Bird Conservation International (2022) 1–19.
doi:10.1017/S0959270921000502

The effect of shade tree species on bird communities in central Kenyan coffee farms

DEVEN KAMMERICHS-BERKE[1*], FANTER J. LANE[1],
FRANK JUMA ONG'ONDO[1,2], EDSON M. MLAMBA[2], WILLIAM T. BEAN[1,3],
JULIE A. JEDLICKA[4], PETER NJOROGE[2] and MATTHEW D. JOHNSON[1]

[1] *California State Polytechnic University, Humboldt, Arcata, California, USA.*
[2] *National Museums of Kenya, Nairobi, Kenya.*
[3] *California Polytechnic State University, San Luis Obispo, California, USA.*
[4] *Missouri Western State University, St. Joseph, Missouri, USA.*

**Author for correspondence; email: dk1166@humboldt.edu*

(Received 12 February 2021; revision accepted 01 November 2021)

Summary

Shade coffee is a well-studied cultivation strategy that creates habitat for tropical birds while also maintaining agricultural yield. Although there is a general consensus that shade coffee is more "bird-friendly" than a sun coffee monoculture, little work has investigated the effects of specific shade tree species on insectivorous bird diversity. This study involved avian foraging observations, mist-netting data, temperature loggers, and arthropod sampling to investigate bottom-up effects of two shade tree taxa - native *Cordia* sp. and introduced *Grevillea robusta* - on insectivorous bird communities in central Kenya. Results indicate that foliage-dwelling arthropod abundance, and the richness and overall abundance of foraging birds were all higher on *Cordia* than on *Grevillea.* Furthermore, multivariate analyses of the bird community indicate a significant difference in community composition between the canopies of the two tree species, though the communities of birds using the coffee understorey under these shade trees were similar. In addition, both shade trees buffered temperatures in coffee, and temperatures under *Cordia* were marginally cooler than under *Grevillea.* These results suggest that native *Cordia* trees on East African shade coffee farms may be better at mitigating habitat loss and attracting insectivorous birds that could promote ecosystem services. Identifying differences in prey abundance and preferences in bird foraging behaviour not only fills basic gaps in our understanding of the ecology of East African coffee farms, it also aids in developing region-specific information to optimize functional diversity, ecosystem services, and the conservation of birds in agricultural landscapes.

Keywords: Ornithology, Coffee Ecology, Ecosystem Services

Introduction

Agricultural intensification is one of the greatest threats to biodiversity (Foley *et al.* 2005), particularly because of its association with deforestation, which has a disproportionately negative effect on biological communities (Donald 2004, Betts *et al.* 2017). In the tropics, where most of the world's biodiversity is concentrated (Brown 2014), an emphasis on agricultural habitats is vital for successful conservation for a variety of ecological and socioeconomic reasons (Perfecto *et al.* 2009, Perfecto and Vandermeer 2010, Renwick *et al.* 2014). Currently, agricultural landscapes cover approximately 37% of the earth's land surface, and agricultural production is projected to increase 100–110% by 2050 to meet growing global crop demand (Tilman *et al.* 2011). Meeting this rising agricultural demand will require identifying strategies to minimize the loss of biodiversity while also maximizing agricultural yield (Vandermeer and Perfecto 1997, Fischer *et al.* 2014, Mehrabi *et al.* 2018).

Coffee *Coffea* spp. grown beneath shade trees, called "shade coffee," is a well-studied example of integrating crop production with biodiversity conservation (Perfecto *et al.* 2009, Jha *et al.* 2014, Perfecto and Vandermeer 2015), contrasting with a more industrial strategy, generally referred to as "sun coffee," which involves few to no shade trees to maximize short-term production (Jha *et al.* 2014). In east Africa (Douglas *et al.* 2013, Buechley *et al.* 2015), the Neotropics (Armbrecht and Perfecto 2003, Philpott *et al.* 2008, Philpott and Bichier 2012) and India (Raman 2006), research suggests that the shade strategy supports a high diversity of economically important taxa such as birds (Johnson and Hackett 2016). In turn, insectivorous bird populations can play a key role in the provisioning of natural pest control services in coffee through top-down effects on pest arthropods (Perfecto *et al.* 2004, Kellermann *et al.* 2008, Philpott *et al.* 2009, Karp *et al.* 2014). Bird species richness (Perfecto *et al.* 2004, Van Bael *et al.* 2008), density (Perfecto *et al.* 2004), abundance (Jedlicka *et al.* 2011), and functional richness (Philpott *et al.* 2009) are all positively correlated with the top-down control of pests, especially the coffee berry borer *Hypothenemus hampei*.

In all regions, the term shade coffee belies tremendous variation among and within farms that contain shade trees (Moguel and Toledo 1999). Smaller-scale farms in Kenya tend to have a higher diversity of native trees, either planted intentionally or as remnants of adjacent forests as a form of rustic farm management (Moguel and Toledo 1999, Lengkeek *et al.* 2005, Kindt *et al.* 2006). Conversely, a shade plantation strategy that utilizes one or only a few species of tree, called a "shaded monoculture" (Moguel and Toledo 1999), is common in many regions, including among the large plantations established during the colonial era in Kenya and now run usually by African or international enterprises (Tignor 2015). Often, a few key tree species dominate shaded monocultures within a region, such as *Grevillea robusta* in Kenya, Uganda, and Brazil (Baggio *et al.* 1997, Muchiri 2004, Kiyingi *et al.* 2016), several species of *Inga* in Mexico and Jamaica (Johnson 2000a, Romero-Alvarado *et al.* 2000), and *Erythrina poeppigeana* in Costa Rica (Perfecto and Vandermeer 2015).

The selection of shade tree species has important implications for both farmers and the wildlife that may use coffee farms. Farmers' criteria for selecting shade tree species tend to revolve around ecological or economic benefits provided by the trees, as well as aspects of tree phenology indirectly related to microclimates, which can promote increased crop yield (Beer 1987, Soto-Pinto *et al.* 2000, Pinard *et al.* 2014b). Shade tree products such as fruit and timber can also buffer the impact of coffee income volatility, particularly for coffee farmers with small land holdings (Jassogne *et al.* 2012, Davis *et al.* 2017), and recent evidence suggest shade trees may help farmers adapt to a warming climate (Rahn *et al.* 2018, Schooler *et al.* 2020).

Understanding the ecology of specific shade tree species is also important because they can affect coffee understorey pests by influencing the abundance and richness of natural bird predators that can act as a top-down control on pest populations (Kellerman *et al.* 2008, Railsback and Johnson 2014) and by lowering understorey temperatures, which can slow pest reproduction (Jaramillo *et al.* 2011). Johnson (2000a) found that Jamaican coffee plantations in which the native genus *Inga* was dominant supported the highest abundances of both birds and non-pest arthropods. Similarly, in central Kenyan plantations, Kammerichs-Berke (2020) found higher densities of non-pest arthropods on native *Cordia* trees. This follows ecological theory regarding insect coevolution with plants as summarised by Tallamy (2004). Insects adapt to evolutionarily novel plants slowly (Southwood *et al.* 1982), and coevolution with particular host plants is a strong driving force for species diversification and radiation for many insect taxa (Farrell and Mitter 1998, Becerra and Venable 1999). Most herbivorous insects specialise on one or a few native plant groups with which they have shared an evolutionary history (Erhlich and Raven 1964, Bernays and Graham 1988, Forister *et al.* 2015), with specialisation being more pronounced at lower latitudes (Schemske *et al.* 2009). Thus, ecosystems dominated by non-native plants tend to exhibit lower insect diversity, abundance, and biomass than systems dominated by native host plants (Burghardt et al. 2010, Litt *et al.* 2014). This interaction has implications for the selection of shade tree species and their effects on top-down impacts of insectivorous pest-eating birds in shade coffee farms (Narango *et al.* 2018).

In central Kenya, two of the most common trees on shaded coffee monocultures are *Grevillea robusta* (hereafter *Grevillea*) and several species of *Cordia*, especially *Cordia africana* (collectively hereafter *Cordia*). *Grevillea* is a deciduous tree introduced to Kenya from eastern Australia in the 19th century and is well-regarded amongst farmers because of its moderate to fast growth (as much as 3 m per year in some sites) and a tall branch system that provides a strong windbreak (Negash 1995). *Cordia*, on the other hand, is an evergreen native to East Africa that generally has a shorter and wider branching canopy than *Grevillea*, as well as broader leaves (D. Kammerichs-Berke pers. obs.) that provides high amounts of shade. Both species are often intentionally planted in evenly spaced rows, and both tree species are also appealing as shade trees due to their nitrogen-fixing abilities (Negash 1995, Lott *et al.* 2000). Despite the prominence of these two shade tree species, ecological aspects of shade tree selection on East African coffee farms remains understudied.

