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Special Issue Article: Tropical Insectivores

Importance of Ethiopian shade coffee farms for forest bird conservation

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ABSTRACT

Coffee is the most important tropical commodity and is grown in high-priority areas for biological conservation. There is abundant literature on the conservation value of coffee farms internationally, but there has been little research on this topic in Africa. Ethiopia is a diverse and little-studied country with high levels of avian endemism, pressing conservation challenges, and where *Coffea arabica* originated. We sampled bird communities in shade coffee farms and moist evergreen Afromontane forest in Ethiopia utilizing standard mist netting procedures at seven sites over three years to evaluate bird species richness, diversity and community structure. Although species diversity did not differ between shade coffee and forest, shade coffee farms had over double the species richness of forest sites and all but one of the nine Palearctic migratory species were captured only in shade coffee. There was a greater relative abundance of forest specialists and understory insectivores in forest, demonstrating that little-disturbed forest is critical for sustaining these at-risk groups of birds. Nonetheless, all species recorded in primary forest control sites were also recorded in shade coffee, indicating that Ethiopian shade coffee is perhaps the most “bird-friendly” coffee in the world. This is an important finding for efforts to conserve forest birds in Africa, and for shade coffee farmers that may benefit from avian pest regulation and biodiversity-friendly coffee certifications.

1. Introduction

1.1. Tropical forest declines and implications for bird populations

Increasing human populations and corresponding land use changes are driving a global extinction crisis (Brashares et al., 2001; Pimm et al., 2006; Vitousek et al., 1997). Tropical forests are the most species-rich terrestrial ecosystem on Earth, supporting up to 70% of plant and animal species, and are being lost at an alarming rate (Dirzo and Raven, 2003; Donald, 2004; Laurance and Bierregaard, 1997; Sodhi et al., 2004). In the last decade, approximately 13 million hectares of forest were cut down each year, with most of the losses occurring in the tropics (UNFAO, 2010). Tropical deforestation represents the single greatest threat to global biodiversity (Donald, 2004): it results in rapid transformations in plant and animal communities, which drastically alters ecological processes and impacts human societies (Clough et al., 2009a; Tilman et al., 2001).

Numerous studies attribute forest bird declines to deforestation and the conversion of tropical forests to agricultural habitats, particularly in forest archipelagos in agricultural landscapes (Bregman et al., 2014; Newmark, 1991; Şekercioğlu, 2012a; Sigel et al., 2006; Sodhi et al., 2011; Stratford and Stouffer, 1999). Currently, 23% of bird species are globally threatened or near threatened with extinction (BirdLife International, 2014), with the vast majority of threatened species inhabiting tropical forests (BirdLife International, 2014; Brooks et al., 1999; Lees and Peres, 2006; Sodhi et al., 2004; Turner, 1996).

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Understanding the ecological drivers underlying avian distributions is critical to evaluate the overall ecological integrity of ecosystems because birds are highly specialized, occupy a variety of ecological niches, have key ecological functions, and are variably susceptible to disturbance (Komar, 2006; Şekercioğlu, 2006a, 2006b; Anjos et al., 2015; Pollock et al., 2014; Pavlacky et al., 2014). Bird extinction risk increases with ecological specialization (Şekercioğlu, 2011). Shifts in bird relative abundance and/or local extinctions are likely to affect ecological processes, including seed dispersal, pollination, nutrient cycling, and even soil formation (Chapin et al., 1998; Heine and Speir, 1989; Lens et al., 2002; Şekercioğlu et al., in press).

Forest understory insectivores are especially sensitive to forest fragmentation and disturbance, and are thus among the most threatened bird species in the world (Tobias et al., 2013). They have relatively high habitat specificity, dependence on forest interior habitats, and limited mobility (Lens et al., 2002; Şekercioğlu et al., 2002; Tobias et al., 2013). Evaluating where and why they are declining is a conservation priority in the tropics (Tobias et al., 2013).

1.2. Agroforests as bird habitat

Preserving biodiversity in habitats that are impacted by human activities is important because (i) these habitats make up an increasingly large portion of the globe (Norris, 2008) and (ii) about one third of the world's ~10,000 bird species have been recorded in human-dominated and mostly agricultural habitats (Şekercioğlu et al., 2007). Agriculture accounts for over 37% of global land cover (World Bank, 2012a) and is a major cause of deforestation. Agroforestry—a farming technique that combines a mixture of trees, shrubs, and crops—is particularly valuable for biodiversity conservation, especially when native tree species are present (Fischer and Lindenmayer, 2007; Perfecto et al., 1996; Pimentel et al., 1992). The conservation value of tropical agroforests is being increasingly recognized (Greenberg et al., 2008; Perfecto and Vandermeer, 2008; Tscharntke and Klein, 2005). Landscape management strategies that maximize biological diversity retention, ecological services, and economic profitability should be investigated and promoted (Bengtsson et al., 2005; Railsback and Johnson, 2014; Rosenzweig, 2003).

A number of factors affect bird assemblages in tropical agroforests, including forest patch size, proximity to other habitat types, percent canopy cover, and shade tree composition. For example, agroforests that have intact forest canopies with high shade tree diversity and native tree species harbor relatively high avian diversity (Gove et al., 2008; Perfecto et al., 1996; Greenberg et al., 1997; Van Bael et al., 2007). Shade coffee is among the most bird-friendly of agricultural habitats, often harboring a high diversity of birds, including forest specialists (Komar, 2006; Perfecto et al., 1996; Greenberg et al., 1997; Van Bael et al., 2007). However, most avian studies only evaluate species diversity or richness, and often overlook the role of community composition in shaping the ecological and conservation importance of bird species utilizing coffee farms. In particular, there is a need to evaluate the degree of habitat specialization, foraging guild structure, and conservation status of bird communities (Komar, 2006). Furthermore, the majority of this research has taken place in the Neotropics and the ecology of birds in coffee farms in Africa, in particular, needs further investigation (Komar, 2006; Şekercioğlu, 2012a).

