

Contents lists available at [ScienceDirect](https://www.sciencedirect.com)

# Global Ecology and Conservation

journal homepage: [www.elsevier.com/locate/gecco](http://www.elsevier.com/locate/gecco)

## Bird abundance and diversity in shade coffee and natural forest in Kenya

Frank Juma Ong'ondo<sup>a,b</sup>, Frank A. Fogarty III<sup>a</sup>, Peter Njoroge<sup>b</sup>,  
Matthew D. Johnson<sup>a,\*</sup>

<sup>a</sup> Department of Wildlife, California Polytechnic University, Humboldt, CA, USA

<sup>b</sup> Department of Ornithology, National Museums of Kenya, Nairobi, Kenya

### ARTICLE INFO

#### Keywords:

Coffee  
Understory  
Insectivore  
Feeding guilds  
Kenya  
Conservation  
Bird  
Biodiversity

### ABSTRACT

Coffee, one of the major traded commodities in the world, has economic value for rural livelihood and potentially as habitat for forest wildlife. Previous work in Central Kenya has demonstrated that when cultivated with shade trees, coffee farms can host high levels of bird diversity. However, questions of how the African bird communities in shade coffee farms compares to those in natural forest remained unanswered. Using three visits to each of 160-point count locations in natural forest (80) and shade coffee sites (80) in Central Kenya, we estimated bird abundance and species richness in natural forest and shade coffee. Specifically, we tested hypotheses that the abundance and diversity of birds in shade-coffee and natural forests varies by feeding guilds and forest-association status. We found that, compared to natural forest, shade coffee had higher bird abundance and species richness of carnivores, granivores, omnivores, and insectivores, including understory forest insectivores specifically. Frugivores and nectivores had similar abundance in forest and coffee, but were more species rich in forest and coffee, respectively. The abundance and species richness of forest specialists and forest visitors were higher in natural forest than in shade coffee, whereas forest generalists and birds with no forest association status were more abundant and species rich in shade coffee. Our study confirms the value of remnant native trees within coffee plantations for the persistence and conservation of avian communities, while also clarifying that some groups of birds are reliant on natural forests and unlikely to be conserved in shade coffee farms.

### 1. Introduction

Birds of tropical forests are among the most threatened species on Earth (Newbold et al. 2013; Şekercioğlu et al. 2019). Tropical forests cover just 10% of the Earth's surface but contain almost two-thirds of its biodiversity, and deforestation rates continue to be high throughout the tropics (Giam, 2017). Much of the deforestation is driven by agricultural expansion and intensification (Geist and Lambin, 2002), which alters habitat and landscape characteristics. The abundance and diversity of birds is a function of resources governed by habitat and landscape characteristics (Block and Brennan, 1993; Bawa et al., 2004; Martensen et al., 2008; Johnson and Wood, 2018). Thus, agriculture strongly impacts bird communities via its effects on food availability, vegetation structure, and habitat connectivity (Dirzo et al., 2014; Ceballos et al., 2017; Şekercioğlu et al., 2019). In particular, the conversion of complex tropical forests to simplified agriculture land cover types (Donald, 2004) destroys microhabitats and resources, prompting the disappearance or

\* Corresponding author.

<https://doi.org/10.1016/j.gecco.2022.e02296>

Received 8 April 2022; Received in revised form 26 September 2022; Accepted 27 September 2022

Available online 28 September 2022

2351-9894/© 2022 Published by Elsevier B.V. This is an open access article under the CC BY-NC-ND license (<http://creativecommons.org/licenses/by-nc-nd/4.0/>).

reduction in abundance of specialized species (Laurance and Bierregaard, 1997; Stouffer et al., 2006; Zurita et al., 2006; Mahiga et al., 2019). For example, several studies in the Neotropics has shown that forest specialists tend to suffer from any conversion of primary forest (Turner, 1996; Donald, 2004; Sekercioglu et al., 2004; Newbold et al., 2013; Alvarez-Alvarez et al., 2022), but very few works have addressed this topic in Africa (Powell et al., 2015).

However, disturbance to tropical forests does not affect all birds negatively (Newbold et al., 2013). Variation within forests creates a range of food resources, nesting sites, and cover (Laurance and Bierregaard, 1997; Otieno et al., 2011). In turn, birds have habitat preferences and feeding habits that affect their response to forest disturbance. "Forest specialists" are found in the interior of forests and are most likely to be extirpated when the forest is modified (Bennun et al., 1996). Forest specialists are particularly responsive to the loss of canopy cover (Reidy et al., 2014), which can diminish the availability of tree cavities for woodpeckers and other cavity-nesters (Bütler et al., 2013) and alter understory microhabitats important for maintaining bird abundance and diversity (Villard and Foppen, 2018). Because of these complex attributes and the rarity of undisturbed forest on the landscape, forests harbor many endangered and specialized species (Bennun et al., 1996; Waceke, 2014). However, forests do not provide the necessary resources for other bird species that are better adapted to open country land cover types, such as grasslands and shrubby fields. These species, including species called "forest visitors," are expected to only use forests occasionally and mainly along their edges (Ndang'ang'a et al., 2013). "Forest generalists" are capable of occupying forests well as more open land cover types, and are expected to show intermediate forest association between forest specialists and visitors, while still other species show no association with forests at all. These forest association categories also correspond with diet (Newbold et al., 2013; Carrara et al., 2015; Carlo and Morales, 2016), as forest specialists tend to include more insectivores and frugivores, whereas forest visitors include many granivores less likely to be negatively affected by forest disturbance (Sekercioglu et al., 2004; Bregman et al., 2014; Morante-Filho et al., 2015). A global review suggest that insectivorous birds of tropical forest understories are especially vulnerable to forest loss, though more work is needed on this topic in Africa (Powell et al., 2015).

Forests are severely threatened in Kenya (Langat et al., 2016). In the past two decades, Kenya lost 49,800 ha of humid primary forest, making up 14% of its total tree cover loss of over 360,000 ha, and over 90% of these losses were caused by shifting agriculture (Global Forest Watch, 2021). Kenya's forests host 4.0% of the known world biodiversity (Mongabay, 2019). Despite their faunal endemism, Kenyan forests have received relatively little conservation attention. Kenyan forests are affected by climate change and human population growth (Cuni-Sanchez et al., 2019). To sustain the latter, there is an urgent need for food and bioenergy, prompting increased forest loss for agricultural expansion, which is a premier threat to forest biodiversity worldwide (Lambin and Meyfroidt, 2011). At a global level, tropical forest loss is estimated at 17% as a result of high demand of agricultural commodities for international markets such as coffee grown under the sun (Vancutsem et al., 2021).

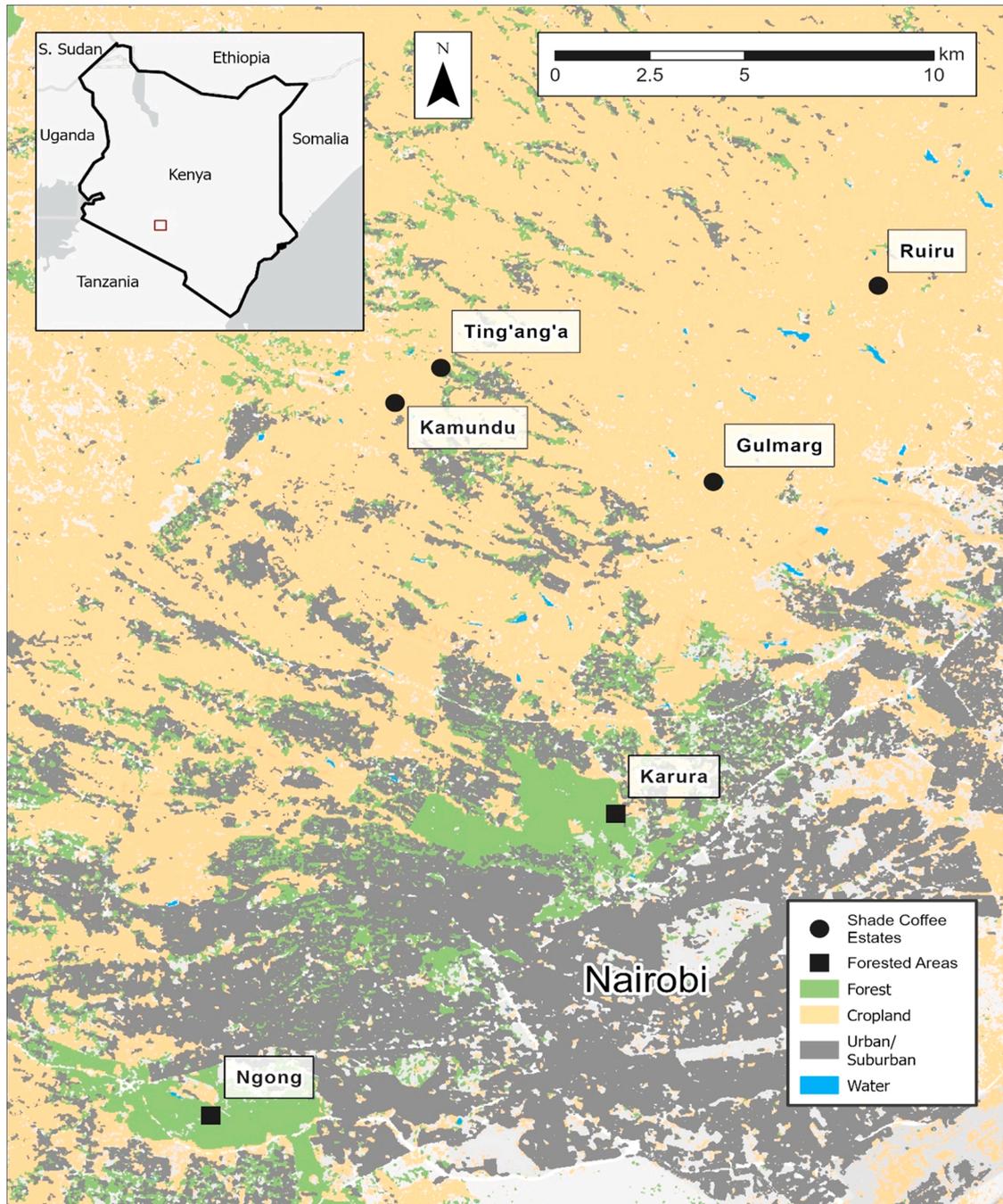
Coffee, one of the major export and cash crops of the tropics, has great influence on biodiversity (Jha et al., 2014). On one hand, deforestation for coffee cultivation is a major threat to forest biodiversity. But coffee can be cultivated in a variety of ways (Jha et al., 2014), and where the coffee shrubs are grown beneath shade trees (shade coffee, hereafter), coffee systems can also provide some habitat for birds species associated with trees and more forested habitats (Perfecto et al., 1996). Native shade trees, in particular, can provide insect resources and microhabitats that are suitable for some forest-associated birds (Narango et al., 2018; Rodrigues et al., 2018; Alvarez-Alvarez et al., 2022; Kammerichs-Berke et al., 2022). Coffee farms provide ground cover that offers suitable habitat for some birds (Komar, 2006), including breeding sites and hiding places for skulking birds as well as foraging habitats for birds such as thrushes (Tejeda-Cruz and Sutherland, 2004; Philpott et al., 2008). Coffee trees themselves also produce flowers that attract insectivorous and omnivorous bird species (Perfecto et al., 1996). Migratory birds also use shade coffee farms as a corridor when moving between temperate and tropical regions (Buechley et al., 2015; Estrada-Carmona et al., 2019). Landscapes with shade coffee may also sustain connectivity and mobility of forest-dependent species moving and feeding from one forest fragment to another (Estrada-Carmona et al., 2019). Nonetheless, shade coffee may not provide resources necessary for the most forest-reliant species (Tejeda-Cruz and Sutherland, 2004; Komar, 2006; Alvarez-Alvarez et al., 2022), and comparisons of bird communities between coffee and intact forests are needed (Mendenhall et al., 2016). Despite the apparent importance of trees in coffee to birds, and the importance of forests to Kenyan avifauna, relatively little work on this topic has been conducted in Kenya, and to date no studies have compared the avifauna in shade coffee and natural forests in Kenya.

