

Impact of Habitat Heterogeneity and Structural Complexity on Nesting Success

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Table of Contents

Abstract.....	2
Introduction.....	3
Methods.....	4
Results.....	6
Discussion.....	10
Acknowledgements.....	10
Supplementary Materials.....	11
Literature Cited.....	12

Abstract

Agricultural intensification has been driving declines in avian biodiversity across the globe, however research has shown that human managed agriculture lands can provide habitat and resources to avifauna in addition to supporting sustainable avian populations. Coffee agroforestry has been spotlighted as an agroecological system that supports abundance and richness of avifauna, though there is limited research on whether these systems support breeding populations and how management decisions impact avian nest success. This study seeks to fill gaps in the literature by comparing avian reproductive success in a shaded coffee farm and a neighboring sun-grown coffee farm. It investigates whether differences in habitat heterogeneity impact nesting success by measuring canopy cover, vertical structure, and constructing a complexity index. It was hypothesized that the less intensely managed shaded coffee agroforestry system would have a higher probability of daily nest success than the more intensely managed sun-grown coffee. Results from this study found that nests in the agroforestry system (n=25) had a 5% higher daily nest survival rate than nests found in the sun-grown coffee system (n=18). Additionally, results suggest a negative correlation between vertical structure surrounding the nest and success of nests, implying a trade-off between nest concealment and risk of failure.

Introduction

Anthropogenic conversion of land for agricultural use has been considered the leading driver of global biodiversity loss seen in the last several decades (Şekercioğlu et al. 2019, Chaudhary et al. 2016). Agricultural intensification, the process of increasing crop yields by increasing inputs such as synthetic fertilizers and pesticides, is one of the greatest contributors to avian biodiversity loss (Rigal et al. 2023, Kehoe et al. 2017). Intensive management practices lower structural complexity which reduces the quality of habitat as resources needed for life history requirements are depleted or removed (Hane et al. 2012). Management decisions such as pruning of understory trees as well as epiphyte removal have been shown to decrease avian abundance and biodiversity (Cruz-Angon and Greenberg 2005). However, human managed agriculture lands can provide habitat and resources to avifauna in addition to supporting sustainable avian populations (Şekercioğlu et al. 2019), while avifauna can provide beneficial ecosystem services such as pest control that can increase farmer crop yields (Mass et al. 2013, Karp et al. 2013).

Coffee agroforestry has been spotlighted as providing quality habitat that supports high avian diversity and abundance (Udawatta et al. 2019, Yashmina-Ulman et al. 2018, Greenberg et al. 1997,) and reduces avian extinction rates (Irizarry et al. 2018, Perfecto et al. 1996). Lower management intensity, specifically retention of floristic structure and floristic diversity, has been linked to greater avian abundance in shaded farms (Bakermans et al. 2012, Najera et al. 2010, Cruz-Angon and Greenberg 2005, Calvo and Blake 1998). Habitat heterogeneity and complexity can provide shelter and resources to avifauna such as protection from predators (Whittingham and Evans 2004, Wilson et al. 2001), materials for nesting (Cruz-Angon and Greenberg 2005) and habitat for food sources (Wilson et al. 2003). This connection between avian abundance and vegetative complexity has been well documented in the Soconusco region of Chiapas, Mexico (Dietsch 2003, Greenberg et al. 1997, Perfecto et al. 1996) where this study was conducted.

Past research of avian populations in the Soconusco region has largely focused on abundance and species richness in these coffee agroforestry systems. These are not indicators of successful, viable populations. Because local populations are affected by emigration and immigration, solely monitoring abundance trends does not provide a full picture of the health of that population. Reproductive success can be impacted by environmental disturbances which may not influence individual adult immigration and could give the appearance of a stable population. Monitoring demographic parameters such as daily nest survival gives us a clearer picture of what is happening within a population and can further lend to insights on whether a population is declining and why a decline is taking place (Martin 1993). Further, understanding the reproductive success of a community or population at a given location allows for the design and implementation of management practices that directly target breeding success to manage a population more effectively (Makan et al. 2014).

