



## Coffee management and the conservation of forest bird diversity in southwestern Ethiopia



Patrícia Rodrigues<sup>a,\*</sup>, Girma Shumi<sup>a</sup>, Ine Dorresteijn<sup>a</sup>, Jannik Schultner<sup>a</sup>, Jan Hanspach<sup>a</sup>, Kristoffer Hylander<sup>b</sup>, Feyera Senbeta<sup>c</sup>, Joern Fischer<sup>a</sup>

<sup>a</sup> Leuphana University, Faculty of Sustainability Science, Lueneburg, Germany

<sup>b</sup> Stockholm University, Dept. of Ecology, Environment and Plant Sciences, Stockholm, Sweden

<sup>c</sup> Addis Ababa University, College of Development Studies, Addis Ababa, Ethiopia

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### ABSTRACT

Moist evergreen forests of southwestern Ethiopia host high levels of biodiversity and have a high economic value due to coffee production. Coffee is a native shrub that is harvested under different management systems; its production can have both beneficial and detrimental effects for biodiversity. We investigated how bird community composition and richness, and abundance of different bird groups responded to different intensities of coffee management and the landscape context. We surveyed birds at 66 points in forest habitat with different intensities of coffee management and at different distances from the forest edge. We explored community composition using detrended correspondence analysis in combination with canonical correspondence analysis and indicator species analysis, and used generalized linear mixed models to investigate the responses of different bird groups to coffee management and landscape context. Our results show that (1) despite considerable bird diversity including some endemics, species turnover in the forest was relatively low; (2) total richness and abundance of birds were not affected by management or landscape context; but (3) the richness of forest and dietary specialists increased with higher forest naturalness, and with increasing distance from the edge and amount of forest cover. These findings show that traditional shade coffee management practices can maintain a diverse suite of forest birds. To conserve forest specialists, retaining undisturbed, remote forest is particularly important, but structurally diverse locations near the forest edge can also harbour a high diversity of specialists.

### 1. Introduction

Tropical forest biodiversity is rapidly declining due to the conversion of forests to agriculture and the intensification of traditional agricultural systems (Wright, 2005). Between 1990 and 2010, the amount of deforested land across the wet tropics increased by 62% (Kim et al., 2015), coupled with a 40% increase in human population numbers (Edelman et al., 2014). For tropical biodiversity conservation to be successful, it needs to promote and ensure viable rural livelihoods. In this context, tropical agroecosystems and in particular shade coffee agroforests have received considerable attention, given their potential benefits for both conservation and livelihoods (Bhagwat et al., 2008; Reed et al., 2016).

Coffee is one of the world's major agricultural commodities grown in tropical areas (Jha et al., 2014) occupying an area of 10.5 million ha worldwide (FAO, 2014). The species *Coffea arabica* represents two

thirds of the world's coffee market (Aerts et al., 2011), and is mostly produced in agroforests (Perfecto et al., 1996; Jha et al., 2014). To date, the vast majority of research investigating the implications of coffee production for biodiversity has focused on Latin America (Philpott et al., 2008 and references therein). However, coffee is also of particular relevance in East Africa, from where it originates (Senbeta and Denish, 2006). The Arabica coffee shrub is native to the biodiversity hotspot of wet Afromontane forests of southwestern Ethiopia, where it naturally occurs at low densities (Labouisse et al., 2008). In Ethiopia, coffee is a highly valued cash crop, with significant economic and cultural value (Petit, 2007).

Coffee in Ethiopia is traditionally grown in agroforests, under the shade of native trees but with varying degrees of management. Management can range from very little or no intervention, to the pruning and thinning of the canopy, coupled with the removal of understorey species that may compete with coffee (Aerts et al., 2011). In

\* Corresponding author at: Leuphana University, Scharnhorststrasse 1, 21335 Lueneburg, Germany.

E-mail addresses: [patricia.rodrigues@leuphana.de](mailto:patricia.rodrigues@leuphana.de) (P. Rodrigues), [dugo@leuphana.de](mailto:dugo@leuphana.de) (G. Shumi), [ine.dorresteijn@leuphana.de](mailto:ine.dorresteijn@leuphana.de) (I. Dorresteijn), [jannik.schultner@leuphana.de](mailto:jannik.schultner@leuphana.de) (J. Schultner), [hanspach@leuphana.de](mailto:hanspach@leuphana.de) (J. Hanspach), [kristoffer.hylander@su.se](mailto:kristoffer.hylander@su.se) (K. Hylander), [feyeras@yahoo.com](mailto:feyeras@yahoo.com) (F. Senbeta), [joern.fischer@leuphana.de](mailto:joern.fischer@leuphana.de) (J. Fischer).

