SHADE TREES PRESERVE AVIAN INSECTIVORE BIODIVERSITY ON COFFEE FARMS IN A WARMING CLIMATE

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ABSTRACT

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Coffee is an important export in many developing countries, with a global annual trade value of \$100 billion. Climate change is projected to drastically reduce the area where coffee is able to be grown. Shade trees may mitigate the effects of climate change through temperature regulation for coffee growth, temperature regulation for pest control, and increase in pest-eating bird diversity. The impact of shade on bird diversity and microclimate on coffee farms has been studied extensively in the Neotropics, but there is a dearth of research in the Paleotropics. I examined the local effects of shade on bird presence and temperature on coffee farms in Kenya and then created regional Maxent models for avian insectivores in East Africa. I adjusted current and future Bioclim layers based on mean differences in temperatures between shade and sun on coffee farms. I then projected models into the future and onto adjusted temperature layers to predict the impact of shade tree removal on climatic suitability for avian insectivores. I found that avian insectivore richness is projected to decrease significantly in the future, as is avian insectivore climatic suitability and suitable area, but this can be mediated by shade trees on coffee farms. Temperature is not currently a limiting factor for avian insectivores on Kenyan coffee farms, indicating that bird presence is determined by site-level factors.

Future temperatures will become a regionally limiting factor for bird distribution in East Africa, but its effects can be potentially mediated through planting and maintaining shade trees on coffee farms.

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INTRODUCTION

Coffee is a crucial source of income for many developing countries, with 25 million people, largely smallholders, depending on its production for their livelihoods (Avelino et al. 2015, Bunn et al. 2015). Additionally, coffee is one of the most important global crops, is one of the most heavily traded global agricultural commodities and is a highly popular beverage consumed by approximately one-third of the world's population (Vega et al. 2003, Donald 2004, DaMatta et al. 2019). However, climate change is predicted to decrease global suitability for coffee growth by as much as 50% before 2050 (Moritz and Agudo 2013, Bunn et al. 2015, Rahn et al. 2018*b*). Climate change is expected to impact coffee production directly (i.e. through physiological response of coffee plants) and indirectly (i.e. through changing pest regimes) (Jaramillo et al. 2011, 2013, Bunn et al. 2015). Direct impacts are generally expected to be negative due to temperature sensitivity of the plants (Bunn et al. 2015, Magrach and Ghazoul 2015, Rahn et al. 2018*a*), although increased atmospheric CO² may mitigate these impacts through increased carbon fertilization (Rahn et al. 2018*b*, DaMatta et al. 2019, Verburg et al. 2019). However, a growing consensus indicates that increasingly negative impacts of coffee pests on production are primarily due to increased pest fecundity caused by warmer temperatures (Bale et al. 2002, Jaramillo et al. 2011, Magrach and Ghazoul 2015). It has been hypothesized that shade trees may mitigate the effects of a warming climate by lowering temperature and increasing humidity on coffee farms (Jha et al. 2014, Rahn et al. 2018*b*).

Coffee has been traditionally grown under a diverse canopy of native shade trees, but as management for higher short-term yields has intensified, the use of shade trees has decreased (Jha et al. 2014). Yet, the supposition that coffee grown without shade (sun coffee) provides higher quantity yields than shade coffee is unproven; in fact, recent research has reported that up to 50% shade cover on farms has a positive effect on coffee yields both in quantity and quality due both to temperature regulation and reduction of coffee pests (Soto-Pinto et al. 2000, Jha et al. 2014, Jonsson et al. 2015, Atallah et al. 2016, Meylan et al. 2017). Shade not only reduces coffee pests by lowering temperatures below pests' thermal optima, but it also contributes to pest control through increased predation by birds (Mäntylä et al. 2011, Kariuki Ndang'ang'a et al. 2013, Classen et al. 2014, Karp et al. 2014, Railsback and Johnson 2014, Nesper et al. 2017). Increased predation may be a function of overall bird abundance or diversity, although this link has been studied more thoroughly in the Neotropics than the Paleotropics (Perfecto et al. 2004, Johnson et al. 2009, 2010, Philpott and Bichier 2012, Classen et al. 2014). Because it has been determined that birds contribute to pest control, and that there are less pests in shade coffee, it can be theorized that, similar to in the Neotropics, greater bird diversity in shade coffee in the Paleotropics contributes to pest control (Classen et al. 2014, Smith et al. 2015, Milligan et al. 2016).

Eastern Africa is one of the few locations in the world projected to become more suitable for growing coffee in the future (Davis et al. 2012, Ovalle-Rivera et al. 2015). With an estimated 20% of the world's 10 million hectares of coffee, more research is needed in this location to predict the impacts of climate change on coffee (Global

Commodity Production Statistics 2016). Although there have been numerous studies on coffee pests, current and future coffee distribution, and effects of shade on coffee production in East Africa, there have been few studies to date on the current and future distribution of insectivorous bird species in East Africa, and how that distribution in relation to shade may affect coffee production (Jaramillo et al. 2011, Milligan et al. 2016, Rahn et al. 2018*b*, Ziska et al. 2018).

Research modeling current and future species distributions relies upon species distribution models, with Maxent (Maximum Entropy Modeling) among the most commonly used methods (Warren and Seifert 2011, Phillips et al. 2017, Yalcin and Leroux 2017). Species distribution models (also called environmental or ecological niche models, habitat suitability models, correlative distribution models, or climatic envelope models) use environmental data such as climate and land cover to predict regional climatic suitability for a given species. The resulting maps are often the basis for estimated species distributions. The theoretical underpinning for these models is that climate is an underlying factor in all coarse-scale species distributions, so climatic factors can serve as a proxy for more complex biotic and abiotic interactions, and thus can correctly predict species distributions on a regional scale (Guisan and Thuiller 2005). Over a large community of species, it is not feasible to measure specific biological impacts such as competition or predation, so species distribution models are especially useful in the face of climate change (Pearson and Dawson 2003).