Studying avian reproductive success can be challenging and labor intensive and research is limited with regard to the avifauna nesting within coffee agroforestry systems (Lindell et al. 2011, Gleffe et al. 2006). Lindell & Smith (2003) investigated distribution and nest success within pastures, sun coffee and understory forest in Costa Rica, however, did not include shaded coffee in their study. A study by Gleffe, et al. (2006) investigated the refugia hypothesis by estimating

nesting success of resident birds between shade coffee and secondary forest in Puerto Rico. Lindell et al. (2011) conducted a species-specific study on White-throated and Clay-colored thrushes comparing nesting success between pastures and abandoned coffee farms in Costa Rica. To date, there is no published literature comparing nesting reproductive success between sun coffee and shade coffee farms and there is no quantitative data available on resident nesting species in coffee agriculture in the Soconusco Region. This research aims to lessen this gap in the literature and provide a starting point for future studies interested in avian breeding ecology in coffee agroforestry systems, possible mechanisms for daily nest survival rate, and how certain management practices that alter habitat heterogeneity and structural complexity can impact breeding populations within these systems.

Methods

Site Selection

This study was conducted within two coffee farms, Finca Irlanda and Finca Hamburgo, located in the Sierra Madre de Chiapas Mountain range in the Soconusco Region of the southern state of Chiapas, Mexico north of the Guatemala border. Finca Irlanda (15°20'N, 90°20'W) is an ~300 ha certified organic, shaded coffee polyculture farm. Vegetation of the farm is diverse with ~200 species of trees (Philpott et al. 2012). Finca Irlanda has the shade-certification from Rainforest Alliance and is part of the Smithsonian's Bird-Friendly program (Philpott et al. 2012). Finca Hamburgo (15°10'N, 92°19'W) shares an eastern border with Finca Irlanda and is a large conventional coffee farm with a limited canopy comprised of *Inga* sp (Jedlicka et al. 2021).

Finca Irlanda and Finca Hamburgo experience semitropical climates with an average annual temperature of 22 C and annual precipitation between 4,500 and 5,000 mm (Jiménez-Soto 2013) primarily occurring in the wet season between May and October (Jedlicka et al. 2021). Both farms have elevation ranges from 950-1150 meters above sea level (Jedlicka et al. 2021, Philpott et al. 2012). Coffee production began in the region in the early 1900s and is now primarily ~90%, commercial coffee agriculture with scattered fragments of forest. The topography of both study sites consists of steep, mountainous terrain (Jedlicka et al. 2021). These two farms have been the site of studies from more than 50 scientific publications providing a depth of background information on the ecology of the coffee agroecosystem (Vandermeer et al. 2010, 2019, Philpott et al. 2012). Of these studies, several focus on the avifauna and include studies on biodiversity conservation (Philpott et al. 2008, Mas and Dietsch 2004, Perfecto et al. 2003) diet (Jedlicka et al. 2021) foraging behaviors (Dietsch et al. 2007, Jedlicka et al. 2006) ecosystem services (Perfecto et al. 2004), disease ecology (Dietsch 2005), and management impacts on population (Philpott et al. 2012) though no research has been published on nesting ecology or nest survivorship within these two farms.

Nest Searching and Monitoring

Nest searching was conducted within a smaller region of the pre-establish study sites at each farm and was done in accordance with methods from Martin (1993). Nest searching occurred from sunrise to ~1200 each day, alternating daily between study sites, with an equal amount of time spent nest searching between each farm. Nests were found primarily by observing parental behavior. Parental behavior indicating the existence of a nest includes material carrying, food

carrying, alarm vocalizations and flushing behaviors. Material carrying occurs during the build stage of the nesting cycle when one or both parents are carrying vegetation, twigs, branches, or spiderwebs to a specific location. Food carrying may happen by one or both parents during the nestling stage when young have hatched and remain in the nest or when one parent is bringing food to the other parent either incubating during the egg stage or brooding, after eggs have hatched. Alarm calling is species specific and can be used to indicate proximity of a nest by a distressed parent. Flushing behavior occurs when a parent is on the nest incubating or brooding and is disturbed by human or predator presence and flushes from, or leaves, the nest in a swift manner discernably different than flying from a perch point.

