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Bird and bat diversity, herbivory and trade-offs with yield in coffee agroforests in Arabica coffee's native range

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ABSTRACT

Agroforestry systems have the potential to provide benefits for conservation, natural pest control and farmer livelihoods. Yet, we need a clearer understanding of how environmental drivers shape different components of biodiversity, how these biodiversity components contribute to suppressing pest levels, and how biodiversity trades off with yield. We focused on the diversity and role of birds and bats across different types of coffee farms in Arabica coffee's native range in southwestern Ethiopia. While elevation, canopy cover, shade tree community composition and surrounding forest cover did not explain bird and bat species richness, the composition of the bird and bat community was significantly influenced by the composition of the shade tree community. Herbivory was unrelated to the species richness and community composition of insectivorous birds and bats. We found no trade-off between bird and bat species richness and coffee yield, but the composition of the bird, but not bat, community changed with increasing yield, where forest specialist birds rapidly declined in abundance from low to mid-yielding sites. Overall, we suggest that the similar levels of bird and bat species richness and an absence of a relationship with herbivory across different types of agroforests are due to the diverse mosaic agricultural landscape and lack of agroforests with very high management intensities (which are common in other parts of the world). From a conservation point of view, intensification of coffee management in the lowest-yielding sites would threaten biodiversity in terms of forest specialist birds. However, is it also important to learn more on the potential positive roles of biodiversity in those parts of the landscape where coffee is managed for high yields. From both a conservation and sustainable management point of view we urgently need more insights into the taxonomy, life-history, habitat preferences and foraging ranges of East African bats.

Introduction

Tropical forests are rapidly disappearing, often due to agricultural expansion (Chaplin-Kramer, et al. 2015; Laurance, Sayer & Cassman 2014). In landscapes threatened by deforestation, agroforestry can provide incentive to conserve some of the forest biodiversity or restore the cover of native trees as shade for the focal agricultural crop (Hylander, et al. 2024; Perfecto, Rice, Greenberg & Van der Voort 1996). While the agroforestry crop provides local livelihoods, the shade trees and forest-like structure can bolster biodiversity and provide ecosystem services such as natural pest control (Clough, et al. 2010; Somarriba, et al. 2004). Nevertheless, we need more knowledge on how environmental drivers shape different components of biodiversity within agroforestry systems, how biodiversity contributes to natural pest control, and the existence and type of trade-offs between biodiversity and crop yield.

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While birds and bats are important components of the biodiversity in many agroforestry systems, there is much variation among individual farms (Ferreira, et al. 2023; Imron et al. 2022; Variar et al. 2021). To improve the conservation of bird and bat diversity in agroforestry systems, it then becomes crucial to understand the abiotic and biotic environmental drivers of bird and bat diversity. Bird species richness is often similar in forests and agroforests, if not slightly higher in the latter (Harvey & González Villalobos 2007). However, the assemblage of bird species may differ, as forests and more natural agroforests can provide habitats for forest specialists, while more open agroforests can provide habitats for generalists and species otherwise found in savannas and other semi-open habitats (Gove, et al. 2008; Harvey & González Villalobos, 2007). Bats often have large home ranges and forage in a variety of different habitats in a landscape (Estrada, Coates-Estrada & Meritt Jr 1993). This might lead to similar species richness and community composition across a landscape, even though open habitat specialists are more likely to be found in agroforests than in forests (Harvey & González Villalobos, 2007; Maas et al. 2016; Williams-Guillén & Perfecto 2011).

In agroforestry systems, birds and bats can play an important functional role by feeding on insects, thereby reducing pest levels (Maas et al. 2016; Williams-Guillén, Perfecto & Vandermeer 2008). Several observational studies and exclusion experiments have indeed shown that birds and bats provide natural pest control services within tropical agroforestry systems (Bael et al. 2008; Karp et al. 2013; Williams-Guillén et al. 2008). As one example, a study by Schmitt et al. (2021) showed that the abundance of herbivorous insects was higher when both birds and bats were excluded from agroforests. Importantly, these pest control services can be stronger in more natural agroforestry systems with a denser canopy cover, greater plant diversity and lower management intensity than in plantation systems (Bianchi, Booij & Tscharntke 2006; Johnson, Levy, Kellermann & Robinson 2009; Perfecto et al. 2004; Shimales et al. 2023). For example, Karp et al. (2013) found greater insectivorous bird abundance and reduced incidence of coffee berry borer (*Hypothenemus hampei*) infestations in agroforestry landscapes with greater forest cover.

Pressure to increase crop yields in agroforestry causes management intensification, which often – but not always – trades off against biodiversity (De Beenhouwer et al. 2016; Geeraert et al. 2019; Zewdie et al. 2022). The shape of the relationship between crop yield and biodiversity can depend on the environmental context and management practices (lesson 2 in Hylander et al. 2024; Mokondoko, Avila-Foucat & Galeana-Pizaña 2022), and differ between organism groups (Clough et al. 2011; Etana et al. 2021; Wurz et al. 2022). For example, butterflies are more sensitive than ants and birds along a management intensity gradient in Mexico (Perfecto, Mas, Dietsch & Vandermeer 2003). While several studies have explored the relationship between crop yields and bird diversity (Bennett, Sillett, Rice & Marra 2022; Felipe-Lucia et al. 2020; Teuscher et al. 2015), few studies exist on the relationship between crop yield and bat diversity (Ferreira et al. 2023; Maas, Clough & Tscharntke 2013).

