Biological Conservation 284 (2023) 110191

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Not all farms are created equal: Shady African cocoa farms promote a richer bat fauna

Diogo F. Ferreira [a,b,c,*], Alexandra Darling [c,d], Crinan Jarrett [c,d,e], Patrick Jules Atagana [c,f], Phallin Roméal Sandjo [c,g], Hermann Taedoumg [h,i], Andreanna J. Welch [j], Hugo Rebelo [a,b,k], Luke L. Powell [a,b,c,d,j]

[a] CIBIO-InBIO, Research Centre in Biodiversity and Genetic Resources, University of Porto, Campus de Vairão, 4485-661 Vairão, Portugal
[b] BIOPOLIS Program in Genomics, Biodiversity and Land Planning, CIBIO, Campus de Vairão, 4485-661 Vairão, Portugal
[c] Biodiversity Initiative, Houghton, MI, USA
[d] Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Glasgow, UK
[e] Swiss Ornithological Institute, Department of Bird Migration, Seerose 1, CH-6204 Sempach, Switzerland
[f] Department of Biological Sciences, Faculty of Sciences, University of Maroua, Maroua, Cameroon
[g] Higher Institute of Environmental Sciences (HIES), Yaoundé, Cameroon
[h] Department of Plant Biology, Faculty of Sciences, University of Yaoundé 1, Cameroon
[i] Consultative Group on International Agricultural Research (CGIAR), Biodiversity International, Yaoundé, Cameroon
[j] Department of Biosciences, Durham University, South Road, Durham, UK
[k] Instituto Politécnico de Setúbal, ESS, Campus da Estefanilha, Setúbal, Portugal

ARTICLE INFO

Keywords:
Bat guilds
Agroforestry systems
Family farms
Smallholder cocoa
Chocolate production
Cameroon

ABSTRACT

Bats provide important pest suppression services with economic value to cocoa farmers, yet the impact of cocoa farm management on bat diversity metrics is still poorly understood. This is especially important if we consider that Afrotropical cocoa farms supply 68 % of the world's chocolate market, with expected increases in production in the forthcoming decades. In this study, we investigated for the first time how bat abundance, richness and diversity varied between African cocoa farms with different levels of shade tree cover, shade tree communities and cocoa characteristics. We found that shade tree cover and shade tree height were the main drivers associated with an increase of Shannon diversity, and abundance and richness of insectivores. Frugivorous and nectarivorous bats were positively associated with the presence of planted shade trees, but richness varied with the size of shade trees. The insectivorous *Hipposideros fuliginosus* was only present in high shade farms, being captured 51 times only in this shade system, while the frugivorous *Myonycteris angolensis* was associated with low shade farms. Our findings show that indeed not all farms are created equal, with high shade farms with large, tall forest shade trees (i.e., containing key plant resources) having richer bat communities. Therefore, policymakers seeking to conserve wildlife within cocoa farming systems should adopt cocoa management systems like those mentioned above and promote a combination of forest and planted shade trees to be able support a rich community of insectivorous, frugivorous and nectarivorous bats and maintain their associated ecosystems services.

1. Introduction

Agricultural expansion is the main drivers of deforestation in the tropics (Curtis et al., 2018), with crop productivity and biodiversity conservation often considered as mutually exclusive objectives (Seppelt et al., 2016). However, agroforestry, where trees are planted or retained with crops, may offer a path forward to preserve biodiversity and ecosystems services, while maintaining livelihoods of local farmer communities (Rice and Greenberg, 2000; Nair et al., 2021).

The diverse and structurally complex shade tree cover in some agroforestry systems can provide wildlife with a structured habitat not unlike the original forest, improving the connectivity between natural landscapes and agricultural systems (Faria et al., 2006). Even though the ecological value and conservation role of agroforests can be dependent on several factors (e.g., type of crop and farm characteristics), agroforestry systems offer a possible alternative to achieve high biodiversity

---

* Corresponding author at: CIBIO-InBIO, Research Centre in Biodiversity and Genetic Resources, University of Porto, Campus de Vairão, 4485-661 Vairão, Portugal.
E-mail address: ferreiradfa@cibio.up.pt (D.F. Ferreira).

https://doi.org/10.1016/j.biocon.2023.110191
Received 14 October 2022; Received in revised form 27 June 2023; Accepted 6 July 2023

alongside high crop yields (Clough et al., 2011). Several studies have shown that increasing the shade tree cover within agroforestry systems can support a higher animal biodiversity across a range of taxa, including birds in cocoa and coffee (Blaser et al., 2018; Bennett et al., 2021; Jarrett et al., 2021) and bats in coffee farms (Williams-Guillén and Perfecto, 2010, 2011).

Cocoa (*Theobroma cocoa*) is an agroforestry cash crop of immense value for many low-income tropical countries (Tscharntke et al., 2011). Its global trade represented $8.6 billion in 2017 (Voora et al., 2019) and it is the fastest expanding export-oriented crop across the Afro-tropics (Ordway et al., 2017). In the last century alone, cocoa cultivation has expanded to over 50 countries (Lass, 2004), with about 70 % of the world's cocoa being produced in small-scale farms in sub-Saharan Africa (FAOSTAT, 2020). Recent policy has increasingly put pressure on farmers to convert their traditional cocoa agroforestry farms into more intensively managed full-sun cocoa systems (Armengot et al., 2016), based on the assumption that sunnier farms produce higher yields (Waldron et al., 2015; but see Clough et al., 2011). In these intensified systems, the shade tree cover is entirely removed, making them less compatible with preservation of ecosystem integrity and diversity (Harvey and González Villalobos, 2007; De Beenhouwer et al., 2013). Currently, in some countries like Cameroon, most cocoa production still comes from small-scale agroforestry farming with cocoa trees planted within native forest (Franzen and Borgerhoff Mulder, 2007). Hence, these areas represent an opportunity to study the impact of farm management on animal communities as well as an opportunity to create win-win scenarios for farmers and nature. Nevertheless, despite the increasing pressures on this system, very few studies have yet to investigate the response of the unique Afrotropical vertebrate community to management intensity in agroforestry cocoa production—there is only two such studies from the Afrotropics both on birds (Jarrett et al., 2021; Sanderson et al., 2022).

Bats are the second most diverse group of mammals in world and contribute to a great variety of ecosystem services worldwide (Sekercioglu, 2006; Kunz et al., 2011). In particular, they are of great importance for the suppression of insect populations, like agricultural pests (Boyles et al., 2011; Maas et al., 2016; Librán-Embid et al., 2017), and for assisting in the vital process of renewing disturbed or damaged areas of natural forest through seed dispersion (van Toor et al., 2019). Studies conducted in Asia (Maas et al., 2013) and South America (Vansynghel et al., 2022) showed that pest suppression by bats and birds increased cocoa yield independently of shade tree cover by 31 % and 114 %, respectively. However, in the only study to date focusing on the role of bats in African cocoa (Curtis et al., 2018), in the only study to date focusing on the role of bats in African cocoa showed that bats and birds can save Cameroonian farmers an average of $478 per ha per year through pest consumption when shade tree cover is maintained at high levels. This study provides evidence that bats and birds may mitigate some of the losses in production caused by interspersing shade and cocoa trees for African farms, as opposed to growing cocoa in full-sun.

