



Original research article

Bird communities in sun and shade coffee farms in Kenya



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ABSTRACT

Agricultural expansion to meet rising crop demand is one of the greatest threats to terrestrial biodiversity. Coffee, one of the most valuable trade items in tropical countries, can provide both economic livelihood and wildlife habitat. Previous work, conducted primarily on Neotropical coffee farms, indicates that birds are generally more abundant and diverse in farms with a canopy of shade trees, though regional variation exists. To date, few studies have examined birds on coffee farms in Africa, which contains 20% of the world's coffee acreage. We studied differences in the bird communities between sun and shade monoculture coffee in central Kenya, and we examined effects of vegetation on bird abundance and diversity. Sun coffee had higher species richness and abundances of all major guilds (omnivores, insectivores, and granivores), and showed low community similarity to shade. Unlike findings from the Neotropics, canopy cover appeared to have a negative influence on all guilds, while understory volume of weeds increased bird abundance and species richness with a similar magnitude as canopy cover. These differences highlight the need for further studies in the general East Africa region with a wider variety of shade coffee systems.

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1. Introduction

Agriculture is one of the greatest threats to biodiversity (Foley et al., 2005, 2011; Gotelli and Ellison, 2013), especially in the tropics, where it is the leading cause of deforestation (Donald, 2004; Geist and Lambin, 2002). Agriculture, including cropland and permanent pasture, currently occupies nearly 40% of the earth's land surface (Ramankutty et al., 2008; World Bank, 2012) and production may need to increase up to 100% by 2050 to meet expected global food demand (Tilman et al., 2011). Identifying strategies to minimize the loss of biodiversity while maximizing agricultural yield is clearly one of the most pressing needs for conservation (Fischer et al., 2008).

Coffee (*Coffea* sp.) is one of the most valuable legally-traded commodities for developing countries (Donald, 2004; O'Brien and Kinnaird, 2003). Cultivated on more than 10 million hectares worldwide (FAO, 2012), typically in forested tropical regions with high biodiversity, coffee significantly influences global biodiversity (Donald, 2004; Mittermeier et al., 1998; Moguel and Toledo, 1999). Coffee is traditionally grown under a canopy of shade trees (Donald, 2004). Empirical data suggest yields may be maximized at intermediate amounts of shade (Soto-Pinto et al., 2000), but coffee is increasingly grown in full sunlight, a global trend driven in part by government incentives to promote agricultural intensification and use of agrochemicals to maximize short-term yields (Donald, 2004; Jha et al., 2014; Rice and Ward, 1996). Due to the expansion

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of sun coffee and its potential influence on tropical biodiversity, it is vital to understand the impacts of sun and shade management strategies.

Studies in the Neotropics and India suggest that bird communities in coffee are generally more diverse and abundant in shade coffee than in sun coffee, especially as cultivation intensifies (González, 1999; Gordon et al., 2007; Greenberg et al., 1997a; Petit and Petit, 2003; Wunderle and Latta, 1996). In a meta-analysis of studies in Latin America, Philpott et al. (2008) found that bird species richness tended to increase with greater habitat complexity, especially higher tree richness, tree density, canopy height, canopy cover, and canopy depth. However, coffee farms exhibit a range of variation in vegetation characteristics, making comparisons of bird communities and effects of vegetation between sun and shade inconsistent and region-specific (Anand et al., 2008; Greenberg et al., 1997b; Mas and Dietsch, 2004; Rao, 2011). Furthermore, the simple label “shade coffee” belies variation in vegetation complexity that can affect bird abundance and diversity among shaded farms (Calvo and Blake, 1998; Moguel and Toledo, 1999; Philpott et al., 2008).

Although bird diversity and abundance in coffee is well studied in the Neotropics and India (Anand et al., 2008; Donald, 2004; Komar, 2006; Philpott et al., 2008; Raman, 2006), there are few studies of bird communities on African coffee farms (Buechley et al., 2015; Gove et al., 2008). Despite the lack of focus on this region, approximately 20% of the world’s 10 million hectares of coffee occur in Africa, and coffee is a leading agricultural export in the East African nations of Ethiopia, Tanzania, and Kenya (FAO, 2012). Bird communities may respond to shade and sun coffee in Africa much as they do in the Neotropics or India. However, regional species pools and the phylogeographic processes, including disturbance history, responsible for creating communities vary between Africa and the Neotropics (Handbook of the Birds of the World Alive, 2014; Jetz et al., 2012) providing an expectation that responses to agricultural disturbance may vary between the two regions.

In East Africa, bird species richness can actually be higher in mixed agriculture than forests, demonstrating the importance of agriculture to birds in this landscape (Buechley et al., 2015; Mulwa et al., 2012). Studies across a variety of agricultural land uses have found that tree density and number of indigenous trees, crop diversity, hedge volume, overall increases in structural diversity, and nearest intact forest all can influence species richness and density in East Africa (Gove et al., 2008; Mulwa et al., 2012; Naidoo, 2004; Otieno et al., 2011). This variety highlights that vegetation factors influencing bird abundance and species richness may vary between crops and habitats, emphasizing the need for coffee-specific research.

Only a small percentage of land in East Africa is protected by parks (Norton-Griffiths et al., 2010; Western et al., 2009), and effective conservation of biodiversity in this region likely needs to involve agricultural landscapes, including coffee. One way to integrate crop production and conservation is to examine the ecosystem services provided by wild species (MEA, 2005; Swift et al., 2004). In the Neotropics, pest removal services and higher coffee yields have been linked to higher bird abundance and species richness on coffee farms (Kellermann et al., 2008; Perfecto et al., 2004; Philpott et al., 2009; Van Bael et al., 2008; Railsback and Johnson, 2014), and understory insectivores and omnivores appear especially important (Greenberg et al., 2000; Johnson et al., 2010; Karp et al., 2013). Similarly, in East Africa, birds increased coffee yield by 9%, though the mechanisms remain unclear (Classen et al., 2014). We investigated the hypothesis that in central Kenya, shade coffee cultivation supports higher bird diversity and abundance than sun coffee. Specifically, we tested the predictions that: (1) shade coffee has higher abundance, species richness, and evenness than sun coffee and these communities show low similarity and (2) bird abundance and species richness correlate positively with canopy cover and other measures of farm vegetation complexity.