At the discovery of the nest, date, time, species, location, nest stage (build, incubating, nestling) and contents (none, number of eggs, number of nestlings) were recorded. Contents were observed directly when nests were found below ~1.5m or when observable from a slope. For nests not directly observable, an extendable pole (3m Bluetooth selfie stick) with attachment for cellular device was used to take a photo via Bluetooth remote from above the nest to determine contents. Location was determined using a handheld GPS device and no physical marker or flagging tape was used in the field to mark locations of nests. For all nests, species was determined through visual identification using the field guide by Howell and Webb (1995). Nests were monitored at each site every other day or every 3rd day where nest searching did not occur on Sundays and nests monitored on Saturday would not be monitored again until Tuesday. Nest monitoring was done concurrently with nest searching to optimize time spent in the field. For nests found in the build stage, monitoring would not begin for an additional 3-5 days after the nest was located. However, nests determined to be in lay stage would continue to be monitored every other day. For nests of species such as the Common Tody-Flycatcher (*Todirostrum cinereum*) and the Rufous-breasted Spinetail (*Synallaxis erythrothorax*) that construct dome-shaped nests where contents is not observable, status was recorded based on parent activity at or around the nest. All nests found above 10 m were recorded and monitored but excluded from data analysis due to difficulty in accurate monitoring.

Failure and success were determined in accordance with methods described in Gleffe et al. (2006) and Lindell et al. (2011). A nest was considered successful if at least one young fledged from the nest. Nest fledges were determined either by visual or audio observation of fledgling near the nest, or parent feeding behavior near the nest, or when the nest was found empty with cues such as flattened rim (Lindell et al. 2011) or without obvious signs of predation, and the median date between the last active nest check and final nest check was approximately 2 days of anticipated fledge date for the species (Haegen 2007). A nest was determined to have failed when the nest was observably no longer active prior to the earliest possible fledge date of the species. This includes nests that were destroyed via weather or predation, and nests found empty of either egg or nestling contents. Nesting cycles were determined for each species using species information from Cornell's Lab of Ornithology's Birds of the World site to accurately determine the earliest possible fledge date. For nests that were found during the nestling stage, where an exact date of hatching was not known, an approximate day of age was given to nestlings based on development.

Vegetation Sampling

Vegetation was quantified in a 3-m radius plot measured from the center of each nest. Sampling was done no sooner than one week after a successful fledge to avoid disturbance of fledglings and within 3 weeks of nest completion for all nests. Canopy openness was measured 3m from the center of the nest at each cardinal direction using a hand-held spherical densiometer held outwardly at chest height. Canopy cover was derived from these measurements and averaged to determine overall cover at each nest site. Vertical structure was measured in accordance with methods from Bailey and King (2019) using a pole held vertically 3m from the nest at each cardinal direction and counting the points of vegetation contact with the pole 3m above and 3m below the nest to produce a single number called vertical structure. A complexity index was calculated by characterizing visual estimates of the level of cover for five different vegetative strata present: overstory (>20m), understory (5-20m), tall shrub layer (1-5m), low shrub layer (20-100cm), and ground layer (< 20cm). Level of cover was determined to be closed, patchy, sparse, open, or absent, and assigned a number 0-4 where 0 = absent (0% cover), 1 = open (1-33% cover), 2 = sparse (34-66% cover), 3 = patchy (67-99% cover) and 4 = closed (100% cover). The numbers for each vegetative strata were then added up to produce a complexity index for each nest site between 0 and 20. The height of nests was measured from the ground to the bottom of the nest, and the site of the nest was recorded for each nest as either tree, coffee, ground, or bank.

