

THE EFFECT OF SHADE TREE SPECIES ON BIRD COMMUNITIES IN CENTRAL KENYAN COFFEE FARMS

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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, and that insectivorous birds have the potential to reduce insect pests, little work has investigated the effects of specific shade tree species on bird diversity, and the capacity for different tree species to help deliver ecosystem services. Previous studies in temperate regions have demonstrated that due to shared evolutionary histories, native plant species are better at promoting native arthropod numbers, which in turn support a greater number of birds in an area. 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 understory under these shade trees were similar. In addition, both shade trees buffered temperatures in coffee, which could help slow the growth of insect pests, 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 promoting ecosystem services. Identifying differences in prey abundance and preferences in bird foraging behavior 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.

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, Mehrabi et al. 2018). 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* sp.) 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 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 higher diversity of economically important taxa such as birds. 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 coffee.

In all regions, the term shade coffee belies tremendous variation among and within farms that contain shade trees (Moguel and Toledo 1999). 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 several species of *Inga* in Mexico (Romero-Alvarado et al. 2000) and Jamaica (Johnson 2000a), *Erythrina poeppigiana* in Costa Rica (Perfecto and Vandermeer 2015), and *Grevillea robusta* in Kenya, Guatemala, Brazil, and India (Baggio et al. 1997, Muchiri 2004, Ambinakudige and Sathish 2009, Jha et al. 2011).

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. 2007, Pinard et al. 2014b). Surveying coffee farmers in Chiapas, Mexico, Soto-Pinto et al. (2007) found that farmers preferred perennial trees that grew quickly, had greater branch hardness and root strength, aided in soil fertilization through fast litter decomposition rates, and/or had moderate foliage density. 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 understory 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 understory 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, an observation also noted by Greenberg et al. (1997a) and Greenberg et al. (1997b) in Guatemala and Mexico, respectively. This follows ecological theory regarding insect coevolution with plants (Tallamy 2004). Insects adapt to evolutionarily novel plants slowly (Southwood et al. 1982), and coevolution with particular host plants is a strong driving force of species diversification and radiation for many insect taxa (Farrell and Mitter 1997, Becerra and Venable 1999). Most herbivorous insects specialize 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 specialization 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 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 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 (Pinard et al. 2014a, 2014b).

This study sought to investigate the influence of these two tree species on the avian community, with a special emphasis on insectivorous birds that may provide pest control services in Kenyan coffee. Native *Cordia* trees were hypothesized to offer more potential for pest control services in Kenyan coffee farms than non-native *Grevillea* because they attract more insectivorous birds that could act as a top-down control on pest populations. Specifically, the following predictions were tested: (1) Non-pest foliage arthropods are more abundant on *Cordia* than *Grevillea*, (2) insectivorous birds forage more in *Cordia* than in *Grevillea*, (3) insectivorous birds foraging in the shade layer also use the coffee understory (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 understory 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 coffee farms along an elevational gradient (1,567 - 1,874 m) in Kiambu County, Kenya from 16 December 2018 through 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 utilized within the shade farms, including acacias (*Acacia* sp.), broad-leaved croton (*Croton macrostaphylus*), Meru oak (*Vitex keniensis*), and Nandi flame (*Spathodea campanulate*), though the two most commonly used species are *Grevillea* and *Cordia*. Vegetation surveys among 41 coffee sites in central Kenya showed that *Grevillea* and *Cordia* comprised 36% and 27% all shade trees sampled, respectively (n = 850, Johnson et al. unpubl. data). Because of the focus on tree species selection, only shade farms with low total tree species diversity and a relatively even distribution of both *Grevillea* and *Cordia* were selected full sun farms were excluded from this study. Surveys were conducted on 6 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).

Field Methods

Arthropod, bird, vegetation, and temperature sampling was organized around individual shade trees at each study site. To select trees, a four-quadrant grid was overlaid on an aerial image of the site, recording the UTM coordinates for the center of each 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 minimize 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. In total, there were 333 trees (184 *Cordia* and 149 *Grevillea*) spread among the 6 farms for avian surveys, of which 146 (75 *Cordia* and 71 *Grevillea*) were also sampled for arthropods, and 72 (36 *Cordia* and 36 *Grevillea*) sampled with mist-nets. Basic vegetation data were recorded for all 333 trees, with more detailed data measured on the 146 trees also sampled for arthropods. Lastly, Maxim iButton temperature loggers were deployed under 12 of the trees (6 *Cordia* and 6 *Grevillea*, 1 per species per site) and at 6 locations nearby under no shade trees that acted as unshaded control samples (1 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

(Garedew et al. 2017). 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 (4 *Cordia*, 4 *Grevillea*, 3 unshaded control).

The branch clipping method described in Johnson (2000b) was used to sample arthropod communities. At each sampled tree, 2 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 2 branches per tree, some trees only had one sample-able branch, leading to an odd number of branches surveyed in total (147 *Cordia* branches and 136 *Grevillea* branches, for a total of 283 branches across all farms). After a branch was selected, the pole 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.

Avian surveys were conducted at the avian observation points from 0600-1000 h 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 optimized 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 behaviors described in Remsen and Robinson (1981). If there were greater than 10 individuals of a species within a tree, observers estimated flock size to the nearest 5; 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 12 2.5 x 9 m, 30-mm mesh nets in the coffee layer under 12 of the survey trees at each site, with nets deployed so that half of the nets 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 5 hours for 3 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.

