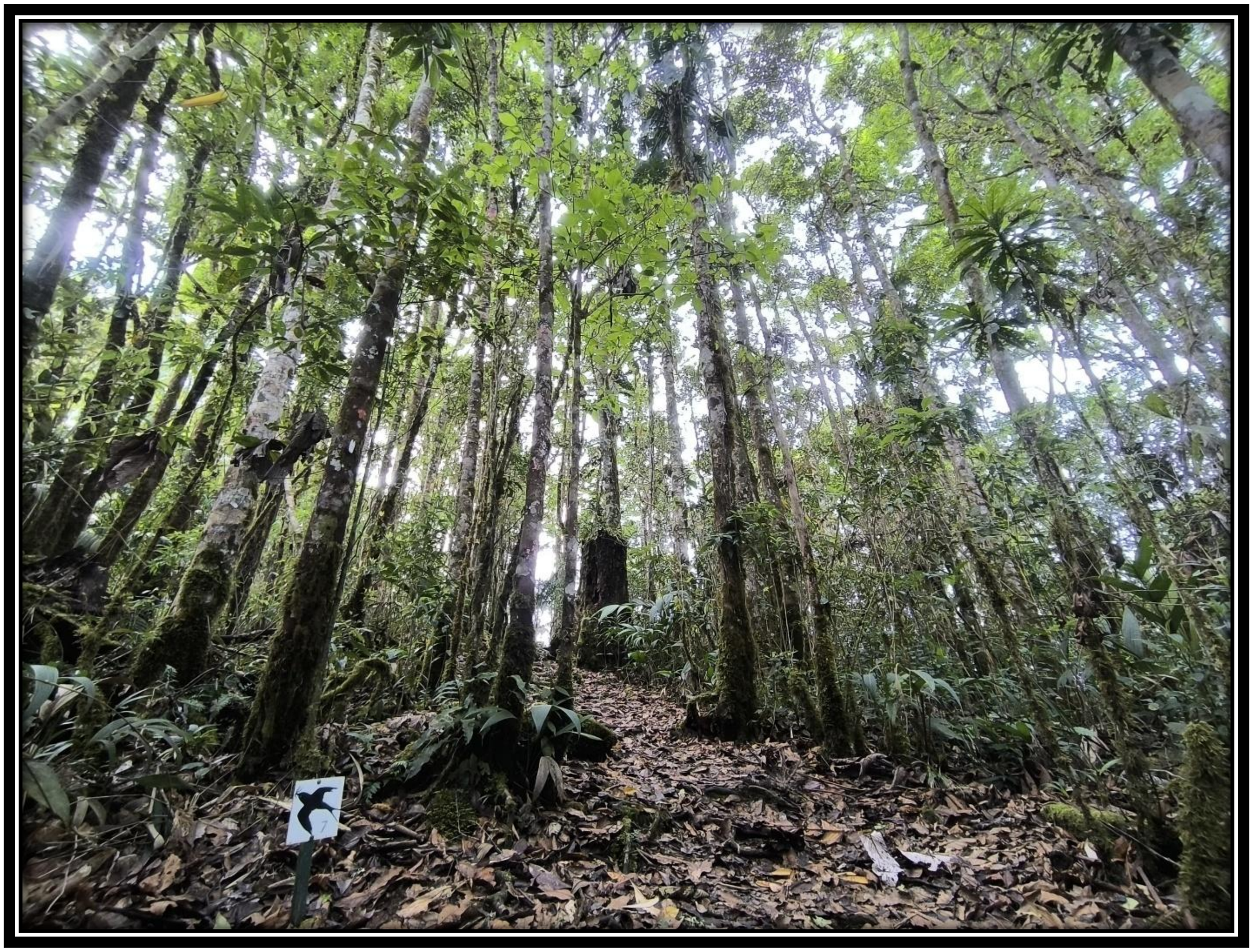

Figure 2 Old-growth habitat on the trail Montaña and Chirripo (Insausti, 2026)

5.2.2 Naturally regenerated forests

The naturally regenerated forests (NR) predate the establishment of the reserve in 2002 and are located adjacent to OG forests, which serve as a proximity for seeds (Cloudbridge Nature Reserve, 2025a). Historical land use consisted of pasture and small-scale farming, abandoned before or during the establishment of Cloudbridge Nature Reserve (Cloudbridge Nature Reserve, 2025a).

NR forests had the lowest mean of DBH for trees larger than 10 cm, which was 20.3 cm. NR was second to OG forest in basal area (3.3 m^2) and mean tree height (10.55 m) (Fleer, 2017). Ground vegetation cover was low and significantly different from both P and OG forests. The dominant tree species is Leathery Colicwood (*Myrsine coriacea*), which is absent in P forests. Leathery Colicwood is described as an important fruiting tree for specialistic frugivorous birds such as the Black Guan (*Chamaepetes unicolor*) (Yu, 2017).

Roughly half of the tree species in NR forests are also found in P (Hoving, 2019). In terms of plant species composition and richness, NR forests show greater similarity to OG forests. NR forests generally occur below 2000 m, within the lower montane cloud forest zone. This zone is characterized by an abundance of palms, ferns, and mosses in the understory and tree densities of about 600-800 stems per hectare (Ibbotson & Cloudbridge Reserve, 2021).

Figure 3 naturally regenerated forest on Montaña and Chirripo trail (Insausti, 2026)

5.2.3 Planted forests

The reforestation of planted (P) forests are among the youngest forest types in Cloudbridge. Reforestation began in 2004 in Montaña area, whereas in 2008-2011 reforestation started on the Jilguero trail. These areas were mainly used for cattle grazing and crop production (Cloudbridge Nature Reserve, 2025a).

Regarding the forest structure, P forests followed OG forests as the second highest in mean of DBH for trees larger than 10 cm (21.1 cm). P forests had the lowest basal area (2.5 m^2) and mean of tree height (10.33 m) (Fleer, 2017).

In P forests, ground vegetation cover was noticeably highest among the three forest types, due to lower tree density and reduced competition for nutrients, water, and light (Petch, 2021). Ground vegetation data at Cloudbridge is scarce but should resemble young lower montane forests, with dense shrub and herb layers and an abundance of ferns (Kappelle & Van Uffelen, 2006). The dominant tree species is the fast-growing pioneer, *Cecropia angustifolia* (Hoving, 2019), which is a valuable fruiting tree for migratory and resident frugivorous bird species (Nickerson, 2023).

Figure 4 planted forest on Montaña and Chirripo trail (Insausti, 2026)

5.3 Frugivorous bird community and richness

Costa Rica is known as a popular birding destination because of the high species richness, hosting 903 bird species (Garrigues & Dean, 2014). At Cloudbridge 360 bird species have been recorded, making up approximately 40% of the country's bird species (Cloudbridge, 2025b).
To be able to conduct the research, a classification needs to be made to classify bird species according to frugivory diet and specialism. Following a description of the methodology used for field data collection.

5.3.1 Classification of frugivorous bird species

Frugivorous bird species are classified according to the following requirements:
- The bird consumes the following fruit types: fleshy fruit, berries, drupes, pomes, aggregated fruits, multiple fruits, and accessory fruits (Lopes et al., 2016).
- The diet consists of a minimum of 10% fruit intake according to the classification of Lopes et al. The threshold helps to exclude bird species that rarely consume fruit, which would have a less meaningful contribution to animal-plant dispersed systems (Lopes et al., 2016).

Migratory birds are included in the analysis because many switch to a frugivorous diet during migration, contributing to reforestation through seed dispersal (Martin, 1985). Only species wintering in Costa Rica were considered, as passing migrants were assumed to have little to no effect on seed dispersal networks.

5.3.2 Frugivorous specialism

In this study, seed dispersal through fruit consumption is seen as the key factor driving diversification in tree species in cloud forests over time. Diversification of tree species leads to restoring ecosystem functioning, which makes a forest type more resilient. For that reason, frugivorous bird specialism is classified according to frugivory dietary characteristics. Diets with high fruit intake contribute more to reforestation efforts (Carlo et al., 2022). To assess the specialization in frugivorous bird species, requirements were established to determine specialist or generalist birds. A generalist was classified through the Eltontrait database and had a diet composed of 10-59% fruits (Wilman et al., 2016). A specialist species was classified through the AVONET database and had a diet that was composed of over 60% fruits (Tobias et al., 2022).

Figure 5 Frugivorous specialists, left photo is Black Guan (Chamaepetes unicolor), right photo is Northern Emerald-Toucanet (Aulacorhynchus prasinus)

5.3.3 Bird protocol

Cloudbridge has established a bird survey protocol, which has been executed from 2016. Across the years, the data of the birds in Cloudbridge Nature Reserve was collected by employees, internees, and graduates (Cloudbridge, 2025b). This study will use the previously collected data between 2016 and 2025. Additionally, new data was collected from October until November 2025, according to the bird survey protocol of Cloudbridge Nature Reserve. For further in-depth description of the used methodology, the extensive bird protocol of Cloudbridge Nature Reserve can be found in appendix B. The database "Master Bird Point Count Database 19March25" provided by Cloudbridge Nature Reserve, includes all observed bird data with the information of spatial variables between 2016 and 2025 (Cloudbridge Nature Reserve, 2016).

Bird surveys consist of permanent point count locations, hereafter referred to as "stations." At the stations, a 20-minute interval is used to identify all bird species observed based on sound and visual recognition. All bird species observed within a radius of 25 m are noted. Bird surveys typically have 4-5 stations along multiple trails (see table 2). These surveys were done in chronological order (from start to end), and the subsequent survey round was done in reverse order to minimize variation of bird abundancy. This methodology ensures that no particular section is always counted in the late morning. This is important because bird activity peaks at sunrise and decreases during the morning (Ramcharan, 2024).

Every trail is done 2 times in chronological order and in reversed order, a total of 4 times. In that way, the fieldwork period covered 4 counts for every station. Variation in observed species is reduced by counting at least 4 times to have a sufficient sample size. Bird counts were supported using binoculars to identify the species.

Table 2: Station-specific information

Survey Group	Station nr.	Trail	Elevation (m)	Forest types
Montaña/Chirripó	1	Montaña	1730	P/NR
	3	Montaña	1830	P
	5	Montaña	1970	NR
	9	Chirripó	2140	OG
Sentinel/Gavilán	34	Gavilán	1950	OG
	15	Gavilán	1805	NR
	16	Gavilán	1735	P/NR
	32	Sentinel	1725	NR
Principal/Río	31	Principal	1625	NR
	17	Río	1660	NR
	18	Río	1650	P/NR
	19	Río	1665	NR
	20	Río	1710	P/NR
El Jilguero	30	El Jilguero Loop	1640	P
	27	El Jilguero	1650	P
	28	El Jilguero	1760	NR
	33	El Jilguero	1845	NR
	12	El Jilguero	1965	OG
Amanzimtoti, Heliconia, and Sentinel	35	Amanzimtoti	1585	P
	37	Heliconia	1600	NR
	38	Heliconia	1690	P/NR
	39	Sentinel	1805	OG

5.4 Spatial variables

Spatial characteristics influence forest structure, resource availability, and microclimatic conditions, which in turn shape frugivorous bird communities. To evaluate how reforestation strategies affect species richness, specialism and species accumulation over time, this study included forest type, forest age, elevation, edge distance, and year as explanatory variables.

All spatial and forest variables were obtained from the "Master Bird Point Count Database 19March25" and supplementary information provided by Cloudbridge Nature Reserve. Station-specific values of the spatial variables are provided in Appendix C. Table 3 summarizes the description, unit of measurement, and ecological relevance of each variable.

Table 3 Overview of variables with a description, unit to measure and ecological relevance

Variable	Description	Unit	Ecological relevance
Forest type	Categorical variable representing four reforestation categories: naturally regenerated (NR), planted (P), planted/naturally regenerated (P/NR) and old-growth forest (OG). Forest type was provided by Cloudbridge Nature Reserve and linked to each station based on its geographic location (see Section 5.2).	P, P/NR, NR, and OG	Represents differences in restoration strategy and successional stage. Allows comparison of bird communities across contrasting habitat conditions. Different forest types are expected to host distinct levels of bird diversity (Jankowski et al., 2021).
Year (2016-2025)	Continuous temporal variable representing the nine-year monitoring period (2016–2025). Included to capture temporal dynamics in bird communities.	Years	Captures temporal trends in species richness, specialism, and species accumulation. Allows evaluation of recovery trajectories and interaction effects with forest type (Forest type × Year).
Forest age	Continuous variable representing years since the last major disturbance (e.g., clear-cutting or pasture use). Baseline forest age was determined in 2016. For subsequent years (2017–2025), forest age was updated by incrementing the baseline value annually to reflect ongoing forest development.	Years	Reflects structural development and vegetation complexity associated with forest succession. Enables assessment of successional effects independently of categorical forest type (Bregman et al., 2016).
Elevation	Continuous variable representing elevation above sea level. Elevation was provided by Cloudbridge Nature Reserve and assigned to each station	Meters	Proxy for climatic and vegetation gradients that influence species composition and diversity. (Rabhek, 1997; Quintero & Jetz, 2018; Dehling et al., 2014)
Edge distance	Continuous variable representing the distance (m) from each sampling station to the nearest boundary with a different forest type. Distances were calculated in ArcGIS Pro 3.5.0. A 25-m buffer was created around each station, corresponding to the radius defined in the Bird Survey Protocol (Appendix B), after which the NEAR function was used to calculate the shortest distance to the nearest adjacent forest type.	Meters	Indicates the degree of edge influence and habitat disturbance. Greater distances generally correspond to more interior-forest conditions and potentially higher diversity (Jankowski et al., 2021).
Station	Permanent point-count location where repeated bird surveys were conducted. Included as a random factor in the statistical models to account for spatial structure and repeated measurements across years	Number	Accounts for repeated surveys at the same location, ensuring that detected temporal patterns reflect ecological change rather than fixed differences among sampling points.
Forest type × Year*	Interaction term between 2 variables	-	Tests whether recovery trajectories vary among reforestation strategies (e.g., increasing diversity in naturally regenerated forests but stable patterns in planted forests).