Analysis

The Mayfield Method (Mayfield 1961) was used to determine probability of daily nest survival for the cumulative nests found at Finca Irlanda and Finca Hamburgo. This number is calculated by dividing the total failed nests at each site by the total number of exposure days and subtracting the quotient from 1 to produce the probability that a nest will survive to the next day. Exposure days are the number of days a nest is exposed, counting from the first day a nest was located until its completion date. This produces a single probability for each site and is not subject to further analysis.

All analysis was conducted using R for statistical computing. Two Sample T Tests were used to compare continuous vegetation variables between farms and continuous vegetation variables between failed and successful nests. A Binomial Linear Regression model was used to determine if site (Finca Irlanda, Finca Hamburgo), nest site (tree, coffee, ground, bank), or vegetation variables (canopy cover, structure average, complexity index, nest height) influenced the outcome of a nest (0:fail, 1:success). A pairwise correlation was conducted for all vegetation variables with a threshold of 0.65 and no strong correlation was found between variables.

Results

A total of 96 nests were found with 62 nests found at Finca Irlanda, and 34 nests found at Finca Hamburgo. Of these nests, 54 were excluded from analysis because they were already inactive, incomplete at the end of study, abandoned during the build stage, unable to be relocated, or found outside of the designated study plot. Final analysis included 18 nests in Finca Hamburgo and 25 nests in Finca Irlanda. Nests comprised 17 species from 11 different families. Finca

Irlanda contained nests of 13 species from 9 families, Finca Hamburgo contained nests of 9 species from 6 families, with nests of 5 species being found at both sites, 8 species' nests only found in Finca Irlanda, and 4 species' nests found only in Finca Hamburgo (Table 1).

Family	Species	Common Name	No. of Active Nests	
			Irlanda	Hamburgo
Cardinalidae	<i>Saltator atriceps</i>	Black-headed Saltator	1	0
Emberezinae	<i>Melospiza biarcuatum</i>	White-faced Ground Sparrow	1	2
Furnariidae	<i>Synallaxis erythrothorax</i>	Rufous-breasted Spinetail	1	0
Parulinae	<i>Basileuterus rufifrons</i>	Rufous-capped Warbler	0	2
Thraupinae	<i>Cyanerpes cyaneus</i>	Red-legged Honeycreeper	6	2
	<i>Euphonia hirundinacea</i>	Yellow-throated Euphonia	0	1
	<i>Piranga leucoptera</i>	White-winged Tanager	0	1
	<i>Thraupis abbas</i>	Yellow-winged Tanager	1	0
	<i>Thraupis episcopus</i>	Blue-gray Tanager	1	0
Trochilidae	<i>Saucerittia cyanura</i>	Blue-tailed Hummingbird	1	0
Troglodytidae	<i>Cantorchilus modestus</i>	Cabanis's Wren	0	1
	<i>Troglodytes aedon</i>	House Wren	1	4
Turdidae	<i>Catharus aurantiirostris</i>	Orange-billed Nightingale-thrush	1	0
	<i>Turdus grayi</i>	Clay-colored Thrush	6	4
Tyrannidae	<i>Contopus bogotensis</i>	Northern Tropical Pewee	1	0
	<i>Todirostrum cinereum</i>	Common Tody-flycatcher	1	1
Vireonidae	<i>Vireo flavoviridis</i>	Yellow-green Vireo	3	0
			25	18

Table 1: Total nests found at each farm organized by family and species.

Trees accounted for the majority of nest site locations at both study sites (Figure 1). Of the 25 nests found at Finca Irlanda, 76% were located in trees, 20% were located in coffee plants, 4% were located in a bank. None of the nests included in analysis were found on the ground at Finca Irlanda. Of the 18 nests found at Finca Hamburgo, 55.56% of nests were located in trees, 16.67% were located in coffee plants, 16.67% were located on a bank and 11.12% were located on the ground (Figure 1).