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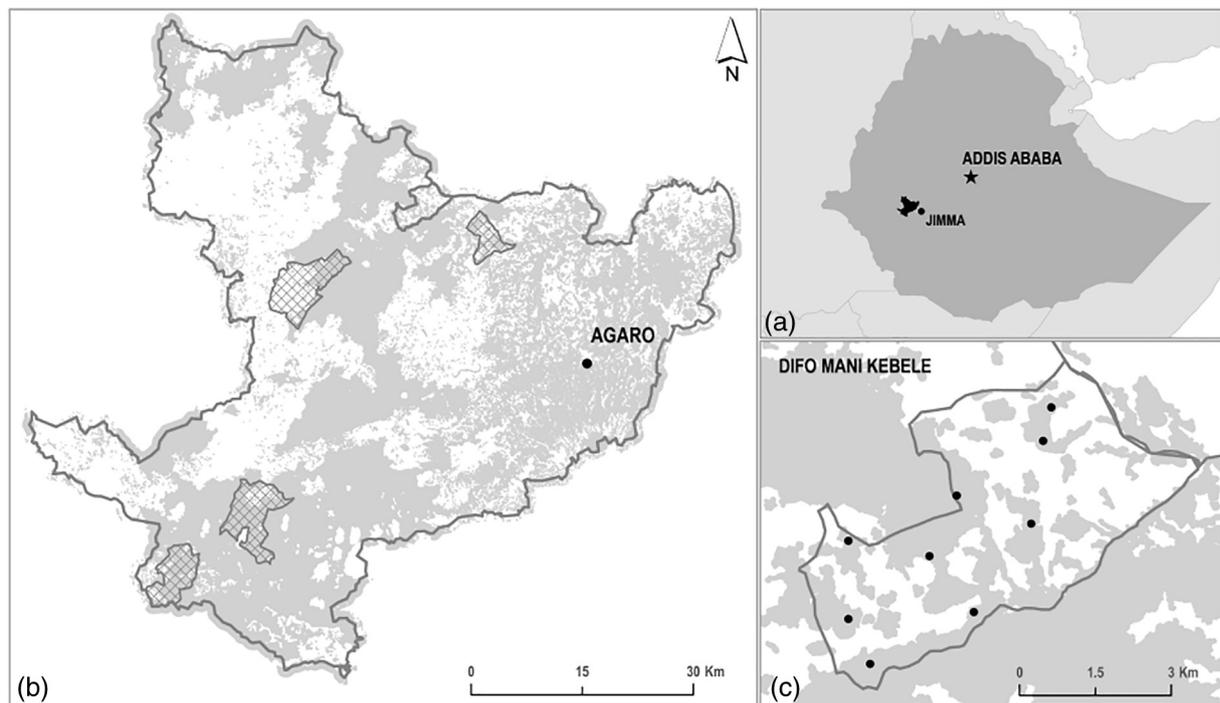


Fig. 1. Location of (a) study area in Jimma zone, southwestern Ethiopia; (b) the five focal *kebeles* in Agaro/Jimma zone (hatched); (c) example of sampling design with survey points (black bullets) in one *kebele*. In (b) and (c) grey colour depicts woody vegetation.

the last few decades, coffee growing areas of southwestern Ethiopia have experienced both high rates of deforestation (mainly for agriculture) and a push towards the intensification of coffee production in state and privately owned plantations (Tadesse et al., 2014a). Intensification is achieved through different management practices, including the reduction of shade tree cover and diversity; an increase in coffee density; the replacement of native shade trees with faster growing exotic species; the use of agrochemicals; and the use of improved coffee varieties (Tadesse et al., 2014b). Accordingly, coffee growing has mixed effects on biodiversity conservation in southwestern Ethiopia. On the one hand, coffee production can help to reduce deforestation, because it provides a source of revenue from remnant forest, thus creating an incentive to maintain it (Philpott and Bichier, 2012; Hylander et al., 2013). On the other hand, a shift towards more intensively managed coffee plots can cause the homogenization and simplification of forest structure and diversity, with potentially negative effects on biodiversity (Aerts et al., 2011; Hundera et al., 2013).

Different species can be expected to respond in different ways to coffee management, and a mixture of positive, negative or null responses of species to coffee management practices have been reported (see Komar, 2006 and Philpott et al., 2008 and references therein). Typically, forest specialist species respond positively to systems with a high degree of naturalness, whereas generalist species tolerate more disturbed or simplified systems (Tejeda-Cruz and Sutherland, 2004). The ability of species to persist in landscapes with different degrees of coffee management will depend on a variety of factors, including: (1) species life history traits and ecological attributes (such as breeding and feeding strategies and habitat affinity) (Newbold et al., 2013); (2) site-specific conditions (such as vegetation structure and composition) (Leyequién et al., 2010); and (3) landscape context (such as landscape configuration, natural forest cover surrounding a site and distance to edge) (Tejeda-Cruz and Sutherland, 2004; Anand et al., 2008). Site-specific conditions and landscape context, in turn, can be expected to co-vary, with sites near forest edges being more disturbed and structurally different from reference sites deep within the forest (Harper et al., 2005). Both the management of coffee sites and the landscape context are thus important for biodiversity outcomes, but because they

often co-vary, their separate effects remain poorly understood. Therefore, and especially in the context of rapidly changing coffee management in Ethiopia, a better understanding of the effects of landscape context and site-specific conditions is urgently needed to inform appropriate management practices.

Here, we used birds as a focal taxon. Birds play important functional roles in ecosystems, as seed dispersers, pollinators, predators and ecosystem engineers, thereby providing a direct link between biodiversity and ecosystem functions and services (Şekercioğlu, 2006). In Ethiopia, few studies have documented the effects of coffee management on bird diversity (but see Gove et al., 2008; Buechley et al., 2015; Engelen et al., 2016). Existing studies suggest that relatively intensively managed coffee systems had higher species richness than forests with more sparse coffee (Buechley et al., 2015), but that forest specialists may decline with increasing coffee density (Gove et al., 2008). Notably, to date, the value of undisturbed forest areas has not been systematically compared with locations managed at different intensities, and the effects of site-specific characteristics and landscape context remain poorly understood. To overcome these shortcomings, we investigated (i) how bird community composition changes along a gradient of coffee forest management; and (ii) how management intensification and landscape characteristics relate to the richness and abundance of different groups of birds, including functional groups and species with different range sizes.