** Units to measure remained the same as the individual variables Forest type and Year.*

5.5 Statistical analyses and methodological justification

This chapter describes the statistical analyses and methodological choices used in this study.

Due to the COVID-19 lockdown, no bird surveys were conducted between 2021 and 2023 (G. Fallas-Rodríguez, personal communication, October 14, 2025). These years were excluded from the analyses.

Frugivorous bird communities were analyzed across four forest types (NR, P, P/NR, and OG forests) between 2016 and 2025, excluding 2021-2023. Forest age, elevation, and edge distance were included as explanatory variables.

5.5.1 Differences in frugivorous bird species richness

Species richness was defined as the total number of frugivorous bird species recorded per station within a year, based on presence-absence data.

Differences in species richness among forest types were explored using boxplot and tested a one-way ANOVA. This analysis compares mean species richness among the four forest types (NR, P, P/NR, and OG forests).

Each station-year combination was treated as one observation. When significant differences were detected, Tukey HSD post-hoc tests were used to identify which forest types differed. Model assumptions of normality and homogeneity of variance were checked prior to analysis (Bevans, 2020).

While this analysis provides a general comparison of species richness among forest types, it does not account for spatial structure or temporal dynamics in the dataset. Therefore, a more advanced statistical approach was required to analyze patterns across the entire monitoring period. For this purpose, a Generalized Linear Mixed Model was applied.

5.5.2 Differences in frugivorous bird species richness across space and time

To analyze spatial and temporal patterns in frugivorous bird species richness across the full monitoring period, a Generalized Linear Mixed Model (GLMM) was used. GLMMs allow analysis of non-normally distributed data while accounting for hierarchical structures (Nahhas, 2025).

Species richness represents count data and is derived from presence–absence observations. Preliminary exploration indicated overdispersion (variance greater than the mean). For this reason, a negative binomial distribution was selected for the model. The negative binomial distribution is commonly used for ecological count data when observations show greater variability than expected under a standard Poisson distribution (Nahhas, 2025).

A log link function was applied to relate the explanatory variables to the expected value of species richness. The log link ensures that predicted species richness values remain positive, which is appropriate for count data.

The model included year, forest type, forest age, elevation, and edge distance as fixed effects. These variables represent spatial and temporal factors that may influence the presence of frugivorous bird species across the study area.

Station was included as a random intercept to account for repeated surveys at the same locations. Observations from the same station may therefore be more similar to each other than observations from different stations. Including station as a random effect accounts for this spatial dependence and prevents bias caused by repeated measurements.

To improve the interpretability of model coefficients, the variables year, elevation, and edge distance were mean-centered. Mean-centering shifts the variables so that the average value becomes zero, which makes the interpretation of model intercepts and coefficients more intuitive.

OG forests was used as the reference category when interpreting forest type effects. Candidate models were compared using Akaike's Information Criterion (AIC), a commonly used metric that evaluates the balance between model fit and model complexity. Lower AIC values indicate a better performing model relative to competing models (Bevans, 2020).

Model assumptions were evaluated using DHARMa simulated residual diagnostics (Hartig, 2024). This diagnostic approach allows assessment of model fit and potential issues such as overdispersion, zero inflation, and unusual residual patterns. Multicollinearity among explanatory variables was assessed using Variance Inflation Factors (VIFs), which remained within acceptable limits (Nahhas, 2025).

5.5.3 Differences in frugivorous bird community specialism

Community specialism was analyzed as the proportion of specialist species relative to the total number of frugivorous bird species recorded per station per year. Because this response variable represents a proportion, a binomial GLMM with a logit link was applied (Nahhas, 2025). Specialist species were specified as the number of successes, while the total frugivorous species richness per station-year combination was specified as the number of trials.

The model included year, forest type, forest age, elevation, and edge distance as explanatory variables. In addition, an interaction term between year and forest type was included to test whether temporal trends in community specialism differed among forest types.

Station and year were included as random intercepts to account for spatial and temporal dependence within the dataset. Model selection followed the same procedure as described for the species richness analysis (Bevans, 2020). Model diagnostics were evaluated using DHARMa simulated residuals to assess whether the assumptions of the binomial model were met (Hartig, 2024).

5.5.4 Species accumulation among forest types

To evaluate differences in total species richness and potential future development of frugivorous bird communities across forest types, species accumulation curves were constructed. A species accumulation curve illustrates how the cumulative number of species increases as additional surveys are conducted.

Species accumulation curves were constructed separately for each forest type using incidence-based presence–absence data and the Chao2 estimator (Chao et al., 2016). The Chao2 estimator was selected because it is specifically designed for incidence-based datasets and provides an estimate of total species richness that accounts for undetected and rare species (Chao et al., 2016). This approach is particularly suitable for tropical forest ecosystems, where dense vegetation and complex environmental conditions can limit the detectability of bird species.

The Chao2 estimator calculates expected species richness based on the number of species recorded once (Q1) and the number of species recorded twice (Q2) within the total number of sampling units (T) (Chao et al., 2016). In this study, individual bird surveys were treated as sampling units, and surveys with zero detections were retained to represent the full sampling effort.

Because sampling effort differed among forest types, the species accumulation curves were standardized through extrapolation to a common level of survey effort using the iNEXT framework (Hsieh & Chao, 2025). This standardization allows meaningful comparison of estimated total species richness among forest types under equalized sampling intensity.

5.5.5 Software

All analyses were conducted in R (version 2025.09.2, build 418) (Posit Software, 2025) using packages for data processing, visualization, mixed modelling and diagnostics, including *readxl* (*Wickham & Bryan, 2025*), *dplyr* (*Wickham et al., 2023*), *ggplot2* (*Wickham, 2016*) , *glmmTMB* (*Brooks et al., 2017*), *DHARMa* (*Hartig, 2024*), *iNEXT* (*Hsieh & Chao, 2025*), *tidyr* (*Wickham et al, 2024*), *broom.mixed* (*Bolker & Robinson, 2024*), *ggeffects* (*Lüdecke, 2018*), *purr* (*Wickham & Henry, 2025*) and *tibble* (*Müller & Wickham, 2025*)

6 Results

In the following chapter, the results will be discussed for every sub-question. Between the period of 2016 till 2025, 124 frugivorous bird species of twenty-two families have been observed. In naturally regenerated (NR) forests, species richness was highest, with 115 species recorded. Secondly, planted/naturally regenerated (P/NR) forests, with a species richness of 89, followed by planted (P) forests with 83 and lastly old-growth (OG) forests with 71 species. The family represented with the highest species diversity is Tyrannidae with 25 species, followed by Parulidae (16), Thraupidae (13), and Turdidae (11). In appendix D, the supplementary table D1 is given for a complete family list.

Sub-question 1: How does species richness in the frugivorous bird community differ between naturally regenerated, planted, and old-growth forests in 2025?

The mean number of frugivore species differed between the forest types ($p = 0,0015$). The highest mean number of frugivore species was found in NR (*mean = 57.9*), followed by P/NR (mean = 42.9*),* P (mean = *38.6*), and OG (mean = *31.4).*

The boxplot of NR shows not only a higher unique species richness but also a larger spread compared to the other forest types (see figure 6). OG forests on the other hand, showed the lowest unique species richness.

The model assumptions of the one-way ANOVA were not violated. The residual showed a normal distribution. In addition, the Bartlett test showed that the variances were homogenous between the forest types (*Bartlett's* $K^2 = 1.56$, $p = 0.67$). In appendix D, the supplementary tables D2, D3 and D4 can be found, which include the RStudio outputs of the descriptive statistics, one-way ANOVA and Tukey post-hoc test.

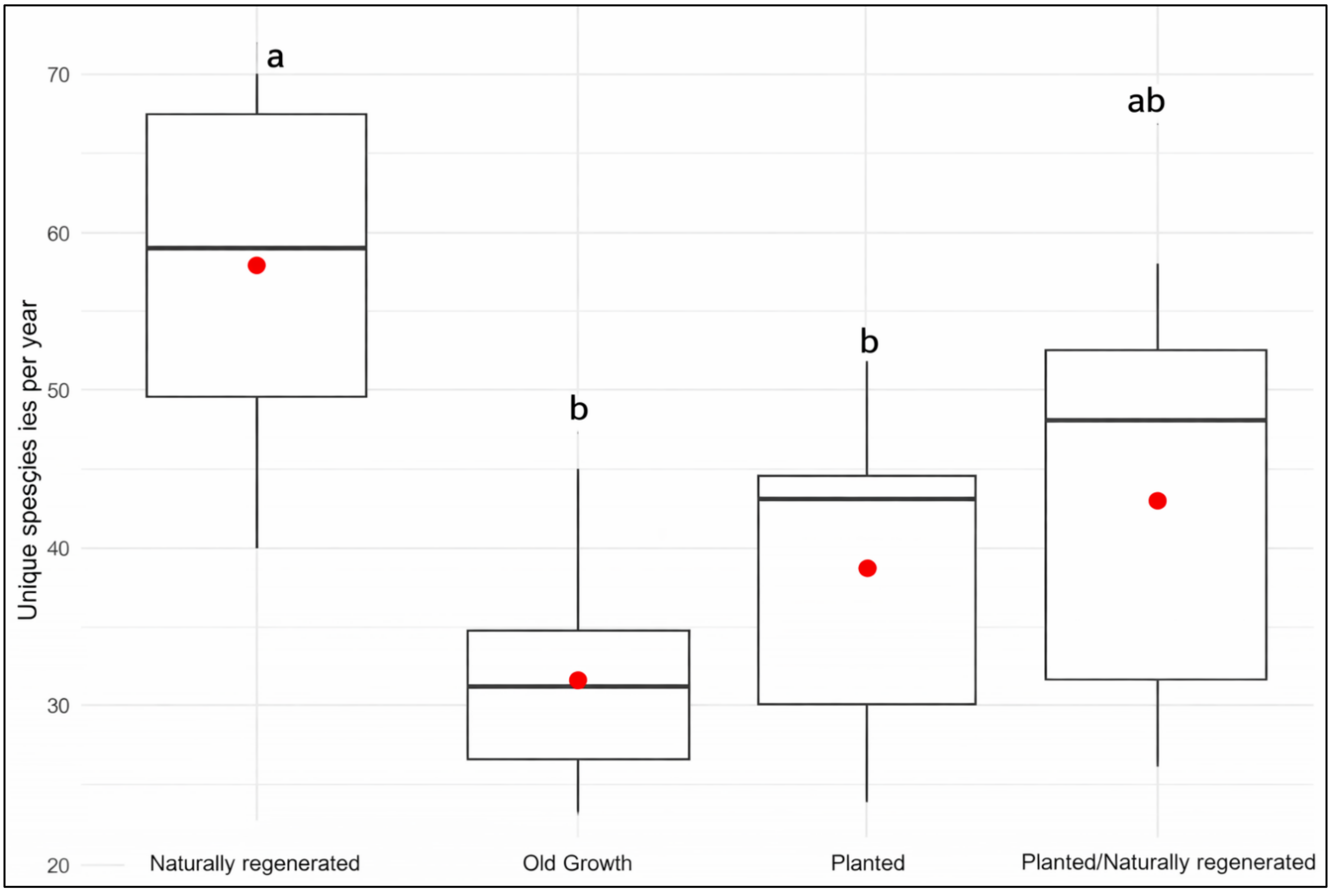

Figure 6: Boxplots showing the annual number of unique species richness across different forest types. Boxes represent the median and interquartile range, whiskers indicate data spread, and red points represent mean species richness. Different letters above the boxes indicate significant differences among forest types based on Tukey's HSD post-hoc test (p <0.05)

The Tukey HSD post-hoc analysis showed that NR significantly had more species richness compared to OG ($p < 0.001$) and P ($p = 0.018$). The difference between NR and P/NR was only marginally not significant ($p = 0.083$). No other significant differences were found between the remaining forest types of combinations.

The findings partly contradict the proposed hypothesis, in which OG forests were expected to have the highest species richness, followed by NR and P forests. Instead, NR forests showed the highest species richness. The results suggest that differences between NR forests and P/NR forests are relatively small, while OG forests showed the lowest species richness.