2. Methods

2.1. Study site

We conducted this study in Nyeri County, Kenya (elevation 1700 m), which averages 208 people/km², of whom 24.5% live in urban areas, primarily in the city of Nyeri (population 120,000; USAID, Kenya and Kenya Bureau of Statistics, 2012). The surrounding landscape has seen a 30%–60% increase of agricultural area from 1975 to 2000 (Brink and Eva, 2009). Locally, coffee is grown on large plantations, where practices on both shade and sun coffee farm plantations include spraying copper as a fungicide (one or two times per year), spot spraying bushes or blocks of coffee with insecticides when pest infestations occur, and either bi-yearly application of herbicides (usually during the rainy seasons, May–June and Nov–Dec) or, more rarely, manual cutting.

This research took place over two years during Dec 2012–Jan 2013 and Dec 2013–Jan 2014 on a total of 21 sites located on five individual farms. Farms were large (>100 ha), and multiple sites were located within each farm, each separated by >250 m and roads and/or hedgerows. Sites were therefore defined as sampling locations located ≥250 m apart, with different management conditions or histories (such as age or density of trees and frequency of herb layer cutting) from nearby sites (Fig. 1).

Observers sampled four sun coffee sites the first year, and seven sun and 10 shade sites the second year, totaling 11 sun sites (on four different farms) and 10 shade sites (on three separate farms). Seven shade sites were located on Sasini farm (210 ha), which borders Aberdares National Park and had shade trees dominated by non-native *Grevillea robusta*. The remaining three shade sites included two with shade dominated by large native *Cordia* sp. (Kihuri Farm: 19 ha) and one with a high diversity of native trees including *Albizia gummifera*, *Albizia schimperiana*, *Croton macrocarpa*, and *Bridelia micrantha* (Jungle Farm: 51 ha; Najma, 2011). Canopy cover over shade sites averaged 38%. Six sun sites were on the coffee farm at

Dedan Kimathi University of Technology (120 ha), with four sampled the first year and two the second year. Three additional sun sites were located on Hill Farm (334 ha), one on Jungle Farm, and one on Sasini Farm. Sun sites had no shade except for sparse short trees and narrow bands of trees (primarily *Grevillea robusta* and *Cordia* sp.) on field margins. Understory height varied from about 0 to 0.3 m high, and was substantially higher only on sites that had not been recently sprayed or manually cut, suggesting management practices drive these differences. Understory plants in both shade and sun farms were similar, including (from most common to least) *Bidens pilosa*, *Oxygonum sinuatum*, *Commelina bengalensis*, *Amaranthus hybridus*, *Brassica rapus*, and *Galium* spp.

2.2. Bird sampling and guild classification

To quantify the bird community, we used mist nets to sample birds found in the crop layer. We focused mostly on birds using the crop layer primarily because these birds are of particular interest in Neotropical coffee, where they often provide significant pest removal services, and are therefore of special interest to local farmers and other coffee researchers. Additionally, understory birds, specifically insectivores are a sensitive group that include many vulnerable species (e.g. Şekercioğlu et al., 2002; Stouffer and Bierregaard, 1995) that are often eliminated by shade coffee development (Komar, 2006). We did not use point counts because they often miss secretive, quiet birds that may be less visible in thick coffee agriculture (Blake and Loiselle, 2001; Ralph and Dunn, 2004; Wang and Finch, 2002). Mist-nets infrequently capture species that forage high in the air, such as aerial insectivores or raptors (Karr, 1981), but are regarded as an effective method for sampling the majority of the bird community in coffee (Buechley et al., 2015; Chandler et al., 2013). Nonetheless, different species likely exhibit different probabilities of being captured, so we also analyzed our data to account for imperfect detection probabilities (Chandler et al., 2013 see below). Each site was sampled for three consecutive days, roughly from 06:00 to 10:00, depending on weather. We identified captured birds to species (taxonomy based on Zimmerman et al., 1999) and age or sex if possible, fitted each with a metal leg band supplied by the National Museums of Kenya, and recorded basic morphometrics (including wing chord, weight, tarsus length, and bill depth, width, and length). Nets within sun and shade sites were >25 m from farm edges, and consisted of two lanes (100 m apart) each with four (2012–2013) or six nets (2013–2015).

To investigate whether guild composition differed between sun and shade coffee, we classified birds into guilds (i.e., insectivore, granivore, frugivore, nectarivore, or omnivore) based on the first and second major diet preferences following Kissling et al. (2007). We then re-classified 12 species (mostly Sunbirds: *Nectariniidae* to either nectarivores or omnivores) based on our own foraging observations and published data from East Africa (Borghesio and Laiolo, 2004; Ndang'ang'a et al., 2013). Birds were also classified by their association with forest habitat and migratory status (Bennun et al., 1996; Handbook of the Birds of the World Alive, 2014). Each species association with forests fell into three categories. Forest specialist species are those characteristic of the interior of undisturbed forests, forest generalists occur in undisturbed forests or secondary forest edges/fragments, and forest visitors are often recorded in forest but not dependent upon it (Bennun et al., 1996).