1.3. Ethiopia: Importance and challenges

Ethiopia is a unique, immensely diverse and little-studied country with a high level of avian endemism. It is located along the critical African-Eurasian migratory flyway (Ash et al., 2009; Şekercioğlu, 2012b). Eastern Afromontane and Horn of Africa Global Biodiversity Hotspots cover most of the country (Conservation International, 2014) and the Ethiopian highlands account for over 50% of the Eastern Afromontane eco-region (Fig. A1). This eco-region is intermittently distributed, is the least explored and least protected eco-region in Africa, and is a major source of endemism (Gole et al., 2008; Küper et al., 2004; Scholes et al., 2006). Approximately three-quarters of plant species (Gole et al., 2008) and 32 bird species are endemic to the Abyssinian Highlands, which include Ethiopia and a portion of neighboring Eritrea (Ash et al., 2009). Despite minimal visitation by ornithologists and birders, especially the unstable border regions with Somalia, Kenya, North and South Sudan, and Eritrea, an impressive total of over 860 species have been documented (Şekercioğlu, 2012b); ranking Ethiopia among the richest countries in the world in terms of bird diversity. This species list is steadily growing with increasing research and tourism. The combination of bird diversity, endemism, globally important migration routes, and scant research make Ethiopia a top priority in Africa for ornithological research and conservation (Şekercioğlu, 2012b).

While Ethiopia has a tremendous wealth of natural resources and biological diversity, it also faces serious conservation challenges. The country's population growth rate is among the highest in the world—currently estimated at 2.6% per year (World Bank, 2013)—which is causing rapid and widespread conversion of forest habitats for human settlements, charcoal and firewood harvesting, and clearing for agriculture, including tea and coffee plantations (Bekele, 2011; Campbell, 1991; Hurni, 1988). Furthermore, there is limited governmental commitment to wild-land conservation. These factors have led to widespread deforestation in the biologically rich Ethiopian highlands: forest cover was reduced from over 15,100,000 ha in 1990 to just under 12,300,000 ha in 2010—a drastic 18.6% decline in 20 years (FAO, 2010).

Global coffee consumption has increased consistently since the early 1980s, at a rate of about 1.2% annually (ICO, 2012a). With an annual value of $100 billion (Donald, 2004), coffee is the second most valuable legal international commodity after oil (O'Brien and Kinnaird, 2003) and is the most important export commodity for many tropical countries (ICO, 2012a). It is produced on approximately 11.5 million hectares of terrain, often in areas of high conservation importance (Donald, 2004). *Coffea arabica*—the most widespread and economically valuable coffee strain—makes up two-thirds of the world's coffee market (Aerts et al., 2011; Labouisse et al., 2008), and is native to southwestern Ethiopia where it has been cultivated for over a thousand years (Aerts et al., 2013; Anthony et al., 2001, 2002).

The agricultural industry accounts for 80% of employment in Ethiopia (United Nations, 2012) and coffee is the primary export crop (ICO, 2012b). From 2000 to 2010, coffee accounted for an average of 33% of export earnings, the second most of any country (ICO, 2012b). Present day coffee cultivation in Ethiopia ranges from the harvesting of near-wild coffee in forest to shade coffee farms with native tree canopies to monoculture sun coffee farms. While Ethiopia has a long history of shade coffee farming, it is following a recent global trend towards sun coffee production, due to the ease of mechanization which can yield higher production per unit area despite decreased production per plant (Donald, 2004; Gove et al., 2008). Intensive sun coffee farms produce a lower quality crop and often face problems with crop pollination and pest outbreaks due to loss of avian ecological function (Kellermann et al., 2008). These biodiversity losses can cause increased reliance on pesticides, which in turn cause further ecological damage (Donald, 2004). As little forest cover remains in Ethiopia and agriculture is the dominant land use, determining the conservation value of agricultural systems is pressing. In addition to being an important step towards determining avian conservation priorities in the tropics, our study also fills an important gap in the existing literature on birds in coffee farms, in a country with high levels of biodiversity, endemism, deforestation rates, human population growth, and economic dependence on agriculture.

2. Material and methods

2.1. Site description

Our study took place in the Oromia Region of southwestern Ethiopia, in the heart of the country's coffee producing region and where *C. arabica* was first domesticated from wild stock (Anthony et al., 2002). Bird community sampling was carried out in two habitat types: shade coffee farms (422 km^2 area; at four localities, Garuke, Eladale, Fetche, and Yebu) and moist evergreen Afromontane forest (920 km^2 area; at three localities, Afalo, Abana Buna, and Qacho) (Fig. 1).

The shade coffee farms are located within the major coffee-producing agricultural mosaic near the city of Jimma (in Kaffa Province, which gave coffee its name) and are all operated by small-scale local farmers with similar growing strategies. The area of the shade coffee farms ranged from two to ten hectares. These shade coffee farms are agroforest fragments in a patchwork of pastures and agriculture. There is extensive canopy and understory thinning and widespread planting of *C. arabica* at high densities and regularly spaced intervals. The coffee cultivars at all of the sites were from wild stocks of *C. arabica* and there was no documented pesticide or fungicide use on the farms. The shade coffee sites have a simplified structure and reduced shrub and tree species composition when compared with the forest sites. Three forest sites were selected from the closest accessible large contiguous forest patches that occurred within the same elevational range, climactic region, and vegetation zone as our shade coffee sites. Located within the Belete-Gera Regional Forest Priority Area, these sites showed only moderate signs of forest management and human alteration, including some clearing of the understory to promote the growth of wild coffee. The forest was complex structurally and compositionally, including diverse herbs, shrubs, lianas and saplings, with an average canopy height of approximately 20 m in the most pristine sections.