Sub-question 2: How does species richness in the frugivorous bird community change in naturally regenerated, planted, old-growth forest between 2016 and 2025?

The GLMM showed the lowest score of AIC (*984.1*), making it the best fitting model of 3 other models *(M0 AIC = 992.5, M1 AIC = 993.2, and M3 AIC = 985.6*). The explanatory variables: year, elevation, edge distance, and forest age have been centered through the scale function in RStudio to make the model more stable and reliable. In appendix D, the supplementary tables D5 and D6 can be found, which have the VIF-values and GLMM outputs of the analysis.

A forest plot was made to visualize the effect of response variables on species richness between 2016 and 2025 (see figure 8). The results of the GLMM of species richness between 2016-2025, show a significant ($p < 0.001$) downward trend in all forest types (see figure 7). The estimation is a 7.6% loss in species richness every year, where the years 2021-2023 are excluded since no data was collected during this time interval. These findings contradict the proposed hypothesis, where an increase in species richness over time was expected. Additionally, forest age did not explain the downward trend in species richness, as it was not significant ($p = 0.47$).

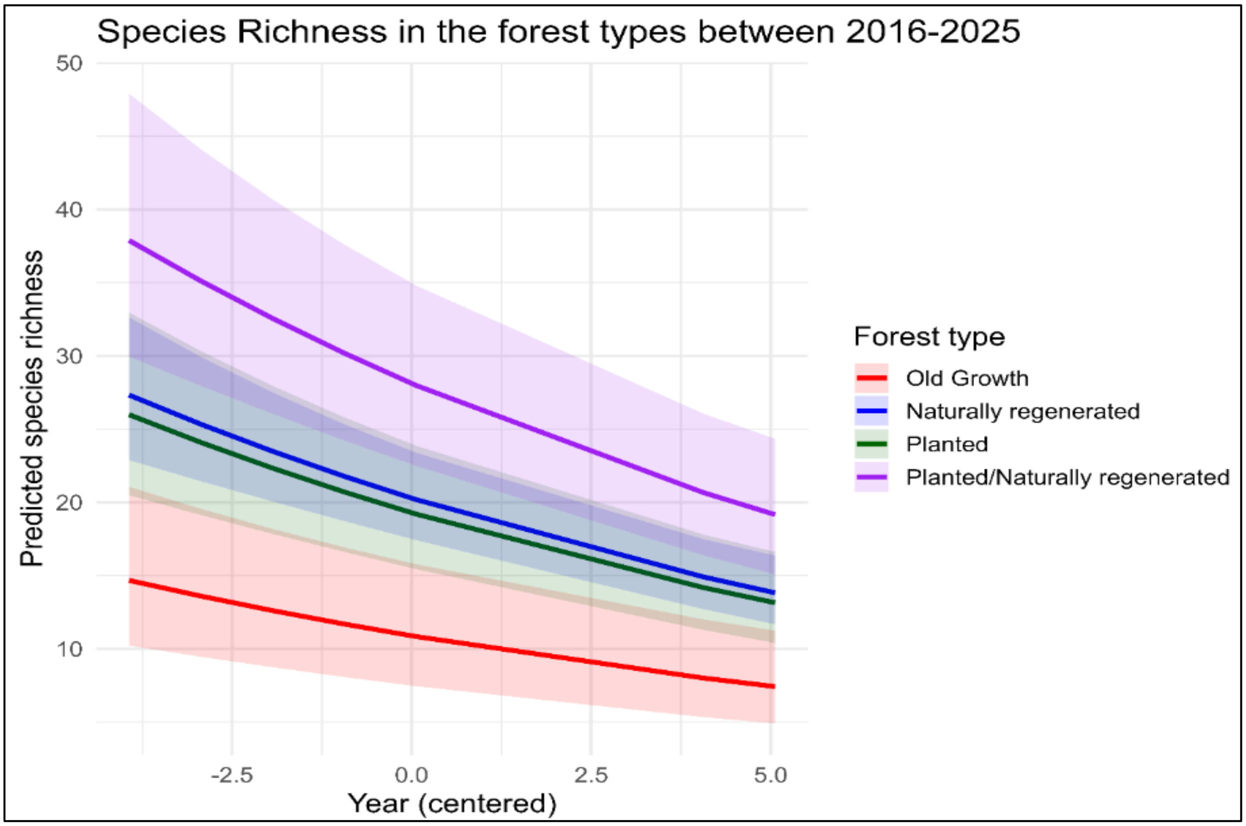

Figure 7: Temporal trend in species richness of frugivorous birds at point count locations between 2016 and 2025. The y-axis represents the predicted species richness derived from the GLMM, while the x-axis represents time (2016–2025). Year was mean-centered to improve model stability and facilitate interpretation of temporal trends.

The OG forest type has been set as the reference forest type, which has a significantly lower species richness than all the other forest types ($p = 0.007$ *(NR), = 0,02 (P),* < 0.001*(P/NR))*. These findings contradicts the proposed hypothesis, were OG was expected to have the highest species richness, followed by NR and P.
Additionally, elevation was expected to be significant, as species richness was expected to decrease with higher elevations above 1500 meters, but proved to be non-significant ($p = 0.21$).

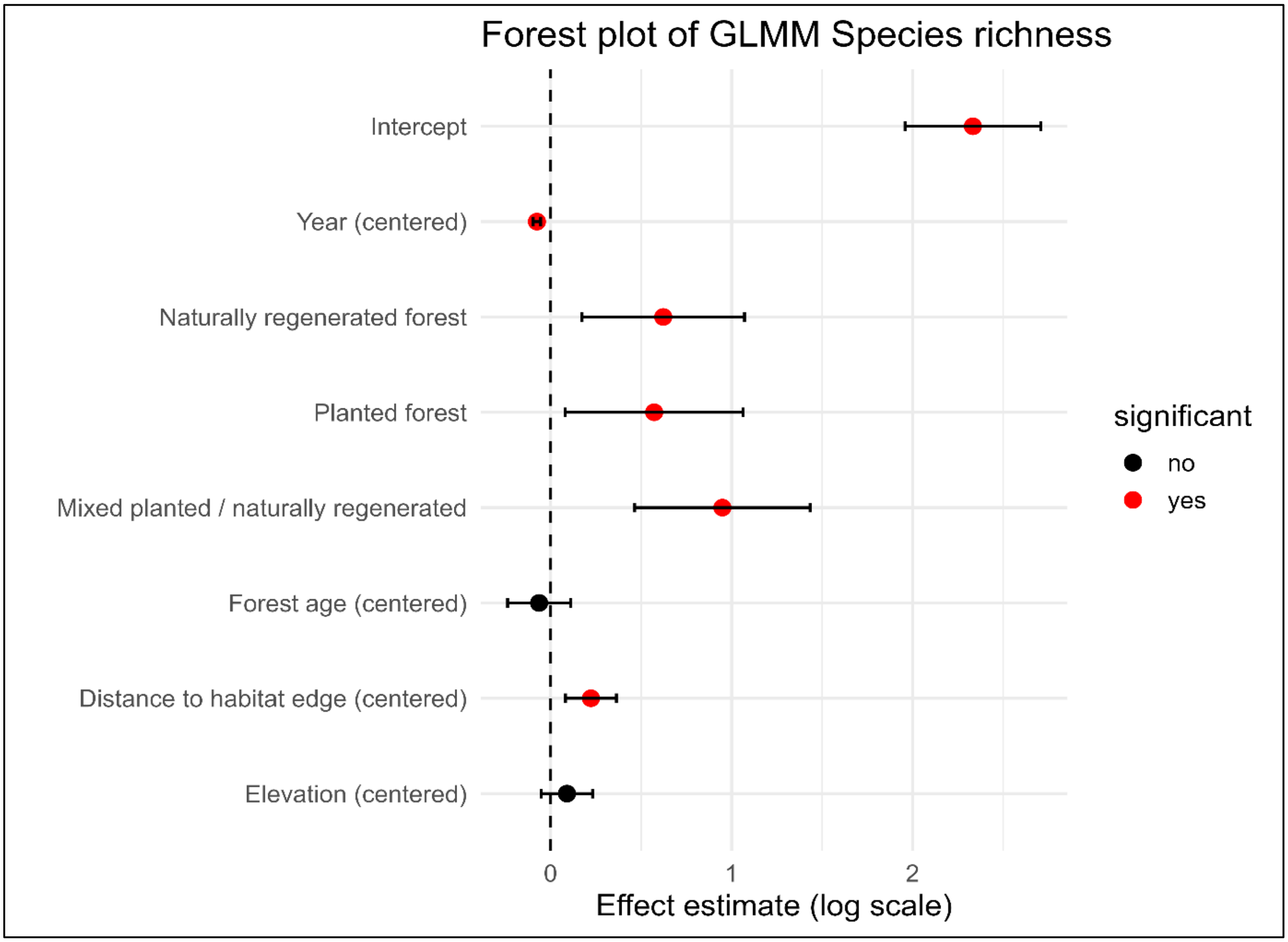

Figure 8: Forest plot of fixed effects from the Generalized Linear Mixed Model (GLMM) explaining frugivorous bird species richness at point count locations between 2016- 2025. Effect estimates are shown on a log scale due to the log-link function of the model. The vertical dotted line represents a zero effect, with positive effects to the right and negative effects to the left. Old-growth forest was used as the reference habitat. Points indicate effect estimates and horizontal lines represent 95% confidence intervals. Significant effects are indicated by red points, whereas non-significant effects are shown in black.

The edge distance also proved to be significant, with a positive estimate explaining species richness increases with greater distance to the edges of a forest type (*p = 0.002)*. The findings contradict the proposed hypothesis, where a smaller edge distance was expected to be associated with a higher species richness.

Sub-question 3: How does frugivorous bird community specialism change in naturally regenerated, planted, and old-growth forest between 2016 and 2025?

The GLMM analyzed the temporal changes in the proportion of specialist species per station between 2016 and 2025, excluding the period 2021-2023. The model included year, forest type, edge distance, and elevation as explanatory variables. Random intercepts for station and year were included to account for spatial and temporal dependence. An interaction between forest age and forest type was included, which was a component left out of previous models. The interaction model showed the best model fit, indicated by the AIC value (*AIC = 3367.2*). The variance components of the random effects were small, suggesting differences among stations between 2016 and 2025 were limited. In appendix D, the supplementary tables D7 and D8, which have the GVIF-values and the GLMM outputs.

A forest plot was made to visualize the effect of response variables on frugivorous bird specialism between 2016 and 2025 (see figure 10). The results show a significant negative effect on the proportion of specialist species in figure 9 (*estimate = -0.193, p = 0.004*). The effect of year was negative and statistically significant (*estimate = -0.036, p = 0.017*). A negative estimate indicates a significant temporal decline in the proportion of specialist species.

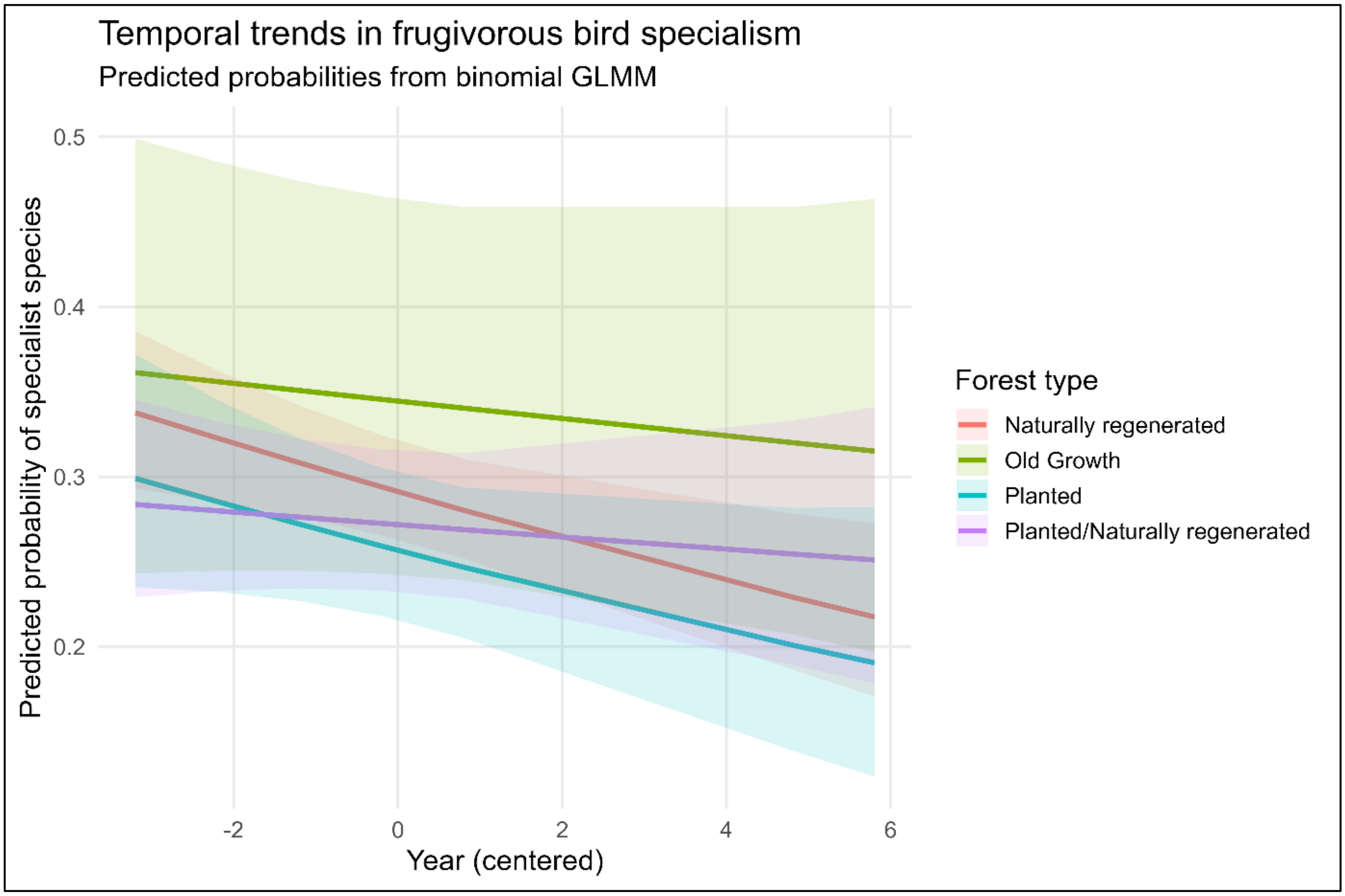

Figure 9: Temporal trends in frugivorous bird community specialism across forest types between 2016-2025. The y-axis represents the predicted probability of a species being classified as a specialist, derived from the GLMM, while the x-axis represents time. Year was mean-centered to improve model stability and comparability among forest types. Shaded areas represent 95% confidence intervals.