## 2. Material and methods

### 2.1. Study area

Our study was conducted in an area of approximately 3800 km<sup>2</sup> in the Jimma Zone, Oromia (Fig. 1). It focused on three districts (*woredas*): Gera, Gummy and Setema. The region is undulating, with steep slopes and flat plateaus in some areas, and elevation ranges from 1900 to 3000 m above sea level. The climate is conditioned by the Inter-Tropical Convergence Zone (Schmitt et al., 2013), with 1500–2000 mm of annual rainfall (Friis et al., 1982), and a mean annual temperature of approximately 20 °C (Cheng et al., 1998). The region is part of the



Fig. 2. Examples of southwestern Ethiopian forests with increasing coffee dominance: (a) deep forest interior without management for coffee production; (b) forest interior with low coffee management intensity; and (c) forest that is intensively managed for coffee production.

Eastern Afromontane Biodiversity Hotspot (Mittermeier et al., 2004), and natural vegetation is dominated by moist evergreen Afromontane forest (Friis et al., 1982). Common canopy tree species include *Olea welwitschii*, *Pouteria adolfi-friederici*, *Schefflera abyssinica*, *Prunus africana*, *Albizia spp.*, *Syzygium guineense*, *Croton macrostachyus* and *Cordia africana* (Cheng et al., 1998). Coffee is native to the region and primarily occurs between altitudes of 1500 and 1900 m (Senbeta et al., 2014). Existing studies suggest a high richness of both trees (> 140 species; Senbeta et al., 2014) and birds (> 110 species; Gove et al., 2008; Engelen et al., 2016), including some endemics. Approximately half of the study area is covered by forest, while the remainder is used for smallholder farming. Human population density in the region has been steadily increasing for several decades (Teller and Hailemariam, 2011). Consistent with this, since the 1970s, forest cover has been decreasing, mainly as a result of the conversion of forest to farmland (Cheng et al., 1998; Hylander et al., 2013).

## 2.2. Selection of survey sites and land cover mapping

We aimed to capture the entire gradient of available forest conditions, both in terms of coffee management and remoteness (Fig. 2). Unlike many other authors, we specifically avoided a priori categories such as “forest coffee”, “semi-forest coffee”, “semi-plantation”, “plantation” and “garden coffee” (e.g. Hundera et al., 2013; Tadesse et al., 2014b; Worku et al., 2015). Despite their intuitive appeal, such classifications are not consistently defined across different studies and regions (Philpott et al., 2008; Moguel and Toledo, 1999).

To establish survey sites, first, we selected five *kebeles*, which represent the smallest administrative unit in Ethiopia. *Kebeles* are meaningful units from both social and biodiversity perspectives. It is at the *kebele* level that important land use decisions are taken. Also, logistics, including research permits, are tied to the *kebele* level. From a biodiversity perspective, *kebeles* are also a relevant unit: they are relatively homogeneous units in terms of policy regime and their size is typically relevant as “landscape context” for organisms such as birds. *Kebeles* were selected to cover different social and landscape contexts: ranging from higher to lower dependence on coffee, from higher to lower levels of isolation from major towns, and from high to low levels of forest cover. Their size ranged from 19 km<sup>2</sup> to 52 km<sup>2</sup>. We used RapidEye satellite images from 2015 (5 m resolution) to derive a map of woody versus non-woody vegetation, using an automatic classification routine, based on Maximum Likelihood in ArcGIS (ESRI, 2013).

Second, we sought to stratify our sites in a way that most likely captured the full gradients of site-specific conditions and landscape context. To this end, and since we had no a priori knowledge of the survey sites, we created a map of the ‘cost distance’ to each point within the forest from the closest point of adjacent farmland. We assumed that management level (and consequently the naturalness of the site) would

be closely related with people’s accessibility to the forest, a proxy for the level of human interference. Therefore, remote sites would have a very low or no management for coffee, whereas more intensive management could be expected in more easily accessible areas.

We used the cost distance analysis tool in ArcGIS, which takes into account the distance to a given point and includes a penalty for steep slopes. A total of 66 survey sites were randomly distributed within the 5 *kebeles* (between 8 and 21 points per *kebele*) in four cost distance classes (low, medium, high and very high cost distance). Thus, our survey sites were located in forests varying in accessibility and in the degree of management for coffee production (Fig. 2). The gradient of environmental conditions thus spanned sites located in intact, remote forest to sites located in relatively intensively managed shade coffee forest. More intensively managed forest coffee sites were characterized by a higher level of understory clearing and canopy thinning and pruning. Despite their reduced diversity in woody species, these sites originated directly from patches of undisturbed forest and still contained relict trees of the original canopy cover.