2.3. Vegetation sampling

To investigate the effects of vegetation characteristics on the bird community, we measured vegetation variables within the coffee and shade layer using 10 m diameter circular plots centered on each net location. Within the coffee layer, we estimated percent coffee (the proportion of the sample plot covered by coffee bushes), and percent cover and height of the weedy understory (height < 1.5 m) and midstory (height 1.5–5 m). Volume of midstory and understory were calculated for each net by multiplying average vegetation height by area covered within the plot. Shade tree variables included: canopy cover (measured using a densiometer), an estimate of shade tree density using point-quarter methods (Krebs, 1989), and distance to the nearest tree (using a range finder) in each quadrant, along with its total height, average canopy depth (measured from top of the tree to the first large patch of canopy nearest the ground), and average trunk height (total height minus canopy depth) using a clinometer. A tree was defined as a woody, non-coffee plant greater than 5 m tall. We identified tree species using field guides (Najma, 2011) and consulted with Professor David Muchiri from Dedan Kimathi University of Technology. We calculated the Shannon–Wiener index (H') for shade tree diversity (Gotelli and Ellison, 2013) at each lane, using only trees within 25 m of plots and excluding trees from forest fragments. Point-quarter methods were used for the second year (Krebs, 1989). Because the first year only recorded the single nearest tree within vegetation plots, we calculated the number of trees within 25 m as a quarter of the total trees within 50 m, and estimated the proportions of each species (only two were observed) based on their relative frequencies.

2.4. Analysis

2.4.1. Variable selection

We used a Bayesian state-space approach to estimate the differences in bird communities between sun and shade sites and to examine the effects of vegetation on bird communities while accounting for imperfect detection probability of mist nets. However, because of the difficulty of performing model selection using a Bayesian framework

(Royle and Dorazio, 2008), we first conducted a model selection exercise using GLMM with Poisson error distributions to identify which of the eight vegetation covariates had the strongest association with bird relative abundance. These analyses were performed at the site and lane level because the probability of capturing a bird was extremely variable at a net level. We ran two groups of GLMM analyses, one using lane nested within site and a second using site as a random effects to investigate which vegetation covariates were most important and whether results differed when lanes were not considered for analysis (preliminary analysis indicated some lanes within a single site differed substantially in abundance). Due to differences in net hours (our measure of effort) between years, year was included as a fixed effect in GLMM models. Response variables included total abundance, species richness, and abundance of omnivores, granivores, and insectivores. Because only two frugivore and three nectarivore species were caught, totaling about 30 individuals for each, we did not specifically analyze these guilds, though these individuals were included in analyses of species richness and total abundance. Similarly, too few migrants and birds associated with forests (which are often of special interest for conservation) were caught to merit in-depth analyses on these groups. Preliminary analyses suggested all vegetation variables were collinear with coffee type (sun or shade); the category of shade or sun coffee was therefore added to the GLMM final candidate model set, involving no other vegetation covariates.

We first used Pearson product-moment correlation coefficients (r) along with variance inflation factors (VIF) to investigate collinearity between variables. Variables with correlation coefficients > 0.80 or VIF numbers > 5 were not used together in the same model (Craney and Surles, 2002; Mason and Perreault, 1991; O'Brien, 2007). We performed two methods for variable selection, both using single vegetation covariates in GLMM models using the lme4 package in Program R (R Core Team, 2012) (1.1–7). We first ranked the eight vegetation covariates using a single-variable model set using AICc values, then calculated marginal R^2 values for each model (following methods described by Nakagawa and Schielzeth, 2013) to select variables to include in the candidate model set. We generally selected variables with both AICc $w_i > 0.10$ (Burnham and Anderson, 2002), and the 3–4 highest R^2 values, or used a single variable if it had most of the model weight and explained a much higher proportion of variance compared with other variables. We then created our final candidate model set using these variables independently and in combination, also including a variable (1|Unit) to estimate overdispersion (Kéry, 2010), and including lane nested within site as a random effect for the net lane analyses. When model selection uncertainty was high for the final candidate model set, we assumed an effect was influential if its model-averaged 95% confidence intervals did not overlap zero (Burnham and Anderson, 2002).

2.4.2. Shade–sun analysis

We followed methods for a removal model using a Bayesian framework as described by Chandler et al. (2013), using a hierarchical model that separated the detection process (i.e. detection probability) from the state process (i.e. underlying abundance). The detection process was modeled using a removal model, which assumed population closure and constant probability of removal (i.e. new capture; Chandler et al., 2013; Pollock, 1991) over the three days each site was sampled. Preliminary analysis suggested that the number of new captures declined over the three days of sampling, confirming a primary assumption of this approach.

Following Chandler et al. (2013), the detection process was modeled by defining capture probability as a logit-transformed linear function of each species (i) at each site (j):

$$\text{Logit}(p_{ij}) = \alpha_0 + \alpha_1 \times \text{Year}_j$$

where p is a different capture probability for each species (i) at each site (j), α_0 is a species-specific intercept, and α_1 is a coefficient representing the effect of year (Year_j). The parameter α_0 was assumed to be a normally distributed random variable with mean μ and variance σ . Within each site, cumulative net hours varied little across occasions (1, 2 and 3) in a single year (mean and SD of day 1, 2 and 3 from 2012: 29.8 and 1.58, 29.9 and 1.88, 29.75 and 1.08 and 2013: 48.9 and 2.29, 49.7 and 1.24, 48.7 and 1.24). However eight nets were used in 2012 and 12 were used in 2013, making effort different between years; the effect of Year_j was thus used to take into account this discrepancy. See Appendix A for full model details.