These findings suggest an overall decline in the proportion of specialist frugivorous species over time. These findings contradict the proposed hypothesis, which expected frugivorous specialism to increase over time.

Additionally, elevation showed a significant negative effect (*estimate = -0.157, p = 0.020*). Increasing elevation reduces the probability of a species classified as a specialist. These findings contradict the proposed hypothesis, which expected frugivorous specialism to increase with higher elevations.

To summarize the remaining variables: forest age (*p = 0.76*), forest type (*p = 0.39 (OG), = 0.16 (P), = 0.43 (P/NR)*), edge distance (*p = 0.55*), and the interaction between year and forest type (*p = 0.31 (OG), = 0.97 (P), = 0.21 (P/NR)*) did not show any significant effects on frugivorous specialism.

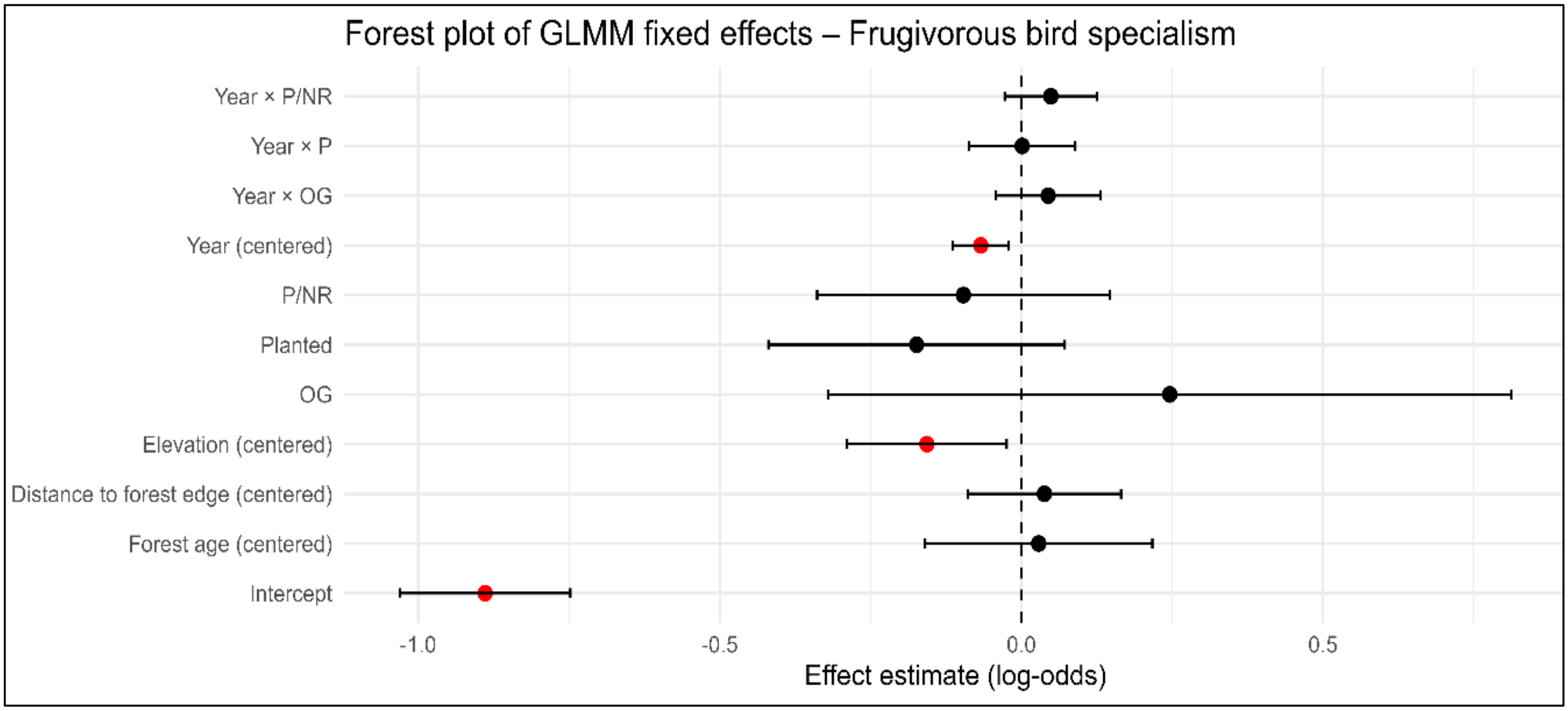

Figure 10: Forest plot of fixed effects from the Generalized Linear Mixed Model (GLMM) explaining frugivorous bird community specialism between 2016 -2025. Effect estimates are presented as log-odds, with the vertical dotted line indicating a zero effect. Effects to the left of the line indicate a negative effect on the probability of a species being a specialist, while effects to the right indicate a positive effect. Points represent effect estimates and horizontal lines denote 95% confidence intervals. Significant effects are highlighted in red, whereas non-significant effects are shown in black.

Sub-question 4: How does species accumulation differ among naturally regenerated, planted, and old-growth forest between 2016 and 2025?

The species richness curve in figure 11 was made through a Chao2 estimator. The forest types show an uneven distribution of sampling effort, where NR is represented the most with 1383 surveys. Next follows P/NR with 628 surveys, P with 625 surveys, and lastly OG with 406 surveys. To even out the number of surveys, the SAC has extrapolated estimated species richness for OG, P, and P/NR until 1383 surveys.

All the curves of the forest types show a rapid increase in estimated species richness, caused by the common frugivorous species. After the increase, the curve flattens, caused by rare or difficult to detect species. The trajectories of OG and P/NR seem to reach the asymptote of the SAC. The P/NR shows a stable curve in the middle of the estimated species richness, whereas the OG remains with the lowest species richness. An explanation for the low species richness in OG could be a greater sampling variance because of the lower sampling effort.

NR is consistently estimated with the highest species richness among the forest types, but P seems to reach a higher species richness at 1050 surveys. These findings suggest P and NR will have similar species accumulation curves, meaning differences might be small between accumulated species richness over time.

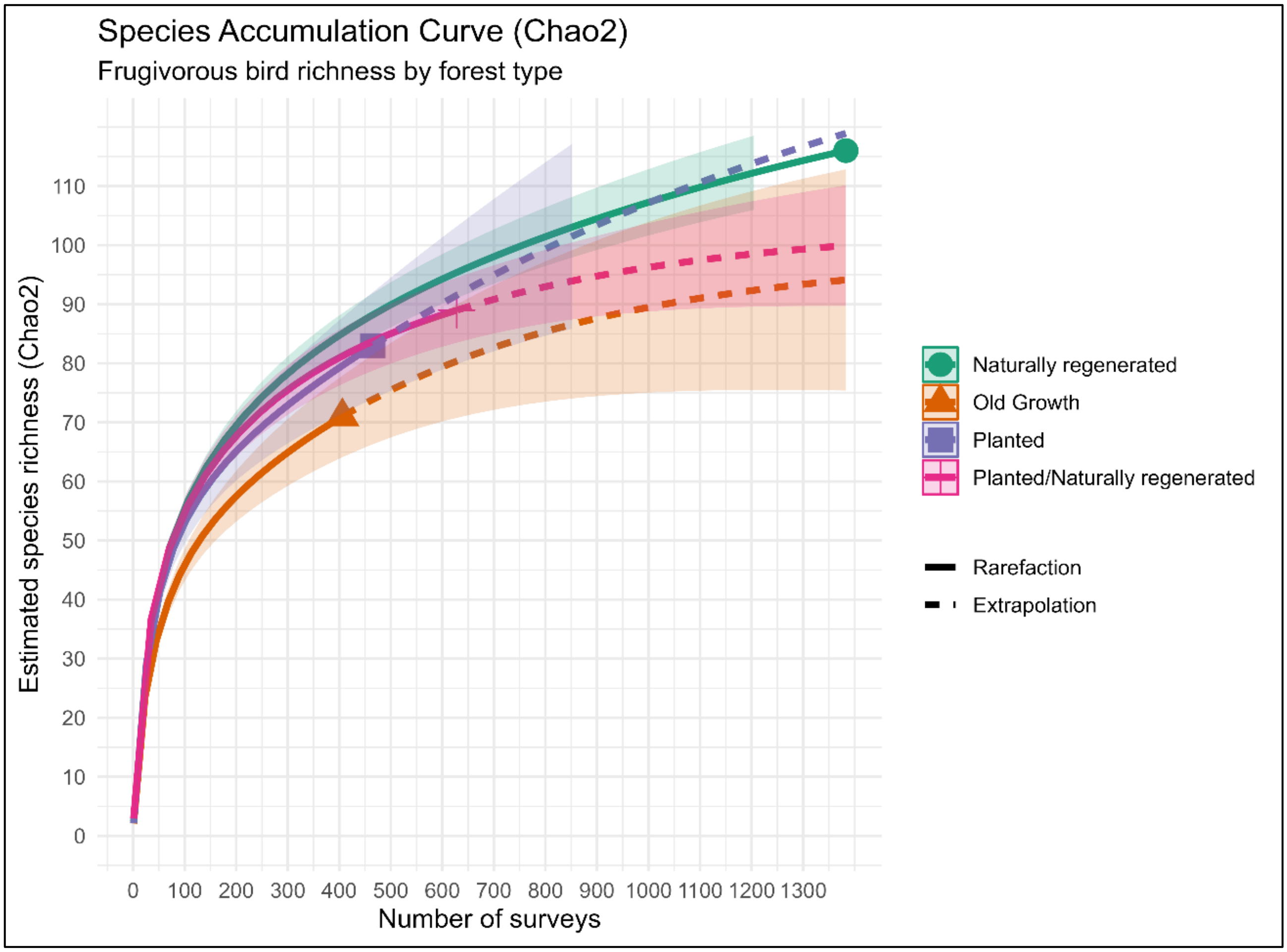

Figure 11: Species accumulation curves (SACs) for frugivorous birds across forest types based on incidence data, estimated using the Chao2 estimator. Solid lines represent estimated species richness based on observed sampling effort, while dotted lines indicate extrapolated estimates up to 1,383 surveys to standardize sampling effort among forest types. The y-axis shows estimated species richness, and the x-axis represents the number of surveys.

7 Discussion

This study investigated the temporal trends in frugivorous bird species richness (hereafter referred to as species richness), specialism and accumulation and how these patterns are influenced by spatial variables across forest types in a cloud forest in Costa Rica between 2016 and 2025. By combining ANOVA, boxplots, generalized linear mixed models, and species accumulation curves, this study provides an integrated approach to understanding how forest restoration methods and spatial variables shape frugivorous bird communities.

In this study species richness differed significantly among forest types in 2025, with naturally regenerated (NR) forests showing the highest frugivorous bird species richness, followed by planted/naturally regenerated (P/NR), planted (P), and old-growth forests (OG) (see sub-question 1). Between 2016 and 2025, frugivorous bird species richness declined significantly across all forest types, with an estimated annual decrease of 7,6%, while increasing edge distance showed a positive effect (see sub-question 2). Furthermore, the proportion of specialist frugivorous bird species declined significantly over time between 2016 and 2025, with higher elevations further reducing the probability of specialist species (see sub-question 3). Finally, species accumulation curves indicated that NR forest support the highest estimated species richness overall, while P forests may reach similar levels over time and OG forests remain lowest (see sub-question 4).