Hundera et al. (2013) studied forest composition and structure within our same study sites in detail. They documented a total of 69 woody plant species across all sites, with 44 species found in forest, while 26–38 species were found on different shade coffee farms. When comparing forest to shade coffee, there was a 70–95% reduction of seedlings, tree abundance was reduced by 30–68%, and basal area decreased by up to 75%, respectively. Emergent tree species, such as *Pouteria adolfi-friederici*, *Olea welwitschii*, and *Afrocarpus falcatus*, are often the first removed in the conversion from forest to shade coffee. While mean tree and canopy height did not vary significantly between habitats, regeneration of late successional tree species was significantly greater in forest than in shade coffee. Hundera et al. (2013) conclude that cutting of saplings in shade coffee inhibits recruitment of late-successional and secondary tree species.

We determined the elevation and mean annual rainfall for all study localities (Table A1). Elevation was extracted from a high resolution digital elevation model (Hijmans et al., 2005), and rainfall values were determined using a world climate database

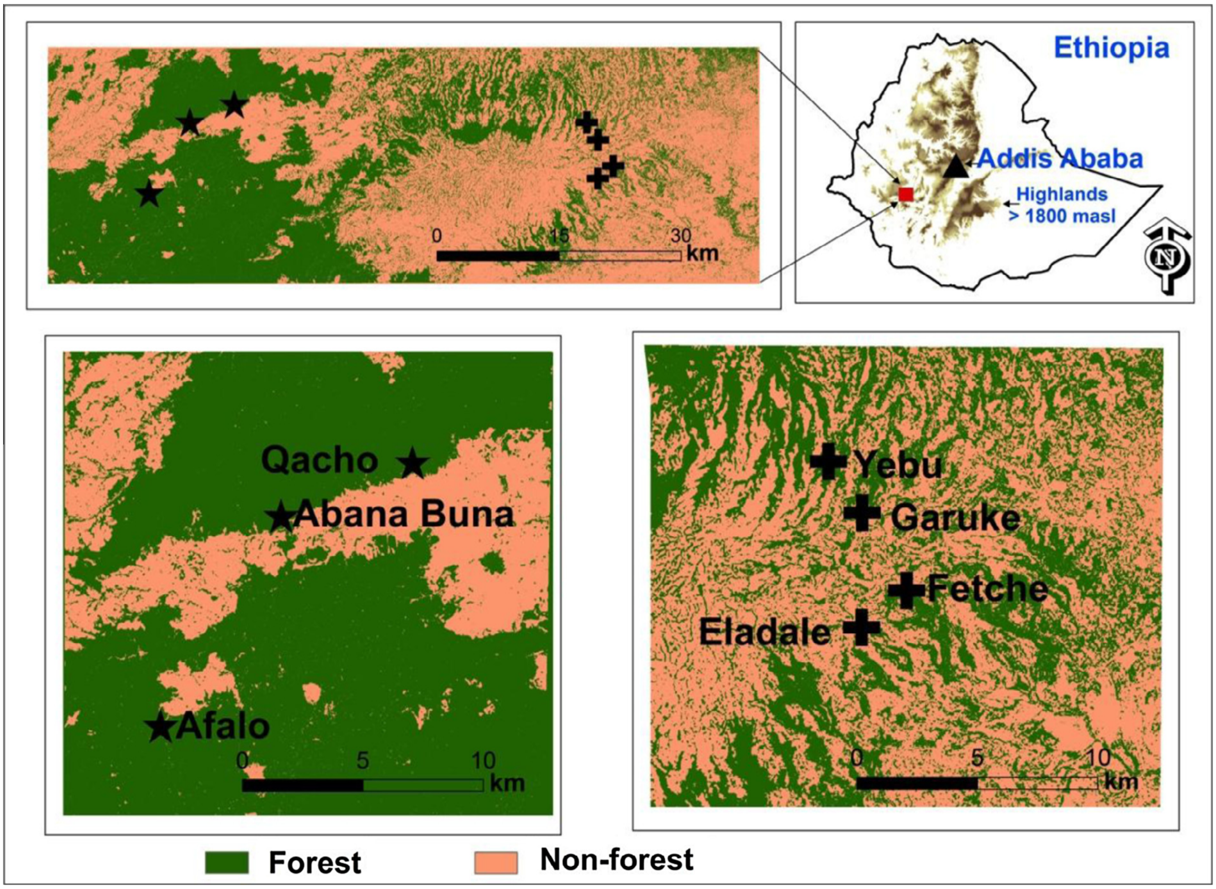

Fig. 1. Location of four shade coffee farms (+) and three moist evergreen Afromontane forest sites (★) where mist netting took place in southwestern Ethiopia. The map shows regional forest cover from a 30 m resolution LandSat image (WorldClim.org, 2014) and classified using ERDAS Imagine Software (Leica Geosystems, 2004).

(WorldClim, 2014). All study sites are located in a 110 m elevational band. The sites are at least 3 km apart and the maximum distance between the two most distant localities is 57 km. All sites occur within the Moist Evergreen Montane Forest vegetation zone and the Warm Temperate 1 and 2 climatic regions as described in Ash et al. (2009). There are distinct weather seasons in the region; a wet season from March to mid-September, with peak rains occurring in April and August, and a dry season from September to February.

2.2. Study design and sampling

Birds were sampled at all sites using standard mist-netting procedures as described in Karr (1979). Mist-netting is regarded as an effective method for sampling understory bird communities, as it can detect species that are cryptic and/or less vocal and is repeatable with few observer biases (Karr, 1981). Sampling took place during the dry season, from December to February, over a three-year time frame, from 2010 to 2012. At each site, we positioned twenty 12 × 2.5 m nets within a 1 ha area and at least 50 m from any bordering habitat type. As much as the terrain and vegetation allowed, net placement approximated a square of 60 m on each side. We used the same net lanes throughout the three-year study period. Each site was sampled at least six times every season, with approximately two weeks between each sampling session. A sampling session consisted of opening the nets half an hour before sunrise and keeping the nets open for six continuous hours. The nets were routinely checked at 30-min intervals so as to promptly remove, process, and release the birds. To process each bird we identified the species, banded it, took standard measurements, and released it (Redman et al., 2009; Stevenson and Fanshawe, 2002).