## 2.3. Data collection

### 2.3.1. Bird data

We sampled birds using two repeated 15 min point counts, within 1 ha circular sites (radius = 56 m) around each of the 66 previously identified locations, between November 2015 and February 2016. Sampling took place between 06 h00 and 10 h30 in the morning. All birds seen or heard within the sites were recorded. A recorder (Linear PCM Olympus LS-14) was used to aid post hoc identification of birds not identified in the field. Surveys were cancelled on rainy and foggy days and all birds flying over, plus raptors, swifts and swallows were excluded. Bird species were classified into different ecological groups according to (1) diet, (2) foraging strategy, (3) migration status, (4) forest dependency, and (5) degree of endemism. Diet and foraging strategies described the use of forest resources in terms of major food sources and vertical strata explored, while migration status described the degree of seasonal movements and residency of birds. Forest dependency referred to the level of association with forest habitat. Diet and foraging strategy were gathered from the Elton Traits Database (Wilman et al., 2014). Forest dependency, migration status and the degree of endemism were derived from Birdlife International’s World Database, 2016 (retrieved at <http://www.birdlife.org/datazone>) and complemented with data from The Handbook of the Birds of the World (Del Hoyo et al., 2014). The degree of endemism was calculated for each species as the inverse of their documented spatial extent of occurrence.

### 2.3.2. Vegetation and environmental data

We surveyed woody vegetation at each survey point, in a plot of

20 m by 20 m. In each plot we quantified three management-related variables: (1) woody plant species richness, (2) mean diameter at breast height of woody species (dbh), and (3) coffee dominance. Woody plant species richness was assessed for shrubs and trees with heights  $\geq 1.5$  m and dbh  $\geq 5$  cm. Mean dbh per plot was calculated as the average dbh of all woody plant species that met these criteria. Coffee dominance was assessed as ranging from 0 to 1, and calculated as the ratio of the number of coffee plants to the total number of woody plants in each plot. In addition to vegetation data, we considered three landscape-related variables: (1) distance to the forest edge, (2) a wetness index, and (3) proportion of canopy cover within a 200 m radius. Distance to the forest edge was calculated from the centre of the survey site to the closest edge. Here, we used Euclidean distance (ranging between 10 and 900 m) rather than the cost distance used for site selection because the two measures were highly correlated, and Euclidean distance had a more direct interpretation. The topographic wetness index was derived using the ArcHydro Toolbox in ArcGIS (ESRI, 2013), based on the ASTER Global Digital Elevation Model v2 (30 m resolution; <https://reverb.echo.nasa.gov/>). Canopy cover within a 200 m buffer around each survey site was calculated from the map of woody vegetation derived from RapidEye imagery.

#### 2.4. Data analysis

To investigate patterns in bird community composition and their relation with environmental variables we used detrended correspondence analysis (DCA) and canonical correspondence analysis (CCA). We first used the DCA to explore the length of the environmental gradient and to determine the degree of species turnover in the community (a first axis length  $> 4$  standard deviations represents a complete turn in species composition (Hill and Gauch, 1980)). We then performed a CCA to explore the patterns of community composition in relation to the environmental variables (ter Braak, 1986). Both DCA and CCA were performed on the bird community matrix of raw abundances, with rare species downweighted. For the CCA all vegetation and environmental predictors were scaled and tested for significance ( $p < 0.05$ ) using 999 permutations (package *vegan* (Oksanen et al., 2013) in R (R Core Team, 2016)).

For visualization purposes, we divided survey sites into two groups according to their degree of coffee dominance. Coffee occurs naturally at very low densities in unmanaged forest. Therefore, we adopted a cut-off value of coffee dominance to visualize relatively natural conditions as follows: sites with coffee dominance  $< 0.2$  included minimal or no management for coffee (“without management”), whereas the remaining sites (coffee dominance  $\geq 0.2$ ) were considered to be managed for coffee production (“with management”). Indicator species analysis was used to explore the composition of bird assemblages at sites with and without coffee management. An indicator value (IndVal; varying between 0 and 1) was estimated for each species according to Dufrêne and Legendre (1997). Here, the maximum value (IndVal = 1) is attributed to a species when it is found in all sites of a group (maximum specificity) and exclusively within that group (maximum fidelity). A species was considered to be an indicator when its IndVal  $\geq 0.5$  for a  $p < 0.1$  (randomization procedure based on 999 permutations). The analysis was performed using the function *multipatt* in the package *indicspecies* (De Cáceres and Legendre, 2009) in R (R Core Team, 2016).

To model the effects of predictors on richness and abundance of different groups of birds we used generalized linear mixed models (GLMM). We used a Poisson distribution with log-link function for count data response variables and a Gaussian distribution with identity link for endemism (Zuur et al., 2009). *Kebele* was used as a random effect to account for spatially nested survey sites. We inspected models for overdispersion by examining residual plots. Models did not show evidence of overdispersion. Given high variation and multicollinearity among environmental predictors, we performed a principal components analysis (PCA) with varimax rotation to summarize the variation in

environmental variables. We then used the rotated axes of the PCA as fixed effects in all models. All variables were scaled and centred before the PCA. Richness and abundance of the different bird groups were used as response variables. Total species richness was derived based on pooled data from both survey rounds, and total abundance was calculated as the maximum of individuals observed in a single survey. Modelling was performed in R (R Core Team, 2016) using packages *lme4* (Bates et al., 2015) and *DHARMA* (Hartig, 2016).