The contribution of coffee farms to the conservation of biodiversity in agricultural landscapes has long been recognized (Perfecto et al., 1996), although their value for forest specialists remain unresolved (Tejeda-Cruz and Sutherland, 2004; Jha et al., 2014). This understanding increases the need for a land use planning strategy that incorporates the management and diversification of the anthropogenic matrix in which natural areas are embedded (Bawa et al., 2004; Kremen and Merenlender, 2018). Many scientific studies focus on overall bird species richness (Sekercioglu, 2002; Mulwa et al., 2012; Smith et al., 2015), but questions remain about species abundance and composition of bird communities in forests and coffee farms, especially with respect to forest specialization, feeding guilds, and understory association (Newbold et al., 2013). Working in Kenyan and Ethiopian coffee farms, respectively, Smith et al. (2015) and Buechley et al. (2015) found bird community patterns that differed from those reported from Neotropical coffee farms, including a high diversity in sun coffee compared to the Neotropics, further underscoring the need to better understand Afrotentative bird communities in agro-ecological matrices.

We investigated how bird abundance and species richness varied between shade coffee farms and natural forests of central Kenyan highlands. Specifically, we examined two hypotheses based on research previously conducted in the Neotropics. The *forest specialization hypothesis* posits that while shade coffee farms harbor many habitat generalists and species able to use both forest and more open land cover types, they are not able to support many forest specialists (Tejeda-Cruz and Sutherland, 2004; Newbold et al., 2013; Reidy et al., 2014). Similarly, the *feeding guild hypothesis* posits that shade coffee farms are well-suited for granivorous birds, but they are not as good as forests at supporting insectivores and frugivores (Komar, 2006; Sekercioglu, 2012; Newbold et al., 2013). A corollary of the

feeding guild hypothesis asserts that shade coffee farms, which have understories that differ from natural forests, cannot support forest understory insectivores present in natural forests (Powell et al., 2015). To examine these hypotheses, we tested the following predictions.

- Natural forest has higher species richness and abundance of forest specialists, frugivores, and insectivores (including forest understory insectivores) than does shade coffee.
- Shade coffee has higher species richness and abundance of forest visitors, forest generalists, those species with no forest association at all, and granivores than does natural forest.



**Fig. 1.** Study area and sampling sites for bird species detected in natural forest and shade coffee on 3 visits to each of 160-point count locations in natural forest (80) and shade coffee sites (80) in Central Kenya, February to April 2020. Map created by Samantha Chavez.

## 2. Materials and methods

### 2.1. Study area

The study was conducted within and around shade coffee farms and natural forest sites in the vicinity of Nairobi, Kenya. The region experiences both wet (April–June and October–December) and dry seasons (August–October and January–early March). The coffee and forest sites receive 865–962 mm of rainfall annually and occur at similar elevations (1500–1850 m asl). Shade coffee farm study sites were on Sasini Coffee Plantation Company in Kiambu County of Central Kenya, in the heart of one of the country's six major areas producing Arabica coffee, *Coffea arabica* (Gakinya, 2014; Smith et al., 2015). The Sasini Coffee Company farms were founded in 1952 (Gakinya, 2014). Sasini Coffee Company adopted two distinct management levels of coffee production: coffee grown under sun and shade coffee. All study sites were in shade coffee. The farms lie in an agriculturally fertile area in Kiambu County and are surrounded by other agricultural land cover, such as tea and maize farms, vegetables, and dairy farming. Sasini Coffee Company has a total of 911 ha under coffee cultivation with eight farms in Central Kenya. We selected 8 sites (2 sites per coffee farm x 4 coffee farm estates) for the shade coffee sampling points (Fig. 1): Kamundu (1° 08' 10" S, 36° 47' 23" E; 123 ha), Ruiru (1° 06' 28" S, 36° 54' 27" E; 117 ha), Ting'ang'a (1° 07' 35" S, 36° 48' 04" E; 112 ha) and Gulmarg (1° 18' 35" S, 36° 44' 35" E; 99 ha). The shade coffee farms include rows of coffee shrubs with systematically distributed shade tree species of one to several native tree species, corresponding to a "shaded monoculture" cultivation strategy as described by Moguel and Toledo (1999). *Cordia* (*Cordia africana*) was the most common shade tree in this study, with scattered *Prunus africanas*, *Vitex kinyensis* and *Ficus sthoningii*. Farms with the exotic grevillea shade tree (*Grevillea robusta*) were excluded from this study. The dominant understory herbaceous plant present during surveys was exotic and invasive Blackjack, *Bidens pilosa*. Blackjack was spread throughout the farms, both between and within the coffee rows. It is considered a weed and was controlled by physical methods with hand-held hoes or with chemicals (herbicide) where it was intense. Other herbaceous plants detected in the farms included *Oxalis latifolia*, *Sporobolus sp*, *Commelina bengalensis*, *Klenia abyssinica*, and *Gloriosa superba* among others.

In natural forest, two forests were chosen for this study for comparison to the shade coffee farms (Fig. 1), both managed by the Kenya Forest Service. Karura Forest (1° 14' 25" S, 36° 49' 25" E) is located adjacent to the Kenya Forest Service headquarters facilities in Nairobi County. It was gazetted in the year 1932 and is 1041 ha (Karura Management plan, 2010). It is a dry upland forest and a water catchment for the Thigiri, Karura, Ruaka, Gitathura, and Mathare River systems. The forest is situated in the northern part of Nairobi City. The forest supports non-native plantation trees, native trees, and grasslands. All bird surveys were conducted in areas of native forest, which was generally between 50 and 100 years old. Due to its proximity to the capital city, Karura forest underwent rapid logging to provide timber for increased infrastructure in Nairobi. In addition, the size of the forest was reduced due to land grabbers and private developers using part of it to build homes and business hubs. The typical trees in Karura Forest include *Olea europaea cuspidate*, *Croton megalocarpus*, *Warburgia ugandensis* (Muthiga), *Brachyleana huillensis* (Muhugu), *Uvaridendron anisatum*, *Strychnos henningsii*, *Markhamia lutea*, *Newtonia buchananii*, *Salvadora persica*, *Ficus thonningii*, *Trichilia emetic*, *Calondendrum capense* and *Dombeya goetzenii*.

Ngong Road Forest (1° 18' 35" S, 36° 44' 35" E) is a dry land forest located within the purview of western Nairobi city, between 1800 and 1820 m. The forest was gazetted in 1952. Due to increased development of Nairobi city and its environs, Ngong Road Forest has undergone severe reduction in size from its original 2927 ha to the current 1224 ha mostly due to expansion of the Karen and Ngong residential areas. Ngong Road Forest has similar tree species as Karura Forest (see above), although it also has some species associated with drier conditions such as *Drypetes gerrardii*, *Maytenus undata* and *Strychnos henningsii* among others. Ngong Road Forest is managed by Kenya Forest Service (KFS) and the Ngong Road Forest Association, a Community Forest Association formed under the Forest Act of 2005.