Studying the coffee agroforestry system in southwestern Ethiopia offers the unique opportunity of analyzing the agroforestry crop, Arabica coffee (*Coffea arabica*), in its native range, an area characterized by a broad environmental and management gradient ranging from coffee growing in natural forests with extremely low yields to more intensively managed plantations under a canopy of shade trees with high yields (Zewdie et al. 2022). Bird species composition shows some differences, with forests and more natural coffee agroforests holding relatively more forest specialists and insectivores (Buechley, et al. 2015; Gove, Hylander, Nemomissa, Shimelis & Enkossa 2013; Rodrigues et al. 2018). However, bird species richness does not seem to differ when comparing agricultural and forest landscapes (Gove et al. 2013), coffee agroforestry systems and natural forests (Buechley et al. 2015), or coffee agroforestry systems with different levels of management intensity (Rodrigues et al. 2018). Even though a high surrounding forest cover promoted greater attack rates on clay caterpillars by birds in Ethiopian coffee agroforestry, this did not affect observed levels of herbivory (Burger, et al. 2022). In contrast to birds, we know very little about the diversity and role of bats in coffee agroforestry in southwestern Ethiopia (Maas et al. 2013; Mertens, Emsens, Jocqué, Geeraert & De Beenhouwer 2020).

We investigated the diversity and role of both birds and bats in coffee agroforests in southwestern Ethiopia. To this aim, we asked the following questions

1) What is the influence of the abiotic and biotic environment (elevation, canopy cover, shade tree community composition and surrounding forest cover) on the species richness, evenness and community composition of birds and bats?
2) How do species richness, evenness, abundance and community composition of insectivorous birds and bats relate to herbivory on Arabica coffee?
3) What is the shape of the relationship between bird and bat species richness and community composition and coffee yield?

Material and methods

Study system

The study area is located in Gomma and Gera districts in Jimma zone, and forms part of the coffee highlands of southwestern Ethiopia (7°370 - 7°560 N and 36°130 - 36°390 E; Fig. 1). The landscape consists of a mosaic of natural and secondary forests, smallholder coffee farms and plantations, pastures, crop fields and villages (Hylander et al. 2024). While coffee is the main cash crop in the region, khat and various annual crops are also cultivated (e.g. maize, sorghum, teff, wheat and barley) and honey and livestock contribute to local livelihoods as well (Hylander et al. 2024). The average daily minimum and maximum temperatures are 12°C and 28°C, respectively (Gomm et al. 2024; Zignol et al. 2023). Rainfall is unimodal, with a peak during the wet season from May to October, and annual precipitation typically between 1500 and 2100 mm (Gomm et al. 2024; Zignol et al. 2023).

Within the study area, coffee is growing in different management types, including forest coffee where coffee grows as an understory shrub in the natural forests, semi-forest coffee with some management interventions, semi-plantation coffee with a reduced canopy cover and regular management interventions and plantation coffee where management intensity is the highest in the region. In all production systems, coffee is grown under a canopy of native trees, referred to as shade trees, and even the most heavily managed agroforests are relatively natural when compared to the most intensively managed agroforests in other parts of the world, such as Brazil. For example, while herbicides are sometimes used in the more intensively managed sites, pesticides are rarely (if ever) used, and the large majority of shade tree species are native. Species dominating the shade tree layer in the study area are *Acacia abyssinica, Albizia schimperiana, Cordia africana, Croton macrostachyus, Olea welwitschii* and *Syzygium guineense* (Koelemeijer, et al. 2021). Common free-feeding herbivores in southwestern Ethiopia are the coffee giant looper *Acostis selenaria*, the coffee hawkmoth *Cephonodes hylas* and the stinging caterpillar *Parasa lepida* (Shimales et al. 2023).

Site selection and abiotic and biotic environmental variables

To examine the influence of environmental and management variables on the diversity and functional role of birds and bats in coffee agroforests, we selected thirty sites along a broad environmental and management gradient (Fig. 1). These sites are a subset of the sixty sites selected by Zewdie, Tack, Adugna, Nemomissa and Hylander (2020), and were previously extensively characterized in terms of the biotic and abiotic environment. We obtained data on elevation and canopy cover from Zewdie et al. (2020), surrounding forest cover from Koelemeijer