Species distribution models are a valuable tool for determining current and future regional distributions of species based on climate but have limited ability to include the

effects of local microclimate factors, such as shade (Araujo and Pererson 2012, Naaf et al. 2013). Shade drastically impacts temperature and humidity on coffee farms, and thus may decrease a regional model's ability to predict local scale climatic suitability (Rapacciuolo et al. 2014, Evans et al. 2016, Garedew et al. 2017). The impact of shade trees on local climatic conditions may mediate current and future temperature and humidity extremes, preserving suitability for coffee and birds (Pearson and Dawson 2003, Buechley et al. 2015). Determining regional-level current and future species distributions of insectivorous birds is crucial for anticipating future climate effects on coffee yields. However, understanding bird diversity at a regional scale offers little guidance for individual landowners to manage pest reduction services on individual coffee farms. Planting and maintaining shade trees on coffee farms is one of the few management actions available to landowners to mitigate the impacts of climate change (Hirons et al. 2018, Ziska et al. 2018). Because of shade's importance for both coffee growth and bird abundance and diversity, it is important to determine the site-level impacts that shade will have on current and future insectivorous bird distributions. Understanding this relationship will be crucial in the future as temperature extremes become more common (Anwar et al. 2013).

In this study, I modeled regional current climatic suitability for a wide variety of avian insectivores that may contribute to pest control on coffee farms in East Africa. Suitability estimates were then compared to the presence of birds found on coffee farms in South Central Kenya to test whether climatic suitability at a regional scale was correlated with species-level detection at a local scale. Shade measurements from these

farms were used to determine the importance of shade level for local avian insectivore presence compared to modeled prediction of climatic suitability. I also estimated the microclimatic effects of shade trees on coffee farms. Finally, this study projected the regional suitability models into the future, focusing particularly on areas predicted to be suitable for coffee. I compared models with and without the mitigating effects of shade trees in order to evaluate the effects of climate change and shade trees on the important relationship between birds, shade, and coffee.

METHODS

Study Area

To assess large-scale insectivorous bird climatic suitability, I examined bird species distributions across northeast Africa including Kenya, Tanzania, Ethiopia, and Somalia. In this region, particularly Kenya and Ethiopia, coffee is generally cultivated in the highlands between 1300 and 2200 meters above sea level (Bunn et al. 2015). The geography of East Africa ranges from the deserts of eastern Ethiopia to the rainforests of Uganda. Mean annual rainfall varies from 400 mm to over 2500 mm. The region is broadly characterized by two distinct wet seasons, one between March and May ("long rains") and the other during October and November ("short rains").

To assess climatic suitability and richness on a local scale, I collected data from 41 coffee sites with varying shade levels in Kiambu and Muranga counties in Kenya across an elevation gradient from 1450 to 1950 meters [\(Figure 1\)](#page-15-0). Kiambu and Muranga counties are located north and east of Nairobi, Kenya between latitude 1°14'52''S to 0°56'83"'S and longitude $36°39'52''E$ to $37°41'79''E$. Together they cover 5100 km² and are characterized by warm sub-humid climate with annual rainfall from 900 to 1400 mm. An analysis of 82 years (1929 – 2011) of location-specific climate data demonstrated an average increase in temperature at an average rate of 0.005°C per year, matching IPCC estimates for Africa (Houghton et al. 2001, IPCC 2007). Agricultural land, composed of subsistence farming, ranching, and cash crops, predominates in the two counties (78.6 %, 4009 km^2), with coffee and tea as the two major cash crops

(County Government of Kiambu 2018, Murang'a County Development Planning Team 2018). Non-agricultural land consists of built-up land (residential, industrial, and urban), forest, bare land, and water (Njiru 2016, County Government of Kiambu 2018, Murang'a County Development Planning Team 2018). Shaded coffee farms in Kiambu and Muranga counties are relatively open and dominated by three species of quick-growing shade trees: *Grevillea robusta, Cordia africana,* and *Albizia sp.* (Schooler unpublished data, Carsan et al. 2013).

Figure 1. Study sites on coffee farms marked with asterisks in Kiambu County shown with location within Kenya. Thika town is labeled for reference.

Local Scale

To collect data on shade and avian insectivore presence, I surveyed 41 sites in Kiambu County, Kenya between 13 December 2017 and 22 January 2018 [\(Figure 1\)](#page-15-0). Some farms were large (>100 ha) and so multiple sites were located on each farm. Sites were defined as sampling locations with management conditions differing from nearby sites. A minimum of three and a maximum of seven survey points were randomly selected at each site depending on farm area. Points were set at least 50 meters from site edge and at least 150 meters away from other points [\(Appendix A\)](#page-58-0). Point selection was influenced by accessibility: if a point was deemed unsuitable (in a hedgerow or on a path) the point was adjusted 5 meters further away from the nearest point. Deflected points were still placed at least 50 meters from the farm edge.

One ten-minute fixed radius point count was conducted at each point to estimate insectivorous bird species presence (Ralph et al. 1993, Kenya 2016). Counts began approximately 15 minutes after local sunrise (approximately 0630) and were completed before 1100 hours. Birds were detected both by audio and visual cues. Every effort was made to avoid duplicate counting of individual birds. Surveys were conducted by two observers and one data recorder. All field work was conducted in accordance with Humboldt State University Institutional Animal Use and Care Committee approved protocol number 16/17.W.06-A. Tree density at each point was measured using the pointcenter-quarter method (Silva et al. 2017). Bird presence was summarized at the site level while tree density was averaged across the points for each site in order to obtain trees per hectare as a measure for average shade cover at each site.

I characterized microclimate differences in coffee bushes beneath shade trees and in full sun at each site using temperature loggers. Maxim iButton© temperature loggers ("iButtons") were mounted using 3M Command[©] strips on 2 mm thick white plastic cut approximately 3 by 4 cm squares with a 1 mm diameter hole drilled at the top. Loggers were then attached to coffee bush trunks below coffee bush tops averaging 2 m above ground using zip ties (Garedew et al. 2017). Loggers were deployed at the first point of data collection on each day at approximately 0630 hours. If shade trees were located within 50 m of the first point, a second temperature logger was placed underneath the closest shade tree. iButtons were set to collect data once per hour and collected data for approximately three months (until March 2018). They were collected by Kenyan collaborators in November 2018 and returned to Humboldt State University for analysis.