### 2.2. Sampling procedure

This study was conducted between February and April 2020 to include surveys for some wintering migrants and coincide with onset of the breeding season. Using a stratified sampling design, we selected eight replicate study sites on each of the two land cover types (shade coffee and natural forest, 16 sites total). Two sites were located in each of the four coffee estates described above, and four sites were located in each of the two forests described above. Each study site was separated from another by at least 400 m and was chosen to include land cover with relatively consistent structure and species composition (e.g., similar shade tree species and age, similar forest tree composition and age). Within each of these selected 16 study sites, we distributed ten sampling points (total 160) where both bird and vegetation data were recorded. Adjacent sampling points were 150 m apart and at least 200 m from the forest edge or major road. The first point at a site was position just beyond 200 m from the edge, and a walking route was established in each site with subsequent points distributed systematically at 150 m intervals. Areas adjacent to roads, buildings and trails were avoided to reduce disturbance and increase natural observation of the birds. At each study site, point counts were conducted three times (February 2020 through April 2020). We randomized the order sites were visited during our first visit, then maintained that order for subsequent visits to keep a relatively consistent interval between each successive visit to a site (21 days). Vegetation data (described in more detail below) were only collected once during the first session of point counts.

We surveyed birds by a standardized point count protocol (Ralph et al., 1993). On arrival to the sampling point, we allowed birds to settle for 1 min and then recorded all the birds seen or heard for a period of 9 min. This time was selected to be short enough not to overestimate the same individual twice and, in turn, long enough to record most species at each point, including rare species. Flyover birds were not counted because we assumed that they were not using the habitat. To avoid double-counting birds at adjacent sampling

points, we only recorded birds detected within a fixed radius of 50 m, using a rangefinder to aid in distance estimation.

All birds recorded during the surveys were classified into one of six feeding guilds: (1) Carnivores (feeding mainly on vertebrates or large non-insect invertebrates), (2) Insectivores (feeding mainly on insects and spiders), (3) Omnivores (feeding on both plant and animal materials without one strongly dominant), (4) Granivores (feeding mainly on grains and seeds), (5) Frugivores (feeding mainly on fruits) and (6) Nectivores (feeding mainly on nectar and pollen grains) (Gray et al., 2007; Kissling et al., 2007); and one of four forest-association guilds: (1) Forest specialists, (2) Forest generalists, (3) Forest visitors, and (4) No forest association (Bennun et al., 1996). Those insectivores that specialize on forest understoreys were also classified as a distinct group for analysis (insectivores with no forest association status were not included; see Appendix A for all guild classifications).

A total of eight vegetation variables were recorded at each of the 160 sampling points. For each of the four trees reaching canopy height nearest to each sampling point, we measured tree height, canopy depth (via clinometer), and trunk diameter at breast height (1.3 m off the ground via DBH tape). We also measured the canopy (shade canopy) cover at each point using a hand-held densiometer by averaging 4 measurements facing each cardinal direction. Within each quadrant of a 10×10 m plot centered at each sampling point, we recorded the estimate of the percentage of shrub cover (defined as vegetation <2.5 m), the number shrub stems present, the mean height of herbaceous vegetation (with aid of tape measure), and the percentage of the understory herbaceous vegetation that was flowering (estimated visually). The vegetation variables recorded in these four quadrants in each plot were averaged to generate point-level values for analyses. Several of these variables were correlated with each other ( $r > |0.7|$ ; tree height and DBH were correlated with each other and with canopy cover), so to avoid multicollinearity only 6 variables were used in analyses: canopy depth, canopy cover, herbaceous layer height, shrub cover, shrub stems, and shrub stems squared. These variables were selected because of their hypothesized roles in potentially influencing birds in coffee and forests (Smith et al., 2015; Kammerichs-Berke et al., 2022). Shrubs stems squared was included for a potential quadratic relationship between birds and the number of shrub stems because previous work suggested intermediate levels of shrub cover were associated with higher bird abundance in Kenyan coffee (Smith et al., 2015). All the field protocols were approved following Humboldt State University Institutional Animal Care and Use Committee (IACUC) permission number 16/17. W306-A.

All analyses were conducted with R version 4.0.2 (R Core Team, 2020). We tested the association between species' feeding guilds and forest association status using chi-square test of independence. We used species accumulation curves to examine the adequacy of sampling effort in shade coffee and natural forest. Specifically, we calculated species accumulation curves for each land cover type as a function of the number of sample points, using the *vegan* package (Martensen et al., 2008), and the number of individual birds detected, using the *iNEXT* package which also included rarefaction and extrapolation of species diversity (Hsieh et al., 2016). We calculated the species similarity index between shade coffee and natural forest using Jaccard Index formula  $C_j = j/(a+b+j)$ , where  $j$  = species detected in both shade coffee and natural forest,  $a$  = species detected only in forest and  $b$  = species detected only in shade coffee.

We used community N-mixture models to estimate bird abundance and species richness detected during the survey period (Bellier et al., 2016; Kéry and Royle, 2016; Yamaura et al., 2016). We organized count data in a three-dimensional array,  $y$ , where the dimensions are  $i$  = point,  $j$  = visit, and  $k$  = species. The observation process of the model was.

$$2.3. y_{ijk} | N_{ik} \sim \text{Binomial}(N_{ik}, p_{ijk})$$

where  $N_{ik}$  is the latent abundance of species  $k$  at point  $i$ , and  $p_k$  is the species-specific detection probability, which is a logit scale random effect drawn from a normal distribution.  $p$  is species-specific, but estimates of  $p$  are drawn from a common distribution, allowing for information sharing among all species and better estimation for rare species. The latent abundance process of the model was.

$$N_{ik} \sim \text{dpois}(a_{ik} * \lambda_{ik})$$

Where  $a_{ik}$  is an indicator variable denoting whether species  $k$  is present at point  $i$  and  $\lambda_{ik}$  is the mean expected abundance of each species  $i$  at point  $k$ . We modeled effects of point-level covariates on  $\lambda$  with a log link.

$$\log(\lambda_{ik}) = \text{beta}0_k + \text{theta}_{ik} * \text{land cover}_i + \beta X_k$$

where  $\text{beta}0_k$  is a random effect for mean abundance of each species  $k$ ,  $\text{theta}_{ik}$  is a covariate for the effect of land cover (coffee vs natural forest) on species  $k$  at point  $i$ , and  $\beta_k$  is a vector of coefficients estimated for each species  $k$  corresponding to a vector of six vegetation variables  $X_{jk}$  measured at each point  $i$ . We included the indicator variable  $a_{ik}$  to account for zero-inflation in our count data and defined it as.

$$a_{ik} \sim \text{dbern}(\text{phi}_k)$$

where  $\text{phi}_k$  is a species-specific mean likelihood of presence.

We fit the N-mixture community model in JAGS (Bellier et al., 2016) using R version 4.0.2 (R Core Team, 2020). We ran two chains of 70000 iterations, with a burn-in of 1200 iterations. We considered abundances or richness between the land cover types to be significant if their modelled estimates had posterior distributions with < 5% overlap.

### 3. Results

A total of 4318 individual birds belonging to 145 species were recorded across all 160 sampling points during the study period

(Appendix A); 2781 individuals of 127 species were recorded in shade coffee and 1537 individuals of 79 species were recorded in natural forests (Table 1). Species accumulation curves suggested an adequate sampling effort, with the number of species detected approaching an asymptote in both coffee and natural forest beyond 70 sampling points (Appendix B). Rarefied species richness as a function of individuals sampled also suggested that sampling effort was similarly thorough in coffee and natural forest (Appendix B). Feeding guilds and forest-association guilds were not independent ( $\chi^2 = 25.33$ ,  $df = 15$ ,  $P < 0.05$ ). Omnivorous species were somewhat more strongly forest-associated than the other guilds (44% of forest specialists vs. 14% of all species were omnivores), and granivores and carnivores were less strongly forest-associated (11% of forests specialists vs. 18% of all species were granivores or carnivores; Appendix C).

Modeled estimates of species abundance suggested there were strong differences between natural forest and coffee. Of 145 total species analyzed, 57 had a modeled land cover type effect with a 95% credible interval that did not overlap zero, with 18 showing higher modeled abundance in natural forest and 39 showing higher abundance in coffee (Appendix A). Likewise, there were strong differences in the modeled abundance of feeding and forest association guilds between natural forest and coffee (all of the following patterns were significant based on <5% overlap in posterior distributions, Fig. 2 & 3). Among feeding guilds, carnivores, granivores, insectivores, and omnivores all had higher estimated abundance per point count in coffee than in forest (Fig. 2). Nine of the insectivore species were classified as using the forest understory specifically, and these species had higher estimated abundance and diversity in coffee than in natural forest. Among forest-association guilds, forest specialists and forest generalists had higher estimated abundance per point count in forest than in coffee, whereas forest visitors and non-forest associated species had higher estimated abundance in coffee than in forest as per our predictions (Fig. 3). Insectivorous species (even including the understory forest insectivores specifically) were more abundant in the shade coffee than in natural forest, while there was no difference in the abundance of frugivores between shade coffee and natural forest (Fig. 2).