The state process, which described variance in abundance among sites, was defined as a Poisson-distributed variable with mean λ_{ij} , which was a linear function of two vegetation covariates (Veg1 and Veg2, or understory volume and canopy cover respectively) measured for each site (j):

$$\text{Log}(\lambda_{ij}) = \beta_0 + \beta_1 \times \text{Veg1}_j + \beta_2 \times \text{Veg2}_j$$

where β_0 is a species specific intercept, and β_1 and β_2 are species-specific coefficients for the effects of vegetation. Each species-specific beta parameter (i.e. β_1) was assumed to be a variate sampled from a normal distribution with a mean μ and variance σ .

To assess abundance and diversity differences in sun and shade coffee, we categorized abundance of each species at each site (N_{ij}), first into their respective guilds, then further into whether the site was in sun or shade coffee. We used abundance per site as a unit because number of shade and sun sites differed. Species richness was calculated by assuming any species with estimated abundance ≥ 1 was present and summing across each iteration to estimate total number of species present (per site). To investigate whether shade and sun coffee had similar evenness, we calculated Shannon–Wiener diversity indices (H') in two ways: for each site independently, and for results of all sites pooled within either shade or sun categories (Gotelli and Ellison, 2013). We used two methods because pooling results can mask site-specific variation. To assess the community similarity between sun and shade sites, we calculated the abundance-based Chao–Jaccard similarity

index (Chao et al., 2005), using the number of individuals at each site (from the means of posteriors from N_{ij}) and program EstimateS (9.1.0, Colwell, 2013). This assumed all sites came from a larger community, from which 210 site comparisons between every sun and shade site were made, with the mean of these comparisons reported (Colwell, 2013). The mean of comparisons made just among shade sites and just among sun sites was also calculated to determine how similar sites within each community were to each other (Colwell, 2013). Lastly, we calculated a correlation coefficient (r) for the removal model output against the raw data for abundance of each species at each site to examine if raw data served as a useful index of abundance.

To assess the effects of vegetation on bird communities, we created four management scenarios to test effects of the most important vegetation covariates, canopy cover and understory volume (see Results for variable selection justification), on bird abundance. We examined scenarios using all four combinations of high and low values for each of these two vegetation variables. We used standardized covariate values for canopy cover and understory volume we observed on the landscape to create scenarios relevant to farmers. Six study sites (all in sun coffee at Dedan Kimathi University) showed much higher understory volume than others (mean 26.6 vs. 2.6 m³ per plot, which corresponds to the equivalent of a uniform understory cover of 33 cm vs. 3 cm in height, respectively). These were used to create categories of “high” and “low” understory volume, which, along with average canopy cover at shade (high value; 38%) and sun sites (low value; 3%), were used in combination to create these four scenarios. We included abundance of granivores, insectivores, omnivores, and combined totals (per site) as response variables for each scenario. Finally, to investigate whether each guild was affected differently by understory volume or canopy cover, we averaged each vegetation variable’s slope for all species within a given guild, and calculated 95% credible intervals of these estimates.

Although all “high” understory volume in this study was found on sun farms, high understory volume can be found in shade coffee, as evidenced by an understory volume of 27.3 m³ per plot on a farm measured during pilot work for this project (C. Wendt, unpublished data). Because all sites with high understory volume were located in sun farms, it was possible the effect of understory volume would be disproportionately expressed in sun coffee, and thus we excluded these six sites and conducted the analysis again to test whether their exclusion would change the direction of effects for understory volume and canopy cover.

We used a Gibbs sampler (R package rjags 3–13, linked to JAGS 3.4.0) to generate an approximation of the posterior probability distribution of model parameters. Vague uniform or normal priors were used for all model parameters (Kéry, 2010). We assessed convergence and analyzed Markov Chain Monte Carlo (MCMC) chains produced by JAGS using R packages coda (version 0.16–1) and sirt (version 0.47–36). The complicated vegetation model was run for 3 million burn-in iterations, with 3 chains sampled 50,000 times (thinned every tenth iteration), totaling 15,000 pooled iterations. We used the Gelman–Rubin statistic and manual inspection of trace plots of the MCMC chains to assess convergence, considering sets of chains with values under 1.10 and with no trends across trace plots as converged (Gelman and Rubin, 1992). The probabilities that the differences were greater than zero are reported as posterior p -values (Chandler et al., 2013), (Meng, 1994).

3. Results

In a total of 2861 net hours, we captured 2026 birds of 83 species, including 991 omnivores (24 spp.), 604 granivores (19 spp.), 373 insectivores (35 spp.), 33 nectarivores (three spp.), and 25 frugivores (two spp.). We caught 24 forest visitor species, 12 forest generalists, and two forest specialist species (Bennun et al., 1996, Appendix B). Of these, only four forest generalist species and one forest specialist species had >8 total captures (forest generalists: 177 in sun and 118 in shade coffee; forest specialists: 17 in sun and one in shade coffee). A total of seven migrant species were caught, accounting for 11% of raw captures (Appendix B). Overall, the hierarchical model estimated mean abundances per site of 130 omnivores, 133 granivores, 71 insectivores, four frugivores, and 10 nectarivores; estimated migrant abundance was 33.7 individuals per site.

3.1. Variable selection for shade–sun analysis

Based on the model selection process, the most important covariates influencing total abundance, species richness, and abundance of omnivores, granivores, and insectivores were similar at both the lane and site level. We therefore chose to use site as the independent unit to maximize the numbers of captures within each sample unit for easier parameter estimation. Understory volume was influential for nearly every response variable. Canopy cover and tree density also showed model averaged 95% confidence intervals that did not overlap zero (or barely did) for omnivores and insectivores respectively. As these two variables were nearly collinear and represent similar measures of habitat, we chose to focus on canopy cover as a core covariate because of its ease of measurement, interpretation, and intuitive association with sun versus shade coffee. Midstory volume was also influential for three response variables at the lane level. However, as it was nearly collinear with and represented similar habitat measures as understory volume, we chose to only use the latter. Two other variables (canopy height and percent coffee) were also influential, but only for a single response variable each and with slopes that were not biologically relevant (e.g., an increase of 1 bird for 75% increase in coffee). Understory volume and canopy cover were therefore used as the primary covariates influencing bird communities.