Our study quantified the influence of these two tree species on the avian community in large scale Kenyan coffee farms, with a special emphasis on insectivorous birds. We hypothesised that native *Cordia* trees offer more potential for pest control services in Kenyan coffee farms than non-native *Grevillea* because *Cordia* attracts more insectivorous birds that could act as a top-down control on pest populations. Specifically, we tested the following predictions: (1) Non-pest foliage arthropods are more abundant on *Cordia* than *Grevillea*, (2) greater numbers of insectivorous birds forage in *Cordia* than in *Grevillea*, (3) insectivorous birds foraging in the shade layer also use the coffee understorey (at the species level), and this pattern differs between *Cordia* and *Grevillea*, and (4) insectivorous birds are more common in the coffee layer under or near *Cordia* than *Grevillea*. Additionally, we measured understorey temperatures beneath *Cordia* and *Grevillea* shade trees to shed light on potential bottom-up effects of shade trees on pests.

Methods

Study Area

This study was conducted on large-scale coffee plantations along an elevational gradient (1,567–1,874 m) in Kiambu County, Kenya from 16 December 2018 to 19 January 2019. Both sun and shade coffee farms occur along this elevational gradient (Jaramillo *et al.* 2013), with variation in farming intensity, acreage, and habitat components. A variety of tree species are utilised within the shade farms in this region, including acacias *Acacia* spp., broad-leaved croton *Croton macrostaphylus*, Meru oak *Vitex keniensis*, and Nandi flame *Spathodea campanulate*, though on large plantations the two most commonly used species are *Grevillea* and *Cordia* (Johnson *et al.* unpubl. data). Because of the focus on tree species selection, we only selected shade farms with low total tree species diversity and a relatively even distribution of both *Grevillea* and *Cordia*, and full sun farms were excluded from this study. Surveys were conducted on six sites (Figure 1a); each site was a different coffee farm, except in one case a single farm was divided into two sites because it was large (approximately 91 ha) and contained multiple fields (separated by dirt roads or paths) with different characteristics (size and density of shade trees, density of coffee trees).

Survey methods

Arthropod, bird, vegetation, and temperature sampling was organised around individual shade trees at each study site. To select trees, a four-quadrant grid fitted to the size of each farm was overlaid on an aerial image of the site, recording the UTM coordinates for the centre of each

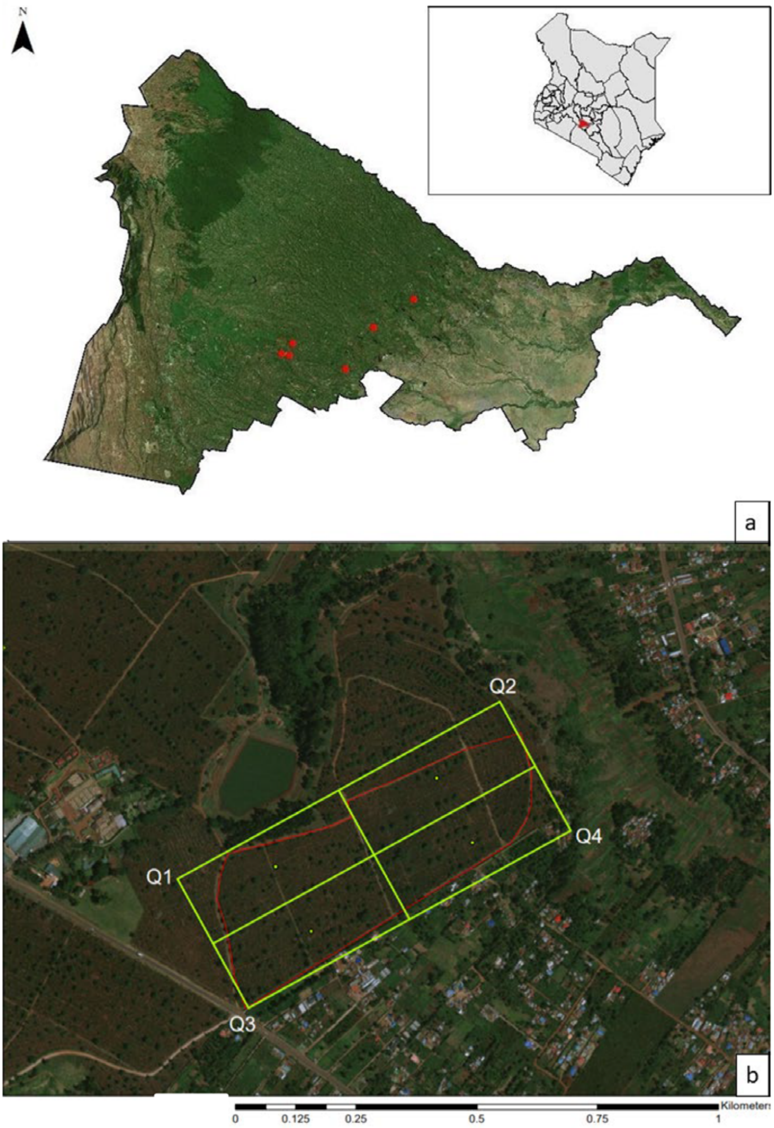

Figure 1. (a) Map depicting the spatial arrangement of the six farms surveyed in Kiambu County, Kenya from 16 December 2018–19 January 2019. (b) Site map depicting 4 quadrants overlaid on one of the coffee farms. Avian observation points were selected by going to the center of each quadrant (green dots) and from there selecting 3–4 points each with 3–4 trees between 23–40 cm diameter at breast height (dbh). All points were at least 50 m from the site edge (shown here in red) and within 20 m of each other

quadrant (Figure 1b). Then, in the field from the centroid of each quadrant, 3–4 avian observation points were selected, defined as locations with 3–4 *Cordia* or *Grevillea* trees that could be visually monitored simultaneously for avian foraging observations and also met the survey criteria: 23–40 cm diameter at breast height (dbh), at least 50 m from the site edge, and within 20 m of each other. This dbh range was selected to minimise the confounding effects of tree size and corresponds to the 25th and 75th percentiles of trees measured in a companion study of these farms in 2017–2018 (Schooler *et al.* 2020, Kammerichs-Berke unpubl. data). An effort was made to survey an equal number of *Cordia* and *Grevillea* trees at each site, though this was not always possible due to their arrangement and availability. Of the 333 trees (184 *Cordia* and 149 *Grevillea*) used in avian surveys, we sampled 146 (75 *Cordia* and 71 *Grevillea*) for arthropods, and 72 (36 *Cordia* and 36 *Grevillea*) sampled with mist-nets. Basic vegetation data were recorded for all 333 trees.

Avian surveys were conducted at the avian observation points from 06h00–10h00 EAT, a time of day when birds are most active (D. Kammerichs-Berke, pers. obs.). Two trained and experienced field technicians conducted all surveys, and they generally alternated between sampling *Cordia* and *Grevillea* trees throughout the morning. Due to the spatial design, one observer surveyed 71 more trees in total than the other, but the difference in proportions of *Cordia* and *Grevillea* was not significant ($\chi^2 = 1.605$, df =1, $P = 0.205$). Once at an observation point, each observer simultaneously monitored the 3–4 focal survey trees that were near the point, for a total of 10 minutes. While this simultaneous design is unusual, we found that the number of birds present in or coming to/from a given tree in a 10-minute period was low (see Results), and the habitat was open and individual trees easily monitored, so this design optimised replication while maintaining precision. For each survey, observers recorded species abundances, and the number of individuals actively foraging in the trees. Foraging was defined as any of the stereotyped behaviours described in Remsen and Robinson (1981). If there were more than 10 individuals of a species within a tree, observers estimated flock size to the nearest five; for groups of a species fewer than 10, observers counted individuals. Observers counted all birds seen in the trees within the 10-minute observation period, including arriving birds.

Mist nets were used to quantify presence/absence and relative abundances of insectivorous birds in the coffee layer. A team of field technicians set up 30-mm mesh nets in the coffee layer under 12 of the survey trees at each site, with nets deployed so that half were near *Grevillea* and half near *Cordia*. Nets were placed no more than 5 m from the base of a tree, parallel to the coffee crop rows. Nets were opened 10 min before sunrise and were run for five hours for three mornings per site. Birds were banded using bands supplied by the National Museums of Kenya. Recaptures from the same day as initial banding were released directly at the net without re-processing, while recaptures from a previous day were processed and recorded. Recaptures from previous days were not included in the analysis as a measure of abundance.

We sampled arthropod communities using the branch clipping method described in Johnson (2000b) to sample arthropod communities. At each sampled tree, two branches were sampled, selected from areas of the foliage profile most similar to those generally used by foliage-gleaning birds (Johnson 2000a) during focal tree observations and within reach of extendable poles (i.e. outer branches <5 m high). Although an effort was made to sample two branches per tree, some trees only had one sampleable branch, leading to an odd number of branches surveyed in total (147 *Cordia* and 136 *Grevillea*, for a total of 283 branches across all farms). After a branch was selected, a pole fitted with a fabric bag was extended to the height of the branch, the branch was enclosed within the bag, and a drawstring pulled to cinch the bag over the branch as quickly as possible. A pruning pole was used to clip the branch free. Once the branch was free, the bagged branch was shaken to dislodge any arthropods. The clipped branches were checked for arthropods afterwards to ensure that all insects were captured in the sample and weighed with a spring scale to obtain wet biomass. The number of arthropods identified to order or class was recorded.