Regional Scale

The primary goal of this project was to model the current and future distributions of East African bird species which could consume coffee pests, and then compare modeled suitability to species presence from field surveys. To determine which bird species to model in East Africa, I used a subset of the bird species detected on coffee farms in this study as well as those identified in Smith et al. (2015). I selected bird species that may eat coffee pests through diet classification and length and weight classification (del Hoyo et al. 2018). Diet classifications included omnivores and insectivores, and bird measurements were used to identify species similar to those known to eat coffee pests in the Neotropics [\(Table 1\)](#page-19-0) (Johnson et al. 2010, Karp et al. 2013,

Martínez-Salinas et al. 2016, Sherry et al. 2016). I included any bird species with lengths \leq 25 cm and weights \leq 73.5 g. These values exceeded the maximum lengths and weights of Neotropical bird species found to eat coffee pests by 4 cm and 27.5 g respectively [\(Table 1,](#page-19-0) [Figure 2\)](#page-20-0). However, existing data are somewhat uncertain because they were collected from mist netting only. I therefore erred on the side of including birds that do not eat pests rather than excluding birds that may eat pests. The final list included 77 bird species from 20 families, with a length range from 9 cm to 25 cm (mean = 14.91) and a weight range from 7 g to 73.5 g (mean = 23.13) [\(Table 1,](#page-19-0) [Figure 2,](#page-20-0) [Appendix B\)](#page-59-0).

Species	Location		Length (cm)	Weight (g)		Reference
		Min	Max	Min	Max	
American Redstart	Jamaica	11	13	6.5	12	Sherry et al. 2016
Black-and-white Warbler	Jamaica	11	13	8.8	15.2	Sherry et al. 2016
Black-throated Blue Warbler	Jamaica	12	14	8.4	12.4	Sherry et al. 2016
Northern Parula	Jamaica	10.5	12	7.1	10.2	Sherry et al. 2016
Prairie Warbler	Jamaica	11	12	5.7	10.8	Sherry et al. 2016
Alder Flycatcher	Costa Rica	13	17	12	14	Martinez-Salinas et al 2016
House Wren	Costa Rica	11.5	12.5	8.9	14.2	Martinez-Salinas et al 2016
Common Tody-flycatcher	Costa Rica	8.8	10.2	4.4	8	Martinez-Salinas et al 2016
Buff-throated Foliage-gleaner	Costa Rica	18	19	30	46	Karp et al. 2013
Rufous-breasted Wren	Costa Rica	14	14	13.5	18.5	Karp et al. 2013
Rufous-capped Warbler	Costa Rica	13	13	7	16	Karp et al. 2013
White-tailed Emerald	Costa Rica	7.5	8	3.1	3.3	Karp et al. 2013

Table 1. Lengths and weights of neotropical birds determined to eat avian insectivores through gastric lavage or guano analysis with location of study and study reference.

Figure 2. Box plot of: length (A) and weight (B) of bird species included in this study (n $= 77$). Dashed lines show maximum and minimum lengths and weights of bird species found to eat coffee berry borer in the Neotropics, and dot-dashed lines indicate mean lengths and weights of bird species found to eat coffee berry borer in the Neotropics (Table 1) $(n = 12)$ (Karp et al. 2013, Martínez-Salinas et al. 2016, Sherry et al. 2016).

Following bird species selection, East Africa bird presence points for selected bird species collected after 1970 were downloaded from the Global Biodiversity Information Facility (GBIF) (GBIF.org 2018). Background points were randomly generated throughout East Africa (Ethiopia, Kenya, Somalia, and Tanzania). The number of background points generated was the same as the number of observed points for each species (Appendix C). Current (1970 – 2000 average) and future climate data was downloaded from WorldClim bioclimatic variables ("Bioclim") using the dismo package in R (Fick et al. 2017). For future climate projection, I analyzed both the most conservative and the most extreme climate scenarios of 2.6 and 8.5 representative concentration pathways respectively projected for 2075. I chose to use the climate model HadGEM2-AO because it has been shown to be an accurate future climate predictor models for East Africa (Onyutha et al. 2016). I included limited results for the 2.6

representative concentration pathway and expanded on results for the 8.5 representative concentration pathway to determine results for the most extreme scenario of climate change.

To minimize the risk of overfitting and aid in interpretation of model results, I selected nine out of nineteen possible Bioclim predictors based on biological underpinnings. The predictors used were: annual mean temperature, mean diurnal range, maximum temperature in the warmest month, minimum temperature in the coldest month, temperature annual range, annual precipitation, precipitation in the wettest month, precipitation in the driest month, and precipitation seasonality (coefficient of variation of monthly precipitation expressed as a percentage).

For each bird species, correlated predictors (threshold of Pearson correlation = 0.75) were removed by selecting the best-fitting predictor (using Akaike information criterion corrected for small sample size (AICc)) (Barbosa 2015). The best predictors from all combinations were determined through the r package enmSdm (Smith 2017). I tested five regularization parameters for each species: 0.5, 1, 1.5, 2, and 5 (Warren and Seifert 2011). Overall best predictors and regularization parameters were determined through AICc model selection. The best Maxent model for each bird species was projected for current climate and future climate.

To evaluate the ability of regional climatic models to distinguish avian insectivore presence on a local scale and to determine if a measure of local shade cover could improve predictions, avian insectivore habitat suitability was predicted at fine scales using logistic regression model selection (Johnson et al. 2004). The predicted variable

was whether the bird was found to be present during point counts at each site. The logistic regression predictors included Maxent suitability at each site and shade level (trees per hectare as determined by point-center-quarter method) at each site. To account for variable detection probability, I also included the total number of points at each site. Additionally, I added latitude and longitude of the site as predictors in order to control for site location. The best logistic model from all predictors was selected using AICc for each bird species individually, then the best overall predictors were summarized.