Win–win scenarios between cocoa farmers and biodiversity can be achieved when a maximum of 30 % to 40 % shade tree cover is maintained in farms (Clough et al., 2011; Waldron et al., 2012; Gras et al., 2016; Blaser et al., 2018). Across the world, several studies have shown that cocoa agroforestry systems can support a considerable amount of the bat diversity found in natural forest, especially when compared to other agricultural land use systems (Faria et al., 2007; Harvey and González Villalobos, 2007; Schroth et al., 2011; Clough et al., 2011; Waldron et al., 2012; Gras et al., 2016; Blaser et al., 2018). Across the world, several studies have shown that cocoa agroforestry systems can support a considerable amount of the bat diversity found in natural forest, especially when compared to other agricultural land use systems (Faria et al., 2007; Harvey and González Villalobos, 2007; Schroth et al., 2011). For example, studies conducted in Brazil showed that shaded cocoa farms can contain a higher proportion of forest specialists than secondary forests (Pardini et al., 2009; Schroth et al., 2011). Furthermore, Atagana et al. (2021) in a study that compared several habitats types, including shaded cocoa farms, showed that African cocoa farms can contain similar levels of bat species richness to forest sites, even though they still have a distinct species composition. Despite the massive deforestation associated with cocoa agroforestry in some African countries (Wessel and Quist-Wessel, 2015; Barima et al., 2016) and the increasing levels of conversion of high to low shaded cocoa across the world (Tscharntke et al., 2011), these studies highlight the importance and potential of shaded cacao for bat conservation.

Remarkably, no study has thus far investigated how bat communities respond to cocoa agroforestry intensification and how bat community composition may vary under different types of management (e.g., degree of shade tree cover and diversity).

Importantly, the few studies that focus on the relationship between biodiversity and cocoa shade management rarely consider other vegetation characteristics associated with shade trees (e.g., type of tree, height and DBH; Faria et al., 2006; Pardini et al., 2009; Maas et al., 2016; Nkrumah et al., 2017; Ocampo-Ariza et al., 2022). These characteristics are important because they represent aspects of shade trees highly relevant to animals: for instance, different shade tree species may provide varying levels of food resources to animals, and height and DBH can capture structural complexity of the shade tree strata as well as resources such as roosting (Zemp et al., 2019; Kusuminda et al., 2022). For example, fig species in Australia provide important keystone food resources both to frugivorous and insectivorous birds (Mackay et al., 2018). However, a study conducted in Mexico showed that bats in coffee farms tend to use timber trees for roosting rather than commonly planted fruit shade trees (Cortés-Delgado and Sosa, 2014). Hence, moving beyond the simplistic view of just considering shade cover and instead considering vegetation characteristics associated with these shade trees can help make cocoa more wildlife-friendly and at the same time create win-win scenarios that improve cocoa yields and farmer income (Wainaina et al., 2021; Asitoakor et al., 2022).

To conserve the current bat diversity within cocoa landscapes, it is vital to study the impact of farm management on bats, especially in the West African cocoa belt. Hence, the aim of our research was to investigate how cocoa farm management (i.e., differences in shade tree cover, shade tree species type and composition, shade tree height and DBH, and cocoa height and DBH) affected bat abundance and richness, and how these responses changed between insectivores, frugivores and nectarivores. In addition, we also aimed to assess how bat species composition, beta diversity and association of species varied between three farm shade systems: low shade cocoa, mixed cocoa agroforestry (medium levels of shade) and rustic cocoa agroforestry (high levels of shade), a metric commonly used as a proxy for farm management intensity (Bennett et al., 2021).

2. Materials and methods

We worked on 28 cocoa farms in south central Cameroon, Africa. Our farms were in 5 different landscapes across Cameroon: Elat (two farms), Ngoumou (six farms), Ebolowa (eight farms), Ayos (eight farms) and Somalomo (four farms; Fig. 1). Farms had varying shade tree cover, were > 1.5 ha and at least 500 m apart.

2.1. Bat surveys

At each farm, we sampled bats using 20 ground-level mist nets (length: 12 m; height: 3.2, 2.6 or 2.5 m; mesh: 20, 18 or 16 mm; denier/ply: 45/1 or 75/2; material: nylon or polyester) from August 2017 to September 2020. We visited each farm from two to six times, and all farms were visited at least once during the dry (January–February) and wet (August–September) season. We opened the nets for six hours from dusk (~18 h30) until midnight (~00 h30) and nets were inspected at intervals of ca. 20 min (for more details see Ferreira et al., 2021). Bats were captured and handled in the field following guidelines approved by

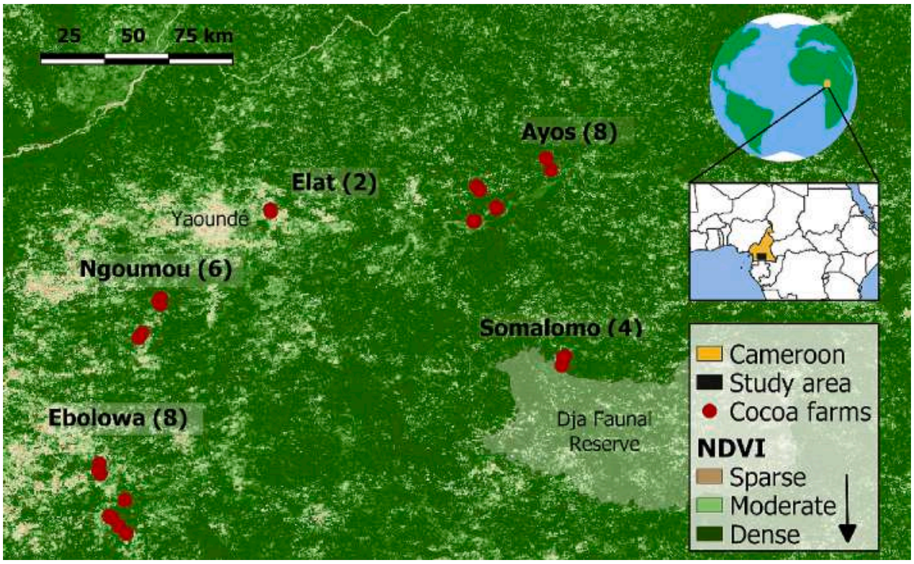

Fig. 1. – Map of 28 focal cocoa farms in Cameroon, Africa. Dots represent cocoa farms and numbers within parentheses represent the number of farms per landscape. Dja Faunal Reserve is a UNESCO World Heritage Site and one of the largest and most biologically diverse tracts of protected rainforest in central Africa. Normalized Difference Vegetation Index (NDVI) is an indicator of vegetation greenness.

the American Society of Mammalogists (Sikes et al., 2011). We identified, measured, and recorded all captured bats. Species identification followed Hayman and Hill (1971), Patterson and Webala (2012), Happold and Happold (2013), and taxonomy followed ACR (2019). Due to the difficulty of morphologically identifying small individuals from the genus Nycteris, Pipistrellus, and Neoromicia (similar-sized individuals without any clear distinctive morphological characteristics), we grouped them at the genus level and treated them as a single taxon. Also, some individuals from the genus *Hipposideros* were grouped into what we believe to be an undescribed or cryptic species (or an isolated population with unique adaptations and thus likely different diet) due to clear differences in echolocation characteristics compared to other species from this genus known for the area.

2.2. Environmental variables

Cocoa agroforestry systems typically have a lower stratum containing cocoa trees (“cocoa stratum”) and a higher stratum with forest or planted trees which provide shade to cocoa trees (“shade strata”). The shade strata in cocoa farms can be composed of dozens of tree species (see Table A.1 for the 135 species found in our farms) and are usually grouped into two groups: native trees that are associated with primary forest (hereafter “forest trees”); and native or exotic trees planted by farmers as a secondary source of income (hereafter “planted trees”). To characterise the shade tree community in our farms, we considered all shade trees that had at least one branch hanging above our mist-net lines (i.e., transects of 240 m). This effectively provided a standardized transect method replicable between farms. Each tree in the transect was identified, measured (height and DBH) and classified as a planted or forest tree. To characterise the cocoa trees in each farm, we measured the height and DBH of 20 cocoa trees that were representative of the trees found in each farm along our mist-net transect.