Tree species, height, and diameter at breast height (dbh) were measured at each surveyed shade tree ($n = 333$). Canopy coverage (via densiometer), crown length, width, and depth, and flowering score were also measured for a third of shade trees ($n = 146$). Tree height and crown depth were calculated from angles to top and bottom of tree and the bottom of crown (excluding small branches at the bottoms, where the bulk of the trees leaves end; measured with a clinometer) and distance to the tree (measured with a rangefinder in m). Crown width was estimated as the average of the crown diameter measured on two axes with a 50-m tape below the tree. Flowering was recorded on a scale of 0–4, representing none, up to 25% of branches with flowers, up to 50%, 75%, and 100%, respectively.

Coffee understorey data were measured in a square 10 x 10 m plot directly adjacent to each surveyed tree ($n = 146$). The number of coffee shrubs (stems) in each quadrant of the 10 x 10m plot was recorded, the percentage coffee cover in each quadrant was visually estimated (to nearest 10%), and the coffee flowering (if any) was recorded using the same scale as the shade tree measurements. Additionally, whether there was prominent flowering (>10 stems) and/or seed prevalence in the understorey was recorded.

Lastly, Maxim iButton temperature loggers were deployed under 12 of the trees (six *Cordia* and six *Grevillea*, one per species per site) and at six locations nearby under no shade trees that acted as unshaded control samples (one sun location per site). Loggers were tied to the stem of coffee shrubs within 3 m of a shade tree (or at least 15 m from a shade tree for unshaded samples), 2 m above ground and not in direct sunlight. The loggers collected data once every half hour to capture the warmest and coolest parts of the day, until the batteries died (approximately 43 days). Temperature loggers were retrieved in April 2019, with 11 successfully located and retrieved (four *Cordia*, four *Grevillea*, three unshaded control).

Statistical analysis

Multiple linear mixed-effects models were used to examine the effects of tree vegetation covariates on arthropod abundance. A two-sample *t*-test showed mean branch weights of *Cordia* and *Grevillea* were unequal (df = 234.37, $t = -5.5236$, $P < 0.001$). As such, arthropod density was used as the response variable, calculated as the number of individual arthropods per g of clipped and inspected branch biomass × 100. A Shapiro-Wilks normality test indicated the raw response variable was not normally distributed, so arthropod density was log-transformed to improve normality (W = 0.9888, $P = 0.03613$). Since arthropods were sampled from the same trees for which full vegetation variables were measured, model selection for predicting arthropod biomass included all vegetation variables. Because multiple branches were sampled from the same trees, tree was treated as a random effect in the model.

Generalized linear mixed-effects models (GLMM) with a Poisson distribution were used to examine the effects of vegetation variables on bird communities in the canopy of shade trees on farms. Although data were collected for all bird species detected on the farms regardless of foraging guild (Appendix S1 in the online supplementary material), analysis of bird communities was limited to insectivores, since that is the guild most relevant to farmers in terms of potential pest control services. Species were classified as insectivorous based on major dietary preferences (HBWA 2018). Three separate stepwise model selection analyses were conducted for the bird community data, using species richness, total abundance of individuals, and abundance of foraging individuals specifically as response variables, respectively. Rarefaction revealed that the bird community was sampled adequately with the full sample size ($n = 333$ trees; Appendix S2), but not with the subset of trees that also included arthropod and detailed vegetation sampling ($n = 146$ trees), so predictive models for the bird community included only the vegetation data collected at all trees (tree species, dbh, height). None of the final vegetation variables had a strong correlation with each other (all $r < 0.75$, VIF <5), so collinearity was not an issue. A Poisson distribution was used to account for the zero-inflated nature of the detection data and helped meet the model assumptions necessary for GLMMs. For each analysis, site was treated as a random effect to account for unmeasured farm-level variation that may have influenced species richness or abundance (e.g. elevation).

GLMMs with a Poisson distribution was also used to examine the effects of vegetation variables on bird communities sampled by mist-nets in the crop layer. The number of captures per net and number of species per net were used as indices of abundance and species richness of birds as the response variables (see Smith *et al.* 2015), with tree species, height, canopy cover, dbh, coffee flowering score, and average percentage understorey cover as predictor variables; site was again used as a random effect. For both canopy and crop layer GLMM analyses, Akaike Information Criterion corrected for small sample size (AICc) was used to establish model weights and select top models and (Burnham and Anderson 2002).

Non-metric multidimensional scaling (NMDS) was used to ordinate Bray-Curtis dissimilarity indices and to identify patterns in the bird community composition data. Because ordinations cannot be constructed using zero values, the survey data was subsampled to only include trees that had at least one detection of any species (n = 139 trees). Bird community matrices were then constructed for the canopy and understorey of each tree species from the foraging and banding data, respectively. Bray-Curtis dissimilarity distances were calculated between each tree, which were ordinated using a NMDS with no more than 1,000 random starts and 4 dimensions ($k = 4$). Four dimensions were used because any scaling done with fewer dimensions failed to converge after 1,000 starts. A pairwise Permutational Multivariate Analysis of Variance (PERMANOVA) with a Bonferroni P-value correction was conducted to compare the community composition of each analysis of canopy and understory, under the null hypothesis that there is no difference in community composition between four vegetation levels (canopy and understory each of *Cordia* and *Grevillea*). In all, 999 permutations were used for the PERMANOVA. A multivariate analogue of Levene's test was used to test for homogeneity of group variances (Anderson 2006). Simpson's indices of diversity and evenness were calculated to determine community diversity and evenness for each vegetation level. Lastly, an analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test were used to compare differences in daily maximum, minimum, and mean daily temperatures between each tree species and the control.

Results

Overall, 2,386 individuals across 23 arthropod taxa groups were detected on native *Cordia*, while 682 individuals across 18 arthropod groups were detected on non-native *Grevillea*. The top performing model predicting arthropod density included tree species and height (Table 1), with *Grevillea* and tree height both negatively associated with arthropod density (Figure 2). The mean

Table 1. AICc results of the competing linear regression model set which included tree species, tree height, and diameter at breast height (dbh) as predictors to arthropod biomass on coffee farms in Kiambu County, Kenya, winter 2018–2019.

Response Variable	Model	K[a]	$\mathrm{Log_e(L)}$[b]	$\mathrm{AIC_c}$[c]	$\Delta\mathrm{AIC_c}$[d]	Wi[e]
Arthropod Biomass	Tree Species + Height	5	-392.29	794.81	0.00	**0.65**
	Tree Species	4	-393.90	795.96	1.15	0.35
	Tree Species + Height + Av. Crown Spread.	6	-394.46	801.23	6.42	0.03
	Tree Species + Height + Av. Crown Spread + Canopy Cover	7	-398.79	812.00	17.19	0.00
	All Vegetation	8	-401.63	819.81	25.00	0.00
	Height	4	-406.21	820.58	25.76	0.00
	Null	3	-420.67	847.43	52.61	0.00
	Av. Crown Spread	4	-421.29	850.72	55.91	0.00
	Canopy Cover	4	-422.17	852.50	57.69	0.00
	Dbh	4	-423.71	855.58	60.77	0.00

[a] Number of parameters

[b] $\mathrm{Log_e}$(likelihood)

[c] Akaike's Information Criterion corrected for small sample size

[d] Difference between $\mathrm{AIC_c}$ and top model $\mathrm{AIC_c}$

[e] $\mathrm{AIC_c}$ weight

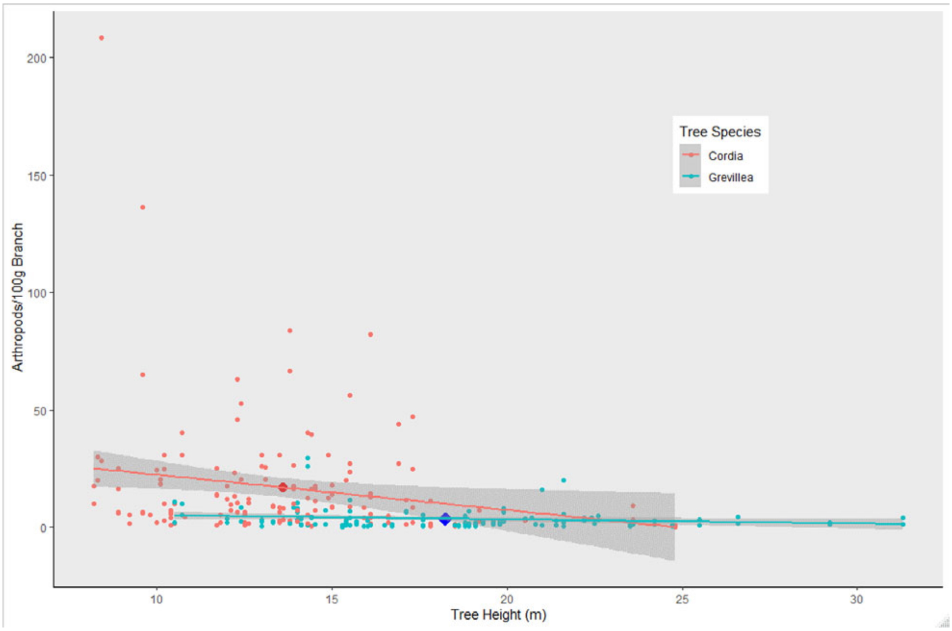

Figure 2. Arthropod density (arthropods per 100 g clipped and inspected vegetation) on *Cordia* and *Grevillea* trees on coffee farms in Kiambu County, Kenya, winter 2018-2019. *Cordia* had significantly higher arthropod density than *Grevillea* ($P = 0.0002$), and shorter trees had higher biomass regardless of tree species ($P = 0.0167$). Enlarged dots represent the mean arthropod density for each tree species and mean height.

density of arthropods per 100 g of clipped and inspected branch vegetation was over four times higher on *Cordia* branches (17.07 ± 2.10) than on *Grevillea* (3.39 ± 0.39).