Projections

I then evaluated insectivorous bird species at a regional level using individual species distribution models. To estimate richness, each model of continuous suitability was thresholded to create areas of presence and absence. I used a threshold value based on equal errors in sensitivity (proportion of accurately predicted presences) and specificity (proportion of accurately predicted absences) for each bird species (Bean et al. 2012). Areas that had a suitability over the thresholded value were coded as the bird species being present. I examined mean suitability for avian insectivores and compared total thresholded suitable area for present and future climate models. I determined avian richness over East Africa by adding all thresholded layers together. I then calculated predicted bird richness on known locations of coffee farms determined from data for *Coffea arabica* and *Coffea robusta* locations from GBIF and from the International Center for Tropical Agriculture (CIAT) (Ovalle-Rivera et al. 2015). I extracted

thresholded predicted bird richness data for the projected climate scenarios at each coffee farm.

Finally, to characterize the mitigating impact of shade trees on local scale climate on coffee farms, I extracted mean monthly temperature, maximum monthly temperature, minimum monthly temperature, mean overall temperature, maximum overall temperature, and minimum overall temperature, and daily range from iButtons placed in sun and under shade trees on sites. The calculations used for monthly temperatures were the same as WorldClim temperature calculations (O'Donnell and Ignizio 2012, Fick et al. 2017). The mean, maximum, and minimum monthly values for sun and shade sites for all farms were compared to the mean, maximum, and minimum monthly temperatures from WorldClim data extracted from site locations (average over 1970-2000) for December, January, February and March (the months the iButtons were deployed). Since the mean temperature of WorldClim layers for December through March at our site locations was similar to temperatures observed on shade and less than temperatures observed on sun farms (see Results; [Table 2,](#page-26-0) [Figure 3\)](#page-27-1), I added the difference between sun and shade from the iButtons to temperature Bioclim layers maximum temperature of warmest month, minimum temperature of coldest month, and annual mean temperature for current and future (2075, 8.5 RCP) climates creating adjusted Bioclim layers. Models were then reprojected on adjusted Bioclim layers to simulate climatic conditions if shade trees were removed from coffee farms. I then conducted the same calculations of richness, suitability, and suitable area on adjusted climate layers as non-adjusted climate layers.

RESULTS

Local Scale

A total of 75 avian insectivore species were observed during point counts on sites. Two avian insectivores found by Smith et al. (2015) that have been previously sighted in Kiambu County (GBIF.org 2018) were not detected by our point count surveys: Redheaded Weaver (*Estrilda rhodopyga*) and Crimson-rumped Waxbill (*Anaplectes rubriceps*). The greatest number of bird species detected at a single site was 31, the fewest was 14, and mean bird richness at sites was 21 with a standard deviation of 5. Sites had a range of shade levels as measured by the point-center-quarter method, from a minimum of 0.01 trees per hectare to 123.46 trees per hectare with an average of 20.44 trees per hectare and a median of 16.40 (standard deviation = 31.71). There was low correlation between bird richness and shade trees per hectare in study sites (Pearson correlation $= 0.13$). Trees per hectare on sites was not a good predictor of bird richness (linear model, $\beta = 0.019$, $SE = 4.60$) nor was number of points surveyed at a given site (linear model, $\beta = 1.15$, $SE = 4.30$, Pearson correlation 0.37). The mean number of sites at which a species was detected was 11 sites [\(](#page-61-0)standard deviation $= 11$) (

[Appendix](#page-61-0) C). Two species were detected at all sites $(n = 41)$ (Common Bulbul (*Pycnonotus barbatus*) and Baglafecht Weaver (*Ploceus baglafecht*))[\(Appendix C\)](#page-62-0). Nine bird species were detected only at a single site [\(](#page-61-0)

[Appendix](#page-61-0) C). Number of observations in GBIF had a Pearson correlation of 0.40 with number of sites at which the bird species was observed.

In total, 19 out of 43 iButtons were recovered, with readable data on 16 loggers from 13 sites. Worldclim mean monthly temperature, maximum monthly temperature, and minimum monthly temperature averaged across the sites and months the iButtons were deployed differed from both sun and shade similarly-averaged iButton temperatures. The mean temperature from WorldClim was 0.32º C cooler than mean shaded temperature on sites and 0.98º C cooler than mean sun temperature on sites [\(Table](#page-26-0) [2,](#page-26-0) [Figure 3\)](#page-27-1). The maximum monthly WorldClim temperature was 2.37º C lower than the maximum monthly shade iButton temperature and 6.64º C lower than the maximum monthly sun iButton temperature [\(Table 2,](#page-26-0) [Figure 3\)](#page-27-1). The monthly minimum WorldClim temperature was 0.42º C lower than the minimum monthly shade iButton temperature and 0.17º C lower than the minimum monthly sun iButton temperature [\(Table 2,](#page-26-0) [Figure 3\)](#page-27-1).

Table 2. Extracted temperature values (°C) and 95% confidence intervals from data recorded by 16 iButtons placed under shade trees $(n = 7)$ and in sun $(n = 9)$ with corresponding WorldClim temperature values from 13 sites.

Value		Shade		Sun	WorldClim		
	Mean	95% CI	Mean	95% CI	Mean	95% CI	
Mean Monthly		20.17 19.53, 20.80 20.83 20.29, 21.37 19.85 19.65, 20.05					
Maximum Monthly		30.45 27.50, 33.40 34.72 31.72, 37.72 28.08 27.80, 28.36					
Minimum Monthly		12.67 11.77, 13.57 12.42 12.07, 12.76 12.25 12.09, 12.40					
Mean Overall		20.03 19.50, 20.56 20.79 20.28, 21.31					
Maximum Overall	34.57	30.51, 38.63 38.70 35.90, 41.50					
Minimum Overall	8.93	7.41,10.45 8.55		7.71, 9.38			
Daily Range	21.67	18.17, 25.16 26.21		23.40, 29.02			

Figure 3. Comparison of extracted temperature metrics of iButtons ($n = 17$ from 13 sites) placed in the sun versus iButtons placed in the shade compared with WorldClim layers for mean monthly temperature (A), maximum monthly temperature (B), and minimum monthly temperature (C).