### 3. Results

We recorded 1344 individual birds from 76 species and 32 families (Table A1). Orioles (*Oriolus monacha* and *O. larvatus*), montane white-eye (*Zosterops poliogastrus*), green-backed camaroptera (*Camaroptera brachyura*), Rueppell's robin-chat (*Cossypha semirufa*) and Ethiopian boubou (*Laniarius aethiopicus*) were the most frequently encountered species. Twenty-one species were endemic to the Horn and Eastern Africa (Table A1), six of which were endemic to the highlands of Ethiopia and Eritrea: the yellow-fronted parrot (*Poicephalus flavifrons*), black-winged lovebird (*Agapornis taranta*), Abyssinian slaty flycatcher (*Melaenornis chocolatinus*), thick-billed raven (*Corvus crassirostris*), Abyssinian woodpecker (*Dendropicos abyssinicus*) and wattled ibis (*Bostrychia carunculata*). The number of bird species ranged from 4 to 20 per site, and the number of individuals from 5 to 37. We recorded 92 woody plant species (4 to 31 per site).

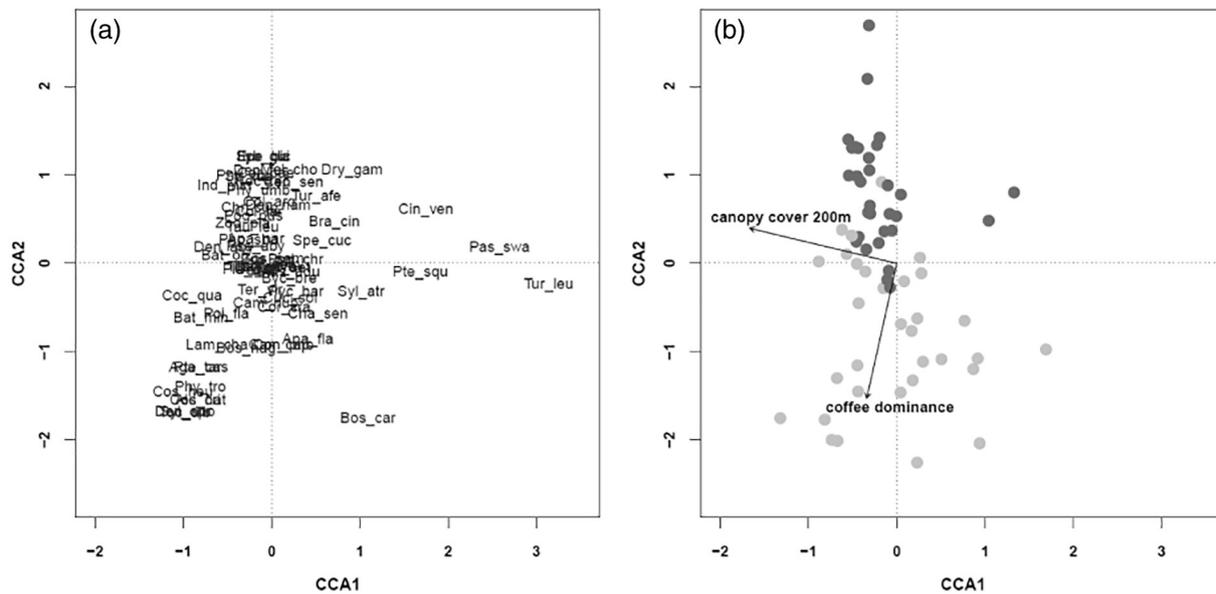
#### 3.1. Community composition

The first DCA axis suggested less than one complete species turnover (length of 2.18 standard deviations), indicating substantial species overlap between sites. The CCA showed that bird community composition significantly correlated with environmental predictors ( $F = 1.597$ ,  $p < 0.05$ ). Significant environmental predictors associated with bird community composition were “coffee dominance” ( $F = 2.064$ ,  $p < 0.01$ ; Fig. 3) and “canopy cover 200 m” ( $F = 2.349$ ,  $p < 0.05$ ; Fig. 3). Four indicator species were found for sites without coffee management: the narina trogon (*Apaloderma narina*), white-cheeked turaco (*Tauraco leucotis*), brown woodland-warbler (*Phylloscopus umbrovirens*), and African hill-babbler (*Pseudoalcippe abyssinica*). One indicator species, the paradise flycatcher (*Terpsiphone viridis*), was found for sites with coffee management.

#### 3.2. Bird responses to environmental gradients

The first two axes of the rotated PCA together explained 54% of variation in environmental data (Table 1). The first rotated axis (rPC1) explained 28% of the variation and represented a management gradient. Positive values of rPC1 indicated higher plant species richness and larger mean dbh values, whereas negative values indicated a higher dominance of coffee shrubs, lower plant species richness and smaller mean diameters. Thus, rPC1 represented a gradient from high naturalness (at high values) to intensive coffee management (at low values). The second rotated axis (rPC2) explained 26% of variation, and described a gradient of landscape context. Low values were assigned to sites closer to the forest edge, with little surrounding canopy cover, whereas high values described sites far from the edge, with more surrounding canopy cover (Table 1).

In the mixed models, total species richness and total abundance did not respond to either gradient (Table A2). However, richness and abundance of highly forest dependent species, as well as richness of midhigh foragers responded positively to both lower intensity of management (rPC1) and higher canopy cover (rPC2) (Table 2, Fig. 4). Richness of insectivores responded positively to increasing canopy cover and distance from the edge. Both richness of frugivores and abundance of insectivores increased with less intensive management (Table 2, Fig. 4).