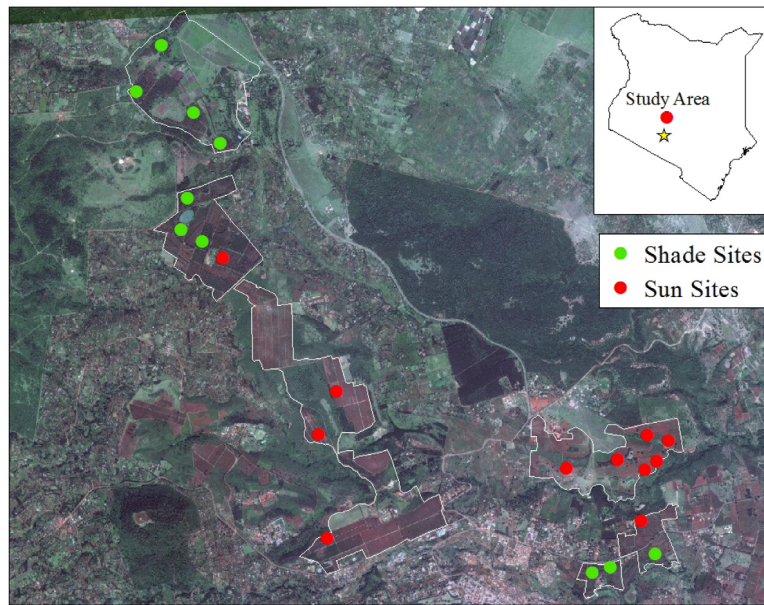


Fig. 1. Locations of the study sites with farm boundaries outlined in white. The inset shows location of our study area (red dot) in relation to Nairobi, Kenya (yellow star). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

Table 1

Species richness estimates and proportion of community per site for five feeding guilds in sun and shade coffee farms in central Kenya. Estimates are corrected for capture probability by the removal model, with means of posterior distributions presented here.

| | Omnivore | Granivore | Insectivore | Frugivore | Nectarivore |
|-------|------------|------------|-------------|-----------|-------------|
| Total | 12.1 (32%) | 9.1 (24%) | 14.8 (39%) | 0.7 (2%) | 1.6 (4%) |
| Shade | 8.1 (32%) | 5.6 (22%) | 10.3 (41%) | 0.4 (2%) | 1.1 (4%) |
| Sun | 15.8 (30%) | 14.8 (28%) | 18.9 (36%) | 0.9 (2%) | 2.1 (4%) |

3.2. Shade–sun analysis

Contrary to our predictions, estimates of bird abundance and species richness per site were generally greater in sun compared with shade coffee. The estimates of bird abundance in sun coffee were always higher compared to shade coffee: 6.8 times larger for omnivores, 10.6 times larger for granivores, and 3.3 times larger for insectivores (posterior $p > 0.99$ for all comparisons; Fig. 2). Species richness followed a similar pattern with richness in sun 1.95 times higher for omnivores, 2.66 times higher for granivores, and 1.82 times higher for insectivores compared with shade coffee; frugivores and nectarivores made up a relatively small proportion of both communities (Table 1). Sun coffee sites also contained 4.6 times more forest visitors, 2.3 more times forest generalists, and a similar amount of forest specialists compared to shade sites, although all three forest categories made up a higher proportion of the overall community caught in shade sites (Table 2). Communities were relatively similar in the proportion of species present for each guild, although granivores made up a slightly higher proportion in sun coffee and insectivores made up a slightly higher proportion in shade coffee (Table 1). However, the mean Chao–Jaccard similarity index between sun and shade coffee comparisons was 0.40, suggesting these two communities were relatively different. Additionally, similarity within sun sites (mean = 0.86) and within shade sites (mean = 0.84) was much higher, suggesting similar communities are found within each management type. Shannon–Wiener diversity indices for each site in sun and shade showed substantial overlap of evenness (Fig. 3), with a mean H' within shade sites of 2.83 and 3.07 in sun sites. Estimates from all sites pooled into sun and shade also showed little difference (posterior $p = 0.38$) in evenness. Lastly, we found the correlation coefficient of predicted bird abundance to raw capture data totals (excluding six high abundance outliers with high leverage) was relatively high ($r = 0.55$), suggesting that raw data provide a relatively good index of abundance in our study system.

The effect of vegetation on bird communities showed a surprising negative coefficient for canopy cover ($\beta_2 = -0.68$), and a similar but positive coefficient of understory volume ($\beta_1 = 0.72$) with 95% credible intervals of slopes that did not overlap zero. Similarly, the mean of all slope estimates for granivores ($\beta_1 = 0.96$, $\beta_2 = -0.71$), insectivores ($\beta_1 = 0.63$, $\beta_2 = -0.49$), and omnivores ($\beta_1 = 0.69$, $\beta_2 = -0.91$) suggested canopy cover and understory volume predicted relatively similar influences on all guilds (similar in magnitude, but in opposite directions), with no 95% credible intervals overlapping zero (Fig. 4). Under the four management scenarios we created using combinations of low and high amounts of canopy cover and understory volume, the model predicted substantial differences between nearly every scenario (most posterior p -values