Regional Scale

Of the 77 selected bird species, the minimum number of GBIF observations was 96 (*Bradornis pallidus*, Pale Flycatcher), the maximum was 27,498 (*Pycnonotus barbatus,* Common Bulbul), with a mean number of observations of 4,390 [\(Appendix C\)](#page-62-0). Overall, based on the 77 model selection processes run for each individual bird species, precipitation in the driest month and precipitation seasonality were selected in the best model for 85.7% of bird species, while minimum temperature in the coldest month was selected in the best model for only 5.2% of bird species [\(Table 3\)](#page-28-0). The best regularization parameter for all birds was selected as 0.5. Mean modeled climatic suitability for avian insectivores across all sites sampled in Kiambu County was 0.53 (CI 0.52, 0.54).

Predicted bird richness using sensitivity-specificity thresholding on all sites surveyed in

Kiambu County was 77 bird species.

Table 3. Percent of best Maxent models and number of bird species' $(n = 77)$ best Maxent models (selected by AICc out of all possible combinations of predictors) that included specified climactic predictors.

Predictor	Percent of Models	Number of Species
Precipitation Driest Month	85.7	66
Precipitation Seasonality	85.7	66
Annual Precipitation	70.1	54
Annual Mean Temperature	57.1	44
Temperature Annual Range	54.5	42
Maximum Temperature Warmest Month	35.1	27
Mean Diurnal Range	32.5	25
Precipitation Wettest Month	16.9	13
Mean Temperature Coldest Month	5.2	$\overline{4}$

Neither shade nor Maxent-predicted suitability were determined to be the most frequent best predictors in logistic models for bird species' presence on sites [\(Table 4\)](#page-29-0). Only six species' presence on sites was best predicted by shade levels only, and three species' presence was best predicted by Maxent suitability only. Longitude was the most common predictor in best logistic models, included in 49.3 percent of the models. Shade was included in 35.6 percent of the models, and Maxent suitability was included in 30.1 percent of the models. Two of the models failed to converge because the species were present at all sites. Two of the species were not included in logistic modeling because they were not observed on our point counts. Coefficients for shade and Maxent in birds that had those variables as best predictors varied widely between species (shade $n = 26$, mean $= -10.86$, standard deviation $= 41.51$, range $= -181.16 - 5.29$; Maxent n $= 22$, mean $= -5939.38$, standard deviation $= 20649.21$, range $= -66757.70 - 27209.22$), becoming especially extreme if the species was observed on few sites. For this reason, I removed bird species that were present on fewer than three sites to further examine trends in model coefficients (for species' that were present on greater than three sites: shade $n = 17$, mean $= -0.001$, standard deviation $= 0.11$, range $= -0.22 - 0.26$; Maxent n $= 22$, mean $= -34.30$, standard deviation =72.99, range = $-161.75 - 122.79$) [\(Figure 4\)](#page-30-0).

Table 4. Percent of best logistic models and number of bird species' $(n = 73)$ best logistic models (selected by AICc out of all possible combinations of predictors) including specified parameters. Shade was calculated as number of trees per hectare on sites, Maxent suitability values were the bird species' climatic suitability at a given site, and number of points were the number of points surveyed at that site.

Parameter	Percent of Models	Number of Species
Longitude	49.3	36
Number Pts	37.0	27
Shade	35.6	26
Maxent	30.1	22
Latitude	27.4	20
Null	13.7	10

Figure 4. Histograms of effect sizes for species with greater than three observations that: had shade as a predictor in their best models ($n = 17$)(A) and species' that had Maxent as a predictor in their best models $(n = 15)(B)$.

Projections

Suitability from Maxent projections was thresholded based on equal errors in sensitivity and specificity. The mean suitability threshold value across the 77 species was 0.24 (standard deviation $= 0.19$), with a maximum threshold value of 0.54, and a minimum of 0.08.

Given a representative concentration pathway of 8.5, biodiversity on coffee farms is projected to decrease from a mean of 73 bird species on East African coffee farms (95% CI 71.87, 73.43) to a mean of 49 bird species (95% CI 48.16, 50.98) for a RCP of 2.6 (95% CI 48.16, 50.98) and 41 bird species for an RCP of 8.5 (95% CI 39.92, 42.36) [\(Figure 5,](#page-32-0) [Figure 6\)](#page-33-0). Mean suitability for avian insectivores over all of East Africa is projected to decrease by 16.37 percent for a RCP of 2.6 and 33.24 percent for a RCP of 8.5 (Figure 6). Similarly, mean area suitable for avian insectivores is projected to decrease by 38.08 percent for a RCP of 2.6 and 51.25 percent for a RCP of 8.5 (calculated through area from thresholded suitability predictions) by 2075 [\(Figure 7\)](#page-34-0).

Using the differences in temperature observed using iButtons on coffee farms under shade and in sun, we projected climatic changes if all shade trees on coffee farms were removed immediately by adding the differences in temperature in sun and in shade on coffee farms to the corresponding Bioclim layers. We found that given estimated climatic changes if all shade trees were removed immediately, current projected richness of birds on coffee farms would decline from an average of 73 species to an average of 50 species solely based on changes in microclimate temperature (95% CI 48.49, 50.80) [\(Figure 5,](#page-32-0) [Figure 6\)](#page-33-0). Simulating the removal of all shade trees by 2075 (using an RCP of

8.5), projected bird richness decreases further to a mean of 35 bird species on each farm $(CI = 33.78, 36.10)$ [\(Figure 5,](#page-32-0) [Figure 6\)](#page-33-0). Additionally, using the 8.5 RCP climatic scenario and simulating the removal of shade trees by 2075 through adjusting temperatures of the Bioclim layers, mean suitable area is projected to decrease by 33.8 percent, and mean suitability is projected to decrease by 45.9 percent [\(Figure 7\)](#page-34-0).

Figure 5. Predicted bird richness across 201 East African coffee farms for current, shade tree removed current (adj. current), future, and shade tree removed future (adj. future) climate scenarios for 77 avian insectivores using sensitivity-specificity thresholding.

Figure 6. Predicted bird richness using thresholded suitability values for current climate conditions (A), current climate conditions adjusted if shade trees were removed on farms (B), future climate conditions (C) and future climate conditions adjusted if shade trees were removed on farms (D).

Figure 7. Comparison of projected mean climatic suitability (A) and projected mean climatically suitable area (B) (using sensitivity-specificity thresholding) in East Africa for current, shade tree removed current (adj. current), future, and shade tree removed future (adj. future) climate scenarios for 77 avian insectivores.