In total, 841 individuals of 19 insectivorous bird species were detected in the avian surveys: *Batis molitor, Terpisphone viridis, Melaniparus albiventris, Sylvietta whytii, Apalis flavida, Phylloscopus trochilus, Ploceus baglafecht*, two species of sylviid warblers (Family Sylviidae), two white-eyes (Family Zosteropidae), two Old World flycatchers (Family Muscicapidae), and six species of sunbirds (Family Nectariniidae; Table 2). Tree species and height were the top predictors of avian species richness, total abundance, and abundance of foraging individuals (Table 3). *Grevillea* was negatively associated with richness ($\beta = -0.743 \pm 0.097$, 95% CI = -0.935, -0.554), total abundance ($\beta = -1.019 \pm 0.092$, 95% CI = -1.203, -0.835), and foraging abundance ($\beta = -1.327 \pm 0.133$, 95% CI = -1.595, -1.069). Tree height was positively associated with richness ($\beta = 0.038 \pm 0.009$, 95% CI = 0.019, 0.057), total abundance ($\beta = 0.035 \pm 0.008$, 95% CI = 0.018, 0.053), and foraging abundance ($\beta = 0.039 \pm 0.012$, 95% CI = 0.015, 0.063; Table 4). Relative to *Grevillea*, a 10-min survey of *Cordia* trees on average contained +0.98 species, +1.61 total birds, and +1.1 foraging birds (Figure 3).

In total, 278 individuals of the same 19 insectivorous bird species were detected by mist-nets in the understorey of shade farms. Average coffee flowering score, canopy cover, and understorey cover were the top predictors of total relative abundance in the crop layer, whereas average coffee flowering score and canopy cover were top predictors of species richness (Appendix S3). Average coffee flowering score was negatively associated with total abundance ($\beta = -0.688 \pm 0.184$, 95% CI = -1.061, -0.333), whereas canopy cover was positively associated with abundance ($\beta = 0.013 \pm 0.003$,95% CI = 0.006, 0.019), as was understorey cover ($\beta = 0.006 \pm 0.003$, 95% CI = 0.0008, 0.013). Average coffee flowering score was negatively associated with species richness

Table 2. Detected abundances of each focal insectivorous bird species for each vegetation level on coffee farms in Kiambu County, Kenya, winter 2018–2019. Birds were detected at the canopy level using 10-minute focal tree observations and at the understory level using mist nets.

		Vegetation Level			
Common Name	Latin Name	Canopy-Cordia	Understory-Cordia	Canopy-Grevillea	Understory-Grevillea
Chinspot Batis	*Batis molitor*	2	4	0	2
African Paradise-Flycatcher	*Terpsiphone viridis*	3	7	2	11
White-bellied Tit	*Melaniparus albiventris*	1	9	0	3
Red-faced Crombec	*Sylvietta whytii*	1	7	1	9
Yellow-breasted Apalis	*Apalis flavida*	1	8	5	5
Willow Warbler	*Phylloscopus trochilus*	17	7	1	7
Eurasian Blackcap	*Sylvia atricapilla*	4	6	0	7
Garden Warbler	*Sylvia borin*	1	1	0	1
Pale White-Eye	*Zosterops flavilateralis*	7	3	7	2
Kikuyu White-Eye	*Zosterops kikuyuensis*	9	47	13	19
Pale Flycatcher	*Agricola pallidus*	7	4	0	2
White-eyed Slaty-Flycatcher	*Melaenornis fischeri*	4	2	0	5
Collared Sunbird	*Hedydipna collaris*	1	4	0	0
Green-headed Sunbird	*Cyanomitra verticalis*	1	1	1	0
Amethyst Sunbird	*Chalcomitra amethystina*	1	0	1	1
Scarlet-chested Sunbird	*Chalcomitra senegalensis*	4	1	1	9
Bronze Sunbird	*Nectarinia kilimensis*	12	20	2	15
Variable Sunbird	*Cinnyris venustus*	16	12	3	13
Baglafecht Weaver	*Ploceus baglafecht*	2	12	1	12

($\beta = -0.899 \pm 0.241$, 95% CI = -1.393, -0.440), while canopy cover was positively associated with richness ($\beta = 0.007 \pm 0.003$, 95% CI = -0.0001, 0.0147; Appendix S4). Shade tree species was not strongly associated with bird abundance or richness sampled by mist-nets in the understorey.

All 19 focal species were detected in the canopy of *Cordia*, 18 in the understorey of *Cordia*, 12 in the canopy of *Grevillea*, and 17 in the understorey of *Grevillea*, with 10 species detected in all four vegetation levels (Table 2). In the ordination, a stress level of 0.141 was obtained at convergence, indicating good ordination goodness-of-fit. The canopy community of *Cordia* was marginally more even than in *Grevillea*, and the understory community of *Grevillea* was the most even and most diverse of all four vegetation levels (Appendix S5). Pairwise PERMANOVA indicated that the bird community composition in the *Grevillea* canopy was significantly different from the *Cordia* canopy ($r^2 = 0.086$, $F = 6.437$, $p_{adj} = 0.006$, df = 1), the *Cordia* understory ($r^2 = 0.103$, $F = 7.857$, $p_{adj} = 0.006$, df = 1), and the *Grevillea* understory ($r^2 = 0.100$, $F = 7.185$, $p_{adj} = 0.006$, df = 1). The community composition did not differ significantly between any other pair of vegetation layers (Table 5, Figure 4). Variance was also shown to be unequal between most groups ($F = 21.596$, $P < 0.001$, df = 3), with only *Cordia* understorey and *Grevillea* understorey communities having equal variance. However, pairwise PERMANOVAs are resilient to heterogeneity of variance in balanced designs such as this one (Anderson and Walsh 2013), so the results of the pairwise PERMANOVA should not be a result of inequal variances.

Shade trees buffered temperatures in coffee, and this affect was similar under *Cordia* and *Grevillea*. The maximum daily temperature was 3.2–3.5 °C lower under shade trees than in the unshaded control, and this affect was significant for both *Cordia* and *Grevillea* ($P < 0.01$; Appendix S6). Likewise, the minimum daily temperature was warmer under shade than in the unshaded

Table 3. AICc results of the competing general linear model set which included tree species, tree height, and diameter at breast height (dbh) as predictors to insectivorous bird species richness, abundance, and foraging on coffee farms in Kiambu County, Kenya, winter 2018-2019.

Response Variable	Model	K[a]	Log$_e$(L)[b]	AIC$_c$[c]	Delta AIC$_c$[d]	Wi[e]
Richness	**Species + Height + (1 | Site)**	**4**	**-620.70**	**1249.51**	**0.00**	**0.69**
	Species + Height + dbh + (1|Site)	5	-620.48	1251.15	1.64	0.30
	Species + dbh + (1|Site)	4	-624.85	1257.82	8.31	0.01
	Species + (1|Site)	3	-628.83	1263.73	14.22	0.00
	dbh + (1|Site)	3	-643.92	1293.91	44.40	0.00
	Height + dbh + (1|Site)	4	-643.03	1294.17	44.66	0.00
	1 + (1|Site)	2	-651.96	1307.95	58.44	0.00
	Height + (1|Site)	3	-651.85	1309.77	60.26	0.00
Abundance	**Species + Height + (1 | Site)**	**4**	**-825.37**	**1658.86**	**0.00**	**0.68**
	Species + Height + dbh + (1|Site)	5	-825.15	1660.48	1.62	0.30
	Species + dbh + (1|Site)	4	-829.42	1666.96	8.10	0.01
	Species + (1|Site)	3	-833.29	1672.64	13.78	0.00
	Height + dbh + (1|Site)	4	-875.74	1759.60	100.74	0.00
	dbh + (1|Site)	3	-875.74	1772.28	113.42	0.00
	Height + (1|Site)	3	-892.08	1790.23	131.37	0.00
	1 + (1|Site)	2	-893.32	1790.67	131.80	0.00
Foraging	**Species + Height + (1 | Site)**	**4**	**-614.42**	**1236.95**	**0.00**	**0.69**
	Species + Height + dbh + (1|Site)	5	-614.36	1238.89	1.94	0.26
	Species + dbh + (1|Site)	4	-617.27	1242.65	5.70	0.04
	Species + (1|Site)	3	-619.43	1244.92	7.97	0.01
	Height + dbh + (1|Site)	4	-658.99	1326.10	89.15	0.00
	dbh + (1|Site)	3	-666.94	1339.96	103.00	0.00
	Height + (1|Site)	3	-671.36	1348.79	111.84	0.00
	1 + (1|Site)	2	-673.43	1350.90	113.95	0.00

[a] Number of parameters
[b] Log$_e$(likelihood)
[c] Akaike's Information Criterion corrected for small sample size
[d] Difference between AIC$_c$ and top model AIC$_c$
[e] AIC$_c$ weight

Table 4. Results from top models for insectivorous bird species richness, abundance, and foraging on coffee farms in Kiambu County, Kenya, winter 2018-2019.