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 2 axes with a 50m 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 understory data were measured in a square 10x10 m plot directly adjacent to each

surveyed tree ($n = 146$). The number of coffee shrubs (stems) in each quadrant of the 10x10m plot was recorded, the percent 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 understory was recorded.

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 $\times 100$. 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 A), 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 B), but not 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 influence species richness or abundance (e.g., elevation).

GLMM with a Poisson distribution was used to examine the effects of vegetation variables on bird communities sampled by mist-nets in the crop layer. Smith et al. (2015) used Bayesian modeling to assess bird density in Kenyan coffee farms using very similar field procedures as in this study, and they found that a simple measure of number of captures was adequate as a relative measure of bird abundance. Therefore, 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, with tree species, height, canopy cover, dbh, coffee flowering score, and average percent understory 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 select top models and establish model weights (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 understory of each tree species from the foraging and banding data, respectively. Bray-Curtis dissimilarity distances were calculated between each tree community, 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*). 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 *Cordia*, while 682 individuals across 18 arthropod groups were detected on *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 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*, *Terpsiphone 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 for 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 more species, 1.61 more total birds, and 1.1 more foraging birds (Figure 3).

In total, 278 individuals of the same 19 insectivorous bird species were detected by mist-nets in the understory of shade farms. Average coffee flowering score, canopy cover, and understory cover were the top predictors for total relative abundance in the crop layer, whereas

average coffee flowering score and canopy cover were top predictors of species richness (Appendix C). 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 understory cover ($\beta = 0.006 \pm 0.003$, 95% CI = 0.0008, 0.013). Average coffee flowering score was negatively associated with species richness ($\beta = -0.899 \pm 0.241$, 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 D). Shade tree species was not strongly associated with bird abundance or richness sampled by mist-nets in the understory.

All 19 focal species were detected in the canopy of *Cordia*, 18 in the understory of *Cordia*, 12 in the canopy of *Grevillea*, and 17 in the understory of *Grevillea*, with 10 species detected in all 4 vegetation levels (Table 2). 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 E). In the ordination, a stress level of 0.141 was obtained at convergence, indicating good ordination goodness-of-fit. Pairwise PERMANOVA indicated that the bird community composition in the *Grevillea* canopy was significantly different from the *Cordia* canopy ($r^2 = 0.086$, $F = 6.437$, $p_{\text{adj}} = 0.006$, $df = 1$), the *Cordia* understory ($r^2 = 0.103$, $F = 7.857$, $p_{\text{adj}} = 0.006$, $df = 1$), and the *Grevillea* understory ($r^2 = 0.100$, $F = 7.185$, $p_{\text{adj}} = 0.006$, $df = 1$). 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* understory and *Grevillea* understory 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 unequal 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 F). Likewise, the minimum daily temperature was warmer under shade than in the unshaded 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, $P = 0.08$).

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 (Narango et al. 2019), and the implications for shade tree use for conservation and ecosystem services (Narango et al. 2018, Narango et al. 2019). As predicted by ecological theory (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 (*Phylloscopus trochilus*, Willow Warbler) accounted for 18% of all individual detections. In contrast, 12 of the focal insectivorous bird species were detected in *Grevillea*, and one species (*Zosterops kikuyuensis*, Kikuyu White-eye) 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 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 specialize 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 ~~non-pest~~ 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 behavior (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 2014).

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 (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 understory (64.7% species overlap), with several species detected in the *Grevillea* understory 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 suggest *Cordia* attracts greater numbers of insect-eating birds to both the canopy and 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). 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 et al. 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* sp.) 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 fiber, and were rarely seen actively foraging.

Cordia may be preferred by farmers for other reasons besides their attractiveness to insect-eating birds. *Cordia* are a generally wider canopied tree, 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, Jaramillo et al. 2011), and temperature data indicate 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 provide a greater windbreak than *Grevillea*, offering greater crop protection during rainy season storm events (J. Murithi, pers. comm.).

Research Priorities

The clear next step is to confirm that species detected in the crop understory 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 this study area, fecal samples were collected from birds captured in mist nets, and on-going molecular analysis will reveal diet compositions of insectivorous birds (Jedlicka et al., unpubl. data).

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 sub-tropical countries in Central and South America, Asia, and Africa, and the industry supports roughly 125 million people worldwide (Osario 2002, FAO 2016). With roughly 20% of the world's 10 million hectares 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 hectares of land are harvested for coffee, and the industry supports about 5 million people within these areas (KALRO 2015). 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. Few studies have been conducted on coffee 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.

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Figure Captions

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

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.

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.

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 Understory-*Grevillea* (adj- $p = 0.006$). Ellipses represent 95% CI around the centroids of each community.

Tables

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	Log_e(L)^b	AIC_c^c	ΔAIC_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

^aNumber of parameters

^bLog_e(likelihood)

^cAkaike's Information Criterion corrected for small sample size

^dDifference between AIC_c and top model AIC_c

^eAIC_c weight

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.

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

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

^aNumber of parameters

^bLog_e(likelihood)

^cAkaike's Information Criterion corrected for small sample size

^dDifference between AIC_c and top model AIC_c

^eAIC_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

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	R²	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 ($p_{adj} < 0.05$)