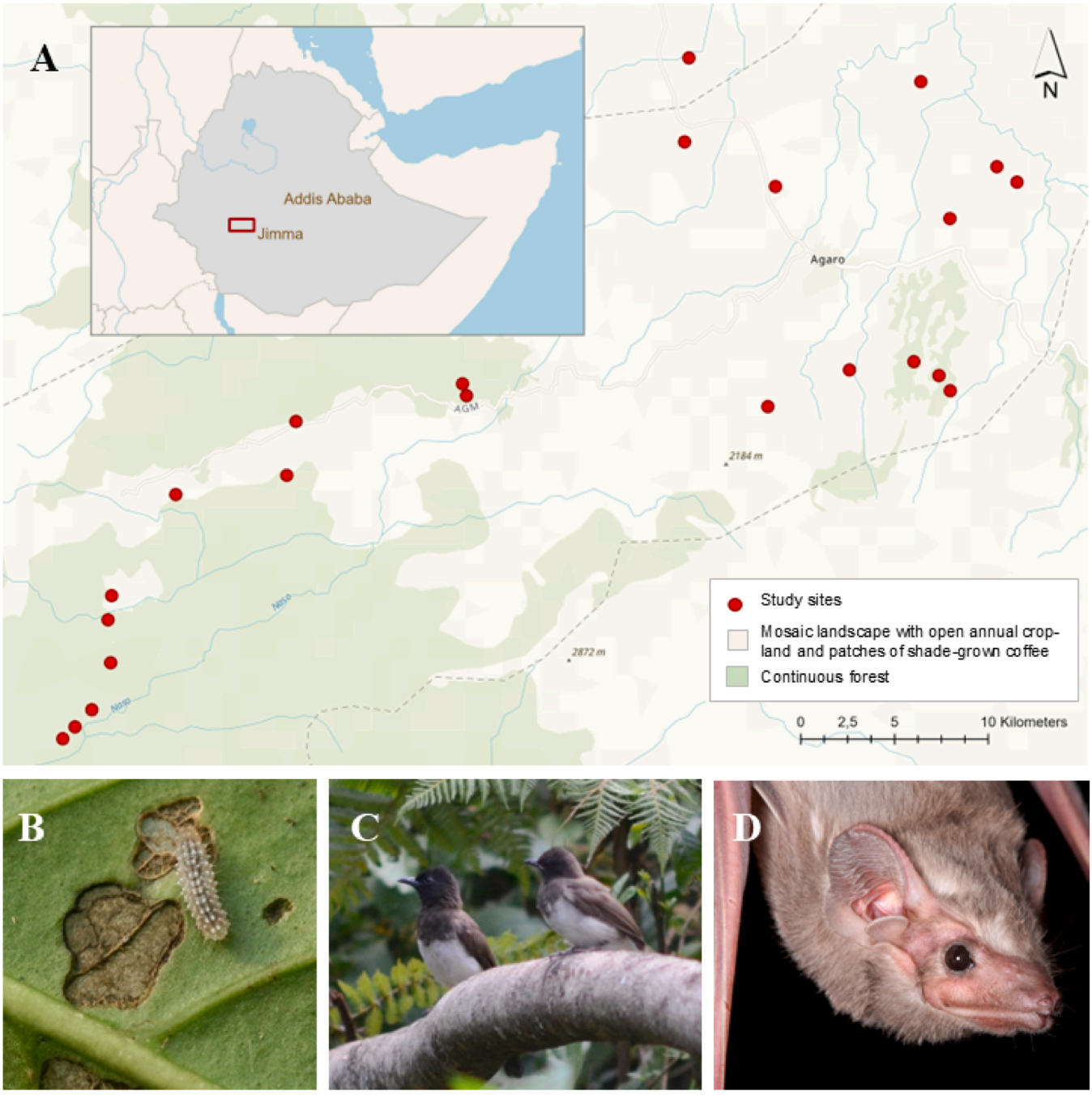

Fig. 1. Overview of the study system. Panel A shows a regional map with the locations of the 23 study sites marked in red, with an inset of the national map in the top-left with the study area in southwestern Ethiopia marked with a red square. The photos below the regional map illustrate B) herbivory (coffee leaf skeletonizer; *Leucoplema dohertyi*; photo by Ayco Tack) and examples of the local C) bird (common bulbul *Pycnonotus barbatus;* photo by Kristoffer Hylander) and D) bat community (Egyptian tomb bat *Taphozous perforatus*, photo by Jens Rydell).

et al. (2021), shade tree species composition and yield from Zewdie et al. (2022), and herbivory from Burger et al. (2022) at each of these sites. The elevation of the studied coffee farms ranged from 1506 up to 2003 m a.s.l. For a detailed description of each variable, see Table 1, Text S1 and Fig. S1.

Recording birds and bats

To characterize the bird and bat community, we placed one AudioMoth acoustic monitoring device (Open Acoustic Devices; Hill et al. 2018) in each of the 30 study sites. During the wet season of 2019, the AudioMoths were set to record at sunrise and sunset for an average of 7 consecutive days per site (range: 5 - 9). Three and four AudioMoth devices were lost to theft and technical failure, respectively. Thus, we used data from a total of 23 study sites in the analyses. For details on the settings of the Audiomoth devices, see Text S1. From a methodological perspective, passive acoustic monitoring of birds and bats is increasingly applied as it enables efficient biodiversity monitoring at large-scales (Darras et al. 2025) and has been shown to perform equally well or better than observer-based monitoring (Hoefer, McKnight, Allen-Ankins, Nordberg & Schwarzkopf 2023; Somveille et al. 2024), even though some less vocal species will be underreported (Buechley et al. 2015; Engelen, Lemessa, Şekercioğlu & Hylander 2017; Hoefer et al. 2023).

Table 1
Description of the variables used in our study. All variables were measured at the same set of thirty sites where we recorded the bird and bat community in the wet season of 2019. For the correlation structure between the environmental variables, see Fig. S1.

Variable name	Description	Data source
Elevation	Meters above sea level of the central point of the study site, measured in the dry season of 2017.	Zewdie et al. (2020)
Canopy cover	Using ImageJ v. 1.50i, we calculated canopy cover in each study site from five photos taken in the dry season of 2017. The five photos were taken above the height of the coffee shrubs, aiming vertically upwards, from the central point of the study site and the four corners of an inner 30 × 30 m plot.	Zewdie et al. (2020)
Surrounding forest cover	In the wet season of 2018, we calculated the proportion of surrounding area with forest cover in a one-kilometer radius for each study site using ArcMAP v. 10.6.1.	Koelemeijer et al. (2021)
Shade tree species composition	Shade tree species composition was calculated in each study site from a species-by-site matrix with the number of individuals of trees and shrubs in a 50 × 50 m plot that were identified in the wet season of 2017. For this, we ran an NMDS-ordination with two dimensions and Bray-Curtis distance measure (stress-value 0.185). We also ran a PCA on the same data and noted that the NMDS-axis 1 correlated well with the first PCA-axis. Since species compositional differences are better represented by Bray-Curtis than Euclidean distances, we chose to use the NMDS axis 1 as our predictor variable in the analyses. Common tree species in the lower end of the gradient are *Chionanthus mildbraedii, Schefflera abyssinica, Olea welwitschii* and *Syzygium guineense* and in the higher end *Cordia africana, Croton macrostachyus, Albizia gummifera* and *A. schimperiana*.	Zewdie et al. (2022)
Yield	Average yield (kg/ha). Coffee yield was estimated for each site from coffee berry numbers of 16 selected coffee shrubs. These counts were performed during the wet seasons of 2017, 2018, 2019 and 2020.	Zewdie et al. (2022)
Herbivory	Free-feeding herbivory was measured on two randomly selected branches of each of 16 permanently marked coffee shrubs per site. On these branches, we noted the proportion of leaves damaged by externally-feeding insects out of the total amount of leaves on the two selected branches. These measurements were taken during the wet season of 2018.	Burger et al. (2022)