Response	Covariate	β	SE	CI (95%)
Richness	Intercept	0.327	0.147	0.036, 0.616
	Species (Grevillea)	-0.743	0.097	-0.935, -0.554
	Height	0.038	0.009	0.019, 0.057
Abundance	Intercept	0.700	0.183	0.316, 1.084
	Species (Grevillea)	-1.019	0.092	-1.203, -0.835
	Height	0.035	0.008	0.018, 0.053
Foraging	Intercept	0.096	0.232	-0.381, 0.572
	Species (Grevillea)	-1.327	0.133	-1.595, -1.069
	Height	0.039	0.012	0.015, 0.063

control, and this was significant for *Cordia* (+1.2° C, P <0.01) but not *Grevillea*-Control: +0.8° C, P =0.15). Mean daily temperatures were similar among both shade tree species and in the unshaded control sites, though mean temperatures were marginally cooler under *Cordia* than *Grevillea* (-0.5° C difference, 95% CI = -0.043, 1.096, P =0.08).

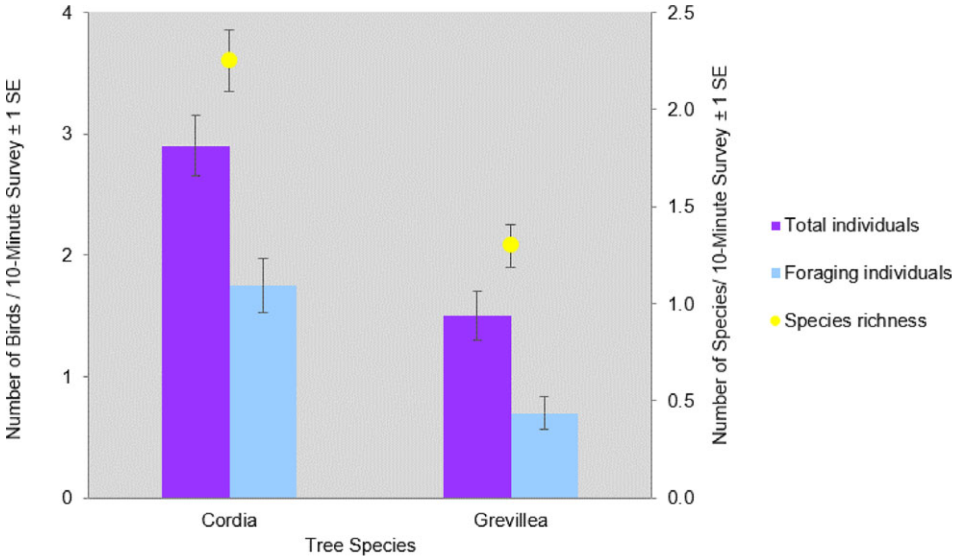

Figure 3. Mean number ($\bar{X}$ / 10-minute survey ±1 SE) of total individuals, foraging individuals, and bird species richness per 10-minute survey of *Cordia* and *Grevillea* shade trees on coffee farms in Kiambu County, Kenya, winter 2018-2019.

Table 5. Pairwise PERMANOVA results for insectivore community similarities between each pair of vegetation levels on coffee farms in Kiambu County, Kenya, winter 2018-2019.

Pairs	Df	Sum of Squares	F	R^2	P_{adj}
Canopy-Cordia / Understory-Cordia	1	0.530	3.269	0.043	0.054
Canopy-Cordia / Canopy-Grevillea	1	0.795	6.437	0.086	0.006**
Canopy-Cordia / Understory-Grevillea	1	0.366	2.233	0.031	0.300
Understory-Cordia / Canopy-Grevillea	1	1.046	7.857	0.103	0.006**
Understory-Cordia / Understory-Grevillea	1	0.170	0.981	0.014	1.000
Canopy-Grevillea / Understory-Grevillea	1	0.957	7.185	0.100	0.006**

** Statistically significant ($p_{adj} < 0.05$)

Discussion

Shade coffee is important for the conservation of birds globally, but there is a need to better understand the effects of particular shade tree species on bird communities and the implications for shade tree use for conservation and ecosystem services (Narango *et al.* 2018, 2019). As predicted by ecological theory relating native vegetation to species diversity (Tallamy 2004), native *Cordia* trees in Kenyan shade coffee farms hosted not only a higher density of arthropods than did non-native *Grevillea* (Figure 4), but *Cordia* also had higher abundance of insectivorous birds and specifically more foraging individuals than *Grevillea* (Figure 5). *Cordia* also had greater bird species richness than did *Grevillea*. All 19 focal species were detected in *Cordia*, and the most abundant species (Willow Warbler *Phylloscopus trochilus*) accounted for 18% of all individual detections. In contrast, only 12 of the focal insectivorous bird species were detected in *Grevillea*, and one species (Kikuyu White-eye *Zosterops kikuyuensis*) accounted for 34% of all detections.

Optimal foraging theory predicts that animals distributed in patchy environments should select the most profitable patches to forage in and decide when to leave the patch they are using, given

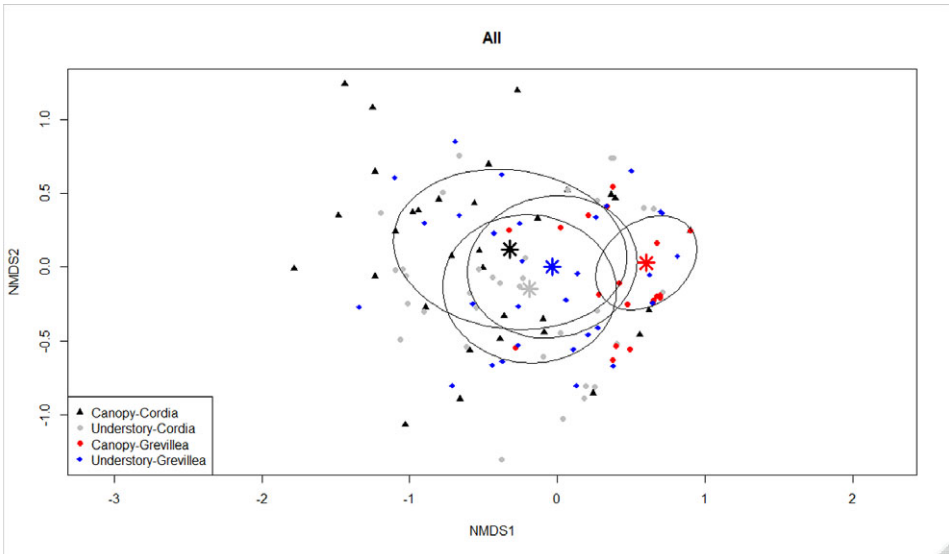

Figure 4. Non-metric multi-dimensional scaling (NMDS) plot of insectivorous bird community similarities between each vegetation level on coffee farms in Kiambu County, Kenya, winter 2018-2019. Canopy-*Grevillea* differs significantly from Canopy-*Cordia* (adj-p = 0.006), Understory-*Cordia* (adj-p = 0.006), and Understorey-*Grevillea* (adj-p = 0.006). Ellipses represent 95% CI around the centroids of each community.

that the intake rates will vary among patches (Pyke 1984). Based on the functional response of animals to prey density (Holling 1965), feeding insectivorous birds should distribute among feeding patches according to their supply of insects, the so-called "habitat matching" rule (Fretwell 1972, Fagen 1987, Johnson and Sherry 2001). Because most insect taxa specialise on one or few native host plants, it is expected that herbivorous insects should be more common on native than exotic plants (Burghardt *et al.* 2010, Litt *et al.* 2014), and correspondingly insect-eating birds should forage more on natives than exotics (Narango *et al.* 2018). Although this study involved only a single pair of native and non-native tree species, the results are consistent with ecological theory of higher abundances of arthropods on native plants, which in turn would support more insectivorous birds that can forage on pest arthropods in the crop layer (Narango *et al.* 2018). This is relevant to farm managers because many of the ecosystem services that birds provide in agricultural landscapes result from their dietary preferences and foraging behaviour (Wenny *et al.* 2011). Insectivorous birds are more likely than other foraging guilds to provide beneficial top-down control of pest species (Kellermann *et al.* 2008, Philpott *et al.* 2008, Johnson *et al.* 2010), and are generally also at higher conservation risk due to their stronger associations with forest habitats (Bennun *et al.* 1996, Sekercioglu *et al.* 2002, HBWA 2018).