To measure shade tree cover, we took 10 photographs of the canopy at 10 different points separated by 24 m along our mist-net transect within each farm using a camera with a fish-eye lens attached to a 6 m pole (i.e., to rise above the cocoa tree understory). We converted the photographs to binary black and white using the software ImageJ (Schneider et al., 2012), and then calculated the percentage of black (vegetation) in each photograph using the default settings. Our estimate of farm shade tree cover was the mean of the 10 pictures.

Finally, following Bennett et al. (2021) we used our estimates of farm shade tree cover to classify our farms into three farm shade systems. However, because farms with 0 % of shade tree cover (full-sun farms) are very rare in Cameroon, our shade tree cover values were adapted to meet our on-the-ground reality. Hence, we divided our farms into: “rustic cocoa agroforestry” with >65 % shade tree cover; “mixed cocoa agroforestry” between 35 and 65 % shade tree cover; and “low shade cocoa” between 20 and 35 % shade tree cover (Table A.2). We used shade tree cover to classify our farms because shade is considered a proxy of farm intensification, with farms with high shade tree cover maintaining a relatively undamaged tree canopy while full-sun farms have no shade trees (Rice and Greenberg, 2000; Bennett et al., 2021). See Table A.2 for average values of the different metrics associated to each farm shade system.

2.3. Statistical analysis

2.3.1. Influence of farm management on bat abundance, species richness and diversity

For each farm we estimated the Shannon-Wiener diversity Index (H') using the “vegan” package. Here larger H' indicates more diverse community (Oksanen et al., 2013). To observe the effects of farm management on bat abundance and richness we used general linear mixed-effects models (GLMMs), while for diversity we used a Linear Mixed Model (LMM). Prior to the analysis, all nine predictors (“shade tree cover”, “shade tree height”, “shade tree DBH”, “number of forest shade trees”, “richness of forest shade trees”, “number of planted shade trees”, “richness of planted shade trees”, “cocoa tree height” and “cocoa tree DBH”) were standardized to a mean of zero and a standard deviation of one. Spearman’s rank correlation coefficient and variance inflation factors (VIF) were calculated to test for multicollinearity (Dormann et al., 2013), whereby we considered variables with $\text{VIF} \geq 10$ and/or with a Spearman correlation >0.7 to be collinear, justifying their exclusion from the analysis. We therefore excluded cocoa tree height and cocoa tree DBH, which were positively correlated with shade tree height and shade tree DBH, respectively (Fig. A.2).

We built eight different models using the abundance and richness of all bats, insectivorous bats, frugivorous bats and nectarivorous bats, respectively, and the Shannon-Wiener diversity index as response variables. Bats were attributed to the different guilds based on their main diet items (Happold and Happold, 2013; ACR, 2019). Because we only captured one nectarivore species, we only used abundance as response variable for this guild. For these count data, we fitted Poisson distributed models, however when data were overdispersed, we used a Negative Binomial or Generalised Poisson distribution depending on their goodness-of-fit (Yadav et al., 2021). For the diversity model, we used Gaussian distribution after checking for normality and homoscedasticity. The fit of models was investigated visually and statistically using a simulation-based approach in the package "DHARMa" (Hartig and Hartig, 2017). Models with good fit showed no significant deviation in the QQ plot of simulated residuals and passed a non-parametric dispersion test.

To account for the nested sampling design and repeated visits in our models, we included a nested random effect containing farm within landscape (i.e., landscape/farm) and one containing field season. Finally, we included as an offset the mist-net hours to account for differences in sampling effort (log number of mist net hours; 1 mist net hour [mnh] equals one 12-m net open for 1 h; Ferreira et al., 2021); Ferreira et al., 2021). We performed backwards model selection using Likelihood Ratio Tests on fully nested models (LRTs, cut-off probability $P > 0.1$) and then used best fit models to estimate coefficients. To determine the relative importance of each predictor within the minimal adequate models, we performed a hierarchical partitioning analysis using the "hier.part" package in R (Mac Nally and Walsh, 2004) that was modified to incorporate a model offset Jeppsson et al. (2010). Following Ferreira et al. (2017), hierarchical partitioning analysis was conducted only considering the fixed effects. We ran all GLMMs using the package glmmTMB (Brooks et al., 2017).

2.3.2. *Relation between bat species community and farm shade system*

For each farm shade system, we compared species richness using individual-based rarefaction and extrapolation curves in iNEXT package (Hsieh et al., 2016)). We estimated species richness after extrapolating to 1000 individuals and estimated the 95 % confidence intervals by a bootstrap method based on 500 replications, where nonoverlapping confidence intervals indicated significant differences (Chao et al., 2014).

To characterised differences in assemblage composition between shade systems we use a non-metric multidimensional scaling (NMDS) ordination based on a Bray-Curtis dissimilarity matrix. We used a community matrix with the number of captures per farm standardized by mist-net hours and square root transformed to reduce the influence of extreme values. We tested for compositional differences between shade systems using a permutational multivariate analysis of variance (PERMANOVA; adonis function). PERMANOVA tests had 9999 permutations to test for significant differences between the permuted datasets compared to the observed differences between clusters. Also, the permutations were constrained by landscape using the "strata" argument, to account for non-independence between farms within the same landscape. To visually compare community groups between farm shade systems, we highlighted clusters of communities using the "ordiellipse". Finally, to see if beta diversity varied between farm shade systems, we used the "betadisper" function and PERMANOVA with 9999 permutations. We conducted all above analyses using the "vegan" package (Oksanen et al., 2013).

To identify the species that were significantly associated with each farm shade system, and thus driving the patterns observed, we conducted an indicator analysis using the package "indicspecies" (De Cáceres and Legendre, 2009). The indicator index value together with permutation tests (set to 9999 permutations) allowed us to identify groups of farms, i.e., farm shade systems, that were more strongly associated with observed bat species distribution patterns (De Cáceres and Legendre, 2009). We considered two farms (five nights) as outliers due to the presence of large roosts within the farm and removed them from abundance, diversity, and composition analyses. We caught dozens to hundreds of individuals of the same species in these farms rather than the typical <10 individuals per night. We conducted all analysis in R v4.0.3 software (R Core Team, 2020).

3. Results

During this study we sampled on 71 nights (8397.5 mnh) and captured 957 bats belonging to 28 species (Table A.3). Insectivorous bats composed >60 % of all captures and were represented by 20 different species, with *Hipposideros* cf. *ruber* (150 captures) and *Rhinolophus alcyone* (151 captures) being the most common. We captured seven species of frugivorous bats, with *Epomops franqueti* representing >50 % of all captures within this guild. The single nectarivorous bat species captured, *Megaloglossus woermanni*, represented 10 % of all captures. We captured 625 bats of 27 species in rustic cocoa agroforestry (5859 mnh), 169 bats of 16 species in mixed cocoa agroforestry (1241 mnh) and 163 bats of 17 species in low shade cocoa (1297.5 mnh; Table A.3).

3.1. *Influence of farm management on bat abundance, species richness and diversity*

For all bats, we found for Shannon-wiener index a positive association with shade tree cover and shade tree height, with the latter explaining more 55 % of the variance (Fig. 2). When looking at all guilds together, bat abundance and richness was positively associated with shade tree cover and number of planted shade trees (Fig. 2). However, when looking at each guild separately we found that bat responses to farm management varied between the three different guilds (Fig. 2; Table A.4).

For insectivorous bats, both abundance and richness were associated positively with shade tree cover and negatively with the number of forest shade trees (Fig. 2). However, shade tree cover explained most of the variance, with >50 % for abundance and >80 % for richness. The abundance of frugivores and nectarivores was positively associated with the number of planted shade trees present in the farms. For these two guilds, this predictor was the only variable selected in the minimum adequate models (Fig. 2). For the richness of frugivorous bats, shade tree DBH was the only predictor retained in the minimum adequate model and was negatively associated to it (Fig. 2).