7.1 Differences in frugivorous bird species richness in forest types

Significant differences in mean species richness between the forest types were found in 2016 and 2025 (figure 6). NR forests were highest in species richness and only differed significantly from OG and P forests. These findings are consistent with a long-term study in Costa Rica. The study emphasizes that planted forests have a relatively quick structural recovery of the vegetation, which promotes an initial gain in species richness by colonization of forest-dependent birds. NR forests recover more slowly, because tree seedlings experience competition from weeds and grasses (Chazdon & Guariguata, 2016; Francis et al., 2024). Therefore, an initial structural recovery of NR forests is slow, but species richness tends to increase at a higher rate in comparison to P forests (Francis et al., 2024). The high observed species richness observed in NR forests compared to P forests would suggest that NR forests have already accumulated at a higher rate in time. Therefore, the observed patterns in this study may confirm the high rate of species richness in NR forests, which was also observed by Francis et al., 2024 in a temporal study about active restoration and tropical bird assemblages in southern Costa Rica.

Another explanation of this pattern might be the dominance of common generalist frugivores in regenerating landscapes, as these species account for the majority of fruit consumption and seed-dispersal events in disturbed Neotropical ecosystems (Carlo et al., 2022). NR forests might prove to have consistently better fruit resources compared to planted forests, which may lead to a higher species richness (Morrison & Lindel, 2011).

The relatively low species richness observed in OG forests were unexpected and do not support the initial hypothesis. One explanation may be that moderately disturbed habitats, such as NR and P forests, often contain higher habitat heterogeneity, allowing the co-occurrence of forest interior and open-area species (Almazán-Núñez et al., 2014; Gomes et al., 2008). As a result, species richness may be higher in regenerating forests than in mature forests, according to the intermediate disturbance hypothesis (Connell, 1978; Moi et al., 2020).

No significant differences were found in species richness between NR and P/NR forests. P/NR forest sites were expected to resemble intermediate disturbances, because these represent the edge between 2 forest types. Edge environments can support both forest interior and edge species, potentially increasing species richness (Connell, 1978; Moi et al., 2020). The lack of differences observed may indicate that NR forests structurally resemble edge environments such as P/NR forests.

7.2 Effect of temporal and spatial variables on frugivorous bird species richness

The generalized linear mixed model revealed a significant downtrend in species richness, but these could not be explained through temporal and spatial variables (e.g., forest age, elevation, and forest types), except for edge distances. The observed decline of species richness may reflect small ecological changes in the forest type that are difficult to detect. The dataset consisted of presence-absence observations, favoring rare or vagrant frugivorous bird species. Tropical bird communities often contain a large proportion of rare species detected only once or a few times.

Therefore, the subtle ecological changes and methods used could have explained the observed decrease in species richness, while the core community of frugivorous birds might still be intact (Poulsen & Krabbe, 1997).

The effect of edges proved to be significant on species richness (see figure 10). The further away stations were from an edge, the greater the species richness. This pattern is consistent in studies showing that fragment shape, rather than fragment size, is determinant for bird species richness. Irregular fragment shapes increase edge habitat that benefits edge-associated species. Contrary to interior forest species, which are more strongly influenced by fragment size, emphasizing increased species richness further away from edges might be related to forest type size (Martínez-Morales, 2004). Therefore, the effect of edge distance may capture broader spatial and ecological context rather than a single effect (Martínez-Morales, 2004).

The consistent decline of species richness could not be explained through forest age, implying successional age is not a driving factor. Forest age was expected to be correlated to successional change, because aging of forests increases structural complexity through vegetational changes in undergrowth, mid-story, and canopy level. A possible explanation could be that the nine-year study period could not capture the successional changes caused by forests aging.

While elevation could not explain overall species richness, a previous study has shown that elevation strongly influences species composition rather than richness. Local assemblages of species richness can be weakly related to elevation due to high species turnover and relative range (Martínez-Morales, 2004; Quintero & Jetz, 2018).

7.3 Frugivorous bird specialism: effect of spatial variables

The study considered generalist when the diet composed between 10-59% of fruits, whereas specialists' diet composed over 60% of fruit. A similar declining trend in species richness was also observed in frugivorous specialism (see figure 9). Generalist-dominated communities still contribute importantly to seed-dispersal networks (Carlo et al., 2022). However, increasing dominance of generalists also indicates reduced habitat suitability for specialist species (Martínez-Morales, 2004).

Larger-bodied birds, who are obligatory fruit-eaters are vulnerable to disturbances, which may contribute to the decline in specialism (Gomes et al., 2008; Martínez-Morales, 2004). Whereas generalist frugivores species are often small to medium-sized bird species with partial or obligatory diets, that are less susceptible to disturbances (Gomes et al., 2008; Martínez-Morales, 2004). In addition, frugivory breadth specialism classification likely has overshadowed large-bodied obligatory frugivores species, as ecological specialization in frugivorous birds is shaped by multiple traits, including body size and fruit preference (Gomes et al., 2008; Carlo et al., 2022). Frugivorous birds may display functional flexibility independent of dietary traits, suggesting simplified classifications overgeneralizes ecological specialization (Quitián et al., 2018).

The declining trend in frugivorous specialism may further indicate that fruit resources of late successional forests remain limited, suggesting forest recovery is incomplete despite a relatively high species richness (Carlo et al., 2022; Gomes et al., 2008; Liebsch et al., 2008). Although animal-dispersed vegetation tends to recover relatively quickly, plant community composition needs approximately 120 years to resemble OG forests (Poorter et al., 2021). This may explain why forest age showed little effect and why forests older than 70 years may still lack frugivorous specialism. The nine-year study period might therefore not capture enough successional changes, highlighting the importance of continued monitoring. Active planting of absent fruiting vegetation could potentially accelerate ecosystem recovery (Gomes et al., 2008; Liebsch et al., 2008).

Finally, the decline in specialism across forest types suggests that broader environmental drivers, such as climate change, are impacting frugivorous bird communities. Increased temperatures and more frequent dry days can reduce mist frequency and alter environmental conditions, such as precipitation (Pounds et al., 2008).

7.4 Potential of frugivorous birds in different forest types

Even though a downtrend in species richness and specialism was noted, the species accumulation curves suggest that additional species may still be detected or colonize P/NR, OG, and P forests in the future (see figure 11). The curves show a rapid initial increase, indicating that common frugivorous bird species were likely detected, while rare species may have remained undetected (O'Dea et al., 2006; Poulsen & Krabbe, 1997). NR forests showed the highest species accumulation curve, which likely contributed to higher observed species richness and sampling effort. Even NR forests have note reached the asymptote of the curve. This suggests that a future stabilization of the declining species richness and specialism cannot be excluded, but much uncertainty remains around the long-term recovery (Liebsch et al., 2008).

The accumulation curves further indicate that differences in species richness between P and NR forests may remain relatively small over time, whereas P/NR forests may reach an asymptote more quickly. This pattern could reflect increasing structural similarity along edges between P and NR forests, resulting in earlier stabilization of species accumulation (O'Dea et al., 2006). The relatively high estimated richness in P and P/NR forests likely reflects the dominance of generalist frugivorous species observed in specialism analysis.

Sampling coverage in NR forests suggests that most rare and uncommon species present have likely all been detected, whereas the accumulation curves of P, P/NR, and OG forests remain far from asymptote. This indicates that sampling effort in these forests may still be insufficient, highlighting the importance of continued long-term monitoring.

8 Conclusion

This study investigated temporal trends in frugivorous bird species richness, specialism, and species accumulation across different forest types in a cloud forest in Costa Rica between 2016 and 2025. In doing so, the study addressed the lack of insight into the development of frugivorous bird communities across different reforestation methods and spatial variables in Cloudbridge Nature Reserve, providing information to help evaluate past reforestation efforts and inform future restoration planning.

Naturally regenerated forests supported the highest frugivorous bird species richness, while planted forests showed similar species accumulation trajectories over time. These findings suggest that both passive and active restoration approaches can contribute to the recovery of frugivorous bird communities. However, a consistent decline in both species richness and frugivorous specialism was observed across forest types, indicating that functional recovery of the frugivorous bird community remains limited despite relatively high observed species richness.

Spatial analyses showed that edge distance significantly influenced species richness, with higher richness occurring further from forest edges. In contrast, forest age and elevation did not significantly explain variation in species richness within the nine-year study period, suggesting that longer monitoring periods may be required to capture successional changes in cloud forest ecosystems.

The increasing dominance of generalist frugivorous species and the decline in specialist species suggest that ecological functions associated with late-successional forests remain limited. However, these patterns should be interpreted with cautions as factors such as sampling method, rare species detection, fruit resource availability, and broader environmental drivers such as climate change may also influence the observed trends. In addition, species accumulation curves suggest that additional species may still be detected in several forest types, highlighting remaining uncertainty about long-term trajectories.

Overall, the results indicate that both naturally regenerated and planted forests can contribute to frugivorous bird diversity, but also highlight that current restoration outcomes remain difficult to fully evaluate. Continued long-term monitoring combined with data on fruit resources, vegetation structure and environmental conditions, will therefore be essential to determine whether reforestation efforts ultimately lead to an ecosystem functioning recovery in Cloudbridge Nature Reserve.

9 Recommendations for restoration

1. Improve long-term bird monitoring

This study found a decline in frugivorous bird species richness and specialism over time. However, the dataset consisted of presence-absence observations, which makes it difficult to determine whether species are actually declining or simply detected less frequently.

To gain a clearer understanding of changes in frugivorous bird communities, future monitoring should include abundance-based data. Recording the number of individuals per species would allow a better detection of population trends and changes in community composition

2. Investigate and enhance fruit resources in restored forests

The decline in frugivorous specialism may indicate that important fruit resources of late-successional forests are still limited. However, this study did not directly measure fruit availability or vegetation structure, making it difficult to determine whether food resources are limiting specialist frugivorous birds.

To better understand the relationship, Cloudbridge Nature Reserve should collect vegetation and fruit-resource data, such as the presence and abundance of fruit-bearing trees. If fruit availability proves to be limited, restoration strategies could include planting of late-successional fruit-bearing tree species that support specialist frugivorous birds. In tropical cloud forests, species within the Lauraceae family, such as *Ocotea* species, are known to provide important food resources for these birds (Wilms & Kappelle, 2006).

3. Prioritize natural regeneration where possible

Results from this study showed that naturally regenerated forests supported the highest species richness, while planted forests showed similar species accumulation trajectories over time. This suggests that both passive and active restoration methods can contribute to frugivorous bird diversity.

For future restoration projects and land acquisition, Cloudbridge Nature Reserve should prioritize natural regeneration in areas located near existing forests. Adjacent forests can facilitate in natural seed dispersal, whereas areas lacking surrounding forests, active planting of a mixture of early pioneer and fruit-bearing tree species may be necessary to accelerate forest recovery (Poorter et al., 2021).

4. Continue long-term monitoring

The nine-year study period may be relatively short to detect ecological changes in cloud forest succession. In addition, species accumulation curves suggest that additional species may still be detected in several forest types.

Continued long-term monitoring of frugivorous bird communities will therefore be essential to evaluate whether current reforestation efforts ultimately lead to ecological recovery in Cloudbridge Nature Reserve. Integrating bird monitoring with environmental variables such as fruit availability, vegetation structure, and climate data would provide a more complete understanding of the drivers shaping frugivorous bird communities.

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Appendix

Appendix A Hypothesis table

Table 4 Proposed hypotheses for species richness and specialism for frugivorous birds

Variables	Hypotheses of the frugivorous bird community	Literature supporting
Elevation (meters above sea level)	Species richness peaks at intermediate elevations 500-1500 m), forming a parabolic pattern. Environmental filters become increasingly more restrictive from 1500 meters, which limits existence of wide-ranging species. Only species adapted to harsh abiotic conditions can persist. Cloudbridge is located at 1500 meters and therefore will follow a linear decrease in species richness.	(Rabhek, 1997) (Quintero & Jetz, 2018)
	Specialism within species increases with elevation because environmental filters increase with elevation, leaving species only adaptable to these harsh abiotic conditions.	(Dehling et al., 2014)
Forest type: planted, naturally regenerated and old-growth forests	Species richness peaks in chronological order: old-growth, natural regenerated and planted forests, because of complexity of forests increase niches and therefore more species richness.	(Bregman et al., 2016)
	Specialism increases in old-growth, because complexity and niche partitioning is highest and support the most specialists. Followed by naturally regenerated, because of heterogeneity in horizontal and vertical vegetational structures. As last planted, because of a more homogenous structure.	(Falconí-López et al., 2024) (Vargas-Daza et al., 2023)
Forest age (in years, since last disturbance)	Species richness increases with forest age, because maturity of forests supports a heterogenous niche diversity.	(Bu et al., 2014)
	Specialism increases with forest age, because complexity and niche partitioning increases with age, which promotes more specialists.	(Vargas-Daza et al., 2023)
Edge distance in meters	Species richness increases near edges of a forest type, because species of both forest types are present. This is related to the intermediate disturbances hypotheses (IDH).	(Moi et al., 2020) (Terraube et al., 2016)
	Specialism decreases with decreasing edge distance because specialists are more confined to interiors of habitats.	(Vallejos et al., 2024)

Appendix B Bird count Protocol Cloudbridge Nature Reserve

Introduction

This document outlines the protocol for bird studies at Cloudbridge Nature Reserve (Cloudbridge). This study has been set-up to accomplish two main goals:

1. Build and maintain a bird species list for Cloudbridge; and,
2. Assess differences in species composition and abundance between different successional habitat types, and monitor how that changes as the forest continues to regenerate.