2.3. Bird classification

We classified each bird species using four main criteria: (i) migratory status, (ii) forest dependence, (iii) foraging guild, and (iv) habitat strata association. Bird taxonomy follows *Clement's 6th Edition*, updated in 2014 (Clements, 2014).

We first classified each species as either a Palearctic migrant or an Afrotropical resident. We then used the established classification of East African forest birds (Bennun et al., 1996) to create a forest dependence rank. In this work, species are classified as forest specialists (FF), forest generalists (F), and forest visitors (f). For a small number of study species that were not included in Bennun et al. (1996), we followed the authors' methods to classify species, using habitat association information found in Ash et al. (2009), del Hoyo et al. (1992), and Redman et al. (2009).

Bird species' foraging guilds were determined using a dataset containing the ecological traits of all of the bird species in the world (hereafter "Birdbase"), as described in Şekercioğlu et al. (2004). This dataset was initially compiled from an extensive literature survey of 248 sources, is updated regularly, and has been used in numerous ecological studies and meta-analyses of bird populations (e.g. Bregman et al., 2014; Burivalova et al., 2014; Redding et al., 2015; Şekercioğlu, 2012a). Herein, seven food categories are identified (plant material, seeds, fleshy fruits, nectar, invertebrates, carrion, and vertebrates) and ordered by priority in each species' diet on a ten-point scale to determine primary diet and foraging strategy. The species' first diet choice was used to classify it into one of the following guilds that were present in our study: frugivore, nectarivore, granivore, and insectivore. Consulting the Birdbase, Ash et al. (2009), del Hoyo et al. (1992), and Redman et al. (2009), we also categorized each species' occurrence within the understory, midstory, and canopy.

Using these categories, we identified two additional groups: understory insectivores, and resident understory insectivores. These groups are composed of species that are insectivorous and consistently frequent the understory, with the latter including only Afrotropical resident species. These groups are of particular interest in this study for two main reasons: (i) pan-tropical studies have shown that understory insectivores are highly impacted by forest modifications (e.g. Bregman et al., 2014; Burivalova et al., 2014), making them good indicators of forest health; (ii) understory insectivores have been shown to contribute ecosystem services to coffee farmers in the form of pest-regulation in other regions of the world (Şekercioğlu et al., in press), and may likewise be of economic importance to coffee farmers in Ethiopia. (See Table A2 for a list of species along with their classifications included in the analysis.)

2.4. Data analysis

We made several modifications to the dataset prior to analysis, to account for limitations and potential biases associated with mist net data (Remsen and Good, 1996) (see Section 4 for full treatment of these issues). We removed species that do not consistently frequent the understory and species that are not reliably caught in mist nets due to their large size, such as raptors, owls, and ravens (Wang and Finch, 2002; see Table A3 for a list of species and the reason they were excluded from the analysis). Individuals were only counted when trapped first (recaptures were excluded from the analysis) to avoid estimation bias from individuals that were recaptured many times (Remsen and Good, 1996). Then, all shade coffee sites and forest sites were combined, so as to compare the two major habitat types.

Using EstimateS 9.1.0 (Colwell, 2013), we calculated estimated species richness S(est), estimated shared species V(est), and Morisita–Horn sample similarity. We used the Chao1 estimator to calculate S(est) for our species relative abundance data. The Morisita–Horn index was used because it has minimal sample size biases and is useful for large species assemblages with many rarely recorded species, as was the case in our study (Magurran, 1988). Rarefaction and extrapolation curves of S(est) were computed with 95% confidence intervals in both habitat types, extrapolating the smaller sample to the number of captures of the larger sample (1208 individuals), in order to directly compare observed and estimated species richness in both habitats. Using this method, statistically robust extrapolation of samples is possible to directly compare sites with different sample sizes, as was the case in our study (Colwell et al., 2012).

Shannon's Diversity (H) was compared between forest and shade coffee by fitting a generalized linear mixed effects model using the package lme4 in R (Bates et al., 2008). Average Shannon's Diversity for each one of the 142 sampling sessions from the seven sites was used as the response variable, site as the random effect and habitat (shade coffee or forest) as the fixed effect. The frequency of breeding birds was determined for both habitats, using the number of individuals in breeding condition, as evidenced by cloacal protuberance or brood patch, divided by the total number of captures (Ralph and Dunn, 2004). The ratio of juvenile to adult birds was then determined. Birds in their first year were classified as juveniles and all birds in their second year or after were classified as adults, with species of undetermined age excluded. Relative abundance was determined from the capture rate (number of birds per net hour), an index which controls for differing effort between habitats (Karr, 1982; Newmark, 1991). To compare relative abundance between habitats, we (i) identified the capture rate of each individual species and each bird classification category and (ii) divided this by the total capture rate in each habitat respectively. We then ran a chi-square analysis in SPSS 21.0 (IBM Corp., 2012) to test for significant differences in relative abundance between habitats.