Characterizing the bird community

To characterize the bird community, we randomly selected 18 morning recordings of five minutes for each site within the time period of 06:15-07:00 AM (i.e. during sunrise). Within each recording, we identified all bird species (Text S1). The presence-absence of each bird species in each of the five-minute intervals was noted by two bird experts (see acknowledgements) by listening to the recordings. From these data, we obtained three metrics: (i) *Abundance*, which was calculated as the number of 5-minute intervals in which a bird species was recorded (resulting in a maximum abundance of 18 for a given bird species in a given site), (ii) *Species richness*, which is the number of bird species recorded at least once at a site, and (iii) Pielou's *Evenness*. As not all birds are equal from a functional perspective, we classified birds according to their feeding guild based on Mackworth-Praed (1960). Based on this, we also calculated the abundance, species richness and community composition of the insectivorous bird community. For this calculation, we excluded insectivorous birds that do not forage inside of coffee farms (wattled ibis and Hadada ibis).

Characterizing bat community

To characterize the bat community, we analysed all recorded sound files that had no or light rain during a 105-minute period at sunrise and three ten-minute periods at sunset. Due to the lack of a reliable call library for Ethiopian bats (Kaipf & Meinig, 2017; Monadjem, Taylor & Schoeman 2020) it was not possible to accurately identify bat species from their echolocation calls and instead bat passes were assigned to distinct sonotypes (Text S1). This resulted in a total of eight sonotypes (Figs S2 and S3). From the sonotypes classifications, we obtained three metrics: (i) *Abundance*, which was calculated as the number of bat passes of each sonotype recorded at each site, (ii) *Species richness*, which is the number of bat sonotypes recorded at least once at a site, and (iii) Pielou's *evenness*.

Statistics

We conducted all analyses in R v 4.3.2 (R Development Core Team 2023). We modelled the univariate response variables with generalized linear models using the functions *glm* and *lm* in the base package of R. We validated model fit using the packages *sjPlot* (Lüdecke, 2025) and *DHARMa* (Hartig, 2024), and tested for significance ($P < 0.05$) using the function *Anova* in the package *car* (Fox & Weisberg, 2019). We modelled the multivariate response variable community composition using the function *adonis2* (with the term *by* = *"margin"* and a Bray-Curtis dissimilarity matrix) in the package *vegan* (Oksanen et al., 2022).

To examine the impact of the abiotic and biotic environment on the bird and bat community, we modelled species richness, evenness and community composition of birds and bats as functions of elevation, canopy cover, shade tree species composition and surrounding forest cover. For species richness, we specified a Poisson distribution with log link, and for evenness, we used a Gaussian distribution with identity link. For community composition, we used a species-by-site matrix with abundances. We used backward selection of the predictor variables, with a cut-off at $P = 0.1$ to retain predictor variables. We illustrated the results for community composition with an NMDS-ordination of the species-by-site matrix with superimposed correlations of the environmental predictors (i.e., those retained after model selection in the *adonis2*-analysis) using the *envfit* function in the package *vegan*.

To investigate the relationship between herbivory by free-feeding insects and the community structure of insectivorous birds and bats, we modelled herbivory as a function of species richness, evenness, abundance and community composition, separately for the bird and bat community. To fulfill model assumptions, we ln-transformed free-feeding herbivory. In order to create univariate variables that describe variation in the composition of insectivorous birds and bats, respectively, we extracted site scores of the first two axes from an NMDS with the function *metaMDS* from the package *vegan*.

To examine the shape of the relationship between the community structure of the birds (from all guilds) and bats and coffee yield, we modelled the community descriptors (species richness and community structure, separately for birds and bats) as a function of coffee yield using generalized additive models with the function *gam* from the *mgcv* package in R (Wood 2011). In order to create univariate variables that describe variation in the composition of birds and bats, respectively, we extracted site scores of the first two axes from an NMDS with the function *metaMDS* from the package *vegan*. We then ran separate models with NMDS1 and NMDS2 as response variables.

As not all abiotic and biotic environmental variables were collected within the same year, we make different assumptions for each of the questions. Regarding question one, we note that while elevation, canopy

cover, surrounding forest cover and shade tree composition were collected one or two years before we characterized the bird and bat community, these variables are close to static at a time scale of one or two years (personal observations by BZ and BA). Regarding question two, the herbivory data is collected in the wet season of 2018, and the bird and bat community was characterized in the wet season of 2019. Hence, we make the explicit assumptions that the bird and bat community, as well as herbivory, in the wet season in year t is related to the bird and bat community and herbivory in the wet season in year t+1. While we strongly expect the bird and bat community in a given place to correlate between years, the consistency of herbivory between years could be further examined in future work (see *Discussion*). Regarding question three, we wanted to understand how the long-term average yield at the farm (reflecting intensification and farmer livelihood through the role of coffee as a cash crop) is related to biodiversity. As coffee yield is characterised by biennial yield (i.e., a high harvest year is followed by a low harvest year), and there might be spatial asynchrony in the pattern of biennial yield among sites, we averaged yield across four years. As such, we do not test the causal relationship between birds, bats and yield within a given year, but explore the relationship between farms with long-term high yields and the bird and bat biodiversity. The common assumption made here is that the bird and bat biodiversity within a site can be assessed within a single year (Buechley et al. 2015; Engelen et al. 2017; Rodrigues et al. 2018).

Results

We detected a total of 32 bird species across the 23 study sites (Table 2). The average species richness per site was 12.6 (SD: 2.6; range: 8 – 17; Table S1). Out of the 32 bird species, we detected one carnivorous (African fish eagle), four frugivorous (e.g. the silvery-cheeked hornbill and the white-cheeked turaco), three granivorous (e.g. the red-eyed dove and tambourine dove), 19 insectivorous (e.g. the green-backed camaroptera and Rüppell's robin-chat) and five omnivorous (e.g. the Ethiopian oriole and the common bulbul) bird species (Tables 2 and S1). From the bat calls, we identified eight different sonotypes, of which sonotype 2 and 8 were the most common (Tables S2 and S3).