The notion that shade trees could attract insectivorous birds helpful for control of pests on coffee shrubs rests on the assumption that birds using the shade trees also forage in the associated understory, but this has rarely been examined explicitly (but see Smith *et al.* 2012). Because the preferred vegetation profiles for foraging vary among bird species, some natural variation between canopy and crop level bird communities is expected. Nonetheless, the bird communities were nearly identical between the *Cordia* canopy and the crop layer (94.7% species overlap), whereas they were much less so between *Grevillea* canopy and understorey (64.7% species overlap), with several species detected in the *Grevillea* understorey but not its canopy. The crop layer under both *Cordia* and *Grevillea* trees more closely resembled the canopy-level communities in *Cordia* trees, suggesting that *Grevillea* had comparatively less influence on the crop-level bird communities. The resemblance between the crop layer, regardless of shade tree species, and the *Cordia* canopy suggests that *Cordia* attracts birds to the canopy with its high abundance of non pest arthropods, and birds then move down and spread out to forage throughout the crop layer. These results, coupled with the relatively low arthropod abundance on in the crop layer (Milligan 2014, Smith *et al.* 2018), suggest *Cordia* attracts greater numbers of insect-eating birds to the canopy that subsequently spill over into the crop layer, increasing the potential for birds to predate on pest species such as coffee berry borer, white coffee stem-borer *Xylotrechus quadripes*, and scale insects (Superfamily Coccoidea). Our data did not suggest that native trees increased the abundance of pest species, because none of the species observed during the arthropod sampling were known coffee pests. In the Neotropics, avian predators of coffee berry borer and other coffee insects are mainly small-billed, small bodied, foliage gleaning insectivores, such as Parulid warblers (Karp and Daily 2014, Sherry *et al.* 2016). Diet data are not yet available for the birds inhabiting East African coffee, but based on morphology, white-eyes (*Zosterops* spp.) may be a likely candidate for pest control. Notably, there were considerably more *Z. kikuyuensis* in the crop layer below *Cordia* than *Grevillea*, even though *Z. kikuyuensis* comprised the majority of individuals detected in the canopy of *Grevillea*. While more *Z. kikuyuensis* were detected in the canopy of *Grevillea* than *Cordia*, most of the individuals were observed collecting nesting material such as spiderweb and tree fibre mand were rarely seen actively foraging. Of course, insectivorous birds could remove more pest-eating insects than the pests themselves, and this intra-guild predation could result in a net negative effect of birds on coffee pests (Müller and Brodeur 2002, Perfecto *et al.* 2014).

Cordia may be preferred by farmers for other reasons besides their attractiveness to insect-eating birds. *Cordia* are generally wide-canopied trees, which, while sometimes taking up more space on the farm, provide the coffee crop with greater amounts of shade that may help adapt to expected climate warming (Kammerichs-Berke 2020). Coffee berry borer reproductive rates are associated with warming temperatures (Jaramillo *et al.* 2009, 2011), and data indicate that coffee under the canopy of both *Cordia* and *Grevillea* trees had a more restricted temperature range than in the sun, with marginally cooler mean temperatures under *Cordia* than *Grevillea*. These buffered temperatures could affect the productivity of pests that would proliferate under warmer temperatures (Jaramillo *et al.* 2009) and help adapt to expected climate warming (Schooler *et al.* 2020).

Grevillea robusta proliferated as a shade tree in central Kenya in the latter half of the 20th century largely due to the growth of the Greenbelt Movement. With the mission of community empowerment and conservation, the Green Belt Movement planted millions of trees throughout Kenya, particularly in agricultural areas such as the Kiambu region (Chikwendu 2008). *Grevillea* was chosen largely because it grows quickly (up to 3 m per year; SelecTree 2020) and yields high, immediate material benefits such as firewood. However, in recent decades the Greenbelt Movement has shifted its stance to encourage the use of native species, including *Cordia*, in environmentally sensitive areas (Murithi *et al.* 2009). *Cordia*, while slower growing, may yield greater environmental conservation benefits as well as similar material benefits in the long term (Alemayehu *et al.* 2016). *Cordia* has various uses as medicine, food, firewood, fodder, and mulch (Alemayehu *et al.* 2016), and is considered an attractive species for beekeeping and honey production (Fichtl and Adi 1994). *Cordia* also provides a greater windbreak than *Grevillea*, offering better crop protection during rainy season storm events (J. Murithi pers. comm.).

Research priorities

The clear next step is to test if species detected in the crop understorey are in fact removing insects from coffee plants. Insectivorous birds have been confirmed to help control coffee pests in the Neotropics (Kellermann *et al.* 2008, Johnson *et al.* 2010, Karp *et al.* 2013, Sherry *et al.* 2016), but this phenomenon has been much less studied in East Africa. Exclosure experiments in Tanzanian coffee farms confirmed a significant increase in herbivory rates on bushes from which birds and bats were excluded (Classen *et al.* 2014), and a sentinel pest removal experiment in Nyeri County, Kenya, documented greater insect removal rates in shade versus sun farms (Milligan *et al.* 2016). However, confirmation of Kenyan birds as pest predators awaits examination of their diets and additional experimental exclosure studies. In our study area, fecal samples were collected from birds captured in mist-nets, and on-going molecular analysis should reveal diet compositions of insectivorous birds (Jedlicka *et al.* unpubl. data).

Despite the economic, cultural, and ecological significance of coffee in Africa, its role in conservation on the continent is poorly understood, especially compared to the abundance of coffee-related ecological research done in the western hemisphere. With a combined worth of US$ 70 billion, the coffee industry plays a significant role in the global economy (Osorio 2002). Coffee is a major export of several tropical and subtropical countries in Central and South America, Asia, and Africa, and the industry supports approximately 125 million people worldwide (Osorio 2002, FAO 2016). With roughly 20% of the world's 10 million ha of harvested area, Africa is one of the world's leading producers of coffee. Coffee is a major cash crop in Kenya, third only to tea and horticulture produce in export earnings. Approximately 110,000 ha of land are harvested for coffee, and the industry supports about 5 million people within these areas (KALRO 2015). Few studies on birds and coffee have been conducted in East Africa, but among them they show conflicting results (Pinard *et al.* 2014a, Buechley *et al.* 2015, Smith *et al.* 2015, Milligan *et al.* 2016). These various results arise from the first few studies of birds in East African coffee farms, and they have followed basic survey designs completed much earlier and replicated many times in the Neotropics, from which broad observable patterns have now emerged (Philpott *et al.* 2008). It is therefore vital to continue examining birds and other wildlife in coffee systems in East Africa to gain a more complete understanding of the agroecosystems in this region.

Supplementary Materials

To view supplementary material for this article, please visit http://doi.org/10.1017/S0959270921000502.

Acknowledgements

We are grateful to James Murithi of Sasini Ltd and Duncan Kanyi of Theta Country Farm for granting us permission to work on their coffee farms. We thank Mark Colwell and Erik Jules, whose input, particularly with the multivariate analyses, was invaluable. Kristina Wolf, Manny Hernandez, and Christopher Watson helped with data collection in the field. This project was funded by the National Science Foundation (IRES award #1657973 and #1657836).

References

Alemayehu, G., Asfaw, Z. and Kelbessa, E. (2016) *Cordia africana* (Boraginaceae) in Ethiopia: A review on its taxonomy, distribution, ethnobotany and conservation status. *Internatn. J. Bot. Stud.* 1: 38–46.

Anderson, M. J. (2006) Distance-based tests for homogeneity of multivariate dispersions. *Biometrics* 62: 245–253.

Anderson, M. J. and Walsh, D. C. I. (2013) PERMANOVA, ANOSIM, and the Mantel test in the face of heterogeneous dispersions: What null hypothesis are you testing? *Ecol. Monogr.* 83: 557–574.

Armbrecht, I. and Perfecto, I. (2003) Litter-twig dwelling ant species richness and predation potential within a forest fragment and neighboring coffee plantations of contrasting habitat quality in Mexico. *Agric. Ecosyst. Environ.* 97: 107–115.

Baggio, A. J., Caramori, P. H., Filho, A. and Montoya, L. (1997) Productivity of Southern Brazilian coffee plantations shaded by different stockings of Grevillea robusta. *Agroforest. Syst.* 37: 111–120.

Becerra, J. X., and Venable, D. L. (1999) Macroevolution of insect-plant associations: The relevance of host biogeography to host affiliation. *Proc. Natl. Ac. Sci.* 96: 12626–12631.

Beer, J. (1987) Advantages, disadvantages and desirable characteristics of shade trees for coffee, cocoa and tea. *Agroforest. Syst.* 5: 3–13.

Bernays, E. M. and Graham, M. (1988) On the evolution of host specificity in phytophagous arthropods. *Ecology* 69: 886–892.

Bennun, L., Dranzoa, C. and Pomeroy, D. (1996) The forest birds of Kenya and Uganda. *J. East Afr, Nat. Hist.* 85: 23–48.

Betts, M. G., Wolf, C., Ripple, W. J., Phalan, B., Millers, K. A., Duarte, A., Butchart, S. H. M. and Levi, T. (2017) Global forest loss disproportionately erodes biodiversity in intact landscapes. *Nature* 547: 441–444.

Brown, J. H. (2014) Why are there so many species in the tropics? *J. Biogeogr.* 41: 8–22.

Buechley, E. R., Şekercioğlu, Ç. H., Atickem, A., Gebremichael, G., Ndungu, J. K., Mahamued, B. A., Beyene, T., Mekonnen, T. and Lens, L. (2015) Importance of Ethiopian shade coffee farms for forest bird conservation. *Biol. Conserv.* 188: 50–60.