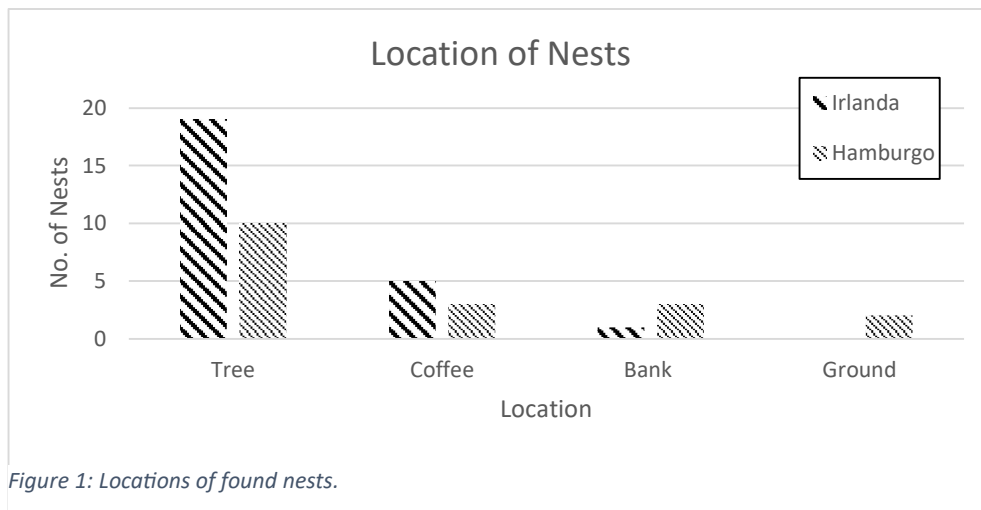


Figure 1: Locations of found nests.

There were significant differences for all vegetation variables between nests found in Finca Irlanda and nests found in Finca Hamburgo. Canopy cover, vertical structure, complexity index and height of nests found in Finca Irlanda were all significantly higher than for nests found in Finca Hamburgo (Figure 2). Means for vegetation variables were consistently higher for failed nests than for successful nests, however these differences were not statistically significant (Figure 3). Figure 4 shows visualization of downward trend from 1 (success) to 0 (fail) with increase in vegetation variable values for canopy cover, structure average and complexity index, however analysis did not show statistical significance.

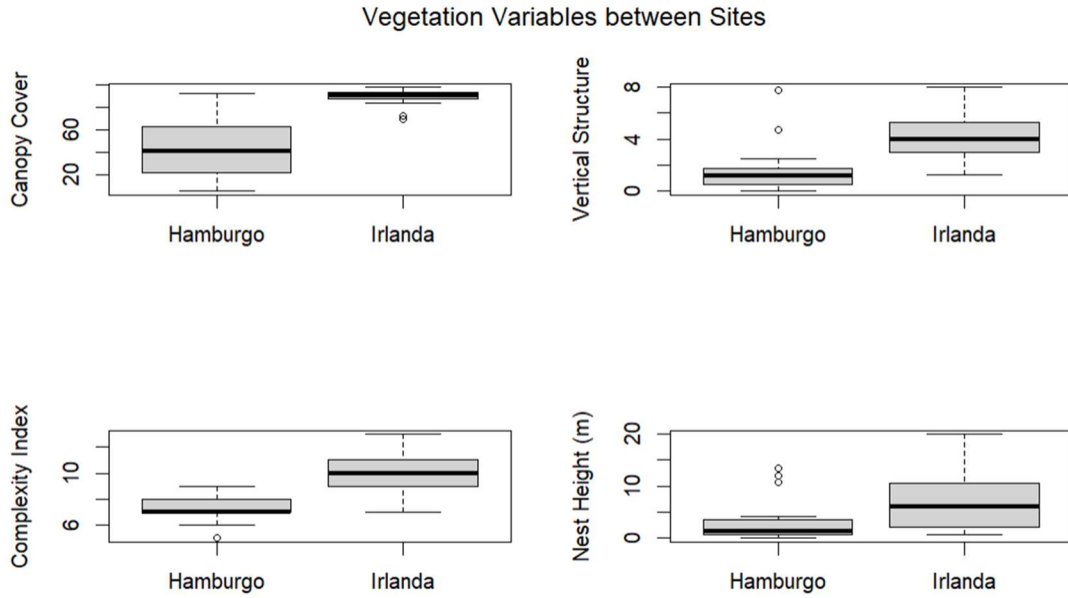


Figure 2: Boxplots of vegetation means between sites.