3.2. *Relation between bat species community and farm shade system*

Overall, individual-based rarefaction and extrapolation curves showed more bat species in the farms with a rustic cocoa agroforestry system. However, due to the high variability within low shade cocoa system farms, the 95 % confidence intervals overlapped between these two shade systems. Hence, differences were only significant between rustic and mixed cocoa agroforestry (Fig. 3A).

Beta diversity did not vary significantly between farm shade systems (PERMANOVA: $F = 0.447$, $P = 0.646$; Fig. 3B), indicating homogeneity of dispersion among shade systems. The NMDS ordination showed clustering among assemblages captured in the three different farm shade systems and had a stress value of 0.18, conveying a good representation of the data along two dimensions. Bat assemblage composition varied significantly between shade systems (PERMANOVA: $F = 2.311$, $P = 0.018$), with bat communities being significantly different between rustic cocoa agroforestry and low shade cocoa (Fig. 2C). Mixed cocoa agroforestry showed intermediary bat community when compared with the other two shade systems.

Based on the indicator species analysis, we identified one bat species significantly associated with each shade system (Table A.1). A frugivorous bat, *Myonycteris angolensis*, exhibited the strongest association with low shade cocoa (Indicator value = 0.479; *P*-value = 0.049), whereas for the other two shade systems that role was occupied by two insectivorous bats. *Hipposideros* cf. *caffer* had the strongest association with mixed cocoa agroforestry (Indicator value = 0.440; P-value = 0.046) and *Hipposideros fuliginosus* with rustic cocoa agroforestry (Indicator value = 0.594; P-value = 0.010). Nycteris sp., a complex of insectivorous bat species, was associated with the former two shade systems, but results

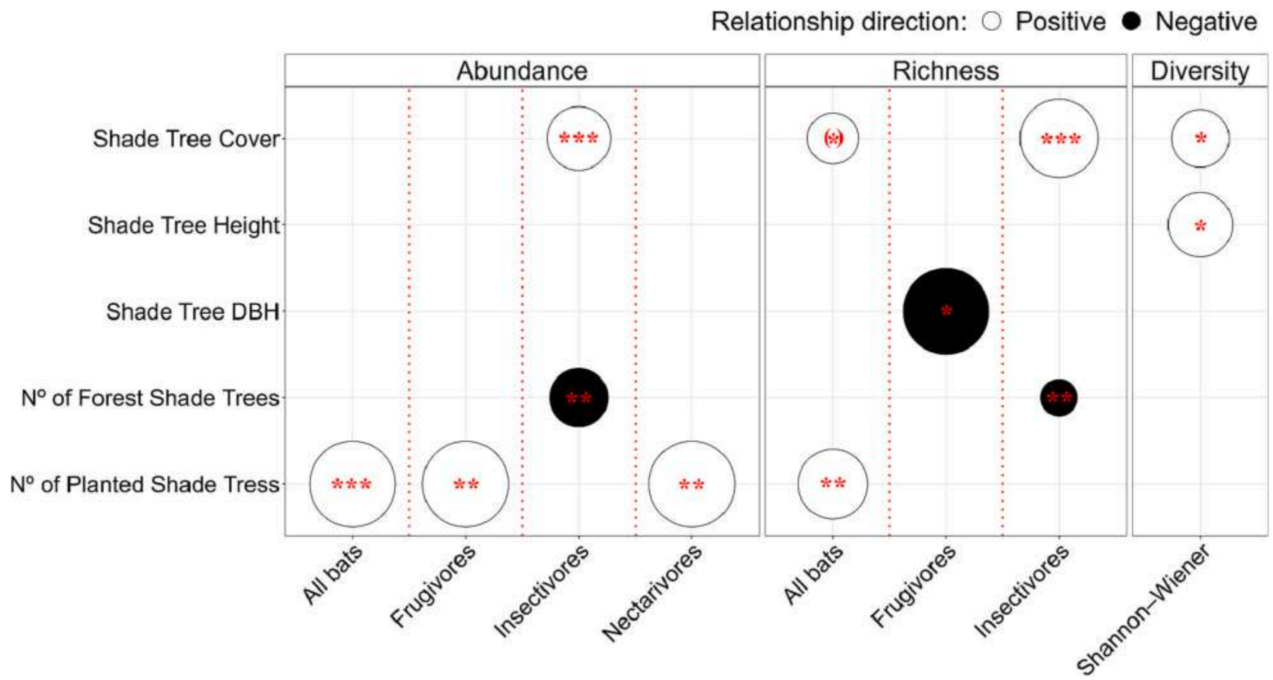

Fig. 2. - Summary results of the minimum adequate models exploring the association between farm managent and diversity, abundance and richness for all bats, frugivores, insectivores and nectarivorous in 28 cocoa farms (26 for the abundance) in Cameroon, Africa. Circle size is proportional to the variation explained by the respective predictor variable based on hierarchical partitioning (largest circle represents 100 % while the smalleste represents 7.7 %). Hierarchical partitioning analysis was conducted only considering the fixed effects. Color denotes the direction of the relationship (based on the effect size). Significant results are indicated as *** $p < 0.001$, ** $p < 0.01$, and * $p < 0.05$, while marginal results as (*) $p < 0.1$. See Tables A.4 for additional modeling results.

were only marginally significant (Indicator value = 0.458; P-value = 0.062).

Furthermore, based on indicator values, each shade system had at least one shade tree species associated with it: *Macaranga monandra* and *Dacryodes macrophylla* with low shade cocoa, *Inga edulis* with mixed cocoa agroforestry, and *Ceiba pentandra var guineensis* and *Ricinodendron heudelotii* with rustic cocoa agroforestry. *Ficus mucuso* was associated with mixed and rustic cocoa agroforestry (Table A.1).

4. Discussion

We investigated for the first time the impact of different cocoa farm management on the community of bats. We found that insectivores and bat diversity was associated strongly with the degree of shade tree cover, while non-insectivores depended on the number of planted shade trees in the farms. Furthermore, bat diversity and frugivorous richness were dependent on the size of shade trees (i.e., height or DBH). Bat communities varied significantly between rustic cocoa agroforestry and low shade cocoa, with mixed cocoa agroforestry showing a bat community shared by the other two shade systems. Also, we found that three insectivorous bats species were strongly associated with the farm shade systems with more shade (rustic and mixed cocoa agroforestry), while a frugivorous species was associated with the low shade cocoa.

4.1. Influence of farm management on bat abundance, species richness and diversity

We found that when considering the abundance and richness of all guilds together results vary from the ones observed when guilds are considered separately. This is in line with other studies conducted in other areas that showed that bat responses to habitat disturbance are guild-specific (Williams-Guillén and Perfecto, 2010; Shapiro et al., 2020; Ocampo-Ariza et al., 2022).

Abundance and richness of insectivorous bats, and bat diversity, as measured by the Shannon-Weiner Species Diversity Index, were positively associated with the amount of shade tree cover (Fig. 2). The similar patterns between these predictors are probably related with the fact that >60 % of our captures and >70 % of our species were insectivores (Table A.3). Studies conducted in coffee agroforestry system showed that insectivorous bat activity and diversity were similar between farms with high and medium levels of shade tree cover but different from farms with low shade (Williams-Guillén and Perfecto, 2010, 2011). Although similar studies were not conduct with bats in cocoa farm, we previously found that African birds' communities in the same cocoa farms are as diverse as forest areas but lack the more specialized insectivores (e.g., forest specialists and ant-followers), with the proportion of these species being five times higher in shady relative to sunny farms (Jarrett et al., 2021). This is in line with our findings, which have also shown a richer insectivorous bat community within shadier farms. Insectivorous bats are usually more sensitive to deforestation and habitat conversion, with gleaning insectivores and forest-dependent aerial insectivores usually showing the sharpest declines (Meyer et al., 2016). The insectivorous community in our rustic farms was mostly composed by gleaning bats such as *Rhinolophus* and *Hipposideros* species (Table A.3; ACR, 2019). The presence of this guild in shaded farms shows the potential of these farms to support high pest suppression services, explaining the possible positive link between cocoa production and bats in an exclusion experiment conducted in the same area (Ferreira et al., 2023).