Burghardt, K. T., Tallamy, D. W. Philips, C. and Shropshire, K. J. (2010) Non-native plants reduce abundance, richness, and host specialization in lepidopteran communities. *Ecosphere* 1: art11.

Burnham, K. P. and Anderson, D. R. (2002) *Model selection and multimodel inference: A practical information-theoretic approach.* New York, New York: Springer-Verlag.

Classen, A., Peters, M. K., Ferger, S. W., Helbig-Bonitz, M., Schmack, J. M., Maassen, G., Schleuning, M., Kalko, E. K. V., Böhnig-Gaese, K. and Steffan-Dewenter, I. (2014) Complementary ecosystem, services provided by pest predators and pollinators increase quantity and quality of coffee yields. *Proc. Roy. Soc.* 281: 20133148.

Chikwendu, E. (2008) Wangari Maathai: Nobel laureate, environmentalist, and engagement with the Kenya state. Pp. 29–44 in C. J. Korieh and P. E. Okeke-Ihejirika, eds. *Gendering global transformations: Gender, culture, race, and identity.* Abingdon-on-Thames, UK: Routledge.

Davis, H., Rice, R., Rockwood, L., Wood, T. and Marra, P. (2017) The economic potential of fruit trees as shade in blue mountain coffee agroecosystems of the Yallahs River watershed, Jamaica W.I. *Agroforest. Syst.* 93: 581–589.

Donald, P. F. (2004) Biodiversity impacts of some agricultural commodity production systems. *Conserv. Biol.* 18: 17–38.

Douglas, D. J. T., Nalwanga, D., Katebaka, R., Atkinson, P. W., Pomeroy, D. E., Nkuutu, D. and Vickery, J. A. (2013) The importance of native trees for forest bird conservation in tropical farmland. *Anim. Conserv.* 17: 256–264.

Eagen, R. (1987) A generalized habitat matching rule. *Evol. Ecol.* 1: 5–10.

Ehrlich, P. L, and Raven, P. H. (1964) Butterflies and plants: A study in coevolution. *Evolution* 18: 586–608.

FAO (2016) FAOSTAT. Food and Agriculture Organization of the United Nations. <http://www.fao.org/faostat/en/#home>. Accessed 6 Sep 2018.

Farrell, B. D. and Mitter, C. (1998) The timing of insect/plant diversification: might *Tetraopes* (Coleoptera: Cerambycidae) and *Asclepias* (Asclepiadaceae) have co-evolved? *Biol. J. Linn. Soc.* 63: 553–577.

Fichtl, R. and Adi, A. (1994) *Honeybee flora of Ethiopia*. Weikersheim, Germany: Margaf Verlag.

Fischer, J., Abson, D. J., Butsic, V., Chappell, M. J., Ekroos, J., Hanspach, J., Kuemmerle, T., Smith, H. G. and von Wehrden, H. (2014) Land sparing versus land sharing: Moving forward. *Conserv. Lett.* 7: 149–157.

Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., Chapin, F. S., Coe, M. T., Daily, G. C., Gibbs, H. K., Helkowski, J. H., Holloway, T., Howard, E. A., Kucharik, C. J., Monfreda, C., Patz, J. A., Prentice, I. C., Ramankutty, N. and Snyder P. K. (2005) Global consequences of land use. *Science* 309: 570–574.

Forister, M. L., Novotny, V., Panorska, A. K., Baje, L., Basset, Y., Butterill, P. T., Cizek, L., Coley, P. D., Dem, F., Diniz, I. R., Pavel, D., Fox, M., Glassmire, A. E., Hazen, R., Hrcek, J., Jahner, P., Kaman, O., Kozubowski, T. J., Kursar, T. A., Lewis, O. T., Lill, J., Marquis, R. J. Miller, S. E., Morais, H. C., Murakami, M., Nickel, H., Pardikes, N. A., Ricklefs, R. E., Singer, M. S., Smilanich, A. M., Stireman, J. O., Villamarin-Cortez, S., Vodka, S., Volf, M., Wagner, D. L., Walla, T., Weiblen, G. D. and Dyer, L. A. (2015) The global distribution of diet breadth in insect herbivores. *Proc. Natl. Ac. Sci.* 112: 442–447.

Fretwell, S. D. (1972) *Populations in a seasonal environment*. Princeton, USA: Princeton University Press.

Handbook of Birds of the World Alive [HBWA] (2018) Species home page. <https://www.hbw.com/species>. Accessed 6 Sep 2018.

Holling, C. (1965) The functional response of predators to prey density and its role in mimicry and population regulation. *Memoirs Entomol. Soc. Canada* 97 (S45): 5–60.

Jaramillo, J., Chabi-Olaye, A., Kamonjo, C., Jaramillo, A., Vega, F. E., Poehling, H. M. and Borgemeister, C. (2009) Thermal tolerance of the coffee berry borer *Hypothenemus hampei*: predictions of climate change impact on a tropical insect pest. *PLoS ONE* 4: e6487.

Jaramillo, J., Muchugu, E., Vega, F. E., Davis, A., Borgemeister, C. and Chabi-Olaye, A. (2011) Some like it hot: the influence and implications of climate change on coffee berry borer (*Hypothenemus hampei*) and coffee production in East Africa. *PLoS ONE* 6: e24528.

Jaramillo, J., Setamou, M., Muchugu, E., Chabi-Olaye, A., Jaramillo, A., Mukabana, J., Maina, J., Gathara, S. and Borgemeister, C. (2013) Climate change or urbanization? Impacts on a traditional coffee production system in East Africa over the last 80 years. *PLoS ONE* 8: e51815.

Jassogne, L., van Astern, P. J. A., Wanyama, I. and Baret, P. (2012) Perceptions and outlook on intercropping coffee with banana as an opportunity for smallholder coffee farmers in Uganda. *Internatn. J. Agric. Sustain.* 11: 144–158.

Jedlicka, J. A., Greenberg, R. and Letourneau, D. K. (2011) Avian conservation practices strengthen ecosystem services in California vineyards. *PLoS ONE* 6: e27347.

Jha, S., Bacon, C. M., Philpott, S. M., Ernesto Méndez, V., Läderach, P. and Rice, R. A. (2014) Shade coffee: Update on a disappearing refuge for biodiversity. *BioScience* 64: 416–428.

Johnson, M. D. (2000a) 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. (2000b) Evaluation of an arthropod sampling technique for measuring food availability for forest insectivorous birds. *J. Field Ornithol.* 71: 88–109.

Johnson, M. D. and Sherry, T. W. (2001) Effects of food availability on the distribution of migratory warblers among habitats in Jamaica. *J. Anim. Ecol.* 70: 546–560.

Johnson, M. D., Kellermann, J. L. and Stercho, A. M. (2010) Pest reduction services by birds in shade and sun coffee in Jamaica. *Anim. Conserv.* 13: 140–147.

Johnson, M. D. and Hackett, S. C. (2016) Why birds matter economically: Values, markets, and policies. Page 29 in *Why birds matter: Avian ecological function and ecosystem services*. Chicago, Illinois: University of Chicago Press.

KALRO (2015) *Annual report 2014-2015*. Nairobi, Kenya: Kenya Agricultural and Livestock Research Organization.

Kammerichs-Berke, D. (2020) The effect of shade tree species on bird communities in central Kenyan coffee farms. Master's thesis, Humboldt State University, Arcata, California.

Karp, D. S., Mendenhall, C. D., Sandi, R. F., Chaumont, N., Ehrlich, P. R., Hadly, E. A. and Daily, G. C. (2013) Forest bolsters bird abundance, pest control and coffee yield. *Ecol. Lett.* 16: 1339–1347.

Karp, D. S. and Daily, G. C. (2014) Cascading effects of insectivorous birds and bats in tropical coffee plantations. *Ecology* 95: 1065–1074.

Karp, D.S., Judson, S., Daily, G. C. and Hadly, E. A. (2014) Molecular diagnosis of bird-mediated pest consumption in tropical farmland. *SpringerPlus*: 3: 630.

Kellermann, J. L., Johnson, M. D., Stercho, A. M. and Hackett, S. C. (2008) Ecological and economic services provided by birds on Jamaican Blue Mountain coffee farms. *Conserv. Biol.* 22: 1177–1185.

Kindt, R., Van Damme, P. and Simmons, A. J. (2006) Tree diversity in western Kenya: using profiles characterize richness and evenness. *Biodivers. Conserv.* 15: 1253–1270.

Kiyingi, I., Ocama, D., Mujuni, D. and Nyombi, K. (2016) A bioeconomic analysis of the carbon sequestration potential of agroforestry systems: A case study *Grevillea robusta* in Western Uganda. *Uganda J. Agric. Sci.* 17: 219–229.

Lengkeek, A. G., Kindt, R., van der Maesen, L. J. G., Simons, A. J. and van Oijen, D. C. C. (2005) Tree density and germplasm source in agroforestry ecosystems in Meru, Mount Kenya. *Genet. Resour. Crop Evol.* 52: 709–721.

Litt, A. R., Cord, E. E., Fulbright, T. E. and Schuster, G. L. (2014) Effects of invasive plants on arthropods. *Conserv. Biol.* 28: 1532–1549.