3. Results

3.1. Bird captures, richness and diversity

A total of 1692 individuals of 71 species were captured in 18,177 net-hours; 1281 individuals were captured in shade coffee and 411 in forest. Nine species were excluded from analysis due to their large body sizes and 11 species were excluded because they do not consistently frequent the understory. After these refinements to the dataset were made, 1605 individuals (94.9% of all individuals captured) of 51 species (71.8% of all species captured) were included in the analysis. All 51 species were captured in shade coffee, while 19 of these were caught in forest. Because shade coffee had more land cover, mist netting effort in shade coffee (13,690 net hours) was more than double the effort in forest sites (4487 net hours), while the overall capture rate was identical (0.085 and 0.082 birds per net-hour in forest and shade coffee, respectively). Six species had significantly greater relative abundance in forest, as determined from the capture rate: Lemon Dove (*Columba larvata*), African Hill Babbler (*Sylvia abyssinica*), Abyssinian Ground-thrush (*Geokichla piaggiae*), Eastern Olive Sunbird (*Cyanomitra olivacea*), Abyssinian Crimson-wing (*Cryptospiza salvadorii*) and Green-backed Twinspot (*Mandingoa nitidula*). Nine species had significantly greater relative abundance in shade coffee: Tambourine Dove (*Turtur tympanistria*), Yellow-fronted Tinkerbird (*Pogoniulus chrysoconus*), Willow Warbler (*Phylloscopus trochilus*), Blackcap (*Sylvia atricapilla*), Common Chiffchaff (*Phylloscopus collybita*), Broad-ringed White-eye (*Zosterops poliogastrus*), Abyssinian Slaty-Flycatcher (*Melaenornis chocolatinus*), African Paradise-flycatcher (*Terpsiphone viridis*), and Tree Pipit (*Anthus trivialis*). Palearctic migrants were predominantly found in shade coffee, where they were captured nearly twice as frequently. All but one (Blackcap, *S. atricapilla*) of the nine migratory species were captured only in shade coffee. (See Table A3 for a full list of species included in the analysis with relative abundance values.)

The sites had estimated understory bird species richness S(est) of 51.00 (95% CI [44.49, 57.51]) and 19.25 (95% CI [17.82, 20.67]), for shade coffee and forest, respectively. While sharing an observed 19 species V(obs), estimated shared species Chao V(est) was 20.96. Despite the large difference in species richness between habitats, the Morisita–Horn Sample Similarity Index was 0.728, indicative of a high degree of overlap in bird communities. Species rarefaction and extrapolation curves reached a plateau in forest, while shade coffee curves had a positive slope indicating that continued sampling in this habitat might have yielded additional species (Fig. 2). Analysis of Shannon's Diversity Index showed no significant difference in bird diversity between shade coffee farms and forest (Table A4).

3.2. Community structure analysis

While there were no significant differences in overall bird diversity values between shade coffee and forest, there were differences in the relative abundance of bird community categories, as determined from the capture rate.

Forest generalists (F) were frequently captured in both habitat types, accounting for 58% of captures in shade coffee and 41% of captures in forest. Forest visitors (f) accounted for over one-third of all captures in shade coffee, whereas they were only one-fifth of captures in forest. There was no significant difference in the composition of these 2 groups between habitats, however. Importantly, though, forest specialists (FF) had a greater relative abundance in forest than in shade coffee by a wide margin; they were captured nearly 5 times as frequently in this habitat ($\chi^2 = 9.877$, $df = 1$, $p = 0.001$) (Fig. 3).

Four foraging guilds were found in our study: frugivore, granivore, insectivore, and nectarivore. Frugivores had a greater relative abundance in shade coffee ($\chi^2 = 4.670$, $df = 1$, $p = 0.017$), whereas granivores had a greater relative abundance in forest ($\chi^2 = 18.900$, $df = 1$, $p < 0.001$). Nectarivores constituted less than 1% of all captures, with no significant difference between habitats. Insectivores were by far the most frequently captured in both habitats, comprising 68% of all captures in shade coffee and 64% in forest. There was no significant difference in the overall relative abundance of insectivores between the habitats. However, both understory insectivores ($\chi^2 = 14.195$, $df = 1$, $p < 0.001$) and resident understory insectivores ($\chi^2 = 48.392$, $df = 1$, $p < 0.001$) had greater relative abundance in forest. In contrast, shade coffee sites had greater relative abundance of Palearctic migrants ($\chi^2 = 21.375$, $df = 1$, $p < 0.001$) (Fig. 3).

There was no significant difference in the frequency of breeding birds (as evidenced by cloacal protuberance or brood patch) between forest and shade coffee, with 27% of all captures in breeding condition in shade coffee and 23% in forest ($\chi^2 = 2.476$, $df = 1$, $p = 0.065$). The species that most frequently showed signs of breeding in shade coffee were Yellow-fronted Tinkerbird (*P. chrysoconus*), Green-backed Camaroptera (*Camaroptera brachyura*), Broad-ringed White-eye (*Z. poliogastrus*), and Eastern Olive Sunbird (*C. olivacea*). The species that most frequently showed signs of breeding in forest were two of the same species, Broad-ringed White-eye (*Z. poliogastrus*) and Eastern Olive Sunbird (*C. olivacea*), plus African Hill Babbler (*S. abyssinica*) and Abyssinian Crimson-wing (*C. salvadorii*). The juvenile to adult ratio was 0.19 in shade

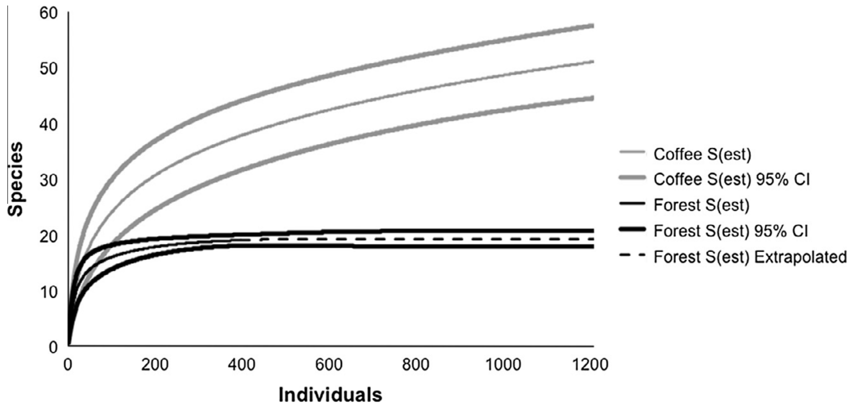

Fig. 2. Observed and extrapolated bird species accumulation curves (S(est)) with 95% confidence intervals (CI) for shade coffee farms and moist evergreen Afromontane forest sites in southwestern Ethiopia.