**Fig. 3.** CCA ordination diagrams of bird community along the environmental gradients: (a) representation of species (species codes provided in Table A1); (b) representation of survey sites (dark grey correspond to sites “without coffee management” and light grey dots correspond to sites “with coffee management”); only variables with a significant relationship ( $p < 0.05$ ) with bird community composition are represented by arrows. Labels of environmental variables: coffee dominance at the site (“coffee dominance”); proportion of tree canopy cover within a 200 m radius (“canopy cover 200 m”). Note that the positive x-axis has been truncated to improve readability and one site (at  $x = 6.994$  and  $y = -0.343$ ) and five species (Vid\_cal, Ser\_str, Ser\_cit, Cen\_mon and Mel\_edo, all with coordinates at  $x = 4.010$  y =  $-0.121$ ) therefore are not shown.

**Table 1**

Principal component analysis loadings after varimax rotation, and variance explained by the first two components (rPC1 and rPC2). Bold values represent the highest loadings on the positive and negative sides of the axes. Both components were used in the generalized linear mixed model analysis as predictor variables.

Variable	rPC1	rPC2
Plant species richness	<b>0.78</b>	0.15
Coffee dominance	<b>-0.65</b>	-0.27
Tree diameter (dbh)	<b>0.78</b>	-0.11
Distance edge	0.19	<b>0.84</b>
Canopy cover (200 m)	0.06	<b>0.86</b>
Wetness	0.11	0.03
% variance explained	28.0	26.0

#### 4. Discussion

The vast majority of studies assessing the effects of management for coffee production on biodiversity focus on the Neotropics. Although Ethiopian shade coffee may in fact be among the most bird-friendly coffee in the world (Buechley et al., 2015), prior to this study, little was known about bird distribution in the moist Afromontane forests of southwestern Ethiopia (but see Gove et al., 2008, Buechley et al., 2015, Engelen et al., 2016). More specifically, the effects of coffee production

of different intensities, in different landscape contexts, and especially as compared to remote areas were virtually unknown in this biodiversity hotspot. In contrast to the common situation where landscape context and site-specific variables strongly co-vary, we found two independent gradients influencing community composition, richness, and abundance of bird groups. First, we identified a management gradient (from a high degree of forest naturalness to relatively intensive coffee management) to affect birds. Second, birds were influenced by a landscape context gradient (from the forest edge towards higher canopy cover in the interior). Our analyses highlighted that (1) despite considerable bird diversity, species turnover in the forest was relatively low; (2) total richness and abundance of birds were not affected by management or landscape context; but (3) the richness of forest and dietary specialists increased with higher forest naturalness, and with increasing distance from the edge and amount of canopy cover. We discuss these findings in relation to existing studies from Ethiopia and other tropical regions, and deduce implications for bird conservation.

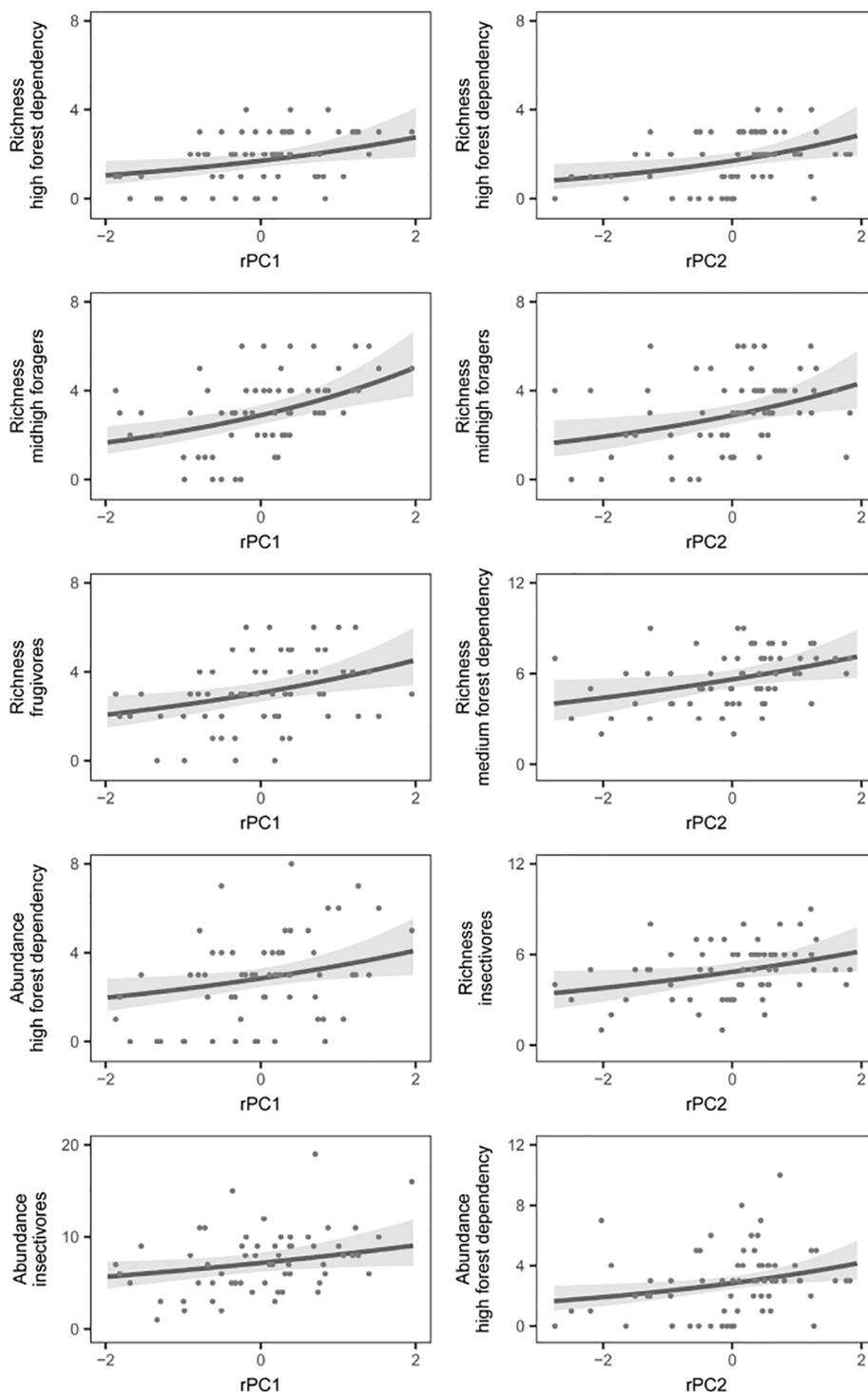
##### 4.1. Findings in relation to existing studies from Ethiopia and other tropical regions