DISCUSSION

This study confirmed the impacts of climate change on species richness and climatically suitable area for East African avian insectivores (Walther 2010, Moritz and Agudo 2013). Specifically, our findings agreed with many other studies establishing that climate change is projected to decrease avian insectivore richness and areas that are climatically suitable for avian insectivores, even without accounting for habitat modification (Jetz et al. 2007, Tingley et al. 2009, Salas et al. 2017). However, the regional impacts of climate change may be mediated locally by the presence of shade. Not only have shade trees previously been found to increase biodiversity by providing structural habitat (Perfecto et al. 1996, Philpott and Bichier 2012, Jha et al. 2014, Buechley et al. 2015), but our study demonstrated that shade significantly lowers temperature on farms, and thus may mitigate the impact of climate change at a local level. It is clear that shade trees currently buffer extreme temperatures (Garedew et al. 2017), and the future effects of shade trees and their possible removal will become more critical for avian insectivores as well as for overall climatic suitability for coffee.

Although Kenya and East Africa generally will become one of the most suitable areas to produce coffee in the future (Bunn et al. 2015, Ovalle-Rivera et al. 2015), coffee plantations, especially at lower elevations, are undergoing wide-spread conversion to urban and suburban landscapes (Jaramillo et al. 2013). To the extent this rapid urbanization shift includes the removal of shade trees on coffee farms, it will have drastic implications on climate, microclimate, and projected bird richness (Philpott et al. 2008,

Rahn et al. 2014). Should urbanization continue, not only will bird richness decrease from habitat loss, but will be exasperated by the drastic changes in temperature from reduction of shade trees (Philpott et al. 2008, Buechley et al. 2015).

My results concur with a comparable study on coffee farms that found similar bird richness on shade and sun coffee farms in Kenya (Smith et al. 2015); this finding differs from some studies in the Neotropics on coffee farms (Greenberg et al. 1997, Kellermann et al. 2008, Railsback and Johnson 2014), but agrees with others (Philpott and Bichier 2012). It is possible that these mixed results are due to lack of accounting for shade tree species. Previous research has revealed that more complex canopies increase bird diversity (Johnson 2000, Philpott et al. 2008, Philpott and Bichier 2012). Smith et al. (2015) suggested that the similarity in bird richness between shade and sun coffee farms in Kenya is due to lack of shade tree diversity in East Africa, as contrasted with coffee farms in the Neotropics and in the Ethiopian highlands, where other studies have taken place (Greenberg et al. 1997, Moguel and Toledo 1999, Jha et al. 2014, Buechley et al. 2015). Our study concurs with these conclusions on a larger scale, given that the majority of shade trees planted on Kenyan coffee farms that we surveyed were limited to *Grevillea robusta*, *Cordia africana,* and *Albizia sp.*, thus lacking a diversity of shade trees found in other forms of shade coffee cultivation. (Moguel and Toledo 1999, Johnson et al. 2010, Karp et al. 2013, Schooler Unpublished Data)*.*

Bird diversity in the Neotropics has been directly linked to pest control services (Kellermann et al. 2008, Johnson et al. 2009, Martínez-Salinas et al. 2016), but the direct connection between bird diversity and pest control has yet to be established in the old-

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world tropics. Regardless of bird species richness, all findings agree that there are decreased pests and increased coffee yield on shaded coffee farms both in the Neo- and Paleotropics (Jaramillo et al. 2009, Nesper et al. 2017). Johnson et al. (2010) identified only five birds that consumed coffee berry borer in Jamaica: American Redstart (*Setophaga ruticilla*), Black-and-white Warbler (*Mniotilta varia*), Black-throated Blue Warbler (*Setophaga caerulescens*), Northern Parula (*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*) [\(Table 1\)](#page-19-0). A similar number of avian insectivores was found to consume pests in Costa Rica [\(Table 1\)](#page-19-0) (Karp et al. 2013, 2014, Martínez-Salinas et al. 2016, Sherry et al. 2016). It is therefore likely that a single abundant avian species or set of species could be responsible for pest removal on coffee farms in Kenya (Maas et al. 2015, Milligan et al. 2016). Anecdotal observations of birds foraging on coffee plants revealed that Willow Warblers (*Phylloscopus trochilus*), Yellow-Breasted Apalises (*Apalis flavida*), African Paradise Flycatchers (*Terpsiphone virdis*), and sunbirds (*Nectariniidae*) flew into the coffee layer and may forage there. White-eyes (*Zosterops abyssinicus* and *Zosterops kikuyuensis*) were observed foraging in the coffee layer multiple times (Schooler Unpublished Data, D. Kammerchs-Berke, pers. comm., 2019). It is therefore possible that these species may be primary pest-control agents for coffee pests, and further analysis should be done to examine whether they have higher presence and abundance in shade versus sun coffee. Additionally, my study did not take into account detection probability or bird abundance, which may be important factors in my findings. However, since detection probability is linked to abundance and abundance is difficult to estimate with location-replicate point counts, it is unclear whether including

detection probability without including abundance estimates in my models would have improved their accuracy (Martin et al. 2005). With the use of a double-observer approach, it is possible that the detection probability was relatively high (Nichols et al. 2000).

When I tested shade level as a predictor of bird species presence on coffee farm sites as compared to Maxent climatic suitability, number of points sampled on that site, and location in latitude and longitude, I did not find that either Maxent suitability or shade alone was a consistently strong predictor of bird species presence for many species. Although they were clearly contributing factors for some species, longitude (used as a proxy for site-based variation) was selected more frequently than shade. Because sitebased variation was selected more frequently as a best predictor than Maxent or shade, we can extrapolate that climate currently is not limiting bird distributions on a regional or local scale in East Africa. Rather, site-level variation such as hedgerows, surrounding landscape, and shade tree diversity likely have greater impacts on bird richness (De la Mora et al. 2015, Nesper et al. 2017). The non-climate habitat impacts of shade on bird species presence should be detected for species for which the model had positive effects of shade on bird presence but no impact of Maxent on presence. This was the case for six species: Abyssinian White-eye (*Zosterops abyssinicus*), Bronze Sunbird (*Nectarinia kilimensis*), Cape Robin-chat (*Cossypha caffra*), Common Chiffchaff (*Phylloscopus collybita*), Common Waxbill (*Estrilda astrild*), and Collared Sunbird (*Hedydiptna collaris*) (in decreasing order of effect size). This result indicates that shade trees currently positively impact these species' occurrence on coffee farms through non-

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climate mediated habitat impacts. As climate warms, more species will become restricted by climate on a region-wide level. Shade trees on farms will help to maintain the avian insectivore species pool on both a regional and a local scale through the mitigating effects of shade on temperature. Conversely, shade tree loss will not only cause biodiversity loss due to loss of habitat, but will also exacerbate warming temperatures causing further declines in richness (Philpott et al. 2008, Scheffers et al. 2014, Frishkoff and Karp 2019).