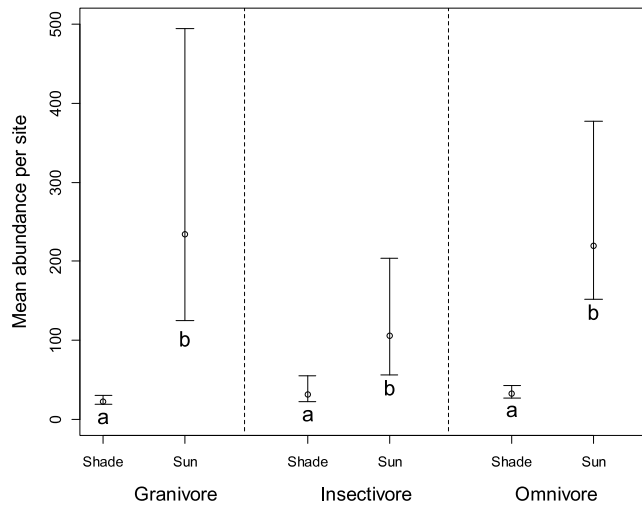


Fig. 2. Average abundance and 95% credible intervals of the three dominant bird guilds in coffee farms in central Kenya, showing abundance (corrected for capture probability) in shade and sun farms. Posterior p -values > 0.95 are indicated by different letters, compared within each guild.

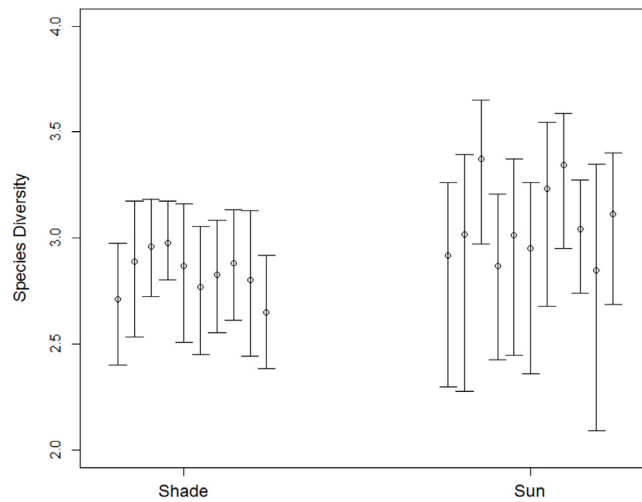


Fig. 3. Shannon–Wiener diversity index mean and 95% credible intervals for bird communities in 10 shade and 11 sun coffee sites in central Kenya, showing relative overlap of community evenness.

Table 2

Abundance estimates and proportion of community per site for sun and shade coffee farms in central Kenya for birds associated with forests, classified into 3 guilds. Estimates are corrected for capture probability by the removal model, with means of posterior distributions presented here. Several species were not classified because they do not use forests.

| | Forest visitor | Forest generalist | Forest specialist |
|-------|----------------|-------------------|-------------------|
| Shade | 51.65 (57%) | 23.2 (25%) | 9.6 (11%) |
| Sun | 235.6 (40%) | 53.5 (9%) | 8.7 (1.5%) |

>0.95 , Fig. 5) for nearly all response variables (total abundance and numbers of omnivores, granivores, and insectivores). We consistently found the combination of low understory with high canopy cover had the fewest birds and high understory with low canopy cover had the most. Finally, results from the second analysis that excluded data from sites with unusually high understory volume revealed slopes with similar direction as the full analysis ($\beta_1 = 0.10$, $\beta_2 = -0.30$), suggesting our results were not driven by these particular sites.

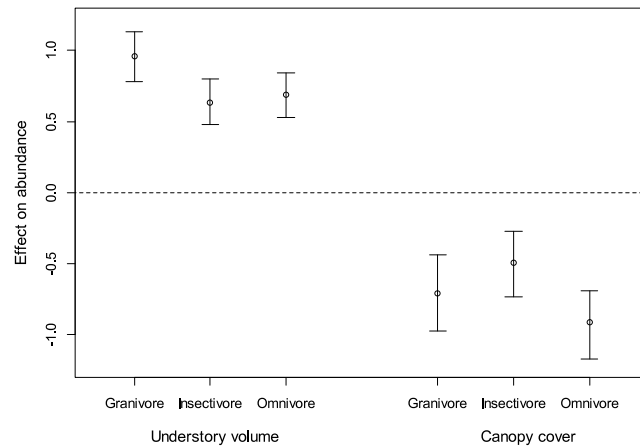


Fig. 4. Mean and 95% credible intervals of effects of understory volume and canopy cover on abundance of granivores, insectivores, and omnivores across all coffee sites. The variables were first standardized to make their effects comparable.