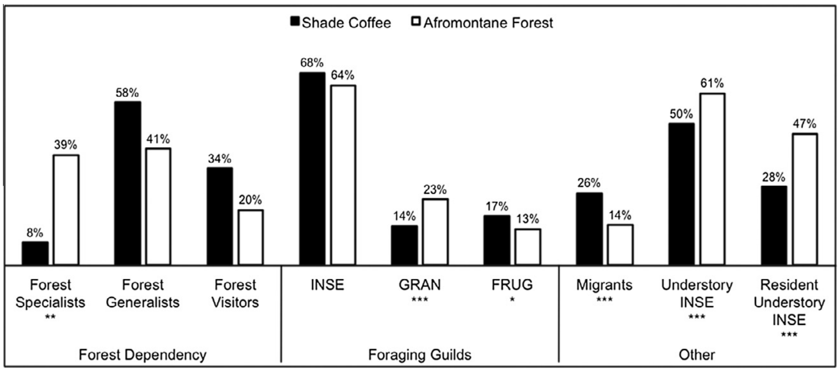

Fig. 3. Summary of the differences in bird relative abundance between shade coffee farms and moist evergreen Afromontane forest sites in southwestern Ethiopia. Bars illustrate the relative abundance of each bird classification category, calculated as the capture rate (# of birds/net hour) in each habitat divided by the total capture rate. Asterisks indicate significant differences in the relative abundance of a category between habitats at the $p < .05$ (*), $p < .01$ (**), and $p < .001$ (***) levels, based on chi-square analysis. Nectarivores were not included in the figure because they accounted for only a fraction of a percent of all captures.

coffee and 0.22 in forest, with no significant difference between sites ($\chi^2 = 2.215$, $df = 1$, $p = 0.080$).

4. Discussion

4.1. Richness and diversity

Results from rarefaction show that shade coffee had over double the species richness of forest. Despite this, the Morisita–Horn Sample Similarity Index indicates high community overlap of nearly 73% between the bird communities. There were no significant differences in Shannon's Diversity. Eight of the nine Palearctic migrants in the study were found only in shade coffee. These results are consistent with numerous tropical studies showing that shade coffee farms harbor high bird species richness and diversity, and provide important habitat for temperate migrants (Jones and Ramoni-Perazzi, 2002; Komar, 2006; Perfecto et al., 2003; Sherry, 2000). The fact that every species we captured in forest was also captured in shade coffee indicates that forest specialist birds may use shade coffee farms in Ethiopia even more than they do in other regions of the world. This is supported by the result that shade coffee had no significant difference from forest in the frequency of birds in breeding condition or the ratio of juveniles to adults. We captured several forest specialist birds in breeding condition in shade coffee, indicating that this habitat may provide viable breeding habitat for some forest specialists, including Lemon Dove (*C. larvata*), Abyssinian Ground-thrush (*G. piaggiae*), Eastern Olive Sunbird (*C. olivacea*), and Green-backed Twinspot (*M. nitidula*). The lack of chemical use in these traditional, organic shade coffee plantations is also likely to contribute to high bird diversity and abundance. However, the viability of shade coffee as breeding habitat for forest birds in this region requires further study. It is possible that shade coffee farms serve mainly as stepping stones for forest birds searching for more suitable habitat, or that these shade coffee fragments are an ecological trap (Battin, 2004) for forest bird species in a highly fragmented and human-dominated landscape. Long-term studies of population dynamics using capture-mark-recapture methods are needed. Nonetheless, the high species richness, diversity, and presence of forest specialist species in organic shade coffee farms in this region are encouraging findings, illustrating the potential importance of shade coffee farms for bird conservation in Africa.

4.2. Community structure

Considering species richness alone, however, could be misleading when assessing the importance of shade coffee farms and forest for bird conservation. Results from community structure analysis show that there are significant differences in the relative abundance of bird species between the two habitats, illustrating the importance of little-disturbed Afromontane forest for particular groups of birds. For example, forest had a much higher relative abundance of forest specialists, understory insectivores, and resident understory insectivores. These results corroborate studies from around the world that have shown that understory insectivores are among the most susceptible of groups to forest disturbance and are often the first species to disappear from altered forests (Şekercioğlu et al., 2002; Stouffer and Bierregaard, 1995; Sodhi et al., 2011; Cordeiro et al., 2015; Pavlacky et al., 2014; Arcilla et al., 2015). In order to conserve forest specialists and understory insectivores in the long term, it is necessary to conserve areas of little-disturbed forest in the Afrotropics as well.

With regard to guild structure, insectivores made up a similar proportion of the community in both forest and shade coffee, a result that is unusual (Hernandez et al., 2013; Şekercioğlu, 2012a). This may be explained by the fact that coffee is a native crop within our study area and a larger portion of the invertebrate prey base for insectivores may be maintained in shade coffee farms here. Furthermore, the lack of chemical use also favors insectivorous birds. A recent study has shown similar incidence of pests on coffee grown in contiguous forest and forest fragments in this region of Ethiopia (Samnegård and Hambäck, 2014). Also of note is a higher proportion of granivores in forest than in shade coffee. This is an unusual result, as well, as granivores typically prefer disturbed and open habitats. Two granivorous species captured frequently in forest, Abyssinian Crimson-wing (*C. salvadorii*) and Green-backed Twinspot (*M. nitidula*), account for the greater relative abundance of granivores in forest. These two species were among the most commonly captured species in forest, accounting for 18% of all captures in this habitat. Unlike many other tropical studies (Şekercioğlu, 2012a), shade coffee farms in our study did not have high numbers of open country granivores. This is an important result, as granivores can be agricultural pests. Frugivores were more common in shade coffee than in forest, a result that parallels pan-tropical findings (Şekercioğlu, 2012a). An increase in frugivores in shade coffee is perhaps the result of selective thinning of the forest in favor of fruiting trees, a frequent practice in agroforests that helps to increase economic production.