None of the environmental predictors (elevation, canopy cover, shade tree species composition and surrounding forest cover) could explain variation in species richness and evenness of the bird and bat community (Table 3). However, the species composition of both birds and bats was significantly related to the gradient in shade tree species composition (Table 3 and Fig. 2). Bird species characteristic for sites with a shade tree community reflective of natural forests were for example white-cheeked turaco, African paradise flycatcher and Abyssinian trush, whereas Abyssinian slaty flycatcher and Ethiopian white-eye were abundant in sites where the shade tree community was reflective of more intensively managed sites. Regarding the bats, sonotypes 3 and 4, which have relatively narrow band calls that are characteristic of bats utilising more open habitats, were more common in sites where the shade tree community was reflective of the more managed sites, while for example sonotype 1, which has a frequency modulated call type characteristic of bats that utilise a broad range of semi-open to more forested habitats, was found in sites along the entire gradient. There was a trend for an effect of surrounding forest cover on the bat community, where sonotype 7 was characteristic for areas with a high surrounding forest cover and sonotype 4 for areas with a low surrounding forest cover (Table 3 and Fig. 2). Sonotype 7 has a rather broadband call type, which could indicate a preference for more forested habitats.

The average proportion of coffee leaves affected by herbivory was 29.1%, ranging from 10.4% to 83.8% among the sites. Species richness, evenness and community composition of birds and bats, as well as bird abundance, were not significantly related to free-feeding herbivory (Table S4). Bat abundance was positively related to herbivory (Table S4).

Table 2
An overview of bird species detected across 23 coffee sites in the Gomma and Gera districts in southwestern Ethiopia. Shown are the scientific and English names, feeding guild, number of sites present and total abundance. Species names follow GBIF and feeding guild during the wet season is based on Mackworth-Praed (1960). Species are ordered by feeding guild.

Scientific name	English name	Feeding guild	Number of sites present	Total abundance[1]
Icthyophaga vocifer	African fish eagle	carnivore	2	2
Bycanistes brevis	Silvery-cheeked hornbill	frugivore	14	69
Columba arquatrix	African olive pigeon	frugivore	4	5
Poicephalus flavifrons	Yellow-fronted parrot	frugivore	3	6
Menelikornis leucotis	White-cheeked turaco	frugivore	8	13
Streptopelia semitorquata	Red-eyed dove	granivore	13	77
Turtur chalcospilos	Emerald-spotted wood dove	granivore	1	1
Turtur tympanistria	Tambourine dove	granivore	4	9
Apaloderma narina	Narina trogon	insectivore	21	123
Batis orientalis	Grey-headed batis	insectivore	1	1
Bostrychia carunculata	Wattled ibis	insectivore	8	25
Bostrychia hagedash	Hadada ibis	insectivore	9	28
Bradypterus cinnamomeus	Cinnamon bracken warbler	insectivore	1	1
Camaroptera brachyura	*Bleating camaroptera*	insectivore	21	182
Campethera nubica	Nubian woodpecker	insectivore	5	9
Centropus superciliosus	White-browed coucal	insectivore	6	35
Chrysococcyx cupreus	African emerald cuckoo	insectivore	1	1
Cossypha albicapillus	White-crowned robin-chat	insectivore	2	9
Cossypha semirufa	Rüppell's robin-chat	insectivore	15	52
Cuculus clamosus	Black cuckoo	insectivore	6	24
Cuculus solitarius	Red-chested cuckoo	insectivore	21	112
Dryoscopus gambensis	Northern puffback	insectivore	1	1
Laniarius aethiopicus	Ethiopian boubou	insectivore	21	213
Melaenornis chocolatinus	Abyssinian slaty flycatcher	insectivore	8	11
Platysteira cyanea	Brown-throated wattle-eye	insectivore	3	10
Terpsiphone viridis	African paradise flycatcher	insectivore	6	8
Zosterops poliogastrus	Ethiopian white-eye	Insectivore[2]	14	69
Corvus albus	Pied crow	omnivore	3	4
Oriolus monacha	Ethiopian oriole	omnivore	21	169
Pogoniulus chrysoconus	Yellow-fronted tinkerbird	omnivore	17	57
Pycnonotus barbatus	Common bulbul	omnivore	23	223
Turdus abyssinicus	Abyssinian thrush	omnivore	7	13

[1] Total abundance represents the total number of five-minute sound recordings in which the species was detected (out of 18 recordings in each of 23 sites).
[2] This species differs in feeding guild between the wet (insectivore) and dry (frugivore and nectivore) season.

Both bird and bat species richness were unrelated to coffee yield ($F_{1,23} = 1.193$, $P = 0.42$ and $F_{1,23} = 1.946$, $P = 0.17$ for birds and bats, respectively, Table S5 and Fig. 3ab). However, there was a significant non-linear change in bird community composition (the first NMDS axis) with yield, resulting in a different composition of the bird community in sites with low and high yields, respectively ($F_{1,23} = 3.85$, P=0.028, R^2 = 0.31 for NMDS1, Table S5 and Fig. 3c). The shift from a more forest specialist bird community to a more generalist community was fast from low to middle sized yields but did not change after that (Fig. 3c). There was no significant change in the community composition of bats along the yield gradient (NMDS1, $F_{1,23} = 2.5$, $P = 0.11$, $R^2 = 0.19$, Table S6, Fig. 3d).

Discussion

We investigated the environmental drivers of the structure of the bird and bat community, the relationship between the bird and bat community and natural pest control, and how bird and bat species richness and composition trade-off with yield across agroforests in southwestern Ethiopia. These agroforests differed strongly in naturalness, ranging from coffee growing with little or no management in the natural forest to more intensively managed sites (but still with a shade tree cover). While both bird and bat species composition shifted with shade tree species composition, bird and bat species richness could not be explained by the tested predictor variables. Variation in herbivory was not related to bird and bat species richness and composition. Only bird, and not bat, species composition changed along the yield gradient.