These goals will be accomplished through a combination of 1) daytime point count surveys, 2) nighttime call-playback surveys (owls) (see Owl Survey Protocol), 3) walking surveys, and 4) incidental observations.

Goal 2: Successional habitat bird study

This goal uses data collected from 1) point count and 2) call-playback surveys to compare the differences in bird species composition and abundance between different successional habitat types throughout Cloudbridge. Bird point counts are surveyed regularly throughout the year in order to monitor seasonal changes in bird presence throughout the reserve and assess diversity and abundance in the different habitat types.

Successional habitat types include:

1. Secondary forest – actively planted areas,
2. Secondary forest – natural regenerated areas under 30 years,
3. Secondary forest – naturally regenerated areas over 30 years,
4. Primary forest – Old-growth forest.

Locations

Twenty-five (25) bird stations are currently in use for point count surveys, shown in Figure 3-1. Each station is marked with a small metal sign at ground level. Each sign is white, with a black bird and the station number painted on them (Figure 3-2). Stations have been added and dropped from the study over the years, meaning that station numbers on a trail are not always sequential, and some stations marked with signs are no longer in use.

Stations are surveyed in groups of 5 per survey day. Summary information on each station is provided in Table 3-1 by survey group.

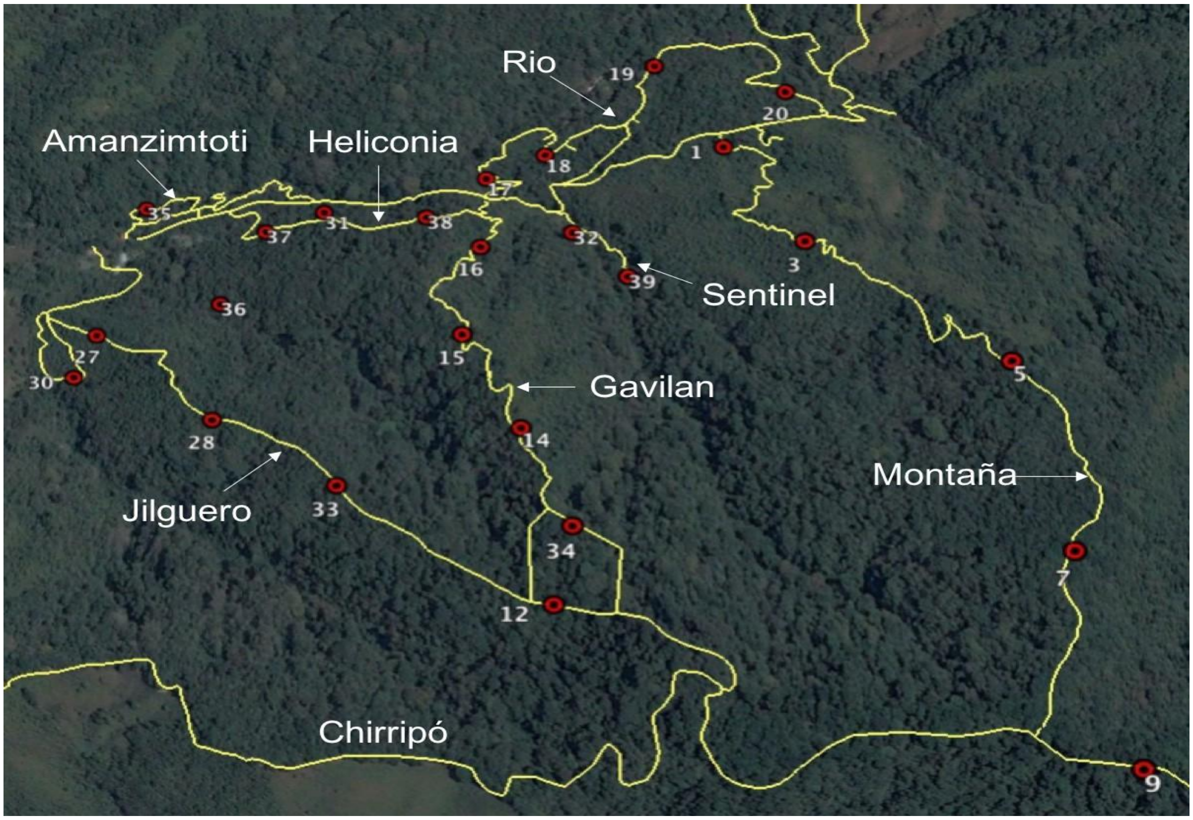


FIGURE 3-1 - LOCATION OF BIRD STATIONS

Survey Timing

All 5 survey groups should be surveyed once per week.

Point count surveys are conducted during the day, starting at approximately 6 am and should be completed by 10 am at the latest (preferably 9 am). For transects that are far away, you can start walking to the transects prior to sunrise, but can only begin sampling after 6:00 am. Approximate times to the furthest and closest stations in each survey group are provided in Table 3-2.

The order in which the stations in each group are surveyed should be varied between sampling events. For example, if one week the El Jilguero group is surveyed in the following order: 30, 27, 28, 33, and 12; the next time it is sampled, it should be surveyed in the other direction: 12, 33, 28, 27, and 30. This helps ensure variations in the sampling results between stations is not due to the time the sites were sampled (i.e. 30 always being sampled at sunrise and 12 always sampled mid-morning).

RAIN

While it almost never rains before 10 am at Cloudbridge, rain during a survey may prevent or stop a survey from being completed. For rain classes of light or drizzle, the survey can continue (see Table C-1 in Appendix C for explanation of rain classes). For a moderate amount of rain, wait 10-15 minutes and if the rain dies down to light or drizzle, continue with the survey. If the rain remains at a moderate level, or is heavy or severe, the survey should be stopped and any uncompleted point counts surveyed another day (ideally, the first available day). If moderate or heavier rain begins part way through a point count, that point count will need to be redone from the beginning. The data already collected at the point count can be recorded in the database under the walking survey tab, but should not be included in the point count data.

Materials

- 1 to 3 observers
- Binoculars – One per observer
- Watch or phone with alarm
- Field notebook
- Pencils
- Bird ID book, *The Birds of Costa Rica: A field guide, 2nd edition* (Garrigues and Dean 2007)
- First aid kit
- Plastic bag or dry bag to keep books, electrical equipment dry should it rain
- Camera (optional)

Methods

Survey Area

The survey area is the area within a 25 m radius of the bird point count marker (measured horizontally out from the point, not along the slope), in a cylinder from the ground to the top of the canopy (Figure 3-3). Birds seen or heard outside of that cylinder should be recorded as 'outside' the survey area. Birds that are passing through the area, but are not utilizing the habitat are also recorded as outside. Birds that pass through the area, but do utilize the habitat (ex. catching bugs in flight, resting on vegetation), are recorded as inside (Figure 3-4).

When identifying and recording biological data for the individual birds (see Section 3.4.3), birds inside the survey area should be given priority over birds outside of the survey area.

FIGURE 3-3 – POINT COUNT SURVEY AREA

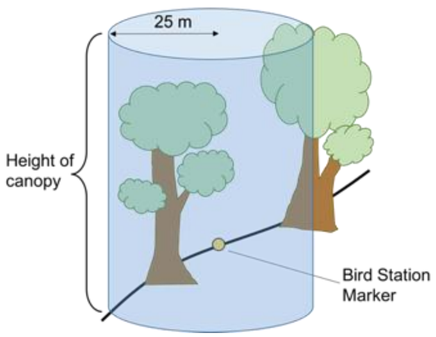
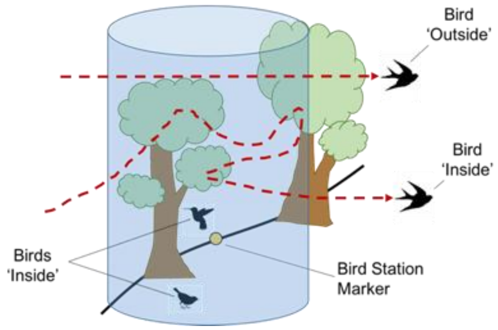


FIGURE 3-4 – INSIDE VS OUTSIDE OF SURVEY AREA



Time Intervals

During a given 20 minute point count, the presence of individual birds is broken into 5 different intervals: 0-2 mins, 2-5 mins, 5-10 mins, 10-15 mins, and 15-20 mins. This is done to allow the data to be comparable with other bird studies that may have been conducted with different survey durations.

Bird Biological Data

When a bird is seen or heard the following information should be recorded for each individual, whenever it is possible to determine:

- Species or lowest identifiable taxonomic group,
- Sex,
- Age class,
- Breeding status, and
- Nesting behaviour.

When it is not possible to determine the exact species of a bird, the bird should be recorded as the lowest identifiable taxonomic group. This may be as large a group as passerine or non-passerine, Hummingbird sp., Wren sp., or it may be you were able to identify it to genus. If it can be identified as one of 2 species in a genus, e.g. Western Wood-Pewee (*Contopus sordidulus*) and the Eastern Wood-Pewee (*Contopus virens*), the bird would be recorded as Eastern or Western Wood-pewee. If it occurs that a bird is identified to 1 of 2 species that are not closely related, e.g. Philadelphia Vireo (*Vireo philadelphicus)* and the Tennessee Warbler (*Oreothlypis peregrine*), it should be recorded to the smallest taxonomic group to which they both belong. In the case of the Philadelphia Vireo and the Tennessee Warbler, it would be recorded as Passerine sp., with a note the comments column of the data file indicating which 2 species were under debate.

Sex is recorded as either: 1) male, 2) female, or 3) unknown. Males and females of many bird species can be differentiated based on the colouration of their plumage. For some species, however, there is little difference between the sexes and they can not be differentiated visually and therefore should be recorded as 'Unknown'.

Age class is recorded as either: 1) adult, 2) juvenile, 3) fledgling, or 4) chick (see Appendix B, Table B-1). Adults and juveniles are told apart by plumage, the characteristics of which are species specific. Fledglings are juveniles that have left the nest, but that are still being fed by adults. A fledgling should only be recorded if it is seen being fed. Chicks are juveniles still in the nest. Be aware that for some species, an adult may be fed while sitting/brooding on eggs and is not a fledgling or chick. Chicks still in the nest are unlikely to be the same size as an adult and will most likely have the plumage of juveniles, or a duller representation of the adult plumage.

Breeding status is recorded as either: 1) breeding, 2) non-breeding, or 3) unknown (see Appendix B, Table B-2). A bird is considered to be 'Breeding' either by noting that the bird is in breeding plumage, or by observing breeding behaviour (ex. bird(s) are observed mating, nest building, caring for chicks, etc.). A bird is considered 'Non-breeding' only if its species has unique breeding and non-breeding plumage and it is currently displaying the non-breeding plumage. All other birds should be recorded as 'Unknown'.

Nesting behaviour is recorded as either: 1) mating, 2) nest building-1, 3) nest building-2, 4) brooding, or 5) feeding (see Appendix B, Table B-3). 'Mating' is recorded when the bird is seen actively mating and is recorded for both individuals. 'Nest building-1' is recorded when a bird is seen carrying nest building materials (this could be in its beak or in its feet). 'Nest building-2' is recorded when an individual is seen building a nest. 'Brooding' is recorded when an adult is seen sitting on eggs, while 'Feeding' is recorded when and adult is seen feeding chicks or chicks can be seen in the nest.

When examining birds to determine species or biological characteristics, priority should always be given to the birds inside the survey area. All data should be collected on an individual inside the survey area before examining an individual outside the survey area.

Procedure

1. Arrive at the first station in the survey group around 6am. Be as quiet as possible while approaching the station and while preparing yourself at the station. Do not start the first survey until 6 am.
2. Record:
    a. Date,
    b. Station number,
    c. Observer's names,
    d. General weather using the tables in Appendix C, including:

        i. Rain class,
        ii. Wind class,
        iii. Cloud cover class, and,
        iv. Any other significant weather (eg. storms, thunder/lightening, earthquake).
3. Record the start time and begin silent observation.
4. Identify all individual birds seen or heard for 20 mins both inside and outside of the survey area (see Section 3.4.1).
5. Record the presence of individual birds in the following intervals: 0-2 mins, 2-5 mins, 5-10 mins, 10-15 mins, and 15-20 mins (see Section 3.4.2).
6. For each bird, record:
    a. Species,
    b. Biological characteristics using the tables in Appendix B.
        i. Sex,
        ii. Age class,
        iii. Breeding status, and
        iv. Nesting behaviour.
    c. Whether they were inside or outside of the survey area,
    d. Whether they were seen or heard, and,
    e. Presence across the 5 time intervals.
7. Record the end time of the survey.
8. Record any changes in the weather conditions.
9. Continue to the next bird station in the survey group and repeat steps 2 through 7.
10. After returning from survey, enter the data into the 'Master Bird Count Project Data' file on the 'Point Counts' tab.
11. Enter a data to e-bird including any incidental birds encountered.