These results indicate an important difference in overall community composition from specialists in forest to generalists in shade coffee. These findings are consistent with previous research (Komar, 2006; Şekercioğlu, 2012a). Generalists are more widespread, relatively common, and less threatened than forest specialists (Şekercioğlu, 2012a). Thus, while the high species richness in shade coffee is an encouraging result, the lower relative abundance of forest specialist species in shade coffee is illustrative of the importance of little-disturbed forest for many species.

4.3. Caveats

Mist netting is regarded as likely the best technique for assessing the relative abundance of tropical understory birds because it can detect species that are cryptic and/or less vocal and is repeatable with few observer biases (Karr, 1982; Newmark, 1991). Nonetheless, there are limitations and potential biases associated with mist netting data (Remsen and Good, 1996). For example, habitat modifications, such as removal of canopy trees and clearing of the understory may alter flight height of species, thereby changing their susceptibility to mist-net capture without changing their relative abundance (Arcilla et al., 2015; Remsen and Good, 1996). We recognize that the number of captures by species is therefore a result, at least in part, of how susceptible a species is to be caught by mist nets and of the habitat structure where the nets are placed. We have therefore made extensive efforts in this study to control for these potential biases. Accordingly, we restricted our analysis by removing species that do not consistently frequent the understory, and species that are not reliably caught in mist nets due to their large size, such as raptors, owls, and ravens (Wang and Finch, 2002). It should therefore be stressed that our results are restricted to interpreting differences in the understory bird community—not the entire bird community—between these habitats. While there was considerable difference in the structure between our shade coffee and forest sites, the average canopy tree height at our sites did not differ (Hundera et al., 2013). We also recognize that the three-year time period of our study could affect the relative abundance estimates of long-lived versus short-lived species. However, in one of the most rigorous studies of tropical forest bird longevity, results from Korfanta et al. (2012) show that the average life span of forest species in Tanzania's Usambara Mountains is 11.8 years. Taking this into account, we believe that a 3-year study period is relatively short compared to the average longevity of tropical forest species. Furthermore, longevity is positively related to body mass in most terrestrial organisms, including birds (Jones et al., 2003; Laurance, 1991), and we have excluded species of large body size from the analysis, which should help minimize any bias in this regard. Lastly, we believe that audio-visually obtained data, such as from point counts (e.g. Aerts et al., 2008), would substantially add to our understanding of bird community composition in Afromontane forest and shade coffee sites. Accordingly, a multi-year point count study is currently being conducted to improve our understanding of the bird communities in these habitats.

4.4. Agroforests and conservation

While shade coffee provides important habitat for many bird species, particularly those migrating from temperate regions, it is substantially different from forests and likely does not provide suitable habitat for all forest species. As evidenced in our study sites by the work of Hundera et al. (2013), shade coffee farming practices often involve the clearing of much of the diverse understory and mid-story of saplings, shrubs, and forbs, as well as the selective removal of large canopy trees. Native tree species are often replaced with those of greater economic value, including fruit and timber producers. Importantly, not all agroforests are created equally, and different farming practices can have profound impacts on biodiversity. For example, agroforests with higher percent shade cover and greater shade tree diversity have been shown to host a greater richness and diversity of birds (Clough et al., 2009a). Retaining shade cover and shade tree diversity on coffee farms may help preserve forest specialist birds, as well as insectivores and nectarivores, which can in turn benefit crop production (Johnson et al., 2010; Maas et al., 2009; Şekercioğlu, 2012a; Şekercioğlu et al., in press). Further research on bird communities on coffee farms with different structural and floral components is needed to evaluate how these factors may impact bird communities.

Shade coffee farms may not provide viable habitat for all species found therein. Rather, some species may use these farms as stepping-stones between forest patches. Research globally has shown that "suboptimal" forest habitats, such as agroforests, secondary forest, plantations, and even individual trees can help increase connectivity of forest patches in agricultural landscapes (Berens et al., 2008; Ferraz et al., 2012; Neuschulz et al., 2011; Uezu et al., 2008). Research in northern Ethiopia demonstrated that forest restoration sites with suboptimal habitat can help connect forest fragments and also provide suitable habitat for some forest species (Aerts et al., 2008). Similarly, shade coffee farms in southwestern Ethiopia may help connect populations of species that rely on forests for breeding. Thus, the location of shade coffee farms may be important in determining their ecological value as links between forest patches.

4.5. Climate change threats

Climate change is predicted to have profound impacts on biodiversity (Thomas et al., 2004). It may cause as many as 900 bird extinctions over the next century, with the vast majority expected to occur in the tropics (Şekercioğlu et al., 2012). Tropical montane forest birds are among the most threatened of all bird species from climate change (Wormworth and Şekercioğlu, 2011) because they are often sedentary and have small ranges. Our study took place in and near Ethiopia's montane forests, which have a large number of endemic and range-restricted bird species that are expected to experience further range contractions with climate change. The distributions of montane birds in East Africa are predicted to shrink and become more isolated as arid areas expand in the region (Huntley et al., 2006). Human-induced habitat loss is likely to further exacerbate the effects of climate change on forest birds by reducing viable habitat and creating barriers to dispersal (Şekercioğlu et al., 2008). In order to preserve forest birds in Ethiopia—and forest biodiversity in general—reserves should incorporate wide elevational distributions and have high connectivity (Noss, 2001; Şekercioğlu et al., 2012). Shade coffee farms that are strategically located near forest patches may help improve connectivity of forests and help mitigate predicted extinctions. Furthermore, trees help buffer against climate change impacts, by improving water quality, reducing topsoil erosion, and creating microclimates (Bonan, 2008; Şekercioğlu, 2010). Encouragingly, there is evidence that Ethiopian farmers recognize these benefits, and are already working to mitigate the effects of climate change on crops by planting trees (Deressa et al., 2009).