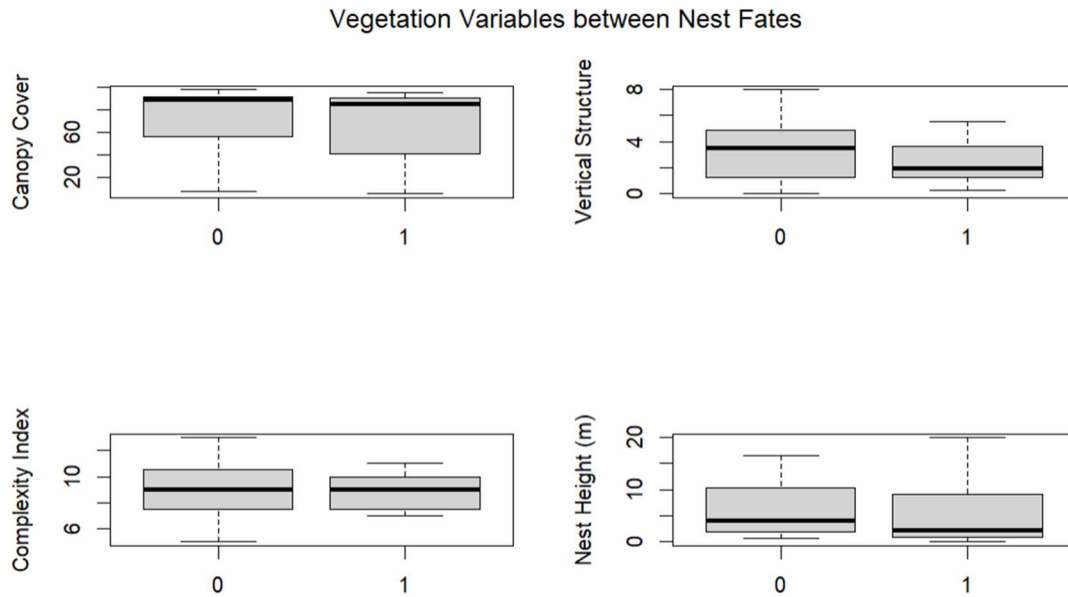


Figure 3: Boxplots of vegetation means between nest fates. (0=failed, 1=success)

Results from the binary regression investigating response variables effect on nest success found vertical structure to be significant in predicting outcome of nest fates. Results show a negative relationship as vertical structure increases by 1, there is an average change of -0.78436 in the log odds of nest outcome of nests being successful. There was additionally a statistical significance and positive correlation between nest outcome and nest site Finca Irlanda. This suggests that, when controlling for all other variables, probability for nest success increases at Finca Irlanda. No other response variables showed any significance in predicting the outcome of nest success.

Probability of Daily Nest Survival					
Site	Total Nests	Successful	Failed	Exposure Days	DSR
Irlanda	25	10	15	288	0.947917
Hamburgo	18	6	12	125	0.904

Table 2: Probability of daily survival rates (DSR) at each farm.

Results from using the Mayfield Method (Table 2) to calculate probability of daily nest survival indicate a slightly higher probability of survival of nests in Finca Irlanda (94.79%) than nests in Finca Hamburgo (90.40%). Species or family specific analysis was not possible due to a lack of sufficient data.