My finding that monthly Bioclim averages match more closely with iButton temperatures in shade than those in sun suggests that use of Bioclim layers for this purpose may rely on assumptions about landcover at any given location. The Bioclim model is interpolated from data collected at weather stations, so it is likely that these weather stations were in shaded areas and thus not capturing the temperatures in full-sun areas of coffee farms (Fick et al. 2017). An alternate explanation for the differences I found between the Bioclim temperatures and temperatures on sun coffee farms is global climatic warming. Given that current Bioclim data is an average of temperatures and precipitation from 1970 through 2000 and our sampling was conducted in 2018, it is possible that the iButton data simply demonstrates a clear trend of global climate change congruent with estimated predictions. Yet, based upon current IPCC estimates, the climate in East Africa has been changing by 0.005º C per year (IPCC 2007). Even assuming that Bioclim temperatures were from 1970, climate change only accounts for a 0.25º C change over 50 years, which our estimates exceed by 376%.

Precipitation in the driest month, precipitation seasonality, and annual precipitation were selected in the best Maxent models for birds more so than temperature.

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This is consistent with some studies which indicate precipitation, especially precipitation extremes, may be more important than temperature in determining climatic suitability (Tingley et al. 2009, Rapacciuolo et al. 2014, Echeverri et al. 2019). Although shade will not have direct effects on precipitation on coffee farms, shade has been linked to higher humidity on coffee farms, which then may mitigate projected future decreases in precipitation due to climate change (IPCC 2007, Mariño et al. 2016, Garedew et al. 2017, Meylan et al. 2017).

Coffee, especially shade coffee, can act in conjunction with forested habitats to maintain bird diversity (Buechley et al. 2015, Karanth et al. 2016). Future research should focus on the impact of shade tree diversity on bird richness on East African coffee farms. In order to increase diversity on shade farms, it may be necessary to plant a greater diversity of shade trees both as to species and structural complexity (Vandermeer et al. 2010, Philpott and Bichier 2012, Narango et al. 2019). Farmers may be able to increase the diversity of birds on coffee farms simply by planting different species of shade trees. Because climate and local factors work in concert, included as part of future research should be the amount of shade produced by a tree of a particular species. Different structural characteristics of trees, such as canopy width, can determine cooling effects (Smithers et al. 2018). Additionally, farmers need to consider other advantages of various shade trees including contributions to insect supply and nitrogen fixing, potential other products such as fruits, and growth rate, along with shade quality and diversity (Johnson 2000, Davis et al. 2017, Narango et al. 2019).

In order to preserve avian insectivore diversity, shade trees must be maintained in East Africa. While temperature is not currently a limiting factor for bird richness and bird distributions appear to be impacted more by local factors, future increases in temperature will limit avian insectivore species distributions at the regional level, thus limiting bird distributions at the site level. Even though predictions were not as extreme in the climatically predicted shade-removed future scenario as in the climatically predicted shade-removed current scenario, this is likely because the temperature adjustment led Maxent to extrapolate to novel environmental scenarios, violating the assumption that relevant environmental gradients were adequately sampled (Elith and Leathwick 2009, Mesgaran et al. 2014, Yates et al. 2018). Thus, my future-adjusted results that are based on an extreme climatic scenario should be taken with that caveat.

This research has also shown that the projected climatic shift from loss of shade trees has almost as dramatic an effect as the most drastic scenario for future climate change. Not only will loss of shade cause increases in temperature, as I modeled, but it will also cause loss of habitat and a disruption of other biotic interactions that we did not model (Philpott et al. 2008, Scherer et al. 2016). This is consistent with evidence that habitat loss in addition to climate change will drastically alter species distributions (Fischer and Lindenmayer 2007, Jetz et al. 2007, Jaramillo et al. 2013, Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services 2019). While coffee farmers may face challenges due to decreased suitability for coffee plants due to climate change and increased urbanization, it is critical to ensure continued existence of

numerous shade trees to mitigate climate change and its impact on bird diversity (Bunn et al. 2015, Njiru 2016).

Since climate for growing coffee will become increasingly unsuitable, especially at low elevations, it is important to maintain shade levels on coffee farms in order to mitigate temperature increases (Bunn et al. 2015). More knowledge on the impact of shade trees, especially shade tree diversity, on coffee farms in East Africa would be beneficial for further refining adaptive strategies for bird diversity and coffee production. In the future, coffee growers will likely need to balance shade tree diversity with shade tree cover in order to optimize climate and bird richness. Refining adaptation strategies for coffee farms is important both for coffee growers as well as preservation of biodiversity, and increased focus on coffee in East Africa is important because it will be one of the most climactically suitable areas in the world for growing coffee in the future (Bunn et al. 2015, Moat et al. 2017, DaMatta et al. 2019).

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Appendix A. Example study design scheme for a single sun-coffee site with three points. Green shapes represent coffee bushes and black points represent locations where point counts were conducted and shade tree density was measured. All points were at least 50 m from coffee farm edge and at least 150 m apart.

Appendix B. Scientific name, common name, guild (identified as G, with omnivores identified as O, and insectivores identified as I), family, length in centimeters (identified as L (cm)), and weights in grams (identified as W (g)) for avian insectivores included in analysis in this study (Smith et al. 2015, del Hoyo et al. 2018). Birds that were not found on point counts in this study, highlighted in grey ($n = 2$), were included because there have been sightings in the area.