We propose that the mosaic landscape in southwestern Ethiopia, with its high levels of heterogeneity and low levels of intensification, allows for the existence of relatively uniform levels of bird and bat species richness and levels of natural biocontrol across all types of agroforestry sites (Engelen et al. 2017; Hylander et al. 2024). Notably, forest specialist birds rapidly declined in abundance from low to mid-yielding sites, indicating that for the conservation of forest specialist birds we need to halt deforestation and the intensification of management in the lowest-yielding sites. More research is urgently needed to understand the implications of our findings for bat conservation.

While elevation, canopy cover, shade tree community composition and surrounding forest cover did not explain bird and bat species richness, the composition of the bird and bat community was significantly influenced by the composition of the shade tree community. The lack of an effect of the environmental predictors on the species richness of birds matches with related studies within the same region. Buechley et al. (2015), Gove et al. (2008; 2013) and Rodrigues et al. (2018) found no differences in bird species richness between forests and agroforests, and Engelen et al. (2017) found no differences between forests and home gardens. These findings might be explained by the heterogeneous agricultural landscape in southwestern Ethiopia, which is characterized by a mosaic of home gardens, relatively small crop fields, grazing lands, and a large diversity and abundance of native trees, which allows for a large diversity of birds not only in the forests but also in the agricultural matrix (see discussion in Engelen et al. 2017). In contrast to our study, and the above cited studies from the same landscape, there are many studies showing lower richness and diversity of birds in human modified, but still tree-rich habitats (e.g. Aycart-Lazo et al. 2025; Bedoya-Durán, Jones, Malone & Branch 2023; Imron et al. 2022). Interestingly, in a global meta-analysis comparing birds in low versus high shade coffee systems, Africa stood out as not displaying lower richness and diversity in low shade systems that otherwise was the general pattern (Manson, Nekaris, Nijman & Campera 2024). In contrast

Table 3
Impact of elevation, canopy cover, shade tree species composition and surrounding forest cover on the species richness, evenness, and composition of the bird and bat community in the Gomma and Gera districts in southwestern Ethiopia, as based on generalized linear models and multivariate analyses. Significant P-values are listed in bold. Horizontal dashes represent predictor variables from the full model that were removed during model selection.

	Bird species richness			Bird evenness			Bird community composition			Bat species richness			Bat evenness			Bat community composition		
	df	χ^2	*P*	df	F	*P*	df	F	*P*	df	χ^2	*P*	df	F	*P*	df	F	*P*
Elevation	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Canopy cover	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
Shade tree species composition	-	-	-	-	-	-	1, 21	3.41	**<0.001**	-	-	-	-	-	-	1,20	4.02	**0.011**
Surrounding forest cover	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	1,20	2.47	0.055

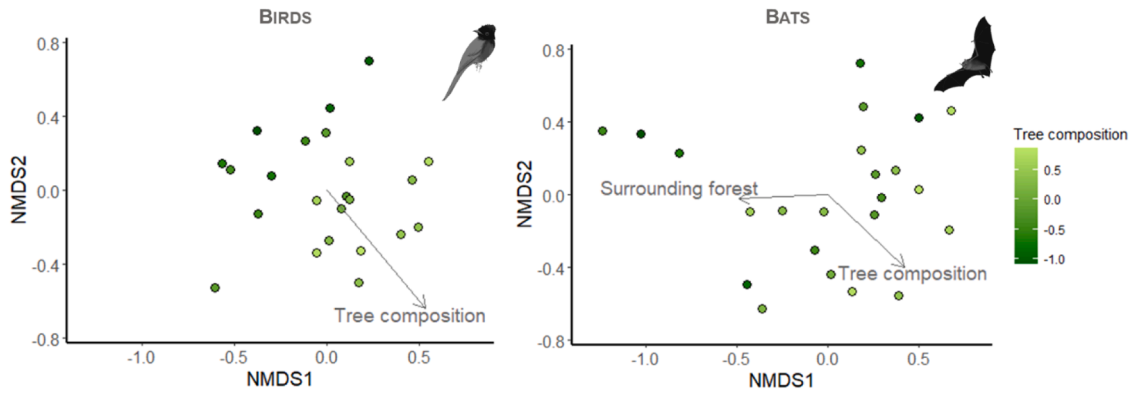

Fig. 2. The relationship between environmental predictors and the a) bird and b) bat community composition, as visualized by an NMDS ordination in two dimensions. Stress values of the three-dimensional NMDS ordinations are 0.15 and 0.01 for the bird and bat community, respectively. Only environmental predictor variables retained after model selection are shown (Table 2). The colours of the circles reflect the shade tree species composition in the study sites. Lower values of the shade tree community composition are reflective of natural forests (e.g. *Chionanthus mildbraedii, Schefflera abyssinica, Olea welwitschii* and *Syzygium guineense*) and higher values of more intensively managed coffee sites (e.g. *Cordia africana, Croton macrostachyus, Albizia gummifera* and *A. schimperiana*).