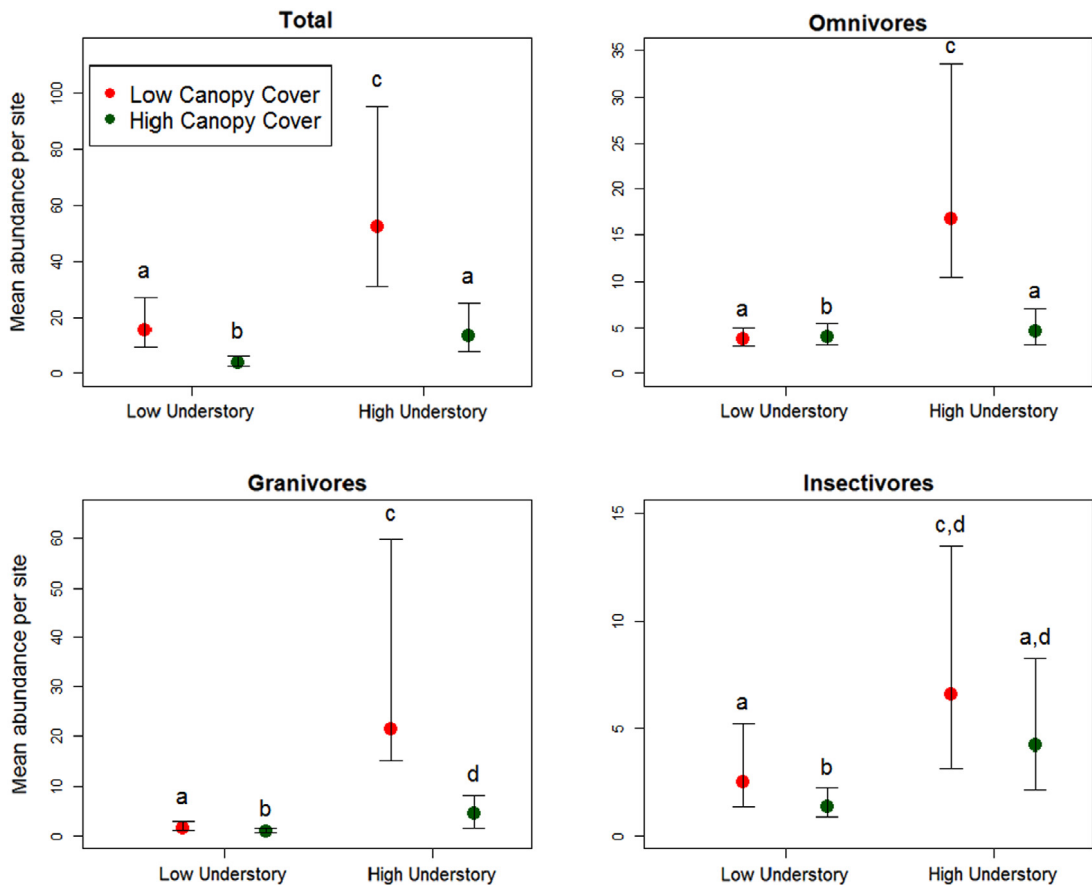


Fig. 5. Predicted values and 95% credible intervals of total abundance and abundance of granivores, insectivores, and omnivores per coffee site under 4 management scenarios as predicted by the removal model. The scenarios are combinations of low and high understory volume (2.6 m³ and 26.6 m³ per plot, respectively) and canopy cover (3% and 38%, respectively), using values observed on farms. Different letters indicate posterior *p*-values > 0.95.

4. Discussion

This is the first comparative study of bird communities in sun and shade coffee farms in East Africa, and our results did not follow patterns previously described in other regions. Unlike farms studied in the Neotropics and India, sun coffee in the central Kenyan highlands appears to support higher abundance and species richness than shade coffee. Shade and

sun sites had relatively similar evenness, but supported distinctly dissimilar species composition of birds. Communities were relatively similar in the proportion of species present for each guild, although granivores made up a slightly higher proportion in sun coffee and insectivores made up a slightly higher proportion in shade coffee. Studies in Neotropical shade coffee suggest overall species richness and total abundance consist primarily of omnivores and insectivores, with granivores making up <11% of species richness or abundance (Greenberg et al., 1997b; Komar, 2006; Tejada-Cruz and Sutherland, 2004). In contrast, granivores appear to make up a much larger proportion of the bird species richness (shade: 22% and sun: 28%) and abundance (shade: 25% and sun: 40%) in Kenyan coffee. In one of the few other studies from Africa, Buechley et al. (2015) also found high numbers of granivores in forest habitat (25%) and shade coffee (14%) in a similar afro-montane landscape in neighboring Ethiopia. Neotropical coffee farms are also renowned for their high abundance and richness of migrant species, especially in Central America, where Nearctic migrants may comprise nearly half of all individuals in birds in coffee (Greenberg et al., 1997b; Johnson, 2000; Leyequién et al., 2010; Wunderle, 1999). We only captured 7 migratory species, and after correcting for capture probability, our model estimated that migrants composed 10% of species richness and 7.7% of abundance per site.

Why do patterns of bird species richness and abundance in sun and shade coffee appear to be so different between Kenya and the Neotropics? A pool of species more associated with open habitats likely plays a role. Of all human-modified landscapes worldwide, granivore numbers are generally highest in open habitats with few trees (Tscharntke et al., 2008). Sub-Saharan Africa has the highest amount of grassland (defined as open habitats including savannah, shrubland and non-woody grassland) in the world: 14.46 million km² or ~60% of its area. In contrast, the Neotropics have few grasslands: the Caribbean and Central America have the lowest area of grasslands in the world (1.05 million km², or ~31% of its area), while South America has only slightly more (4.87 million km², or ~27% of its area) with the majority located in southern South America where little coffee is grown (White et al., 2000). It is possible that the higher proportion of granivores in our study (38% overall) compared to those in the Neotropics (<11%) reflects biogeographic differences in open habitat that over evolutionary time caused differences in guild abundance between these regions. Granivores worldwide may be 4–5 times more abundant in open agriculture than intact forest and agroforestry systems (Tscharntke et al., 2008), possibly also providing an explanation for the smaller-scale effect of higher numbers of granivores in sun than shade coffee. High numbers of granivores in sun coffee may also be associated with the weedy understory found in sun coffee, where weeds produce the seeds that are the primary food source for granivores.

Another explanation for the differences between our results and those from Neotropical coffee may come from regional differences in food availability for birds in shade canopies. In Neotropical coffee farms birds forage mostly in the canopy, with foraging in trees accounting for between 66% and 76% of total observations (Greenberg et al., 1997a; Jones et al., 2002; Komar, 2006; Wunderle and Latta, 1998). Arthropod numbers in Neotropical coffee studies can be higher in canopy trees than in coffee or adjacent forests (Greenberg et al., 2000; Johnson, 2000). It is possible that central Kenya has fewer arthropods in shade trees compared to the Neotropics, thereby making other substrates (such as the understory or ground) more important foraging habitats for birds. Arthropod samples from the dominant shade trees in our study system (*Cordia* sp. and *Grivellia robusta*) revealed low abundance and biomass that did not differ from the coffee layer (M. Milligan unpublished data). These observations suggest that shade trees on coffee farms in Kenya may provide less food (especially insects) compared to shade trees in the Neotropics, thus making other vegetation layers more important for foraging birds in this system. These patterns are especially important to farmers and coffee pest researchers because this may suggest that managing shade tree species and quantity of understory vegetation could affect bird abundance and richness, and therefore the pest removal services they deliver (Kellermann et al., 2008; Philpott et al., 2009). Additional sampling of arthropods and foraging observations are needed in coffee farms in East Africa to confirm or refute these possible explanations for bird abundance and species richness.