By using a spatially fully randomised design, with unbiased placement of survey sites away from roads and major tracks, we were able to cover a gradient of coffee production that was larger than the gradients

**Table 2**

Results of generalized linear mixed models, assessing the effect of forest management on richness and abundance of bird groups. In all models *kebele* was included as a random effect. Only significant models are shown ( $n = 7$  from a total of 21). rPC1 refers to the coffee management effect and rPC2 refers to the landscape context effect. Refer to Table A2 in Supplementary material for the remaining models. Codes for the significance levels: \*\*\* $p < 0.001$ , \*\* $p < 0.01$ , \* $p < 0.05$ .

	Intercept [SE]	rPC1 [SE]	rPC2 [SE]	Variance <i>kebele</i> [SE]
<b>(a) Richness</b>				
High forest dependency	0.531 [0.097]***	0.242 [0.098]*	0.263 [0.101]**	0.000 [0.000]
Medium forest dependency	1.726 [0.052]***	0.096 [0.053]	0.122 [0.054]*	0.000 [0.000]
Frugivores	1.117 [0.071]***	0.197 [0.069]**	0.067 [0.071]	0.000 [0.000]
Insectivores	1.579 [0.056]***	0.102 [0.057]	0.124 [0.058]*	0.000 [0.000]
Midhigh foragers	1.064 [0.074]***	0.278 [0.073]*	0.204 [0.075]**	0.000 [0.000]
<b>(b) Abundance</b>				
High forest dependency	1.045 [0.074]***	0.183 [0.075]*	0.196 [0.077]*	0.000 [0.000]
Insectivores	1.971 [0.072]***	0.118 [0.056]*	0.088 [0.056]	0.013 [0.114]



**Fig. 4.** Responses of different bird groups to rotated PCA axes describing the environment. Only significant responses are represented. Data points are displayed in dark grey and light grey areas indicate 95% confidence intervals for the regression lines. rPC1 refers to the gradient of coffee management, with increasing values representing an increase in forest naturalness and a decrease in coffee management intensity. rPC2 refers to a gradient of landscape context with high positive values describing sites further away from the forest edge and with higher proportion of forest cover.

covered in previous studies in the region. This approach yielded interesting findings. Unlike in most other studies, our data revealed independent effects of site-specific conditions and landscape context, with our results suggesting that both are important in determining richness and abundance of different bird groups.

Site-specific conditions and landscape context are shaped by environmental parameters and human interventions, and can influence species diversity and community composition (Clough et al., 2009). Bird diversity and composition are known to be affected by both local vegetation attributes (MacArthur and MacArthur, 1961) and landscape context (Banks-Leite et al., 2010; Carrara et al., 2015). In most systems, site-specific effects and landscape context effects are confounded (and

thus difficult to separate) because of an interplay of local and landscape processes via edge effects (Harper et al., 2005). In contrast, our analysis identified a clear separation of site-level, management-related attributes and landscape context. This unexpected finding suggests that some patches of forest are intensively managed, even though they are deep within the forest interior; while other patches remain relatively undisturbed, even though they are close to the forest edge. This, in turn, enabled us to assess whether birds responded primarily to management or to landscape context, a finding with important implications for conservation.

Total bird richness and abundance did not respond to either management or landscape context gradients. The lack of response to

management is in line with a study from Tanzania, which found no effect of land-use intensification (from forest to coffee plantations) on the richness and abundance of birds and bats (Helbig-Bonitz et al., 2015). However, Buechley et al. (2015) found higher species richness in relatively intensively managed coffee systems than in forests with more sparse coffee, whereas many other studies have documented declines of overall richness and abundance of birds with coffee management intensification (reviewed in Komar, 2006 and in Philpott et al., 2008). The relatively small contrast between intensively and less intensively managed coffee forest sites in our study area may explain these differences.