Lott, J. E., Howard, S. B., Ong, C. and Black, C. R. (2000) Long-term productivity of a Grevillea robusta-based overstorey agroforestry system in semi-arid Kenya: II. Crop growth and system performance. *For. Ecol. Manage.* 139: 187–201.

Mehrabi, Z., Ellis, E. C. and Ramankutty, N. (2018) The challenge of feeding the world while conserving half the planet. *Nat. Sustain.* 1: 409–412.

Milligan, M. C. (2014) *Quantifying pest control services by birds and ants in Kenyan coffee farms.* Master's thesis, Humboldt State University, Arcata, California.

Milligan, M. C., Johnson, M. D., Garfinkel, M., Smith, C. J. and Njoroge, P. (2016) Quantifying pest control services by birds and ants in Kenyan coffee farms. *Biol. Conserv.* 194: 58–65.

Moguel, P. and Toledo, V. M. (1999) Biodiversity conservation in traditional coffee systems. *Conserv. Biol.* 13: 11–21.

Muchiri, M. N. (2004) Grevillea robusta in agroforestry systems in Kenya. *J. Trop. For. Sci.* 16: 396–401.

Müller, C.B. and Brodeur, J. (2002) Intraguild predation in biological control and conservation biology. *Biol. Control* 25: 216–223.

Murithi, C. W., Ong, C. K., Craigon, J., Mati, B. M., Ngumi, V. W. and Black, C. R. (2009) Gas exchange and water use efficiency of trees and maize in agroforestry systems in semi-arid Kenya. *Agric. Ecosyt. Environ,* 129: 297–307.

Narango, D. L., Tallamy, D. W. and Marra, P. P. (2018) Nonnative plants reduce population growth of an insectivorous bird. *Proc. Natl. Ac. Sci.* 201809259.

Narango, D. L., Tallamy, D. W., Snyder, K. J. and Rice, R. A. (2019) Canopy tree preference by insectivorous birds in shade-coffee farms: Implications for migratory bird conservation. *Biotropica* 51: 387–398.

Negash, L. (1995) *Native trees of Ethiopia: Biology, uses and propagation techniques.* Umea, Sweden: SLU Reprocentralen.

Osorio, N. (2002) *The global coffee crisis: a threat to sustainable development*. Johannesburg, South Africa: International Coffee Organization.

Perfecto, I., and Vandermeer, J. (2010) The agroecological matrix as alternative to the land- sparing/agriculture intensification model. *Proc. Natl. Ac. Sci.* 107: 5786–5791.

Perfecto, I., Vandermeer, J. and Philpott, S. M. (2014) Complex ecological interactions in the coffee agroecosystem. *Annu. Rev. Ecol. Evol. Syst.* 45: 137–158.

Perfecto, I., and Vandermeer, J. (2015) *Coffee agroecology: A new approach to understanding agricultural biodiversity, ecosystem services and sustainable development.* Abingdon, UK: Routledge.

Perfecto, I., Vandermeer, J., Bautista, G. L., Ibarra Nunñez, G., Greenberg, R., Bichier, P. and Langridge, S. (2004) Greater predation in shaded coffee farms: The role of resident Neotropical birds. *Ecology* 85: 2677–2681.

Perfecto, I., Vandermeer, J. and Wright, A. (2009) *Nature's matrix: Linking agriculture, conservation and food sovereignty.* Abingdon, UK: Routledge.

Philpott, S. M., Arendt, W. J., Armbrecht, 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. and 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.

Philpott, S. M. and Bichier, P. (2012) Effects of shade tree removal on birds in coffee agroecosystems in Chiapas, Mexico. *Agric. Ecosyst. Environ.* 149: 171–180.

Philpott, S. M., Soong, O., Lowenstein, J. H., Pulido, A. L., Lopez, D. T., Flynn, D. F. and DeClerck, F. (2009) Functional richness and ecosystem services: bird predation on arthropods in tropical agroecosystems. *Ecol. Applic.* 19: 1858–1867.

Pinard, F., Joetzjer, E., Kindt, R. and Kehlenbeck, K. (2014a) Are coffee agroforestry systems suitable for circa situm conservation of native trees? A case study from Central Kenya. *Biodivers. Conserv.* 23: 467–495.

Pinard, F., Boffa, J. M. and Rwakagara, E. (2014b) Scattered shade trees improve low-input smallholder Arabica coffee productivity in the northern Lake Kivu region of Rwanda. *Agroforest. Syst.* 88: 707–718.

Pyke, G. H. (1984) Optimal foraging theory: A critical review. *Annu. Rev. Ecol. Syst.* 15: 523–575.

Rahn, E., Vaast, P., Läderach, P., van Asten, P., Jassogne, L. and Ghazoul, G. (2018) Exploring adaptation strategies of coffee production to climate change using a process-based model. *Ecol. Model.* 371: 76–89.

Railsback, S. F. and Johnson, M. D. (2014) Effects of land use on bird populations and pest control service on coffee farms. *Proc. Natl. Ac. Sci.* 1320957111.

Raman, T. R. S. (2006) Effects of habitat structure and adjacent habitats on birds in tropical rainforest fragments and shaded plantations in the Western Ghats, India. *Biodivers. Conserv.* 15: 1577–1607.

Remsen, J. V. and Robinson, S. K. (1981) A classification scheme for foraging behavior of birds in terrestrial habitats. *Stud. Avian Biol.* 13: 144–160.

Renwick, A. R., Vickery, J. A., Potts, S. G., Bolwig, S., Nalwanga, D., Pomeroy, D. E., Mushabe, D. and Atkinson, P. W. (2014) Achieving production and conservation simultaneously in tropical agricultural landscapes. *Agric. Ecosyst. Environ.* 192: 130–134.

Romero-Alvarado, Y., Soto-Pinto, L., García-Barrios, L. and Barrera-Gaytán, J. F. (2000) Coffee yields and soil nutrients under the shades of *Inga* sp. vs. multiple species in Chiapas, Mexico. *Agroforest. Syst.* 54: 215–224.

Schemske, D. W., Mittelbach, G. G., Cornell, H. V., Sobel, J. M. and Roy, K. (2009) Is there a latitudinal gradient in the importance of biotic interactions? *Annu. Rev. Ecol. Syst.* 40: 245–269.

Schooler, S. L., Johnson, M. D., Njoroge, P. and Bean, W. T. (2020) Shade trees preserve avian insectivore biodiversity on coffee farms in a warming climate. *Ecol. Evol.* 10: 1–13.

Sekercioglu, C. H., Ehrlich, P. R., Daily, G. C., Aygen, D., Goehring, D. and Sandi, R. F. (2002) Proc. *Natl. Acad. Sci.* 99: 263–267.

SelecTree (2020) "Grevillea robusta Tree Record." CalPoly SelecTree Database (1995-2020). <https://selectree.calpoly.edu/tree-detail/grevillea-robusta>. Accessed 31 July 2020.

Sherry, T.W., Johnson, M. D., Williams, K. A., Kaban, J. D., McAvoy, C. K., Hallauer, A. M., Rainey, S. and 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. J., Johnson, M. D., Campos, B. R. and Bishop, C. M. (2012) Variation in aggression of Black-throated Blue Warblers wintering in Jamaica. *Condor* 114: 831–839.

Smith, C., Barton, D., Johnson, M. D., Wendt, C., Milligan, M. C., Njoroge, P. and Gichuki, P. (2015) Bird communities in sun and shade coffee farms in Kenya. *Global Ecol. Conserv.* 4: 479–490.

Smith, C., M. Milligan, C., Johnson, M. D. and Njoroge, P. (2018) Bird community response to landscape and foliage arthropod variables in sun coffee of central Kenyan highlands. *Global Ecol. Conserv.* 13: e00378.

Soto-Pinto, L., Perfecto, I., Castillo-Hernandez, J. and Caballero-Nieto, J. (2000) Shade effect on coffee production at the northern Tzeltal zone of the state of Chiapas, Mexico. *Agric. Ecosyst. Environ.* 80: 61–69.

Southwood, T. R. E., Moran, V. C. and Kennedy, C. E. J. (1982) The richness, abundance, and biomass of the arthropod communities on trees. *J. Anim. Ecol.* 51: 635–649.

Tilman, D., Balzer, C., Hill, J. and Befort, B. L. (2011) Global food demand and the sustainable intensification of agriculture. *Proc. Natl. Ac. Sci.* 108: 20260–20264.

Tignor, R. L. (2015) *Colonial transformation of Kenya: The Kambu, Kikuyu, and Maasai from 1900-1939*. Princeton, New Jersey: Princeton University Press.

Van Bael, S. A., Philpott, S. M., Greenberg, R., Bichier, P., Barber, N. A., Mooney, K. A. and Gruner, D. S. (2008) Birds as predators in tropical agroforestry systems. *Ecology* 89: 928–934.

Vandermeer, J. and Perfecto, I. (1997) The agroecosystem: a need for the conservation biologist's lens. *Conserv. Biol.* 11: 591–592.

Wenny, D. G., DeVault, T. L., Johnson, M. D., Kelly, D., Sekercioglu, C. H., Tomback, D. F. and Whelan, C. J. (2011) The need to quantify ecosystem services provided by birds. *The Auk* 128: 1–14.