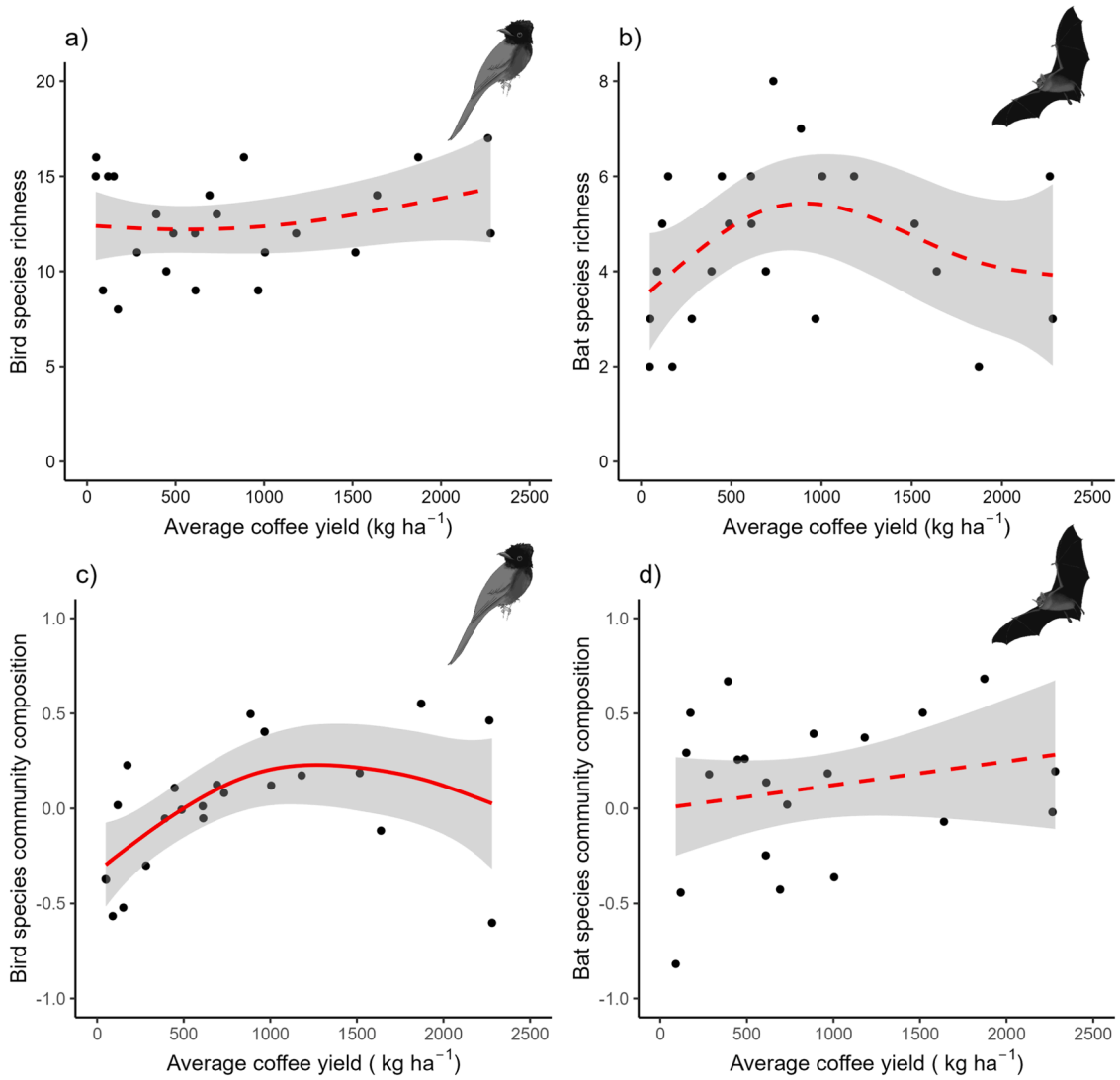

Fig. 3. The relationship between coffee yield and a) bird species richness, b) bat species richness, c) bird community composition (axis 1 of an NMDS ordination) and d) bat community composition (axis 1 of an NMDS ordination) across 23 sites in southwestern Ethiopia. Shown are regression slopes with 95% confidence intervals from a GAM model. Solid lines represent a significant relationship ($P < 0.05$) and dashed lines represent a non-significant relationship ($P > 0.05$). For statistical details, see Table S5. Bird and bat illustrations by Hannah Burger.

to the patterns found for abundance and species richness, as expected, the bird community composition shifted along the gradient from agroforests with natural forest structure to agroforests with less forest specialist trees, which is easily explained by the presence of both forest specialist birds (that are entirely restricted to the natural forest sites; Engelen et al. 2017) and bird species that thrive in semi-open landscapes within the region. Gebremichael et al. (2022) show that especially the presence of very large trees promotes forest specialists in coffee farms in this region. This pattern, of a stronger link between environmental factors and composition than with abundance and richness, is actually frequently reported also from other disturbed tropical forest systems. For example, composition, but not richness, changed with succession after abandonment of cacao agroforests in Trinidad (Arnold et al. 2021) and commercial polyculture coffee fields had similar bird abundance and richness, but different composition, as coffee under a canopy of natural forest trees in Indonesia (Imron et al. 2022). For bats, we also found that the community composition shifted significantly along the gradient from agroforests with natural forest structure to agroforests with less forest specialist trees. However, this pattern differed from that for birds: we detected no clear forest specialist bats, and the sonotype with the strongest association with forests also occurred in many of the more managed sites. Moreover, the highest richness was recorded in two sites (7 and 8 species) with quite intensive management and a simple shade tree structure, indicating that all bat species are also found in more open agroforests. In addition to the significant relationship between bat species composition and shade tree species composition there was a trend for an effect of surrounding forest cover on bat community composition. This matches with the idea that bat species have quite large foraging areas and that the presence or absence in a specific point does not only reflect the local habitat conditions but also the composition of the surrounding landscape (Cassano, Silva, Mariano-Neto, Schroth & Faria 2016; Jones, Jacobs, Kunz, Willig & Racey 2009; Russo et al. 2021). Yet, we know too little about the taxonomy, life history, habitat preferences and foraging ranges of the local bats to conclude whether – like some birds – some of the bat species rely on the more natural forest. For example, even though all species were found to forage (also) in the sites with trees common in the agricultural matrix, bats have often been found to be more abundant and diverse when there are more natural agroforests and primary forest in the landscape (Huang, Rustiati, Nusalawo & Kingston 2019; Williams-Guillén & Perfecto 2010). One important future direction is also the construction of a reference database for bat species sonotypes in Ethiopia and Africa in

general, which would allow for the large-scale inventory and identification of bat communities using passive acoustic devices. Currently, we could not match our recordings to bat species previously recorded within agroforestry systems in the region, such as *Neoromicia guineensis, Rhinolophus clivosus, Sctoophilus dinganii, Trianeops afer, T. persicus* and *Tadarida ventralis* (Kaipf & Meinig, 2017; Kruskop & Lavrenchenko 2008).