The patterns observed in the differential abundance of guilds between land cover types arise from differences in individual species, some of which merit special mention. For example, the higher abundance of nectivores in shade coffee was driven largely by many more detections of Bronze and Scarlet-chested Sunbirds in coffee (168 and 72, respectively) than in forest (2 and 8, respectively, see Appendix A, where all common and scientific names are provided). In contrast, the similar total abundance of omnivores in shade coffee and natural forest came about because some omnivores were far more abundant in coffee whereas other omnivores were more abundant in forest, rather than most omnivore species being similarly abundant in both land cover types. For instance, omnivorous Baglafaecht Weavers were detected primarily in coffee (121 vs. 1 in forest), whereas omnivorous Yellow-whiskered Greenbuls were detected exclusively in forest (136 vs. 0 in coffee). Similarly, there were more omnivorous Kikuyu White-eyes and Common Bulbuls in shade coffee than in natural forest, but more White-starred Robins and Spot-flanked Barbets in forest than in coffee (Appendix A). There were only four species of true frugivores detected, and the most abundant of these showed opposite patterns: Hartlaub's Turacos were detected only in forest, whereas African Green Pigeons were detected only in coffee.

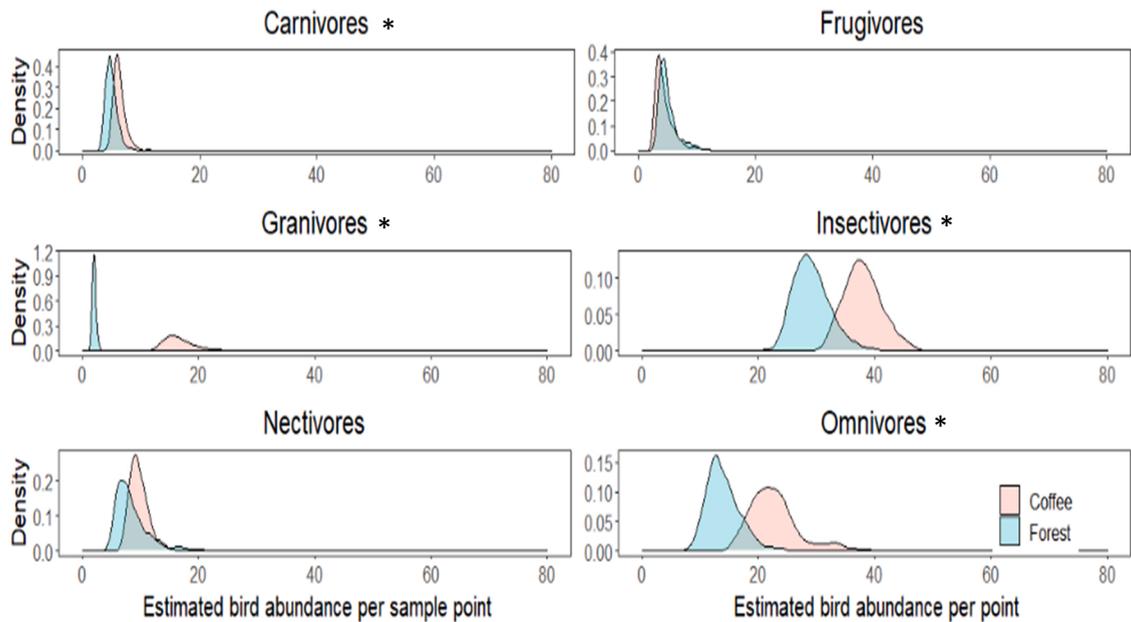
Importantly, several species were not detected at all in one land cover or the other. For example, African Citril, Kenya Rufous Sparrow, Golden-breasted Bunting and Jackson's Francolin among others were detected in coffee but not forest, whereas Brown-chested Alethe, Crowned Eagle, Cabanis's Greenbul, Green-backed Twin-spot, Lemon Dove, and Slender-billed Greenbul were detected in forest but not in coffee (Appendix A). Some species such as Little Swift, Northern Double-collared Sunbird, Tambourine Dove, Tropical Boubou, and Yellow-breasted Apalis among others showed similar detections in shade coffee and natural forest (Appendix A). All nine of the species recorded as forest understory insectivores were recorded in natural forest, whereas two of these species were not detected in coffee: Brown-chested Alethe and Mountain Wagtail.

There were also strong differences in species richness between natural forest and shade coffee (all of the following patterns were significant based on <5% overlap in posterior distributions, Figs. 4 & 5). Overall, the number of species detected was higher in coffee (127) than in the forest (79), with 66 (46%) species detected in coffee only, 18 (12%) in forest only, and 61 (42%) detected in both,

**Table 1**

Total bird detections and total number of species detected (with percentages of total in a land cover type in parentheses) among 7 feeding guilds and 4 forest association guilds on 3 visits to each of 160-point count locations in natural forest (80) and shade coffee sites (80) in Central Kenya, February to April 2020.

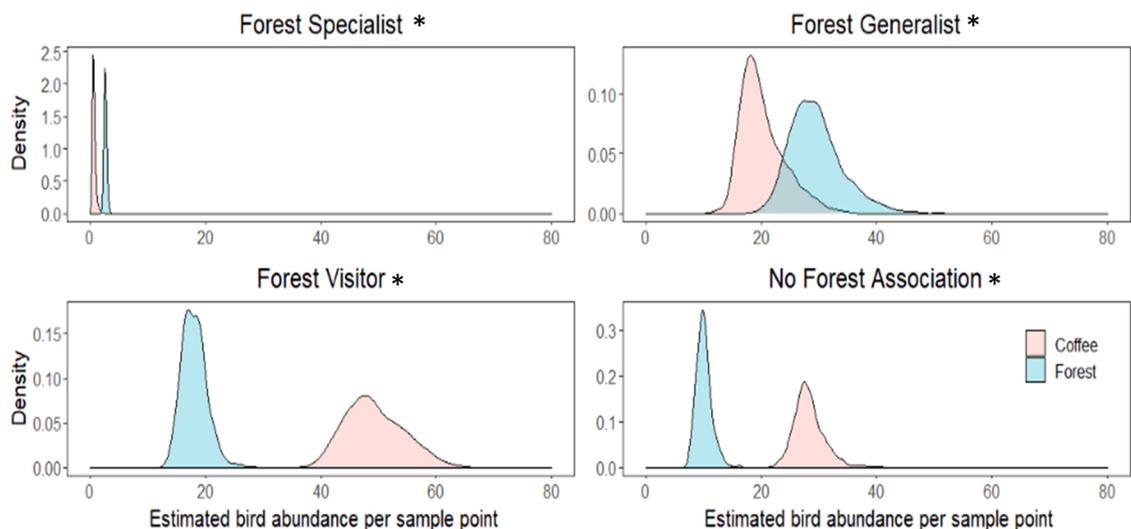
Guilds	Forest		Coffee		Total	
	# detections	# species	# detections	# species	# detections	# species
<b>Feeding guilds</b>						
Carnivore	84 (5%)	10 (13%)	132 (5%)	23 (18%)	216 (5%)	26 (18%)
Frugivore	108 (7%)	2 (3%)	84 (3%)	3 (2%)	192 (4%)	4 (3%)
Granivore	28 (2%)	10 (13%)	486 (17%)	26 (20%)	514 (12%)	26 (18%)
Insectivore	772 (50%)	39 (49%)	1068 (38%)	54 (43%)	1840 (43%)	61 (42%)
Understory ins.	281 (18%)	9 (11%)	357 (13%)	7 (6%)	638 (15%)	9 (6%)
Nectivore	228 (15%)	5 (6%)	428 (15%)	7 (6%)	656 (15%)	7 (5%)
Omnivore	317 (21%)	13 (16%)	583 (21%)	14 (11%)	900 (21%)	21 (14%)
<b>Forest association guilds</b>						
Forest specialist	134 (9%)	8 (10%)	1 (0%)	1 (1%)	135 (3%)	9 (6%)
Forest generalist	709 (46%)	21 (27%)	442 (16%)	20 (16%)	1151 (27%)	25 (17%)
Forest visitor	534 (35%)	28 (35%)	1653 (59%)	35 (28%)	2187 (51%)	37 (26%)
Non-forest-associated	160 (10%)	22 (28%)	685 (25%)	71 (56%)	845 (20%)	74 (51%)
<b>Total</b>	<b>1537</b>	<b>79</b>	<b>2781</b>	<b>127</b>	<b>4318</b>	<b>145</b>



**Fig. 2.** Posterior distributions of mean total bird abundance per sample point for six feeding guilds based on point count surveys in Central Kenya, February to April 2020. Distributions with < 5% overlap are indicated with asterisks.

yielding a community similarity index of 42% between the two land cover types. The estimates of species richness of all feeding guilds except frugivores was higher in shade coffee than in natural forest (Fig. 4). Frugivores were more speciose in natural forest than shade coffee (Fig. 4). Forest understory insectivores had higher estimated species richness in coffee than in forest. Among forest association guilds, species richness of forest specialists and forest generalists were higher in natural forest than in shade coffee, whereas species richness was higher in coffee than in forest for forest visitors and non-forest associated species (Fig. 5). The higher species richness of forest specialists and frugivores in natural forest than in shade coffee, and the higher species richness of forest visitors, non-forest associated species, and granivores in shade coffee than in natural forest (Figs. 4 & 5) are all consistent with predictions of the feeding guild and forest association hypotheses. However, results for insectivores, including forest understory insectivores specifically, were contrary to our predictions. The richness of forest generalists was higher in natural forest than in shade coffee (Fig. 5), suggesting the forest association hypothesis was even stronger than predicted.

As expected, there were very strong differences in the vegetation structure between land cover types (Table 2). Coffee sample points



**Fig. 3.** Posterior distributions of mean total bird abundance per sample point for four forest association guilds based on point count surveys in Central Kenya, February to April 2020. Distributions with < 5% overlap are indicated with an asterisk.