We also found that farm vegetation may drive the unexpected differences we documented between sun and shade coffee, with canopy cover and understory volume having opposing effects. Overall, canopy cover was negatively associated with bird abundance, while understory volume was positively associated with bird abundance. Bird abundance usually increases with increasing canopy cover (Philpott et al., 2008), although in India, increasing *G. robusta* (a species that also dominated some of our shade plantations) has been associated with lower bird abundance (Anand et al., 2008; Rao, 2011). Similarly novel, the strong effect of understory volume has rarely been documented in coffee literature as important (Komar, 2006), and was strong enough in our study that sun farms with low understory were predicted to have similar abundance as shade farms with high understory volume. Patterns of canopy cover and understory volume held for all major feeding guilds (granivore, omnivore, and insectivore), though there were some individual species that showed different patterns (e.g., several flycatchers were positively associated with canopy cover, and the common montane white-eye (*Zosterops poliogaster*) was negatively associated with understory volume).

Together, these data might be taken to suggest that sun coffee has higher conservation value than shade coffee in our study region. However, shade coffee supports a different bird community than sun coffee, specifically supporting higher abundance of many species that rely on canopy cover. Many species or genera within sun coffee are also abundant in other tree-less agricultural crops in East Africa (Mulwa et al., 2012; Ndang'ang'a et al., 2013). In Kenya, crops grown in relatively open agricultural fields represent the majority of agricultural land (FAO, 2012). Crops that are grown under a canopy of trees are relatively rare in Kenya (FAO, 2012). Given the increasing deforestation of the region and paucity of this habitat in agricultural landscapes, the conservation value of shade-coffee may therefore be substantially higher, given that species dependent on canopy structure may have less habitat on the landscape as a whole.

Likewise, increasing the quality of shade coffee may substantially increase its conservation value for bird communities. Our own study sites were predominantly comprised of low-diversity plantation scale shade coffee. In contrast, (Buechley et al., 2015), working in similar high elevation afro-montane forest habitat in the Ethiopian Highlands, found that diverse, small-scale shade coffee farms harbored species richness and abundances that rivaled those found in intact forest habitats. The bird community in Buechley et al. (2015) was notably different from what we found, with the proportion of forest generalists and forest visitors 4–5 times higher compared with our study. Additionally, their study found a higher proportion of insectivores (68%) and frugivores (17%) and fewer granivores (14%) than our study (although they did not classify omnivores as a guild), and migrants also made up a higher percentage (25%) of the bird community. Buechley et al. (2015) appear to have conducted their study on small (2–10 ha) shade sites with higher shade tree diversity and structure, consisting of primarily native trees. Their sites had relatively fewer *Cordia* and no *Grivellia* sp. (Hundera et al., 2013) while our shade sites which were dominated by these species; only 2 of our shade sites had similar tree composition. Carsan et al. (2013) also found many more tree species on the small-scale farms they studied in central Kenya compared to our plantation-scale sites. These results suggest that the quality of “shade coffee” habitat in East Africa may differ substantially based on farm scale, complexity, and/or region. Future research should examine a range of shade coffee farms in East Africa, as has been done in the Neotropics (Komar, 2006; Philpott et al., 2008).

Our estimates of bird communities are also based on mist nets, which inherently have detection biases for canopy bird species. If detection bias associated with this approach explained our results, then we would have found many more species that went completely undetected on shade farms than on sun farms. We believe this is likely not the case, based on more than 500 foraging observations (S. MacDonald unpublished data). Of the 53 species observed foraging in the shade canopy, only 10 (or 19%) were not caught in nets (8 of which were single observations) and a relatively similar fraction of species observed foraging in sun coffee were also not caught in nets (4 of 39 species, or 10%). Any species rarely caught (including canopy species) was also assigned a low capture probability by the removal model, with estimates of abundance and presence adjusted accordingly. Nonetheless, it is possible that capture probability differed between sun and shade habitat, such that a species found in both was rarely caught in sun but present in large numbers in the canopy of shade; this would in turn underestimate its abundance in shade habitat. It would be unrealistic to assume that mist nets sample canopy and understory species equally, and as such, we suggest our results that sun coffee higher species richness and abundance than shade coffee should be considered provisional until surveys that sample canopy birds more thoroughly (such as point counts) are done.

In conclusion, our study represents the first comparison of sun and shade coffee in East Africa, and we found many patterns contrary to a large body of coffee literature (Komar, 2006). Lack of additional research makes it difficult to draw conclusions about broad-scale patterns such as the value of sun and shade coffee habitats, habitat quality differences between shade coffee types, and reasons behind the high abundance of birds observed in sun coffee. However, Kenya, Uganda, and likely other East African countries are dominated by shade monocultures with low shade tree diversity (Jha et al., 2014), and roughly two thirds of species richness and 80% of our bird abundance was made up of species that range extensively throughout Sub-Saharan Africa (Handbook of the Birds of the World Alive, 2014), suggesting that patterns observed here may hold true for many other parts of Africa where shade coffee with low shade tree diversity is widespread.

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Appendix A. Supplementary data

Supplementary material related to this article can be found online at <http://dx.doi.org/10.1016/j.gecco.2015.09.004>.

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