Scientific Name	Common Name	G	Family	L (cm)	W(g)
Amblyospiza albifrons	Thick-billed Weaver	Ω	Ploceidae	18	45.5
Anaplectes rubriceps	Red-headed Weaver	\overline{O}	Ploceidae	13.5	21.5
Anthus trivialis	Tree Pipit	I	Motacillidae	14.5	27
Apalis cinerea	Grey Apalis	I	Cisticolidae	12.5	11
Apalis flavida	Yellow-breasted Apalis	I	Cisticolidae	11.5	8
Batis molitor	Chinspot Batis	I	Platysteiridae	12	9.5
Bradypterus cinnamomeus	Cinnamon Bracken Warbler	$\bf I$	Sylviidae	14.5	18
Camaroptera brachyura	Green-backed Camaroptera	I	Cisticolidae	10.5	10
Chalcomitra amethystina	Amethyst Sunbird	Ω	Nectariniidae	14	13.4
Chalcomitra senegalensis	Scarlet-chested Sunbird	Ω	Nectariniidae	14	12
Cinnyricinclus leucogaster	Violet-backed Starling	O	<i>Sturnidae</i>	16	40
Cinnyris chalybeus	Collared Sunbird	O	Nectariniidae	10	8
Cinnyris venustus	Variable Sunbird	O	Nectariniidae	10.5	7.5
Cisticola cantans	Singing Cisticola	I	Cisticolidae	13	14
Cisticola chiniana	Rattling Cisticola	I	Cisticolidae	13.5	15
Cisticola erythrops	Red-Faced Cisticola	I	Cisticolidae	14	14.5
Cisticola robustus	Stout Cisticola	I	Cisticolidae	14.5	20.5
Cossypha caffra	Cape Robin-Chat	$\bf I$	Muscicapidae	16.5	30.5
Cossypha semirufa	Rüppell's Robin-Chat	I	Muscicapidae	18.5	26.5
Crithagra citrinelloides	African Citril	O	Fringillidae	11.5	13
Crithagra mozambica	Yellow-fronted Canary	O	Fringillidae	12	14
Crithagra sulphurata	Brimstone Canary	O	Fringillidae	15	20
Crithagra xanthopygia	Yellow-rumped Seedeater	O	Fringillidae	11	12
Dicrurus adsimilis	Fork-tailed Drongo	I	Dicruridae	25	50
Dryoscopus cubla	Black-backed Puffback	Ω	Malaconotidae	17	27.5
Emberiza flaviventris	Golden-breasted Bunting	O	Fringillidae	15.5	21
Eminia lepida	Grey-capped Warbler	I	Cisticolidae	15	10
Estrilda astrild	Common Waxbill	O	Estrildidae	11	8.5
Estrilda rhodopyga	Crimson-rumped Waxbill	O	Estrildidae	10	8
Euplectes ardens	Red-collared Widowbird	O	Ploceidae	12.2	19
Euplectes capensis	Yellow Bishop	Ω	Ploceidae	15	21.5
Iduna natalensis	African Yellow Warbler	I	Acrocephalidae	13	13
Lagonosticta rubricata	African Firefinch	O	Estrildidae	10.5	9
Laniarius major	Tropical Boubou	I	Malaconotidae	23	53
Lanius humeralis	Northern Fiscal	I	Laniidae	22	41.5

Appendix C. Scientific name, common name, number of sites observed present (Sites Pres.), and number of GBIF observations (GBIF Obs.) for avian insectivores included in analysis in this study ($n = 77$). Birds that were not found on point counts in this study, highlighted in grey $(n = 2)$, were included because there have been sightings in the area.

Scientific Name	Common Name	Sites Pres.	
Amblyospiza albifrons	Thick-billed Weaver	7	3248
Anaplectes rubriceps	Red-headed Weaver	$\mathbf{0}$	3154
Anthus trivialis	Tree Pipit	10	1202
Apalis cinerea	Grey Apalis	3	1234
Apalis flavida	Yellow-breasted Apalis	32	5732
Batis molitor	Chinspot Batis	16	5628
Bradypterus cinnamomeus	Cinnamon Bracken Warbler	1	1362
Camaroptera brachyura	Green-backed Camaroptera	7	12110
Chalcomitra amethystina	Amethyst Sunbird	10	5060
Chalcomitra senegalensis	Scarlet-chested Sunbird	22	7112
Cinnyricinclus leucogaster	Violet-backed Starling	$\overline{2}$	3412
Cinnyris chalybeus	Collared Sunbird	5	6394
Cinnyris venustus	Variable Sunbird	35	11248
Cisticola cantans	Singing Cisticola	29	3366
Cisticola chiniana	Rattling Cisticola	2	7068
Cisticola erythrops	Red-Faced Cisticola	8	1760
Cisticola robustus	Stout Cisticola	\overline{c}	1868
Cossypha caffra	Cape Robin-Chat	38	4240
Cossypha semirufa	Rüppell's Robin-Chat	15	3906
Crithagra citrinelloides	African Citril	28	204
Crithagra mozambica	Yellow-fronted Canary	$\mathbf{1}$	3402
Crithagra sulphurata	Brimstone Canary	6	2196
Crithagra xanthopygia	Yellow-rumped Seedeater	13	176
Dicrurus adsimilis	Fork-tailed Drongo	10	15032
Dryoscopus cubla	Black-backed Puffback	8	6178
Emberiza flaviventris	Golden-breasted Bunting	25	1920
Eminia lepida	Grey-capped Warbler	11	2802
Estrilda astrild	Common Waxbill	6	3852
Estrilda rhodopyga	Crimson-rumped Waxbill	$\mathbf{0}$	2286
Euplectes ardens	Red-collared Widowbird	$\overline{4}$	2038
Euplectes capensis	Yellow Bishop	1	3476
Iduna natalensis	African Yellow Warbler	1	1470
Lagonosticta rubricata	African Firefinch	15	1848
Laniarius major	Tropical Boubou	26	1278
Lanius humeralis	Northern Fiscal	20	592
Lanius phoenicuroides	Red-tailed Shrike	9	656
Macronyx croceus	Yellow-throated Longclaw	2	4568