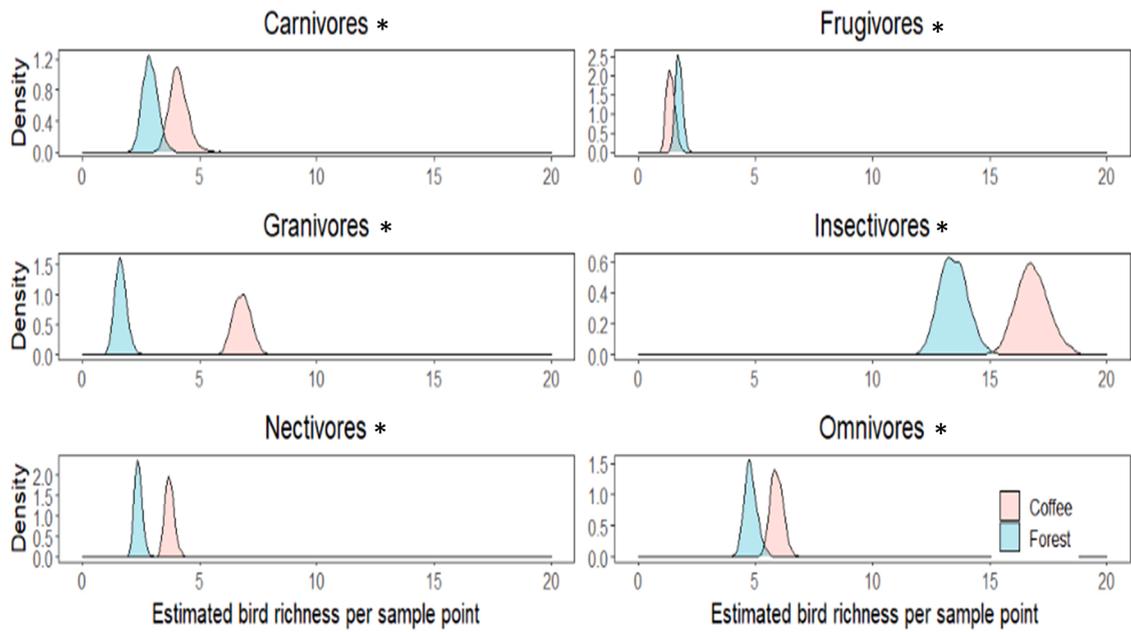


Fig. 4. Posterior distributions of mean total species richness per sample point for six feeding guilds based on point count surveys in Central Kenya, February to April 2020. Distributions with < 5% overlap are indicated with asterisks.

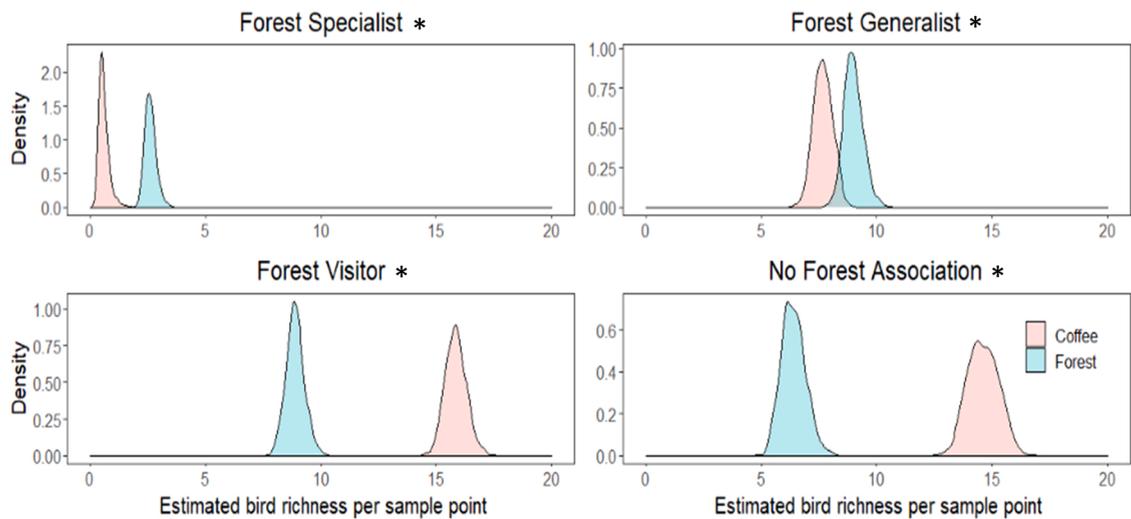


Fig. 5. Posterior distributions of mean total species richness per sample point for four forest association guilds based on point count surveys in Central Kenya, February to April 2020. Distributions with < 5% overlap are indicated with asterisks.

Table 2

Comparison of the mean ± SE of the vegetation variables recorded per point count between two land cover types at 160-point count locations in natural forest (80) and shade coffee sites (80) in Central Kenya, February to April 2020.

Variables	Shade coffee		Natural forest		t	df	P
	Mean	SE	Mean	SE			
Canopy depth (m)	5.3	0.2	4.1	0.2	4.3	158	< 0.01
Densimeter (0–96 “closed” points)	68.8	1.6	81.5	2.2	-4.7	158	< 0.01
Herbaceous layer height (cm)	21.7	1.3	24	1.2	-1.3	158	< 0.01
Shrub cover (%)	47.4	0.1	25.2	0.8	9.1	158	< 0.01
Shrub stems (#)	4.1	0.1	8.6	0.1	-5.4	158	< 0.01
Understory flowering (%)	1.4	1.4	0.4	2.0	9.0	158	< 0.01
Tree height (m)	11.9	0.4	8.5	0.3	6.8	158	< 0.01
Diameter at breast height (cm)	39.3	1.0	20.8	1.0	13.2	158	< 0.01

had, on average, greater canopy depth (+1.2 m), higher shrub cover (+22%), understory flowering (+1%), tree height (+3.4 m), and tree diameter (+18.5 cm), but a lower number of shrub stems per plot (−4.5), lower canopy cover (−13 densiometer points) and shorter herbaceous layer (−2 cm). The modeled vegetation variables showed relatively few significant relationships with bird abundance. Among estimated coefficients of 6 vegetation variables for 145 bird species, only 4 species showed a coefficient with a posterior distribution that did not overlap 0, all for shrub stem<sup>2</sup> (Appendix D).

#### 4. Discussion

Shade coffee farms can provide habitat for many tropical birds (Jha et al., 2014; Alvarez-Alvarez et al., 2022) as well as migratory species (Perfecto et al., 1996), but several authors have noted that shade coffee may not provide resources necessary for all types of birds (Tejeda-Cruz and Sutherland, 2004; Komar, 2006; Alvarez-Alvarez et al., 2022), and more comparisons of bird communities between coffee and intact forests are needed (Mendenhall et al., 2016), especially in Africa (Powell et al., 2015). Our findings support the concept that shade coffee is valuable for birds in Kenya; indeed, we found higher overall bird abundance and species richness in shade coffee farms than in natural forest sites. “Keeping common birds common” is an important bird conservation goal globally (PIF, 2021; Kenya Bird Map, 2022), and shade coffee farms appear to provide habitat for many Kenyan birds. However, the bird communities were somewhat dissimilar between forests and coffee sites (community similarity index = 0.42), suggesting shade coffee farms are not a substitute for natural forests from an avian conservation perspective, but can function as complementary sites for the conservation of birds (Alvarez-Alvarez et al., 2022). While our work focused on coffee, it is important to acknowledge that other woody tree-crops could also serve as useful refugia for some birds, such as cacao plantations, which have been examined by avian ecologists in the Neotropics, Indonesia, and West Africa, though very little has been done in East African cacao (Schroth and Harvey, 2007; De Beenhouwer et al., 2013).

Our findings also provide support for the *forest specialization and feeding guild hypotheses* which posit that the suitability of shade coffee farms for birds varies among forest-association and feeding guilds. We found distinct patterns in abundance and species richness between land cover types based on birds' guild status. These differences are likely due to the fact that shade coffee and natural forests have different vegetation structure and composition attributes (Alvarez-Alvarez et al., 2021). We documented significant differences in vegetation structure between coffee and natural forest, with coffee having higher shrub cover and lower canopy cover, but larger trees. Nonetheless, our modeling showed only a few strong associations between individual bird species abundances and our measured variables. Vegetation was relatively consistent within forest and coffee, but with strong differences between them (Table 2), so the habitat variable (forest vs. coffee) captured some of these effects. We also suggest that measures of foliage height complexity and amount of edge habitat would have revealed the conspicuous ‘layered’ structure of coffee versus a more complex foliage height profile in natural forest, and these measures may have shown stronger associations with bird abundance. Vegetation cover plays an integral role by influencing resource availability (Clough et al., 2009; Milligan et al., 2016), nesting habitat, and cover, which in turn affects bird abundance and species richness (Burke and Nol, 1998; Johnson and Wood, 2018). Even though our study did not focus on plant community and richness, it would be important to include this detail in future studies (Alvarez-Alvarez et al., 2021) in order to shed more light on the apparent differences observed in bird diversity and species richness between shade coffee and forests in East Africa.