Unlike for total richness and abundance, we observed responses to the forest management gradient for the richness and abundance of forest specialists, abundance of insectivores, and richness of midhigh foragers and frugivores. Homogenization of vegetation structure and composition has been reported to be detrimental for both forest specialists and insectivorous birds elsewhere (Şekercioğlu et al., 2002; Perfecto and Vandermeer, 2008). Forest specialists are highly dependent on forest interior habitat and on specific microclimatic conditions. Insectivores, in particular, are known to benefit from high vegetation structural complexity, which is closely associated with food availability for this group (Mas and Dietsch, 2004; Philpott et al., 2008). Management intensification therefore can have detrimental effects for these ecological groups: for example, pruning and thinning of the canopy and slashing of the understorey could reduce the availability and diversity of foraging sites (Waltert et al., 2005). Finally, landscape context also affected some ecological groups: highly and medium forest dependent species, insectivores and midhigh foragers were sensitive to the edge-interior gradient, with more species found in interior sites surrounded by high canopy cover. Species classified as highly dependent on forest showed an increase in both richness and abundance at sites that were located further from the forest edge, highlighting the importance of interior forest, irrespective of management, for some species.

Finally, with respect to bird community composition we found it to be relatively stable along the gradient of forest naturalness versus coffee management. While other studies have reported much higher turnover rates for birds in coffee systems, our results are broadly consistent with previous research in the region (Buechley et al., 2015). Discrepancies with other studies may be explained in two ways. First, many studies of bird communities in coffee growing areas have included homegardens (e.g. Gove et al., 2008; Helbig-Bonitz et al., 2015) or more intensive land uses such as sun coffee plantations (e.g. Greenberg et al., 1997a). This greatly increases the likelihood of finding high species turnover, by adding species that are associated with farmland habitats and open areas. Second, when compared with studies from the Neotropics (e.g. Tejada-Cruz and Sutherland, 2004; Greenberg et al., 1997b), community turnover in our study may be relatively low because evolutionary processes have led to a greater pool of species in the Neotropics (Jetz et al., 2012).

#### 4.2. Conservation implications

There is a lively debate in the scientific community regarding the best approaches to retain biodiversity while securing livelihoods (Fischer et al., 2014, 2017). Two major discourses stand out: “land sparing” versus a focus on “countryside biogeography”. The discourse on land sparing emphasises the supreme importance for conservation – especially of sensitive species – of maintaining large blocks of undisturbed forest (Green et al., 2005; Phalan et al., 2011; Hulme et al., 2013). On the other hand, countryside biogeography highlights the value of integrated management of conservation and production areas throughout the landscape “matrix”, that is, areas outside natural forest (Daily, 2001). Our findings show that these discourses need not be mutually exclusive (Kremen, 2015).

One main finding of our study was the relative stability of community composition and richness and abundance of bird species along

the gradient of coffee management. This suggests that under traditional shade coffee management practices, diverse forest bird communities can persist, as also observed elsewhere (e.g. Greenberg et al., 1997b). Our study thus underlines that appropriately managed forest ecosystems, where habitat complexity and plant species diversity are fostered, can serve conservation purposes while also contributing to rural livelihoods. Yet, our second major finding demonstrates that certain species (e.g. the Abyssinian ground-thrush and African hill-babbler) were primarily found in relatively remote areas with high naturalness. This supports existing evidence that conservation of sensitive species hinges on protecting areas that are largely free from human disturbance, for example via a strategy of “land sparing” (Gibson et al., 2011).

By separating the effects of site-specific conditions and landscape context on bird diversity we showed that both influence the richness and abundance of different bird groups – indicating that conservation measures need to consider both local and landscape scales. For instance, forest specialists and insectivores responded to the gradient of landscape context, implying that to assess only site-conditions would be insufficient. Yet, other species responded strongly to site level conditions, suggesting that looking exclusively at landscape context would ignore the potentially major benefits for conservation of retaining high structural complexity for local bird diversity. From a conservation perspective, we argue that the maintenance and protection of large undisturbed areas of natural forest should receive the highest priority, because many forest specialist are highly dependent on undisturbed areas. However, where the protection of large patches of remote forest is not possible, even fragmented forest managed at low intensities can support a diverse bird community. In the context of rapidly changing coffee production systems in Ethiopia, participatory forest management may help to achieve conservation goals on the ground. In our study area, three of the *kebeles* are within two Forest Priority Areas, the Sigo-Geba and Belete-Gera areas (UNEP-WCMC, 2016). These priority areas were established in the 1980s with the aim to protect and manage the remaining natural forests. To date none of these areas has been legally constituted and only Belete-Gera has a provisional forest management agreement between the government and the local community, which prevents the on-site enforcement of conservation provisions.

#### 5. Conclusion

Traditional coffee agroforests in southwestern Ethiopia host a diverse community of birds. However, some uncertainty still remains regarding the potential of these systems to host sensitive species such as forest specialists. Thus, while coffee agroforests are valuable for bird conservation they should not be considered a replacement for natural undisturbed forests. The landscape of southwestern Ethiopia is vulnerable to the intensification of traditional coffee agroforest systems and to the conversion of natural forests into agricultural land. Because coffee production in the region is of great importance for rural livelihoods, guidelines for coffee production should both secure livelihoods as well as promote biodiversity. Management strategies and certification schemes that encourage traditional practices (i.e. that foster habitat complexity and heterogeneity) and the retention within the matrix of large undisturbed natural forests should be promoted in the region if conservation and rural livelihoods improvement are to be achieved together.

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## Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.biocon.2017.10.036>.

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