Coffee production is also expected to suffer worldwide as a result of climate change. A global model estimates land suitable for growing coffee will decrease by about 50% by 2050 (Bunn et al., 2014). Interestingly, Ethiopia is one of the few locations where the suitability for coffee production is expected to improve. This model shows suitable land for coffee growing in Ethiopia shifting upwards with climate change, from rugged hillsides to the extensive highland plateaus. This scenario presents Ethiopia with a unique opportunity: by investing in shade coffee farming now, it may position itself to control a larger share of the lucrative coffee market in the future, while helping to mitigate the local effects of climate change by planting trees, and simultaneously benefiting the country's rich biodiversity by increasing connectivity of native forests. However, in order to conserve biodiversity, it is also imperative to preserve remaining forest patches with minimal human disturbance.

4.6. Avian ecosystem services and "Shade Grown Coffee" certification

Approximately half of the global human population relies on subsistence or small-scale farming (Donald, 2004). Therefore, changes in ecological processes and ecosystem services can have profound impacts on human livelihood and well-being (Şekercioğlu, 2010). With a per-capita GDP of $374 USD in 2011 (World Bank, 2012b), Ethiopia is one of the most impoverished nations on Earth. However, it has tremendous opportunities for sustainable development based on its high biological diversity, abundant natural resources, and potential for ecotourism. Shade coffee farming with high canopy cover and shade tree diversity have the potential to benefit not only the local ecology and biodiversity, but also the economy.

Birds provide valuable ecosystem services in agricultural areas, including pollination, predation of pests, seed dispersal, and ecosystem engineering (Şekercioğlu, 2006a, 2006b; Wenny et al., 2011; Şekercioğlu et al., in press). In the Neotropics, birds have been shown to provide economically valuable services to coffee farmers in the form of pest control (Clough et al., 2009b; Dietsch et al., 2007; Greenberg et al., 2000a, 2000b; Johnson et al., 2010; Perfecto et al., 2004; Şekercioğlu, 2006a, 2006b; Van Bael et al., 2008). For example, a study in Jamaica concluded that pest reduction by birds economically benefited coffee farmers by $310 USD per hectare (Johnson et al., 2010). Investigating avian usage of and pest-regulating services in African shade coffee farms is a high priority, in order to compare with extensive findings from other regions of the world (Komar, 2006). Our results show that shade coffee farms in southwestern Ethiopia harbor a diverse and abundant insectivorous bird community. This is an important finding with implications for pest regulation on shade coffee farms. Fifteen coffee insect pests have been documented in the vicinity of our study, including the coffee berry borer (*Hypothemus hampei*) and Coffee Berry Moth (*Prophantis smaragdina*), which can drastically damage coffee crops (Abedeta et al., 2014). Indeed, average Coffee Berry Moth incidence on coffee berries in the region was documented at 24.5%, with peak incidence of over 60% in some seasons (Mendesil and Tesfaye, 2009). Coffee berry borer is similarly ubiquitous in the region (Mendesil, 2004). This high prevalence of coffee pests implies that there may be large benefits from avian insectivory on shade coffee farms in Ethiopia. One study within the region documented similar pest infestation rates between shade coffee grown in contiguous forest and forest patches (Samnegård and Hambäck, 2014), but there is need for further investigation of the frequency of pest infestation and avian pest regulation in differing habitats where coffee is grown.

To our knowledge, our study documents the only known location in the world where all forest understory bird species recorded in primary forest control sites were also recorded in shade coffee sites (e.g. Wunderle and Latta, 1996; Tejeda-Cruz and Sutherland, 2004; Philpott et al., 2008; Waltert et al., 2005; Aguilar-Ortiz, 1982). This is not altogether surprising, because coffee is native to our study region, whereas most studies of bird communities on coffee farms have occurred in the Neotropics, where coffee is an exotic crop. However, there is almost no awareness of this in the global "biodiversity friendly" coffee market. Certifying, publicizing and marketing Ethiopian coffee as "organic" "shade-grown" and "bird friendly" has the potential to increase incomes of local coffee farmers and provide them a major financial incentive to maintain traditional shade coffee farms instead of converting them into sun coffee plantations that are poor for biodiversity conservation. Farms in Ethiopia that have "shade grown" certification may receive as much as 15–20% more revenue per unit of crop (Takahashi and Todo, 2013). Furthermore, shade coffee is widely regarded to be of superior quality to sun coffee, and is thus more valuable. These factors should be a significant consideration for local farmers in developing countries attempting to maximize profits (Philpott and Dietsch, 2003).

5. Conclusions

In studies around the world, shade coffee has been shown to support high bird species richness, albeit with fewer forest specialist species, particularly understory insectivores. Our results corroborate these findings. Shade coffee farms in southwestern Ethiopia had over double the species richness of nearby primary forest, while there was a much higher relative abundance of forest specialists, understory insectivores and Afrotropical-resident understory insectivores in primary forest. These groups are among the most extinction-prone birds globally. There were also some results that contrast with most global findings: (i) there was no difference in the relative abundance of all insectivores between the two habitats, and (ii) there was a greater relative abundance of granivores in primary forest. Our results support the consensus that shade coffee farms are an important habitat for forest bird conservation in the tropics. However, differences in the relative abundance of species in shade coffee and forest habitats indicate that intact forest must also be conserved in order to mitigate declines in forest specialist birds. Conserving all types of forested habitat is increasingly important for biodiversity conservation in the tropics (Gibson et al., 2011; Hernandez et al., 2013).

Humans can benefit in turn from conservation of forests and bird communities. Shade coffee farmers can profit from valuable ecosystem services provided by forest bird communities, such as pollination and insect regulation. These benefits can be economically significant, and may help contribute to poverty alleviation in Ethiopia—one of the most impoverished countries in the world. Shade coffee farms located near forest and those that maintain high levels of canopy cover and native tree diversity are particularly likely to benefit from avian ecosystem services. Our results imply that Ethiopian shade coffee is among the most "bird friendly" in the world. By promoting, certifying, and marketing shade coffee, Ethiopia has the potential to substantially increase revenue, while simultaneously helping conserve biodiversity.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.biocon.2015.01.011.

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