Shannon diversity was positively associated with shade tree height (Fig. 2). In agroforestry systems, cocoa trees are planted in the understory and several shade tree species provide cover (Rice and Greenberg, 2000). This creates a structured habitat more similar to native forest with a stratum made up of cocoa crowns ("cocoa stratum") and a strata above cocoa ("shade strata") that can be used differently by animals and humans (Harvey and González Villalobos, 2007; Nakayama et al., 2008; Niether et al., 2020). Even though there are no studies focusing on vertical stratification by bats in agroforestry systems, studies conducted in forest areas showed bat activity can vary between strata and some bat species forage specifically or preferably at certain tree heights (Thiel

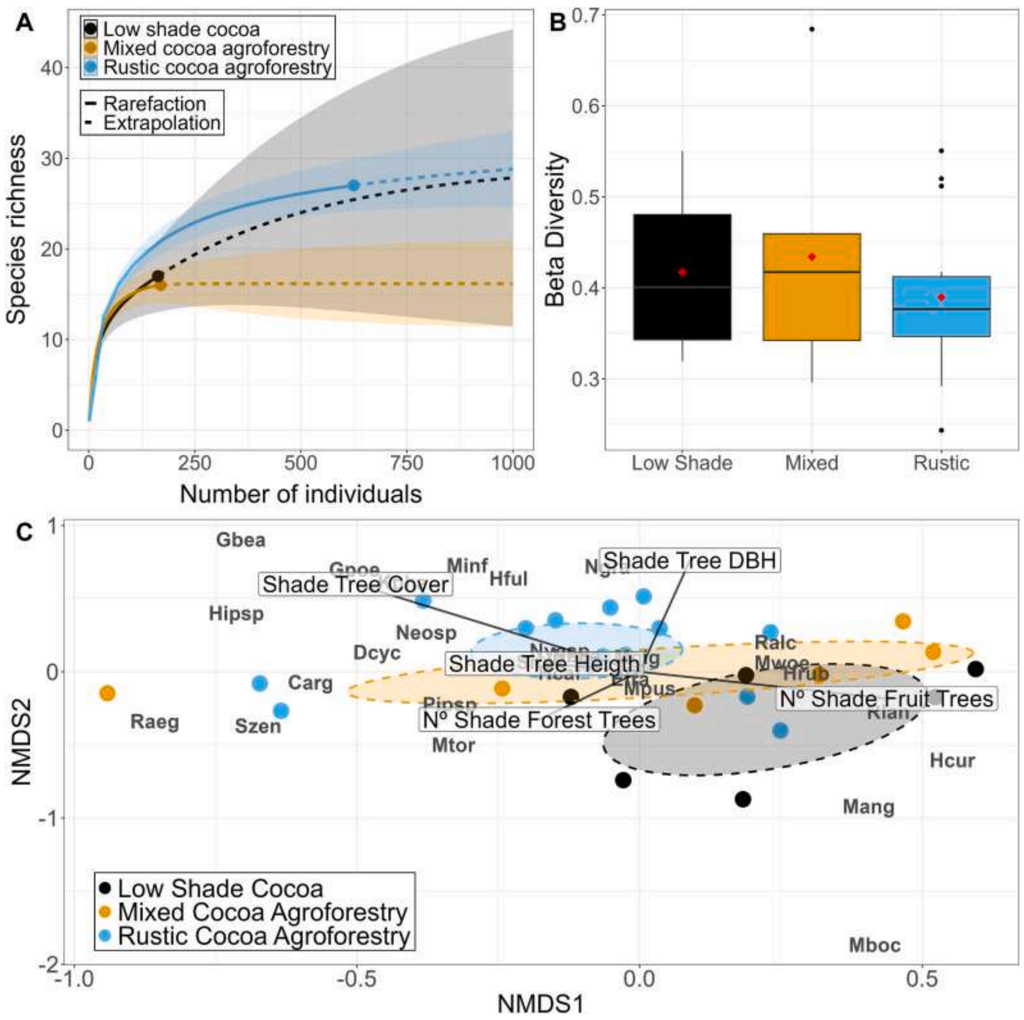

Fig. 3 – **A.** Plot showing individual-based rarefaction with extrapolation curve for the number of bat species caught in the three farm shade systems. We obtained the 95 % confidence intervals by a bootstrap method based on 500 replications. B) Comparison of beta diversity between farm shade systems. Boxplot is represented by the "minimum", first quartile, median, third quartile, and "maximum", while red dots represent the average between farms. C) NMDS plot of bat communities using abundances standardized by mist-net hours. Points represent sampled communities at a given farm. Boxed text represents the five different predictors that characterise farm management, while black four-letter codes represent bat species (see Table A.3 for definitions). Ellipses represent 95 % confidence intervals of clusters by farm shade system. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2021; Basham et al., 2023). Hence, farms with taller shade trees have the potential for having a greater vertical foraging space than farms with shorter shade trees (Bakermans et al., 2012), and thus have the capacity to support a more diverse bat assemblage. However, capture information is required from canopy mist-nets or setup bat detectors in the shade strata to fully understand how bats are vertically stratified in cocoa farms and how this stratification is associated with their dependence on shade tree cover.

Although shade tree cover was the main variable explaining the patterns observed for insectivores, this group also showed a negative association with the number of forest trees (Fig. 2). Shade tree cover in a farm can be provided by several tall shade trees with low DBH or by a few tall trees with high DBH, the latter usually being old forest trees (Diogo F. Ferreira, personal obs.; Table A.1). Since, insectivorous bats in our study area are negative associated to high numbers of shade trees present in a farm, our results indicate an association of this guild with farms that have high shade tree cover provided by a small number of large, mature trees. These findings were similar to a study conducted in coffee farms in India that found an increase in mammal abundance and total richness with increasing basal area and decreasing number of shade trees (Caudill et al., 2014). Most of the insectivores that we captured in our farms were from the Hipposideridae and Rhinolophidae family (Table A.3), which roost in holes in big trees (ACR, 2019), like the big *Ceiba pentandra var guineensis* and *Ricinodendron heudelotii* that were strongly associated to our rustic cocoa farms (Table A.1). This highlights the need to carefully consider the shade trees species used in cocoa farms, as it seems that some of these trees may be acting as keystone plant resources (Cortés-Delgado and Sosa, 2014; Mackay et al., 2018; Kusuminda et al., 2022) and may be central for the conservation of bats in agroforestry systems. However, the presence of old-growth trees within farms does not necessarily guarantee that these trees are as available or of the same quality as the ones present in undisturbed forests areas (Faria and Baumgarten, 2007). Hence, the presence of forest areas adjacent to cacao plantations may facilitate the access of bats to roost resources that are lacking in farms and act as spillover sources of insectivorous bats (Tscharntke et al., 2012).

As expected, we found that the abundance of frugivores and nectarivores was positively associated with the number of planted shade trees present in a farm (Fig. 2). The frugivorous species (Pteropodidae) present in our farms have a diet mostly constituted by fruits, while the only obligate nectarivorous bat species captured in our farms, *M. woermanni*, feeds on the nectar and pollen of several plants (Weber et al., 2009; ACR, 2019). Hence, farms that contain a high number of planted shade trees may have a high availability of flowers and fruits throughout the year, providing resources for these two guilds. However, the richness of frugivores was not explained by the number of planted trees but by the DBH of the shade trees, showing a negative relation with it (Fig. 2). Sanderson et al. (2022) found that the proportion of frugivores in West African bird communities in cocoa agroforest systems was negatively associated with the number of large trees. This may suggest that African frugivorous flying vertebrates may benefit from the overrepresentation of planted trees that produce edible, nutritious fruits in low shade cocoa instead of the larger older trees present in rustic cocoa farms, mimicking the patterns observed in degraded forests (Hawes et al., 2020; Sanderson et al., 2022). Nevertheless, since our rustic farm system contained similar number and richness of planted trees (Table A.2), future studies should try to understand if flower and fruit availability within low shade farm systems is indeed driving the patterns observed and what tree species are responsible for it.