While our results generally support the hypotheses that the value of shade coffee varies depending on birds' feeding guilds and forest association guilds, results were not entirely consistent with our predictions. For example, we predicted that the abundance and species richness of insectivores and frugivores would be higher in natural forest, but our results showed more insectivores in shade coffee (Fig. 2 & 4). This result may be due to resources provided by shade trees. Coffee shrubs themselves support notoriously low insect numbers (Milligan et al., 2016), due to both defenses within the coffee leaves and partially due to insecticide application, but native flowering shade trees, such as *Inga* in the Neotropics and *Cordia* in East Africa, can provide both insect and nectar resources for birds (Feinsinger, 1976; Johnson, 2000; Reitsma et al., 2001; Komar, 2006; Kammerichs-Berke et al., 2022). Additionally, large and widely spaced shade trees can provide excellent feeding opportunities for insectivores and omnivores, especially if the trees are native species (Moguel and Toledo, 1999; Johnson, 2000; Reitsma et al., 2001; Komar, 2006) which is consistent with our results. Vegetation surveys showed that trees were larger on the shade coffee farms than in natural forest in our study sites (Table 2). An important caveat is that the forests in our study, while the best and most representative forest patches available in the region, are fragments variously modified by (heavy) historic and (light) ongoing human activity, and they are close to urban centers. Thus, we do not know if less disturbed forests would harbor more birds or more specialized species.

Farm management activities (Alvarez-Alvarez et al., 2022) could also enhance the availability of insects for birds. For example, we observed a general trend of more detections of insectivorous bird species in sampling sites where farm workers were actively weeding and/or picking, which could cause disturbance and the flushing of insects, thus aiding foraging. Although we did not quantify this possibility, it could merit further research. As predicted, the abundance and species richness of granivores were both markedly higher in shade coffee than in natural forest (Fig. 2 & 4). We suggest that the presence of understory plants seeding and flowering at the time of surveys (F. Ong'ondo pers. obs.) could have contributed to this higher detection of granivores in shade coffee than in the natural forest. In fact, previous work in Kenya has shown that granivores can respond to the temporarily abundant seed sources in shade coffee farms with abundant weeds (Smith et al., 2015).

We hypothesized that the abundance and richness of birds in shade coffee and natural forest would vary with forest association status and predicted that the most strongly forest-associated species (forest specialists) would be more common in natural forest, while the other three forest association categories would be more common on shade coffee farms. Our findings show that the forest-association patterns were even stronger than predicted. Both forest specialists and forest generalists were more abundant and species-rich in natural forest than in shade coffee farms, while forest visitors and those species with no forest association were more

abundant and speciose on shade coffee farms (Fig. 3 & 5). Of the nine species of forest specialists detected in our study, 8 were detected exclusively in the forest (Appendix A); the Thick-billed Seedeater was the only forest specialist species detected in coffee (a single detection). Interestingly, this species was not detected in the forest. We suggest that the bill morphology of the Thick-billed Seedeater enables it to feed on a variety plant material hence presumably able to live in a wide array of land cover types (Forbeseh et al., 2003), and it may therefore be incorrectly classified as a forest specialist. Among the 25 species of forest generalists, nine had a significantly higher abundance in natural forest than in shade coffee farms, while four showed the reverse. Three forest generalist species were dramatically more common in forest, with > 100 detections in forest and < 20 in coffee (Black-backed Puffback, Collared Sunbird, and Yellow-whiskered Greenbul; Appendix A). These results suggest that there are some forest attributes favored by even generalist species that are insufficient or lacking in the shade coffee sites we studied. In addition, forest generalists can use both natural forest and shade coffee (Norfolk et al., 2017), enabling them to shift among habitats to track resources, which may have been limited in the dry season in coffee. Our study did not quantify the variation of forest generalists throughout the year to understand their abundance and richness, therefore calling for future work.

It is unsurprising that forest specialist bird species prefer natural forests (Reitsma et al., 2001; Waltert et al., 2005; Clough et al., 2009; Gilroy et al., 2015; Alvarez-Alvarez et al., 2022) in correspondence to their comparatively narrow ecological needs found in natural land cover (Hinsley et al., 2009; Mulwa et al., 2012), and their susceptibility to habitat modification. Our natural forest sites had higher canopy cover and greater tree species richness than did the coffee farms, which were composed of just a few tree species (though often larger than the trees in the forest, Table 2). Thus, the higher abundance of forest specialists in forests in this study may have been driven mainly by the richer tree-layer in our forest than our coffee sites. The mid canopy of a forest is composed of orchids, mosses, and other epiphytes and lianas that can help support arboreal gleaner bird species (Waltert et al., 2005), while the upper canopy can be utilized by forest raptors (Waceke, 2014). The strong association of the forest specialists in the natural forest suggests that tree density and tree species richness play a crucial role in the conservation of threatened forest associated species. Our findings concur with other studies done elsewhere (Naidoo, 2004; Mulwa et al., 2012; Helbig-Bonitz et al., 2015; Smith et al., 2015; Alvarez-Alvarez et al., 2022) and emphasize the crucial role natural forests play in providing habitat for species less likely to use human-disturbed land cover types such as coffee farms.

It was surprising that we found more understory forest insectivores in coffee than in forest. Although shrub cover was higher in shade coffee than in the natural forest (Table 2), this shrub layer was composed nearly exclusively of a single species shrub (coffee) which is known to harbor relatively few insects (Johnson, 2000). In contrast, the natural forest sample points had a higher diversity of shrub species, nearly all of which were native, and could harbor more insects (Wenninger and Inouye, 2008). Moreover, a global review suggest that understory forest insectivores are especially sensitive to disturbance (Sekercioglu, 2002; Powell et al., 2015). We suggest that because our natural forests experienced some historical and ongoing human disturbance, some of the most vulnerable understory forest insectivores may have already been extirpated from our sites. For example, Orange Ground-Thrush (*Geokichla gurneyi*), Evergreen Forest Warbler (*Bradypterus lopezi*), or Cinnamon Bracken-Warbler (*Bradypterus cinnamomeus*) were not detected in our surveys, but can occur in undisturbed forests in the general region (Kenya Bird Map, 2022). Among the forest understory insectivores we did detect, African Paradise-flycatcher and White-eyed Slaty Flycatcher are well known to be tolerant of disturbance and were markedly more common in coffee than in forest. Others, including Brown-chested Alethe and Rüppell's Robin-chat are more sensitive to disturbance and were more common in forest than in coffee.

Consistent with our predictions, the abundance and species richness of both forest visitors and those birds with no forest association status were higher in shade coffee than in natural forest. This was expected, as there is a large pool of open-country and farmland associated species in East that can make use of the relatively open canopy, herbaceous layer, and widely spaced trees in coffee farms Africa (Luck and Daily, 2003; Mulwa et al., 2012; Smith et al., 2015; Mahiga et al., 2019). For instance, during the survey, most of the herbaceous plants had finished seeding, providing food for granivorous species such as Dusky Turtle Dove, Holub's Golden Weaver, African Citril, Kenya Rufous Sparrow, and Purple Grenadier among others. Widely spaced native trees creates foraging opportunities for species adapted to sallying for insects in open space, such as African paradise flycatcher and White-eyed Slaty-Flycatcher.

Our study was not designed to examine the Palearctic migrant versus Afrotropical resident bird communities specifically, but several trends in our study are worth noting. Our survey period corresponded to a time when some wintering migrants were present (e.g., Blackcap), though some may have begun to migrate in our final survey (April). Overall, we only detected 11 species of Palearctic migrants, and they comprised only 5% of total detections (2% in forest and 7% in coffee) and only 8% of species (5% in forest and 9% in coffee). Most of the individual migrants detected in coffee were of a single species, Willow Warblers (61%). These trends are not dissimilar to results from Ethiopia, where Buechley et al. (2015) also detected 9 species of Palearctic migrants that were disproportionately common in coffee relative to intact forest. In the Neotropics, Nearctic migrants can make up a much larger proportion of the bird communities in shade coffee farms, exceeding half of individuals in some settings (e.g., Greenberg et al., 1997; Tejada-Cruz and Sutherland, 2004; Komar, 2006). Some of the Nearctic migrants appear to be among the most beneficial for consuming insect pests in coffee (Sherry et al., 2016). Additional research is needed on whether Palearctic migrants in African farms are also important providers of pest control services. Finally, it is important to note that bird abundance and species richness are incomplete measures of the quality of habitats for birds (Horne, 1983; Johnson, 2000). A full understanding of the value of shade coffee farms in Kenya and elsewhere will require examination of their capacity to also support reproduction and survival (Gleffe et al., 2006; Komar, 2006).

## 5. Conservation implications

In conclusion, this study has for the first time documented which bird species in Kenya can be abundant in shade coffee farms in comparison to reference natural forest sites. Future work should be conducted in other areas of East Africa to determine if this pattern is

widespread.

Recognizing which species readily use shade coffee farms, and which do not, has important conservation implications because it can both clarify how shade coffee can be a tool for conservation while also highlighting those species, such as forest specialists, which require intact natural forest present in protected areas. Clearly, the natural forests of Kenya are under threat by numerous activities including agricultural expansion, and populations of birds associated with these forests are becoming increasingly dependent on protected areas.

### Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Frank Juma Ong'ondo reports financial support was provided by Humboldt Area Foundation. Frank Juma Ong'ondo reports financial support was provided by US Department of Education.

### Data availability

The authors do not have permission to share data.

### Acknowledgements

The study received financial support from Cal Poly Humboldt (formerly Humboldt State University), The Humboldt Area Foundation, a US Dept of Education HSI STEM Award, #P031C150193 and NSF-funded International Research Experience for Students (IRES) grant #1657973 and #1657836, to whom we are very grateful. We would also like to acknowledge the assistance accorded to us by National Museums of Kenya, Ornithology section of the zoology Department for administrative and field logistics support. To Kenya Wildlife Service and Kenya Forest Services, we want to say thank you for the permission to conduct our field surveys. Finally, we would like to express our deepest appreciation to Sasini Coffee Plantation Limited for the permission to survey birds in their farms, especially James Mureithi (General Manager).

### Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.gecco.2022.e02296](https://doi.org/10.1016/j.gecco.2022.e02296).

### References

- Alvarez-Alvarez, E.A., Almazán-Núñez, R.C., González-García, F., Brito-Millán, M., Méndez-Bahena, A., García-Ibáñez, S., 2021. Shade coffee plantations maintain woody plant diversity and structure in a cloud forest landscape of southern Mexico. *J. For. Res.* 32, 637–648.
- Alvarez-Alvarez, E.A., Almazán-Núñez, R.C., Corcuera, P., González-García, F., Brito-Millán, M., Alvarado-Castro, V.M., 2022. Land use cover changes the bird distribution and functional groups at the local and landscape level in a Mexican shaded-coffee agroforestry system. *Agric., Ecosyst. Environ.* 330, 107882.
- Bawa, K.S., Kress, W.J., Nadkarni, N.M., Lele, S., 2004. Beyond paradise-meeting the challenges in tropical biology in the 21st century. *Biotropica* 36, 437–446.
- Bellier, E., Kéry, M., Schaub, M., 2016. Simulation-based assessment of dynamic *N*-mixture models in the presence of density dependence and environmental stochasticity. In: Hodgson, D. (Ed.), *Methods in Ecology and Evolution*, 7, pp. 1029–1040.
- Bennun, L., Dranzoa, C., Pomeroy, D., 1996. The Forest Birds of Kenya and Uganda. *J. East Afr. Nat. Hist.* 85, 23–48.
- Block, W.M., Brennan, L.A., 1993. The habitat concept in ornithology: theory and applications. In: Power, D.M. (Ed.), *Current Ornithology*. Springer, US, Boston, MA, pp. 35–91.
- Bregman, T.P., Sekercioglu, C.H., Tobias, J.A., 2014. Global patterns and predictors of bird species responses to forest fragmentation: implications for ecosystem function and conservation. *Biol. Conserv.* 169, 372–383.
- Buechley, E.R., Şekercioglu, Ç.H., Atickem, A., Gebremichael, G., Ndungu, J.K., Mahamued, B.A., Beyene, T., Mekonnen, T., Lens, L., 2015. Importance of Ethiopian shade coffee farms for forest bird conservation. *Biol. Conserv.* 188, 50–60.
- Burke, D.M., Nol, E., 1998. Influence of food abundance, nest-site habitat, and forest fragmentation on breeding ovenbirds. *Auk* 115, 96–104.
- Bütler, R., T. Lachat, L. Larrieu, Y. Paillet, and D. Kraus. 2013. Habitat trees: key elements for forest biodiversity. Integrative approaches as an opportunity for the conservation of forest biodiversity, European Forest Institute, pp.84–91, 2013, In Focus – Managing Forest in Europe.: 978–952-5980-06-6. (hal-02599082).
- Carlo, T.A., Morales, J.M., 2016. Generalist birds promote tropical forest regeneration and increase plant diversity via rare-biased seed dispersal. *Ecology* 97, 1819–1831.
- Carrara, E., Arroyo-Rodríguez, V., Vega-Rivera, J.H., Schondube, J.E., de Freitas, S.M., Fahrig, L., 2015. Impact of landscape composition and configuration on forest specialist and generalist bird species in the fragmented Lacandona rainforest, Mexico. *Biol. Conserv.* 184, 117–126.
- Ceballos, G., Ehrlich, P.R., Dirzo, R., 2017. Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc. Natl. Acad. Sci.* 114.
- Clough, Y., Dwi Putra, D., Pitopang, R., Tschamtk, T., 2009. Local and landscape factors determine functional bird diversity in Indonesian cacao agroforestry. *Biol. Conserv.* 142, 1032–1041.
- Cuni-Sanchez, A., Omeny, P., Pfeifer, M., Olaka, L., Mamo, M.B., Marchant, R., Burgess, N.D., 2019. Climate change and pastoralists: perceptions and adaptation in montane Kenya. *Clim. Dev.* 11, 513–524.
- De Beenhouwer, M., Aerts, R., Honnay, O., 2013. A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. *Agric., Ecosyst. Environ.* 175, 1–7.
- Dirzo, R., Young, H.S., Galetti, M., Ceballos, G., Isaac, N.J.B., Collen, B., 2014. Defaunation in the anthropocene. *Science* 345, 401–406.
- Donald, P.F., 2004. Biodiversity impacts of some agricultural commodity production systems. *Conserv. Biol.* 18, 17–38.
- Estrada-Carmona, N., Martínez-Salinas, A., DeClerck, F.A.J., Vélchez-Mendoza, S., Garbach, K., 2019. Managing the farmscape for connectivity increases conservation value for tropical bird species with different forest-dependencies. *J. Environ. Manag.* 250, 109504.