RAIN

While it almost never rains before 10 am at Cloudbridge, there can sometimes be heavy rains in the late morning. For rain classes of light or drizzle, walking surveys can continue (see Table C-1 in Appendix C for explanation of rain classes). For a moderate amount of rain, wait 10-15 minutes and if the rain dies down to light or drizzle, continue with the survey. If the rain remains at a moderate level, or is heavy or severe, the survey can be stopped.

Species identification

When recording the species of an individual bird, only record a species name if 100% sure of the identification. This is especially true for audio identifications. If unsure, the bird should still be recorded, but just to the lowest identifiable taxon (e.g. tyrant flycatcher sp., euphonia sp., raptor sp.). This is done so birds with uncertain IDs can still be used to assess overall abundance in each area.

At Cloudbridge, birds are recorded in notes using their English common names as found in Garrigues and Dean (2007). The 'Master CB Bird Species List' file on the Cloudbridge hard drive, and the 'CB Bird Species List' tab in the 'Master Bird Count Project Data' file have both the English common names and scientific names to allow for cross-referencing. In the Master CB Bird Species List file, the scientific names have been cross-referenced with *The Cornell Lab of Ornithology - Neotropical Birds* website (CLO 2016) to ensure the scientific names used are up-to-date with current scientific classification. The date the scientific names were last updated is recorded in the bird species list file. If the scientific name for a given bird species has not been updated in over a year, check the scientific name against the *Neotropical Birds* website.

Data Entry

Data from all surveys are recorded in the Bird Point Count Field Book, and then manually entered into the 'Master Bird Count Project Data' file on the appropriate tab. Data is also uploaded to the *eBird* website for each point count (each point count is a different checklist)

Any new species recorded during the surveys are added to the 'CB Bird Species List' tab within the project data file and highlighted. At the end of the project, the new species are updated in the 'Master CB Bird Species List' file on the Cloudbridge hard drive.

By the end of the project, all data collected during your project is uploaded to the *eBird* website (Audubon and CLO 2016) and transferred to the Cloudbridge hard drive.

Appendix III: Weather Classification Tables

TABLE C-1 – RAIN CLASS

Rain Class		Conditions
0	None	No rain.
1	Drizzle	Barely raining. Tiny raindrops, very sparse or erratic rainfall. Rain gear not necessary.
2	Light	Rain falling at a steady rate, but sparse. Would get soaked if out for an extended period without rain gear.
3	Moderate	Rain constant and dense. Would get soaked in minutes without rain gear.
4	Heavy	Raindrops large and falling with force. Streams forming on some trails. Would get soaked immediately without rain gear.
5	Severe	Storm conditions. Sheets of rain falling from the sky. Trails become creeks. Dangerous to be out at all.

TABLE C-2 - WIND CLASS

Wind Class		Conditions
0	Calm	Calm. Smoke rises vertically.
1	Faint	Fog and smoke drift indicates wind direction. Leaves stationary.
2	Light	Wind felt on exposed skin. Leaves rustle.
3	Moderate	Leaves and small twigs constantly moving. Light flags extended.
		Dust and loose paper raised. Small branches begin to move.
4	Strong	Branches of a moderate size move. Small trees in leaf begin to sway.
		Large branches in motion. Umbrella use becomes difficult. Empty plastic bins tip over.
5	Severe	Whole trees in motion. Effort needed to walk against the wind.

TABLE C-3 – CLOUD COVER CLASS

Cloud Class		Conditions
0	Clear	No clouds.
1	Mostly Clear	A few scattered clouds.
2	Partly Cloudy	An equal amount of clouds and clear sky.
3	Mostly Cloudy	More clouds than clear sky.
4	Overcast	Full cloud cover.
5	Misty	Low lying clouds (fog).

Appendix C Station-specific information

Station number	Forest type	Forest age in 2025	Elevation	Edge distance	Trail
1	Planted/Naturally regenerated	23	1734	0	Montana
3	Planted	23	1835	48,50	Montana
5	Naturally regenerated	23	1968	68,65	Montana
7	Old-growth/Naturally regenerated	39	2071	0	Montana
9	Old-growth	79	2133	220,20	Chirripo
12	Old-growth	79	1969	188,82	Jilguero
14	Old-growth/Planted	39	1868	0	Gavilan
15	Naturally regenerated	19	1807	24,23	Gavilan
16	Planted/Naturally regenerated	19	1731	0,00	Gavilan
17	Naturally regenerated	23	1654	34,82	Rio
18	Planted/Naturally regenerated	23	1650	0	Rio
19	Naturally regenerated	23	1660	35,80	Rio
20	Planted/Naturally regenerated	23	1705	0	Rio
27	Planted	17	1660	48,48	Jilguero
28	Naturally regenerated	17	1765	172,64	Jilguero
30	Planted	17	1647	31,18	Jilguero
31	Naturally regenerated	34	1624	1,84	Principal
32	Naturally regenerated	15	1711	10,59	Sentinel
33	Naturally regenerated	17	1841	96,67	Jilguero
34	Old-growth	79	1954	79,56	Gavilan
35	Planted	34	1567	40,62	Amanzimtoti
37	Naturally regenerated	34	1603	38,59	Heliconia
39	Old-growth	23	1763	22,41	Sentinel

Appendix D Supplementary data

Supplementary table D1 Family list

Frugivore Species Richness per Family (2016–2025)

Family	Species represented
Tyrannidae	25
Parulidae	16
Thraupidae	13
Turdidae	11
Passerellidae	8
Cardinalidae	7
Picidae	6
Vireonidae	6
Columbidae	5
Fringillidae	5
Psittacidae	5
Tityridae	3
Corvidae	2
Cracidae	2
Ptiliogonatidae	2
Trogonidae	2
Capitonidae	1
Cuculidae	1
Icteridae	1
Momotidae	1
Ramphastidae	1
Tinamidae	1

Supplementary tables D2, D3 and D4 - Supportive question 1

Supplementary Table D2

Descriptive statistics of annual frugivorous bird species richness per forest type

Forest type	**Mean richness**	**Median richness**	**SD**	**Number of years**
Naturally regenerated	57.9	59	12.3	7
Old-growth	31.4	31	7.85	7
Planted	38.6	43	10.7	7
Planted / naturally regenerated	42.9	48	13.1	7

Supplementary Table D3

Results of one-way ANOVA and Tukey HSD post-hoc comparisons
One-way ANOVA

Source	**df**	**Sum of squares**	**Mean square**	**F value**	**p value**
Forest type	3	2617	872.3	6.99	0.0015
Residuals	24	2995	124.8		

Significant effect of forest type on species richness ($p < 0.01$).

Supplementary Table D4

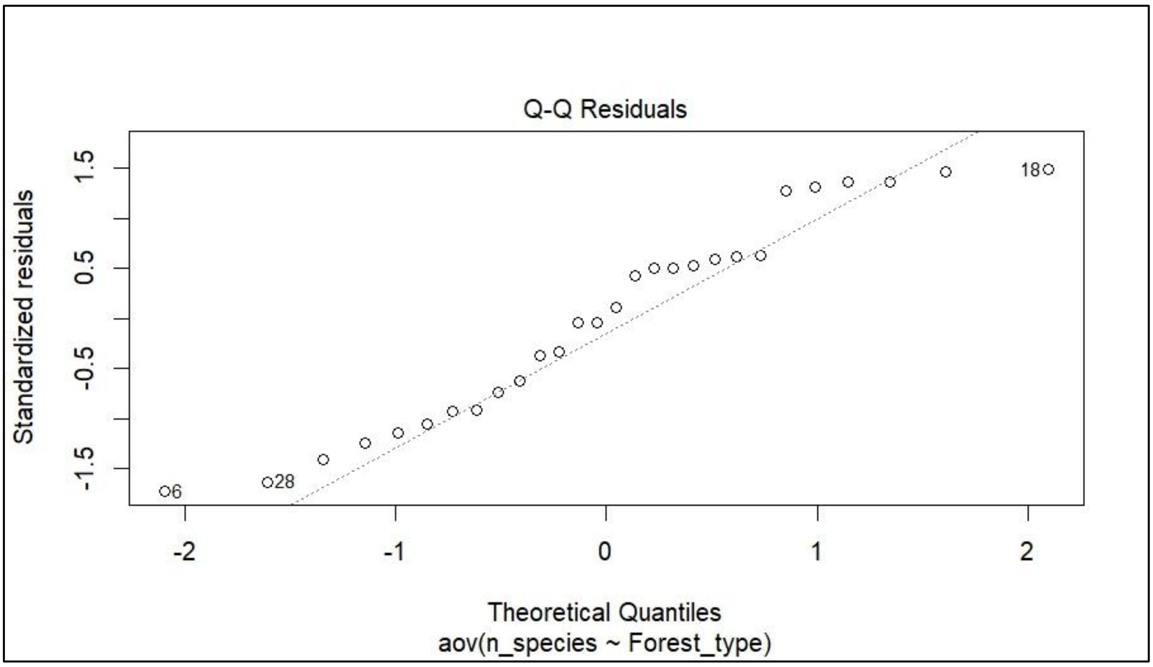
Tukey HSD post-hoc test (pairwise comparisons)

Comparison	**Mean difference**	**95% CI lower**	**95% CI upper**	**Adjusted p**
Old-growth – naturally regenerated	−26.43	−42.90	−9.96	< 0.001
Planted – naturally regenerated	−19.29	−35.76	−2.81	0.018
Planted / naturally regenerated – naturally regenerated	−15.00	−31.47	1.47	0.083
Planted – old-growth	7.14	−9.33	23.62	0.635
Planted / naturally regenerated – old-growth	11.43	−5.04	27.90	0.249
Planted / naturally regenerated – planted	4.29	−12.19	20.76	0.889

Table D4. Results of one-way ANOVA testing differences in annual frugivorous bird species richness among forest types, followed by Tukey HSD post-hoc comparisons. Bartlett's test indicated homogeneity of variances ($K^2 = 1.56$, $p = 0.67$).

Diagnostics for the One-way ANOVA

Figure 12: Q-Q residual plots of One-Way Anova of sub-question 1



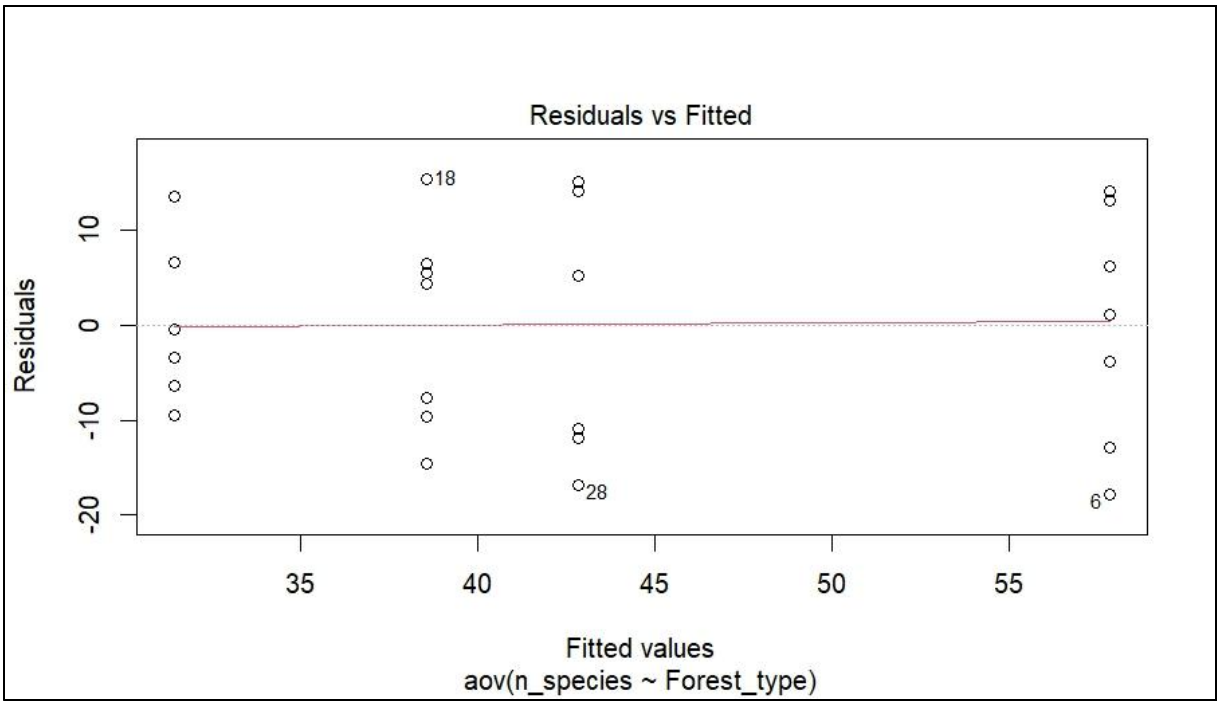


Figure 13: Residuals vs fitted of One-way Anova from sub-question 1

Supplementary tables D5 and D6 - Supportive question 2

Supplementary table D5

VIF multicollinearity output in RStudio

Term	VIF	VIF 95% CI	Adj. VIF	Tolerance	Tolerance 95% CI
Year_c	1.18	[1.0, 1.56]	1.09	0.84	[0.64, 094]
Forestage_c	4.18	[3.25, 5.51]	2.05	0.24	[0.18, 0.31]
Edge_c	2.75	[2.19, 3.57]	1.66	0.36	[0.28, 0,46]
Elev_c	2.74	[2.18, 3.56]	1.66	0.36	[0.28, 0,46]
Forest_type	5.17	[3.98, 6.84]	1.31	0.19	[0.15, 0.25]