4.2. Relation between bat species community and farm shade system

Although we found no differences for species richness and beta diversity between the low shade and rustic cocoa shade systems, our results showed a different species composition between these two shade systems. Beta diversity is a component of regional biodiversity that responds due to inter-site differences between local species assemblages (Socolar et al., 2016). The non-significant result indicates a homogeneity of dispersion among our shade systems and thus shows a similar degree of community differentiation within each of the shade systems. Because PERMANOVA tests can be sensitive to differences in dispersions among groups for unbalanced sampling designs (like ours, see Table A.2; Anderson and Walsh, 2013), a non-significant beta diversity allows us to have confidence that the differences observed in species composition between the low shade cocoa and rustic cocoa shade systems (Fig. 2) are true and not an artifact of heterogeneous dispersions.

We found that farms with low shade had the highest capture rates for frugivores species (0.049 bat/mnh vs 0.023 and 0.030 for mixed and rustic cocoa, respectively) and the lowest capture rates for insectivorous bats (0.059 vs 0.087 and 0.07 for mixed and rustic, respectively; Table A.3). These findings are similar to a study conducted in Neotropical coffee farms that found an increase of large frugivorous bats and a decrease of insectivorous bats in more intensively managed farms (Williams-Guillén and Perfecto, 2010). These results highlight the potential of shaded cocoa farms for the conservation of bats, but this potential may be limited to rustic cocoa systems. Although farms with an intermediary level of shade (mixed cocoa systems) still contained a diverse community of bats, they showed an intermediary species composition with less frugivores than low shade cocoa and less insectivores than rustic cocoa (Fig. 2; Table A.2). Nevertheless, since landscape composition and configuration around cacao farms are known to be important in shaping bat communities (Faria and Baumgarten, 2007; Tscharntke et al., 2015; Williams-Guillén et al., 2016), future studies should investigate if patterns are maintained under different cacao landscape scenarios.

Our findings from the species composition analyses perfectly match the results obtained from the indicator species analysis, which showed a frugivorous bat, *Myonycteris angolensis*, and a forest insectivorous bat, *Hipposideros fuliginosus*, driving the patterns observed for the low shade cocoa and rustic cocoa, respectively (Table A.1). *H. fuliginosus* is a widespread species with a localized and comparatively rare distribution restricted mainly to rainforest that depends on hollow trunks to roost (Happold and Happold, 2013). These type of vegetation characteristics are commonly found in our rustic farms, which might explain why *H. fuliginosus* is strongly associated with this shade system. Even though this species is sympatric with *H.* cf. *ruber* throughout most of its range (Monadjem et al., 2020), the presence of *H.* cf. *ruber* in all of our shade systems, contrary to *H. fuliginosus* that was only captured in rustic farms, may indicate that *H. fuliginosus* is more sensitive to habitat degradation and an indicator of good forests. Although the taxonomy of this species is not resolved due to the presence of two morphotypes, one from East and other from West Africa (Happold and Happold, 2013), the holotype (i.e., type locality) of this species is from West Africa and thus our populations are the true *H. fuliginous*. Contrary to what was expected, an insectivorous bat commonly found in savannahs, *H.* cf. *caffer* (Happold and Happold, 2013), was the only species associated with mixed cocoa agroforestry. This association may indicate that farms with intermediary levels of shade may still be structurally very different from forest areas and more similar to savannas. However, Baldwin et al. (2021) showed that the *H. caffer* complex in Central\West Africa may be formed by at least four distinct species, indicating that maybe the *H.* cf. *caffer* that we captured in our farms is a different species that is not dependent on savannahs. We need more studies focusing on genetics of African bats to properly disentangle the differences in species composition observed between our farm systems and agroforestry systems in other parts of Africa.

5. Conclusion

Although cocoa farms with a maximum of 30 % to 40 % shade tree cover are supposed to maintain win–win scenarios, our study complements the existing literature (e.g., Blaser et al., 2018) by showing for the first time for bats that cocoa farms with intermediary levels of shade tree cover, like the ones proposed in these scenarios, have lower levels of species richness and contain a bat community different from the ones present in high shade farms. In addition, we showed that abundance, richness, and diversity of insectivorous bats increases with increasing shade tree cover. If we consider that cocoa is the fastest expanding export-oriented crop across Africa (Ordway et al., 2017), we need management recommendations that include optimization of shade tree cover and shade tree community composition (e.g., to include keystone forest tree species and planted trees) to be able to preserve all three bat guilds and their ecosystems services (pest suppression, seed dispersion and pollination). To maintain a rich community of insectivorous bats in African cocoa farms, we recommend policymakers and farmers to adopt farm systems with shade tree cover above 65 % and maintain large, tall forest shade trees within farms. In addition, we highlight the importance of combining planted and forest shade tree species in each cocoa farm, not only to maximize bat diversity but also to optimize farmer income through secondary production of shade trees (see Table A.1; (Niether et al., 2020; Wainaina et al., 2021).

CRediT authorship contribution statement

Diogo F. Ferreira: Conceptualization, Investigation, Formal analysis, Writing - Original draft preparation, Funding acquisition. Alexandra Darling: Investigation, Writing - Original draft preparation. Crinan Jarrett: Conceptualization, Investigation, Writing - Reviewing and Editing, Funding acquisition. Patrick Jules Atagana: Investigation, Writing - Reviewing and Editing. Phallin Sandjo: Investigation, Writing - Reviewing and Editing. Hermann Taedoumg: Investigation, Writing - Reviewing and Editing. Andreanna J. Welch: Writing - Reviewing and Editing, Funding acquisition. Hugo Rebelo: Conceptualization, Writing - Reviewing and Editing, Supervision. Luke L. Powell: Conceptualization, Investigation, Writing - Reviewing and Editing, Funding acquisition, Supervision.

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.

Data availability

Data will be made available on request.

Acknowledgments

We thank the 28 cocoa farmers for allowing us to work within their farms and for the support provided, as well Claire, Cyril, Melanie, Fedo, Valery and Arastide for the helped collecting data. We thank International Institute of Tropical Agriculture (IITA), especially Emmanuel Meye, for logistic support. This research was funded by a Durham Junior Research Fellowship, A Marie Curie fellowship, and the Global Challenges Research Fund. LLP was also supported by the European Union's

Horizon 2020 research and innovation program under grant agreement No 854248. H.R. was supported by Portuguese Foundation for Science and Technology (FCT/MCTES) with a contract under DL57/2016. Finally, D.F.F was supported by a FCT fellowship (SFRH/BD/138310/2018).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2023.110191.

References

ACR, 2019. African Chiroptera Report 2019. AfricanBats NPC, Pretoria, South Africa.

Anderson, M.J., Walsh, D.C.I., 2013. PERMANOVA, ANOSIM, and the mantel test in the face of heterogeneous dispersions: what null hypothesis are you testing? Ecol. Monogr. 83, 557–574.

Armengot, L., Barbieri, P., Andres, C., Milz, J., Schneider, M., 2016. Cacao agroforestry systems have higher return on labor compared to full-sun monocultures. Agron. Sustain. Dev. 36, 70.

Asitoakor, B.K., et al., 2022. Selected shade tree species improved cocoa yields in low-input agroforestry systems in Ghana. Agric. Syst. 202, 103476.

Atagana, P.J., Fils, E.M.B., Kekeunou, S., 2021. Responses of bat communities (Mammalia: Chiroptera) to forest loss and habitat conversion in southern Cameroon. Tropical Conservation Science 14, 19400829211010360.