Discussion

Findings from this study show that an increase in habitat complexity more directly surrounding the nest as indicated by vertical structure may play a role in nest survival more than the overall composition of the habitat as indicated by canopy cover or the complexity index. This is congruent with past studies that found nest concealment within 1m of the nest was more closely associated with daily nest survival than canopy cover or other vegetation metrics (Israel et al. 2023, Segura et al. 2012). However, those studies indicated a positive relationship between nest concealment and survival. Further research has shown a trade-off exists between vegetation density offering concealment and protection from predators and inhibiting the ability of parents to protect the nest through detection of predators (King et al. 1999, Götmark et al. 1995). Dense vegetation can also provide nest access route to predators like snakes (Koenig et al. 2007). This could explain the negative correlation found in this study between vertical structure and nest fate. Furthermore, the primary cause of nest failure in the tropics is predation (Söderström et al. 2006, Martin et al. 1992). Although this study did not include predator surveys within these systems, interviews with farmworkers regarding working conditions in Finca Irlanda and Finca Hamburgo mentioned snake bites as more of a threat in Finca Irlanda due to the dense vegetation, as compared to Finca Hamburgo (Jimenez-Soto 2021).

The interpretation of results from this study are highly limited as data was only collected for 12 weeks during a single breeding season. The small data sample limits the inclusion of other factors influencing nest success such as time of nesting within the breeding season, stage of the nest at failure and species-specific trends and makes it difficult to draw conclusions to make management recommendations. A larger sample pool across breeding seasons would allow for a clearer interpretation of correlation between nest fate and habitat complexity. Additionally, the data in the regression are not independent, given phylogenetic relationships amount species.

However, the uneven sample sizes make controlling for phylogenetic relatedness in statistical analysis challenging.

Expansion of this nesting ecology research in the future in conjunction with predator surveys and a more in depth look at habitat use, and requirements of breeding species might lend clearer insights into how these systems can support breeding avian populations. Previous research on avian predation of coffee pests shows that the Red Legged Honey Creeper (*Cyanerpes cyaneus*) and the Rufous Crowned Warbler (*Basileuterus rufifrons*) contribute to the reduction of coffee pests (Jedlicka et al. 2021) and further species-specific research on these resident nesting species and their foraging and nesting requirements could contribute to applicable management decisions for farmers interested in relying more heavily on the beneficial ecology of the area and reduce the need for pesticide inputs.

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Supplementary Materials

Mean Difference in Vegetation between Nest Sites					
Vegetation Variable	Site	Mean	t	df	p val
Canopy Cover (%)	Irlanda	88.57	-7.1581	18	1.01E-06
	Hamburgo	42.92			
Vertical Structure	Irlanda	4.06	-4.2294	36	0.00015
	Hamburgo	1.64			
Complexity Index	Irlanda	10.04	-7.1387	41	1.05E-08
	Hamburgo	7.34			
Nest Height (m)	Irlanda	6.77	-2.6565	40	0.01125
	Hamburgo	3.09			

Table 3: Results of t-test analysis of vegetation variables between farms.

Mean Difference in Vegetation between Nest Fates					
Vegetation Variable	Fate	Mean	t	df	p val
Canopy Cover (%)	Fail	71.56	0.533	29	0.5977
	Success	66.49			
Vertical Structure	Fail	3.38	1.4376	40	0.1583
	Success	2.48			
Complexity Index	Fail	9	0.46741	40	0.6427
	Success	8.75			
Nest Height (m)	Fail	5.56	0.29965	28	0.7667
	Success	5.04			

Table 4: Results of t-test analysis of vegetational variables between nest fates. (0=fail, 1=success)

Variable	Coefficient
Canopy Cover	-0.01052 (0.7787)
Complexity Index	-0.31335 (0.3965)
Vertical Structure	-0.78436 (0.0407*)
Nest Height	0.15693 (0.1413)
Nest Site: Tree	-1.53187 (0.3562)
Nest Site: Coffee	2.41030 (0.1195)
Nest Site: Ground	19.45094 (0.9944)
Site: Irlanda	4.21141 (0.0731*)

Table 5: Results of binary linear regression.

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