Model diagnostics of GLMM

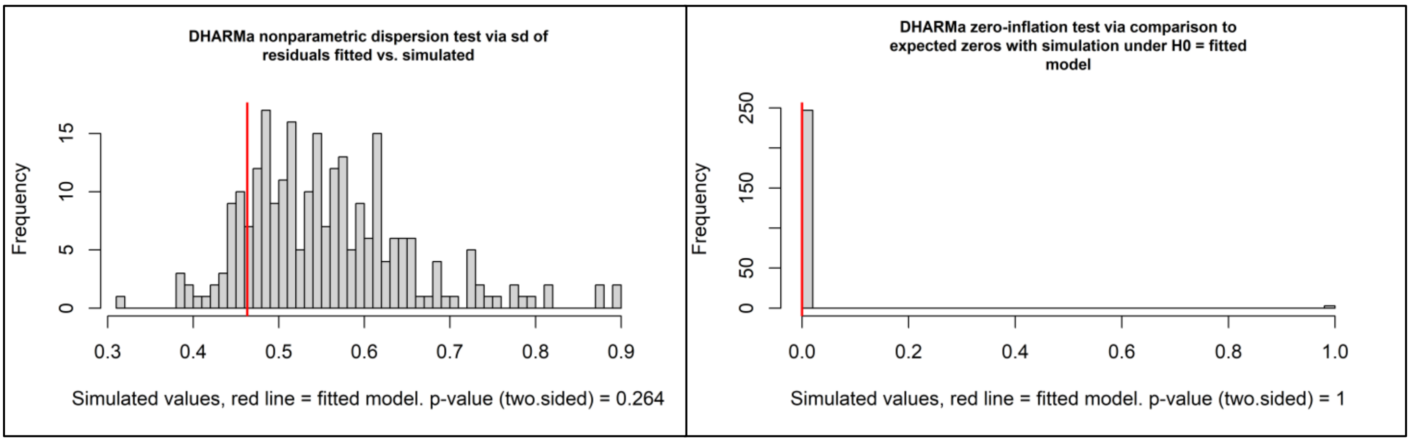


Figure 14 and figure 15: DHARMa diagnostics including overdispersion test and zero-inflation test

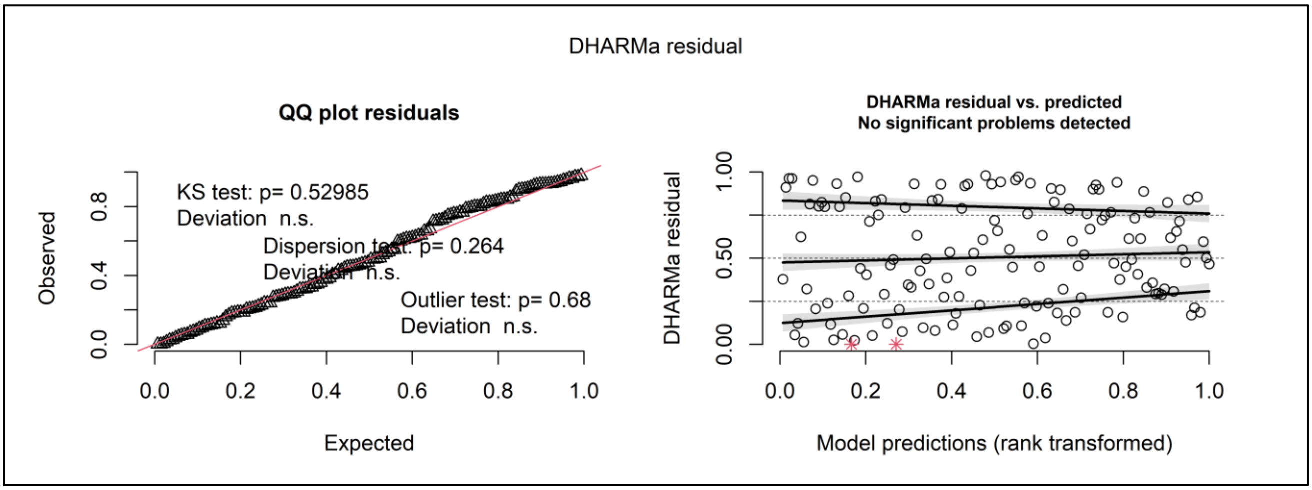


Figure 16 and figure 17: DHARMa diagnostics including Q-Q plot of residuals and Residual vs. predicted.

Supplementary table D6

Negative binomial GLMM results for frugivorous bird species richness (2016–2025)

Predictor	Estimate	SE	z-value	p-value
Intercept (Old-growth)	2.333	0.191	12.20	<0.001 ***
Year (scaled)	−0.076	0.011	−7.21	<0.001 ***
Forest type: Naturally regenerated	0.622	0.229	2.72	0.006 **
Forest type: Planted	0.572	0.251	2.28	0.022 *
Forest type: Planted/NR	0.949	0.247	3.84	<0.001 ***
Forest age (scaled)	−0.064	0.089	−0.72	0.474
Edge distance (scaled)	0.223	0.072	3.11	0.002 **
Elevation (scaled)	0.090	0.072	1.25	0.212

Model details:
Family: negative binomial (nbinom2), log link
Random effects: Station (intercept)
Number of observations: 144
Number of stations: 21
AIC = 984.1
Dispersion parameter = 15.1
Significance levels: *p* < 0.05 (*), < 0.01 (**), < 0.001 (***)

Supplementary Table D7 and D8 - Supportive question 3

Supplementary Table D7

GLMM output from RStudio

Fixed effect	**Estimate**	**Std. Error**	**z value**	***p* value**	**Significance**
(Intercept)	-0.889	0.072	-12.34	< 0.001	***
Year (centered)	-0.193	0.067	-2.86	0.004	**
Forest type: Old-growth	0.246	0.289	0.85	0.394	
Forest type: Planted	-0.174	0.125	-1.39	0.166	
Forest type: Planted / Naturally regenerated	-0.096	0.124	-0.78	0.437	
Forest age (centered)	0.029	0.096	0.30	0.765	
Distance to forest edge (centered)	0.038	0.065	0.59	0.556	
Elevation (centered)	-0.157	0.067	-2.32	0.020	*
Year × Old-growth	0.127	0.127	1.00	0.317	
Year × Planted	0.004	0.129	0.03	0.977	
Year × Planted / Naturally regenerated	0.140	0.112	1.25	0.211	

Supplementary Table D7. *Results of a generalized linear mixed model (GLMM) with binomial error distribution and logit link testing the effects of forest type, temporal trends, and environmental variables on the probability of a species being a specialist. Station and year were included as random intercepts. Significance codes: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$.*

Supplementary Table D8

GVIF values

Predictor	**GVIF^(1/(2Df))**
Year (centered)	2.58
Forest type	1.41
Forest age (centered)	2.22
Distance to edge	1.60
Elevation	1.58
Year × Forest type	1.41

Diagnostic of GLMM proportion of specialist species

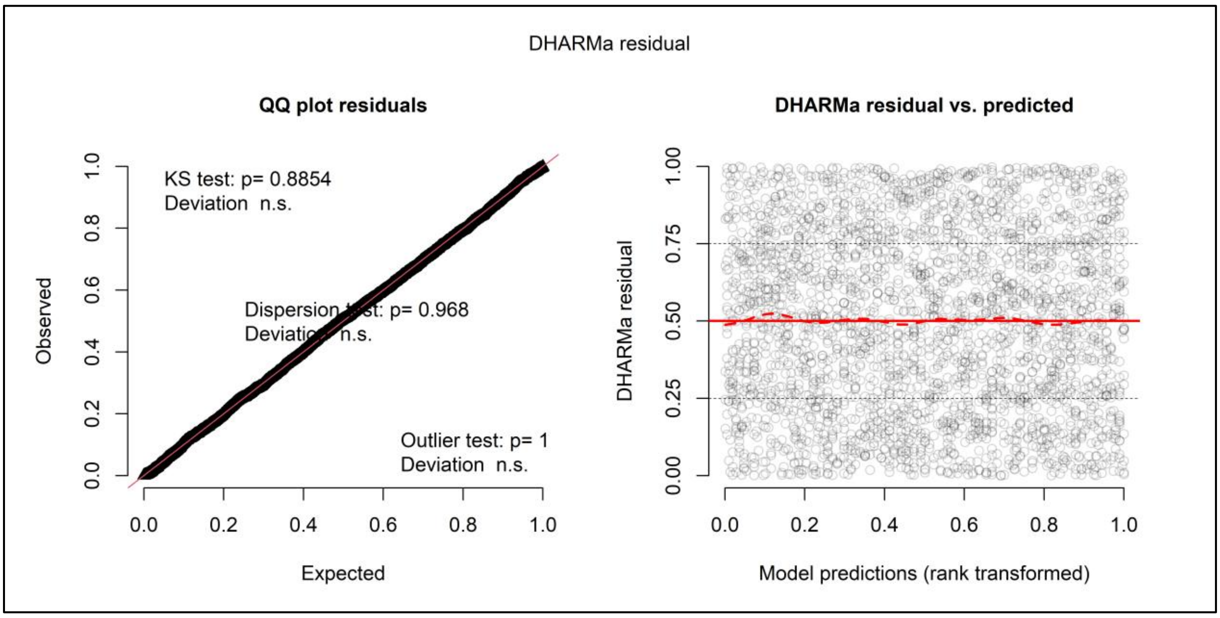


Figure 18 and figure 19: DHARMa diagnostics including Q-Q plot residuals and Residual vs predicted

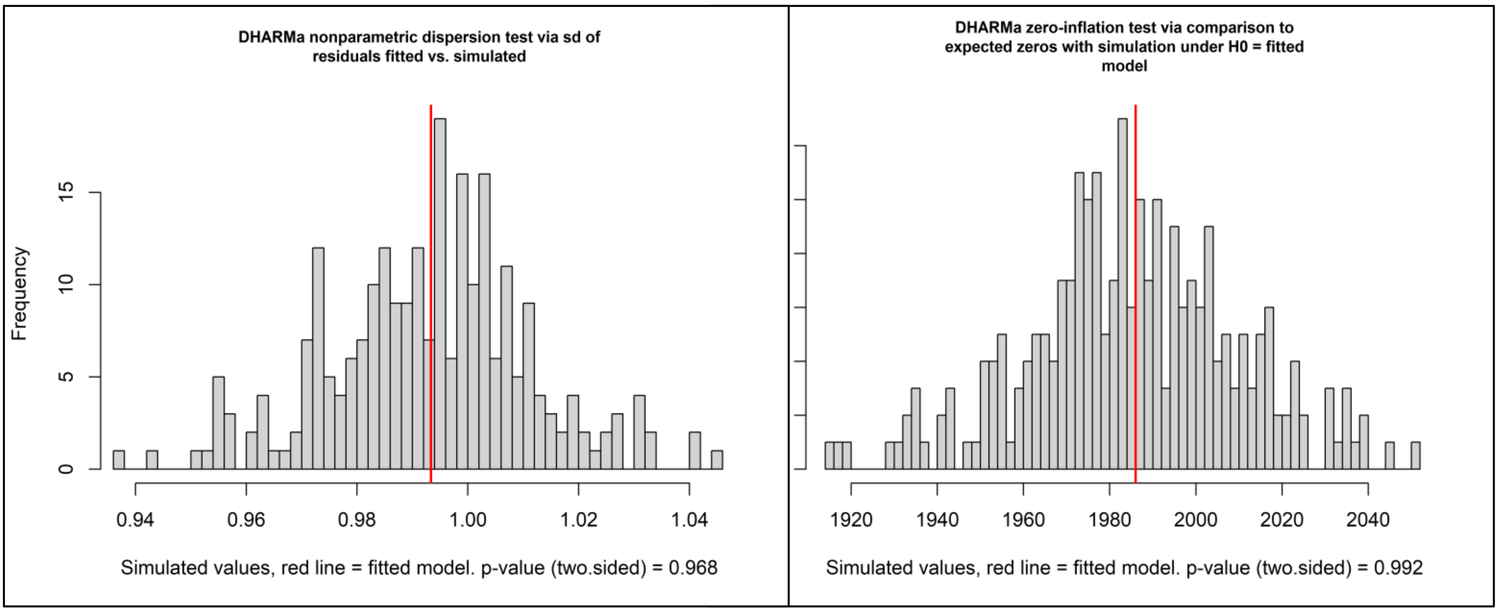


Figure 20 and figure 21: DHARMa diagnostics including overdispersion test and zero-inflation test