Bakermans, M.H., Rodewald, A.D., Vitz, A.C., Rengifo, C., 2012. Migratory bird use of shade coffee: the role of structural and floristic features. Agrofor. Syst. 85, 85–94.

Baldwin, H.J., et al., 2021. Concordant patterns of genetic, acoustic, and morphological divergence in the west African old-world leaf-nosed bats of the Hipposideros caffer complex. J. Zool. Syst. Evol. Res. 59, 1390–1407.

Barima, Y.S.S., et al., 2016. Cocoa crops are destroying the forest reserves of the classified forest of Haut-Sassandra (Ivory Coast). Global Ecology and Conservation 8, 85–98.

Basham, E.W., Baecher, J.A., Klinges, D.H., Scheffers, B.R., 2023. Vertical stratification patterns of tropical forest vertebrates: a meta-analysis. Biol. Rev. 98, 99–114.

Bennett, R.E., Sillett, T.S., Rice, R.A., Marra, P.P., 2021. Impact of cocoa agricultural intensification on bird diversity and community composition. Conserv. Biol. 36, 1–10.

Blaser, W.J., Oppong, J., Hart, S.P., Landolt, J., Yeboah, E., Six, J., 2018. Climate-smart sustainable agriculture in low-to-intermediate shade agroforests. Nature Sustainability 1, 234–239.

Boyles, J.G., Cryan, P.M., McCracken, G.F., Kunz, T.K., 2011. Economic importance of bats in agriculture.pdf. Science 332, 41–42.

Brooks, M.E., et al., 2017. glmmTMB balances speed and flexibility among packages for zero-inflated generalized linear mixed modeling. The R Journal 9, 378–400.

Caudill, S.A., Vaast, P., Husband, T.P., 2014. Assessment of small mammal diversity in coffee agroforestry in the Western Ghats, India. Agrofor. Syst. 88, 173–186.

Chao, A., et al., 2014. Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol. Monogr. 84, 45–67.

Clough, Y., et al., 2011. Combining high biodiversity with high yields in tropical agroforests. Proceedings of the National Academy of Sciences 108, 8311 LP–8316 LP.

Cortés-Delgado, N., Sosa, V.J., 2014. Do bats roost and forage in shade coffee plantations? A perspective from the frugivorous bat Sturnira hondurensis. Biotropica 46, 624–632.

Curtis, P.G., Slay, C.M., Harris, N.L., Tyukavina, A., Hansen, M.C., 2018. Classifying drivers of global forest loss. Science 361, 1108–1111.

De Beenhouwer, M., Aerts, R., Honnay, O., 2013. A global meta-analysis of the biodiversity and ecosystem service benefits of coffee and cacao agroforestry. Agric. Ecosyst. Environ. 175, 1–7.

De Cáceres, M., Legendre, P., 2009. Associations between species and groups of sites: indices and statistical inference. Ecology 90, 3566–3574.

Dormann, C.F., et al., 2013. Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. Ecography 36, 27–46.

FAOSTAT, 2020. Food and Agriculture Organization of the United Nations.

Faria, D., Baumgarten, J., 2007. Shade cacao plantations (Theobroma cacao) and bat conservation in southern Bahia, Brazil. Biodivers. Conserv. 16, 291–312.

Faria, D., Laps, R.R., Baumgarten, J., Cetra, M., 2006. Bat and bird assemblages from forests and shade cacao plantations in two contrasting landscapes in the Atlantic Forest of southern Bahia, Brazil. Biodivers. Conserv. 15, 587–612.

Faria, D., Paciencia, M.L.B., Dixo, M., Laps, R.R., Baumgarten, J., 2007. Ferns, frogs, lizards, birds and bats in forest fragments and shade cacao plantations in two contrasting landscapes in the Atlantic Forest, Brazil. Biodivers. Conserv. 16, 2335–2357.

Ferreira, D.F., et al., 2017. Season-modulated responses of Neotropical bats to forest fragmentation. Ecology and Evolution 7, 4059–4071.

Ferreira, D.F., Jarrett, C., Atagana, P.J., Powell, L.L., Rebelo, H., 2021. Are bat mist nets ideal for capturing bats? From ultrathin to bird nets, a field test. J. Mammal. 102, 1627–1634.

Ferreira, D.F., et al., 2023. Birds and bats enhance yields in Afrotropical cacao agroforests only under high tree-level shade cover. Agric. Ecosyst. Environ. 345, 108325.

Franzen, M., Borgerhoff Mulder, M., 2007. Ecological, economic and social perspectives on cocoa production worldwide. Biodivers. Conserv. 16, 3835–3849.

Gras, P., Tscharntke, T., Maas, B., Tjoa, A., Hafsah, A., Clough, Y., 2016. How ants, birds and bats affect crop yield along shade gradients in tropical cacao agroforestry. J. Appl. Ecol. 53, 953–963.

Happold, M., Happold, D.C.D., 2013. Mammals of Africa. In: Hedgehogs, shrews, and bats, IV. Bloomsbury Publishing, London, United Kingdom.

Hartig, F., Hartig, M.F., 2017. Package 'DHARMa'.

Harvey, C.A., González Villalobos, J.A., 2007. Agroforestry systems conserve species-rich but modified assemblages of tropical birds and bats. Biodivers. Conserv. 16, 2257–2292.

Hawes, J.E., et al., 2020. A large-scale assessment of plant dispersal mode and seed traits across human-modified Amazonian forests. J. Ecol. 108, 1373–1385.

Hayman, R.W., Hill, J.E., 1971. Part 2. Order Chiroptera. In: Meester, J., Setzer, H.W. (Eds.), The mammals of Africa: an identification manual. Smithsonian Institution Press, Washington, D.C., pp. 1–73

Hsieh, T.C., Ma, K.H., Chao, A., 2016. iNEXT: an R package for rarefaction and extrapolation of species diversity (Hill numbers). Methods Ecol. Evol. 7, 1451–1456.

Jarrett, C., et al., 2021. Bird communities in African cocoa agroforestry are diverse but lack specialized insectivores. J. Appl. Ecol. 58, 1237–1247.

Jeppsson, T., Lindhe, A., Gärdenfors, U., Forslund, P., 2010. The use of historical collections to estimate population trends: a case study using Swedish longhorn beetles (Coleoptera: Cerambycidae). Biol. Conserv. 143, 1940–1950.

Kunz, T.H., Braun de Torrez, E., Bauer, D., Lobova, T., Fleming, T.H., 2011. Ecosystem services provided by bats. Ann. N. Y. Acad. Sci. 1223, 1–38.

Kusuminda, T., Mannakkara, A., Gamage, R., Patterson, B.D., Yapa, W.B., 2022. Roosting Ecology of Insectivorous Bats in a Tropical Agricultural Landscape, 86, pp. 134–143.

Lass, T., 2004. In: Flood, J., Murphy, R. (Eds.), Balancing Cocoa Production and Consumption. Cocoa Futures: A Source Book on some Important Issues Facing the Cocoa Industry. Commodities Press.

Librán-Embid, F., De Coster, G., Metzger, J.P., 2017. Effects of bird and bat exclusion on coffee pest control at multiple spatial scales. Landsc. Ecol. 32, 1907–1920.

Maas, B., Clough, Y., Tscharntke, T., 2013. Bats and birds increase crop yield in tropical agroforestry landscapes. Ecol. Lett. 16, 1480–1487.

Maas, B., et al., 2016. Bird and bat predation services in tropical forests and agroforestry landscapes. Biol. Rev. 91, 1081–1101.

Mac Nally, R., Walsh, C.J., 2004. Hierarchical partitioning public-domain software. Biodivers. Conserv. 13, 659–660.