The species richness and composition of the bird and bat community were unrelated to insect herbivory. On the one hand, this suggest that – against expectation – agroforests that are more reminiscent of the natural forest do not provide higher levels of natural pest control. On the other hand, average herbivory levels on coffee were relatively low (72.3% of leaves with no damage; Burger et al. 2022; Shimales et al. 2023) as compared to fourteen subtropical trees (10 – 60% of leaves with no damage; Liu, LeRoy, Wang, Guo, Song et al. 2023), which might mean that natural pest control is benefitting farmers across all types of agroforestry sites. The finding that bat (but not bird) abundance was positively related to herbivory might suggest bottom-up regulation for bats, where higher abundances of herbivorous insects result in higher abundances of insectivorous bats. One caveat of our analysis is that we only have snap-shot data on levels of herbivory as well as species composition of birds and bats. While it is generally assumed that snap-shot recordings of the bird and bat community are representative, we know much less about the seasonal and interannual variation in herbivory. To advance our understanding of the variation in herbivory and natural biocontrol, we suggest that we need a combination of short- and long-term surveys of herbivory and the bird and bat community to assess seasonal and interannual variation, as well as experiments excluding birds, bats and insect predators and parasitoids (Schmitt et al. 2021). Such data can also reveal the exact time scale at which we can link patterns of herbivory with the community composition of birds and bats. We also note that even the most intensively managed agroforests in the landscape are relatively natural as compared with many plantations in other countries (Buechley et al. 2015; Imron et al. 2022; Zewdie et al. 2022). Hence, natural pest control might decrease with further management intensification and homogenization of the landscape. Our finding contrasts with a study within the same region on the natural biocontrol of the coffee blotch miner, where parasitoid diversity decreased, and leaf miner infestation increased, with increasing management intensity (Shimales et al. 2023), suggesting that different types of natural enemy groups have a different sensitivity to management intensity and intensification.

We found a relationship between bird, but not bat, community composition and yield, whereas we found no relationship between bird and bat species richness and yield. Similarly, Zewdie et al. (2022) found that species composition, but not richness, for different groups of plants (trees, herbaceous species and bryophytes) changed along the yield gradient. The shift in community composition with yield in that case, as well as for our results of the bird community, is straightforward: forest specialists disappear from the high-yield sites, and species thriving in more open habitats are more abundant in the high-yield sites. In contrast, the absence of a shift in the bat community along the yield gradient indicates that the same bat species forage in low and high yield sites, possibly due to the absence of clear forest specialists (see above). However, it is important to note that the high-yield sites in this landscape are still relatively natural (Zewdie et al. 2022), and patterns might look different if sites with very high chemical inputs and low tree species diversity (or with non-native trees) would exist within the landscape (Buechley et al. 2015; Hylander et al. 2024; Imron et al. 2022). Also important to note is that we do not assume that the variation in yield between sites is mainly driven by the bird, bat or plant communities. However, an important future research direction is to disentangle the joint effects of the various drivers of yield differences. Such studies need to include both direct biotic (e.g. top-down control by birds, bats and insects), abiotic (e.g. microclimate) and management drivers as well as the indirect effects on both biotic and abiotic drivers imposed by different management (see also Hylander et al. 2024).

Implications for conservation, sustainable agroforestry and livelihood

We found that bird and bat community composition were linked to the shade tree species composition, that the bird and bat community were not related to lower pest levels, and that the bird – but not bat – community shifted with increasing yield. From a conservation perspective, the rapid shift in the bird community composition from low to intermediate yields implies that conserving part of the landscape as forest-like and low-yield agroforests is paramount for forest specialist birds; this is an important message for conservation in a landscape where deforestation rates are high and management intensification is ongoing (Hylander et al. 2024). To retain such parts of the landscape, economic compensation for carbon sequestration is probably more effective than coffee certification since the latter may rather lead to intensification (Schmitt, Senbeta, Denich, Preisinger & Boehmer 2010; but see Takahashi & Todo 2017). For the part of the landscape where coffee production is already intermediate or high, it might be possible to increase yields without compromising biodiversity. To intensify management in a sustainable way, it is important to explore how biodiversity can contribute to sustained yields (e.g. through natural pest control) and how biodiversity and high yields can be maintained simultaneously (Hylander et al. 2024). Experiments that manipulate different biodiversity components at the same time as monitoring yield are important to establish the causal links and effect sizes of these drivers (Cassano et al. 2016). Notably, while we feel comfortable to interpret our findings for birds, for which much background expert knowledge exists, our findings highlight also how difficult it is to infer the mechanisms behind the patterns found for the bat species. To conserve this important and diverse group of mammals, we urgently need studies on the taxonomy, echolocation calls, life-history, habitat preferences and foraging ranges of East-African bats.

CRediT authorship contribution statement

A.J.M. Tack: Writing – review & editing, Writing – original draft, Supervision, Methodology, Funding acquisition, Formal analysis, Conceptualization. **H.F. Burger:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **H. Wood:** Writing – review & editing, Visualization, Methodology, Formal analysis, Data curation, Conceptualization. **B. Zewdie:** Writing – review & editing, Methodology, Data curation, Conceptualization. **T. Shimales:** Writing – review & editing, Methodology, Data curation. **B. Ayalew:** Writing – review & editing, Methodology, Data curation. **E. Mendesil:** Writing – review & editing, Supervision. **K. Hylander:** Writing – review & editing, Visualization, Methodology, Formal analysis, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Supplementary materials

Supplementary material associated with this article can be found, in

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