- Feinsinger, P., 1976. Organization of a tropical guild of nectarivorous birds. *Ecol. Monogr.* 46, 257–291.
- Forbeseh, P.F., Keming, E.C., Toh, C.L., Wultof, I.N.B., 2003. Monitoring of Kilum-Ijim forest bird communities: initial findings. *Bird. Conserv. Int.* 13, 255–271.
- Gakinya, S.K., 2014. Strategic responses by Sasini coffee company limited to environmental changes in Kenya. *Univ. Nairobi.*
- Geist, H.J., Lambin, E.F., 2002. Proximate causes and underlying driving forces of tropical deforestation. *BioScience* 52, 143.
- Giam, X., 2017. Global biodiversity loss from tropical deforestation. *Proc. Natl. Acad. Sci.* 114, 5775–5777.
- Gilroy, J.J., Medina Uribe, C.A., Haugaasen, T., Edwards, D.P., 2015. Effect of scale on trait predictors of species responses to agriculture: Species' Responses to Agriculture. *Conserv. Biol.* 29, 463–472.
- Gleffe, J.D., Collazo, J.A., Groom, M.J., Miranda-Castro, L., 2006. Avian reproduction and the conservation value of shaded coffee plantations. *Ornitol. Neotrop.* 17, 271–282.
- Global Forest Watch. 2021. Tropical forest loss dashboard. <<https://www.globalforestwatch.org/dashboards/global/>> access 24 July 2022.
- Gray, M.A., Baldauf, S.L., Mayhew, P.J., Hill, J.K., 2007. The response of avian feeding guilds to tropical forest disturbance. *Conserv. Biol.* 21, 133–141.
- Greenberg, R., Bichier, P., Sterling, J., 1997. Bird populations in rustic and planted shade coffee plantations of Eastern Chiapas, Mexico. *Biotropica* 29, 501–514.
- Helbig-Bonitz, M., Ferger, S.W., Böhning-Gaese, K., Tschapka, M., Howell, K., Kalko, E.K.V., 2015. Bats are not birds - different responses to human land-use on a tropical mountain. *Biotropica* 47, 497–508.
- Hinsley, S., Hill, R., Fuller, R., Bellamy, P., Rothery, P., 2009. Bird species distributions across woodland canopy structure gradients. *Community Ecol.* 10, 99–110.
- Horne, V.B., 1983. Density as a misleading indicator of habitat quality. *J. Wildl. Manag.* 47, 893.
- Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). In: McInerney, G. (Ed.), *Methods in Ecology and Evolution*, 7, pp. 1451–1456.
- Jha, S., Bacon, C.M., Philpott, S.M., Ernesto Méndez, V., Läderach, P., Rice, R.A., 2014. Shade coffee: update on a disappearing refuge for biodiversity. *BioScience* 64, 416–428.
- Johnson, M.D., 2000. Effects of shade-tree species and crop structure on the winter arthropod and bird communities in a jamaican shade coffee plantation. *Biotropica* 32, 133–145.
- Johnson, M.D., Wood, E.M., 2018. *Habitat Ecology*. Ch. 18 in *Ornithology: Foundation*. In: Morrison, M.L., Rodewald, A.D., Voelker, G., Colón, M.R., Prather, J.F. (Eds.), Analysis, and Application. Johns Hopkins Press.
- Kammerichs-Berke, D., Lane, F.J., Ong'ondo, F.J., Mlamba, E.M., Bean, W.T., Jedlicka, J.A., Njoroge, P., Johnson, M.D., 2022. The effect of shade tree species on bird communities in central Kenyan coffee farms. *Bird. Conserv. Int.* 1–19.
- Karura Management plan, B. L. P. T. 2010. *Karura Forest Strategic Management Plan*.
- Kenya Bird Map. 2022. Kenya Bird Map. <<https://kenya.birdmap.africa/coverage/project/kenya>>.
- Kéry, M., Royle, J.A., 2016. *Applied Hierarchical Modeling in Ecology*. first, Volume one. Academic Press.
- Kissling, W.D., Rahbek, C., Böhning-Gaese, K., 2007. Food plant diversity as broad-scale determinant of avian frugivore richness. *Proc. R. Soc. B: Biol. Sci.* 274, 799–808.
- Komar, O., 2006. Priority Contribution. Ecology and conservation of birds in coffee plantations: a critical review. *Bird. Conserv. Int.* 16, 1.
- Kremen, C., Merenlender, A.M., 2018. Landscapes that work for biodiversity and people. *Sci.* 362:eaau6 020.
- Lambin, E.F., Meyfroidt, P., 2011. Global land use change, economic globalization, and the looming land scarcity. *Proc. Natl. Acad. Sci.* 108, 3465–3472.
- Langat, D.K., Maranga, E.K., Aboud, A.A., Cheboiwo, J.K., 2016. Role of forest resources to local livelihoods: the case of east mau forest ecosystem, Kenya. *Int. J. For. Res.* 2016, 1–10.
- Laurance, W.F., Bierregaard, R.O., 1997. *Tropical forest remnants: ecology, management, and conservation of fragmented communities*. Univ. Chic. Press, Chic., Ill. 616.
- Luck, G.W., Daily, G.C., 2003. Tropical countryside bird assemblages: richness, composition, and foraging differ by landscape context. *Ecol. Appl.* 13, 235–247.
- Mahiga, S.N., Wehala, P., Mware, M.J., Ndag'ang'a, P.K., 2019. Influence of land-use type on forest bird community composition in Mount Kenya Forest. *Int. J. Ecol.* 2019, 1–8.
- Martensen, A.C., Pimentel, R.G., Metzger, J.P., 2008. Relative effects of fragment size and connectivity on bird community in the Atlantic Rain Forest: Implications for conservation. *Biol. Conserv.* 141, 2184–2192.
- Mendenhall, C.D., A. Shields-Estrada, A.J. Krishnaswami, and G.C. Daily. 2016. Quantifying and sustaining biodiversity in tropical agricultural landscapes. *Proceedings of the National Academy of Sciences* 113:14544–14551.
- Milligan, M.C., Johnson, M.D., Garfinkel, M., Smith, C.J., Njoroge, P., 2016. Quantifying pest control services by birds and ants in Kenyan coffee farms. *Biol. Conserv.* 194, 58–65.
- Moguel, P., Toledo, V.M., 1999. Biodiversity conservation in traditional coffee systems of Mexico. *Conserv. Biol.* 13, 11–21.
- Mongabay. 2019. Tropical Rainforest: Deforestation rates tables and chats. [mongabay.com. <https://rainforests.mongabay.com/deforestation/2000/Kenya.htm>](https://rainforests.mongabay.com/deforestation/2000/Kenya.htm).
- Morante-Filho, J.C., Faria, D., Mariano-Neto, E., Rhodes, J., 2015. Birds in anthropogenic landscapes: the responses of ecological groups to forest loss in the Brazilian Atlantic forest. In: Gibbons, P. (Ed.), *PLOS ONE*, 10.
- Mulwa, R.K., Böhning-Gaese, K., Schleuning, M., 2012. High bird species diversity in structurally heterogeneous farmland in Western Kenya. *Biotropica* 44, 801–809.
- Naidoo, R., 2004. Species richness and community composition of songbirds in a tropical forest-agricultural landscape. *Anim. Conserv.* 7, 93–105.
- Narango, D.L., Tallamy, D.W., Marra, P.P., 2018. Nonnative plants reduce population growth of an insectivorous bird. *Proc. Natl. Acad. Sci.* 115, 11549–11554.
- Ndag'ang'a, P.K., Njoroge, J.B., Githiru, M., 2013. Vegetation composition and structure influences bird species community assemblages in the highland agricultural landscape of Nyandarua, Kenya. *Ostrich* 84, 171–179.
- Newbold, T., Scharlemann, J.P.W., Butchart, S.H.M., Şekercioglu, Ç.H., Alkemade, R., Booth, H., Purves, D.W., 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. *Proc. R. Soc. B: Biol. Sci.* 280, 20122131.
- Norfolk, O., Jung, M., Platts, P.J., Malaki, P., Odeny, D., Marchant, R., 2017. Birds in the matrix: the role of agriculture in avian conservation in the Taita Hills, Kenya. *Afr. J. Ecol.* 55, 530–540.
- Otieno, N.E., Gichuki, N., Farwig, N., Kiboi, S., 2011. The role of farm structure on bird assemblages around a Kenyan tropical rainforest: Habitat structure and farm bird assemblage. *Afr. J. Ecol.* 49, 410–417.
- Perfecto, I., Rice, R.A., Greenberg, R., van der Voort, M.E., 1996. Shade coffee: a disappearing refuge for biodiversity. *BioScience* 46, 598–608.
- Philpott, S.M., Arendt, W.J., Armbrrecht, I., Bichier, P., Diestch, T.V., Gordon, C., Greenberg, R., Perfecto, I., Reynoso-Santos, R., Soto-Pinto, L., Tejeda-Cruz, C., Williams-Linera, G., Valenzuela, J., Zolotoff, J.M., 2008. Biodiversity loss in Latin American coffee landscapes: review of the evidence on ants, birds, and trees. *Conserv. Biol.* 22, 1093–1105.
- PIF. 2021. *Partners In Flight*. <<https://partnersinflight.org/blog/>>.
- Powell, L.L., Cordeiro, N.J., Stratford, J.A., 2015. Ecology and conservation of avian insectivores of the rainforest understory: a pantropical perspective. *Biol. Conserv.* 188, 1–10.
- R Core Team, 2020. R: A language and environment for statistical computing. R. Found. Stat. Comput., Vienna, Austria. <<http://www.r-project.org/index.html>>.
- Ralph, C.J., Geupel, G.R., Pyle, P., Martin, T.E., DeSante, D.F., 1993. *Handbook of field methods for monitoring landbirds*. U.S. Department of Agriculture, Forest Service. Pacific Southwest Research Station, Albany, CA.
- Reidy, J.L., Thompson, F.R., Kendrick, S.W., 2014. Breeding bird response to habitat and landscape factors across a gradient of savanna, woodland, and forest in the Missouri Ozarks. *For. Ecol. Manag.* 313, 34–46.
- Reitsma, R., J.D. Parrish, and W. McLarney. 2001. The role of cacao plantations in maintaining forest avian diversity in southeastern Costa Rica. 9.
- Rodrigues, P., Shumi, G., Dorrestein, I., Schultner, J., Hanspach, J., Hylander, K., Senbeta, F., Fischer, J., 2018. Coffee management and the conservation of forest bird diversity in southwestern Ethiopia. *Biol. Conserv.* 217, 131–139.
- Schroth, G., Harvey, C.A., 2007. Biodiversity conservation in cocoa production landscapes: an overview. *Biodivers. Conserv.* 16, 2237–2244.
- Şekercioglu, C.H., 2002. Effects of forestry practices on vegetation structure and bird community of Kibale National Park, Uganda. *Biol. Conserv.* 12.

- Sekercioglu, C.H., 2012. Bird functional diversity and ecosystem services in tropical forests, agroforests and agricultural areas. *J. Ornithol.* 153, 153–161.
- Sekercioglu, C.H., Daily, G.C., Ehrlich, P.R., 2004. Ecosystem consequences of bird declines. *Proc. Natl. Acad. Sci.* 101, 18042–18047.
- Şekercioglu, Ç.H., Mendenhall, C.D., Oviedo-Brenes, F., Horns, J.J., Ehrlich, P.R., Daily, G.C., 2019. Long-term declines in bird populations in tropical agricultural countryside. *Proc. Natl. Acad. Sci.* 116, 9903–9912.
- Sherry, T.W., Johnson, M.D., Williams, K.A., Kaban, J.D., McAvoy, C.K., Hallauer, A.M., Rainey, S., Xu, S., 2016. Dietary opportunism, resource partitioning, and consumption of coffee berry borers by five species of migratory wood warblers (Parulidae) wintering in Jamaican shade coffee plantations. *J. Field Ornithol.* 87, 273–292.
- Smith, C., Barton, D., Johnson, M.D., Wendt, C., Milligan, M.C., Njoroge, P., Gichuki, P., 2015. Bird communities in sun and shade coffee farms in Kenya. *Glob. Ecol. Conserv.* 4, 479–490.
- Stouffer, P.C., Bierregaard Jr, R.O., Strong, C., Lovejoy, T.E., 2006. Long-term landscape change and bird abundance in Amazonian rainforest fragments. *Conservation Biology* 20 (4), 1212–1223.
- Tejeda-Cruz, C., Sutherland, W.J., 2004. Bird responses to shade coffee production. *Anim. Conserv.* 7, 169–179.
- Turner, I.M., 1996. Species loss in fragments of tropical rain forest: a review of the evidence. *J. Appl. Ecol.* 33, 200.
- Vancutsem, C., Achard, F., Pekel, J.-F., Vieilledent, G., Carboni, S., Simonetti, D., Gallego, J., Aragão, L.E.O.C., Nasi, R., 2021. Long-term (1990–2019) monitoring of forest cover changes in the humid tropics. *Sci. Adv.* 7:eabe1 603.
- Villard, M.-A., Poppen, R., 2018. Ecological Adaptations of Birds to Forest Environments. Pages 51–78 in G. Mikusiński. In: Roberge, J.-M., Fuller, R. (Eds.), editors. *Ecology and Conservation of Forest Birds*. First edition. Cambridge University Press.
- Waceke, L., 2014. Impacts of The Southern Bypass Road Construction through Ngong Forest on the African Crowned Eagle. Nairobi Cty. Kenya Univ.
- Waltert, M., Bobo, K.S., Sainge, N.M., Fermon, H., Mühlenberg, M., 2005. From forest to farmland: habitat effects on Afrotropical forest bird diversity. *Ecol. Appl.* 15, 1351–1366.
- Wenninger, E.J., Inouye, R.S., 2008. Insect community response to plant diversity and productivity in a sagebrush-steppe ecosystem. *J. Arid Environ.* 72, 24–33.
- Yamaura, Y., Kéry, M., Andrew Royle, J., 2016. Study of biological communities subject to imperfect detection: bias and precision of community N-mixture abundance models in small-sample situations. *Ecol. Res.* 31, 289–305.
- Zurita, G.A., Rey, N., Varela, D.M., Villagra, M., Bellocq, M.I., 2006. Conversion of the Atlantic Forest into native and exotic tree plantations: Effects on bird communities from the local and regional perspectives. *For. Ecol. Manag.* 235, 164–173.