Mackay, K.D., Gross, C.L., Rossetto, M., 2018. Small populations of fig trees offer a keystone food resource and conservation benefits for declining insectivorous birds. Global Ecology and Conservation 14, e00403.

Meyer, C.F.J., Struebig, M.J., Willig, M.R., 2016. Responses of tropical bats to habitat fragmentation, logging, and deforestation. In: Voigt, C.C., Kingston, T. (Eds.), Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer International Publishing, Cham, pp. 63–103.

Monadjem, A., Taylor, P.J., Coterill, F.P.D., Schoeman, M.C., 2020. Bats of Southern and Central Africa: A Biogeographic and Taxonomic Synthesis, 2nd edition. Wits University Press Johannesburg.

Nair, P.K.R., Kumar, B.M., Nair, V.D., 2021. Definition and concepts of agroforestry. In: Nair, P.K.R., Kumar, B.M., Nair, V.D. (Eds.), An Introduction to Agroforestry: Four Decades of Scientific Developments. Springer International Publishing, Cham, pp. 21–28.

Nakayama, K., Azevedo, C.O., Valverde, M.O., de Siqueira Neves, F., Sperber, C.F., 2008. Sampling parasitoid wasps (Insecta, Hymenoptera) in cacao agroforestry systems. Stud. Neotropical Fauna Environ. 43, 217–226.

Niether, W., Jacobi, J., Blaser, W.J., Andres, C., Armengot, L., 2020. Cocoa agroforestry systems versus monocultures: a multi-dimensional meta-analysis. Environ. Res. Lett. 15, 104085.

Nkrumah, E.E., Opoku, B.A., Badu, E.K., Danquah, E., Tschapka, M., Oppong, S.K., 2017. Estimating bat abundance and diversity in a modified tropical environment in Central Ghana. Trop. Ecol. 58, 751–759.

Ocampo-Ariza, C., et al., 2022. Trait-dependent responses of birds and bats to season and dry forest distance in tropical agroforestry. Agric. Ecosyst. Environ. 325, 107751.

Oksanen, J., et al., 2013. Package "vegan": community ecology package version. R package version 3.4.0 2, 1–296.

Ordway, E.M., Asner, G.P., Lambin, E.F., 2017. Deforestation risk due to commodity crop expansion in sub-Saharan Africa. Environ. Res. Lett. 12, 044015.

Pardini, R., et al., 2009. The challenge of maintaining Atlantic Forest biodiversity: a multi-taxa conservation assessment of specialist and generalist species in an agro-forestry mosaic in southern Bahia. Biol. Conserv. 142, 1178–1190.

Patterson, B.D., Webala, P.W., 2012. Keys to the bats (Mammalia: Chiroptera) of East Africa. Fieldiana Life and Earth Sciences 6, 1–60.

R Core Team, 2020. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria.

Rice, R.A., Greenberg, R., 2000. Cacao cultivation and the conservation of biological diversity. AMBIO: A Journal of the Human Environment 29, 167–173.

Sanderson, F.J., et al., 2022. Forest-dependent bird communities of west African cocoa agroforests are influenced by landscape context and local habitat management. Agric. Ecosyst. Environ. 328, 107848.

Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH image to ImageJ: 25 years of image analysis. Nat. Methods 9, 671–675.

Schroth, G., et al., 2011. Conservation in tropical landscape mosaics: the case of the cacao landscape of southern Bahia, Brazil. Biodivers. Conserv. 20, 1635–1654.

Sekercioglu, C.H., 2006. Increasing awareness of avian ecological function. Trends Ecol. Evol. 21, 464–471.

Seppelt, R., et al., 2016. Harmonizing biodiversity conservation and productivity in the context of increasing demands on landscapes. BioScience 66, 890–896.

Shapiro, J.T., Monadjem, A., Röder, T., McCleery, R.A., 2020. Response of bat activity to land cover and land use in savannas is scale-, season-, and guild-specific. Biol. Conserv. 241, 108245.

Sikes, R.S., Gannon, W.L., Animal Care and Use Committee of the American Society of Mammalogists, 2011. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. J. Mammal. 92, 235–253.

Socolar, J.B., Gilroy, J.J., Kunin, W.E., Edwards, D.P., 2016. How should Beta-diversity inform biodiversity conservation? Trends Ecol. Evol. 31, 67–80.

Thiel, S., Tschapka, M., Heymann, E.W., Heer, K., 2021. Vertical stratification of seed-dispersing vertebrate communities and their interactions with plants in tropical forests. Biol. Rev. 96, 454–469.

van Toor, M.L., O'Mara, M.T., Abedi-Lartey, M., Wikelski, M., Fahr, J., Dechmann, D.K. N., 2019. Linking colony size with quantitative estimates of ecosystem services of African fruit bats. Curr. Biol. 29, R237–R238.

Tscharntke, T., et al., 2011. Multifunctional shade-tree management in tropical agroforestry landscapes – a review. J. Appl. Ecol. 48, 619–629.

Tscharntke, T., et al., 2012. Landscape moderation of biodiversity patterns and processes - eight hypotheses. Biol. Rev. 87, 661–685.

Tscharntke, T., et al., 2015. Conserving biodiversity through certification of tropical agroforestry crops at local and landscape scales. Conserv. Lett. 8, 14–23.

Vansynghel, J., et al., 2022. Quantifying services and disservices provided by insects and vertebrates in cacao agroforestry landscapes. Proc. R. Soc. B Biol. Sci. 289, 20221309.

Voora, V., Bermúdez, S., Larrea, C., 2019. Global Market Report: Cocoa. International Institute for Sustainable Development (IISD).

Wainaina, P., Minang, P.A., Duguma, L., Muthee, K., 2021. A review of the trade-offs across different cocoa production systems in Ghana. Sustainability 13, 10945.

Waldron, A., Justicia, R., Smith, L., Sanchez, M., 2012. Conservation through chocolate: a win-win for biodiversity and farmers in Ecuador's lowland tropics. Conserv. Lett. 5, 213–221.

Waldron, A., Justicia, R., Smith, L.E., 2015. Making biodiversity-friendly cocoa pay: combining yield, certification, and REDD for shade management. Ecol. Appl. 25, 361–372.

Weber, N., Kalko, E.K.V., Fahr, J., 2009. A first assessment of home range and foraging behaviour of the African long-tongued bat *Megaloglossus woermanni* (Chiroptera: Pteropodidae) in a heterogeneous landscape within the Lama Forest Reserve, Benin. Acta Chiropterologica 11, 317–329.

Wessel, M., Quist-Wessel, P.M.F., 2015. Cocoa production in West Africa, a review and analysis of recent developments. NJAS - Wageningen Journal of Life Sciences 74–75, 1–7.

Williams-Guillén, K., Perfecto, I., 2010. Effects of agricultural intensification on the assemblage of leaf-nosed bats (Phyllostomidae) in a coffee landscape in Chiapas, Mexico. Biotropica 42, 605–613.

Williams-Guillén, K., Perfecto, I., 2011. Ensemble composition and activity levels of insectivorous bats in response to management intensification in coffee agroforestry systems. PLoS One 6, e16502.

Williams-Guillén, K., Olimpi, E., Maas, B., Taylor, P.J., Arlettaz, R., 2016. Bats in the anthropogenic matrix: challenges and opportunities for the conservation of chiroptera and their ecosystem services in agricultural landscapes BT - bats in the anthropocene: conservation of bats in a changing world. In: Voigt, C.C., Kingston, T. (Eds.), Bats in the Anthropocene: Conservation of Bats in a Changing World. Springer International Publishing, Cham, pp. 151–186.

Yadav, B., et al., 2021. Can generalized Poisson model replace any other count data models? An evaluation. Clinical Epidemiology and Global Health 11, 100774.

Zemp, D.C., et al., 2019. Mixed-species tree plantings enhance structural complexity in oil palm plantations. Agric. Ecosyst. Environ. 283, 106564.