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# The role of landscape context in shaping bat assemblages in African cacao plantations

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### HIGHLIGHTS

G R A P H I C A L A B S T R A C T

All Guilds

Insectivore:

- Sub-Saharan Africa produces most of the Earth's cacao.
- Landscape structure can shape the communities of bats in African cacao farms.
- Insectivores depend on natural habitats (e.g., tree cover) within cacao landscapes.
- Frugivores and nectarivores are more associated to anthropogenic habitats within cacao landscapes.
- Conceptual designs to manage cacao landscapes need to be tailored to each guild.

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### ABSTRACT

Frugivores

Nectarivore:

22

Cacao production is mostly concentrated in Africa, with this continent exporting an impressive 68.4 % of the world's cacao. The increasing demand for cacao from the Global North has already led to massive deforestation in Ghana and Ivory Coast and cacao-driven deforestation is likely to continue changing landscapes in Sub-Saharan Africa. Bats are affected by these landscape changes due to their dependence on multiple resources spread at a large spatial scale. Although bats can save cacao farmers millions of euros through pest suppression, no study has investigated how landscape context affects bat communities in African cacao plantations. Here for the first time, we studied how abundance and richness of insectivorous, frugivorous and nectarivorous bats within cacao landscapes could be affected by cover type and the distance between these habitats and each cacao plantation. We sampled bats using mist-nets in 38 cacao plantations spread throughout southern Cameroon from 2017 to 2020. We found that guilds responded differently to the distance and amount of cover of each of the land

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cover types, with the scale of response being habitat-dependent. Overall, insectivorous bats were associated positively with high cover of natural habitats (e.g., tree cover, rangeland, and flooded vegetation), and negatively with nearby anthropogenic disturbance (e.g., logging and intensive agriculture). Frugivorous and nectarivorous bats were associated to the presence of natural habitats with water and of nearby anthropogenic habitats (e.g., human settlements, community forests and unpaved roads), probably due to the presence of more fruiting and flowering trees. Considering the associations found between the landscape metrics and bats, we propose three different conceptual designs to manage cacao landscapes: one for insectivores, one for frugivores/ nectarivores and a third design that maximises the trade-offs between these three guilds. By safeguarding the diversity of these three guilds farmers can maintain pest suppression services within their plantations and guarantee healthy and long-lasting sustainable cacao landscapes through bats' pollination and seed dispersal.

### 1. Introduction

Cacao (*Theobroma cacao*) is a valuable crop in many tropical countries, and its cultivation is expanding at a faster rate than any other export-oriented crop in Africa (Ordway et al., 2017). Even though cacao is cultivated in over 50 countries (Lass, 2004), 68.4 % of the world's cacao is produced in mostly small-scale family plantations located in Central/West Africa (FAOSTAT, 2020). The increasing demand for cacao in the last decade (Lass, 2004) will potentially lead to the partial or complete destruction of natural forests in Central/West Africa (Schroth and Harvey, 2007). In countries such as Ivory Coast and Ghana the expansion of cacao agriculture has already led to massive deforestation and the fragmentation of existing protected forest areas, being responsible for 13 % to 40 % of the forest loss in these areas (Asare et al., 2014; Barima et al., 2016; Kalischek et al., 2023).

Bats can be found within agricultural environments across the world and are responsible for several ecosystem services, including pollination, dispersal of seeds and suppression of insect populations (Boyles et al., 2011; Kunz et al., 2011; Russo et al., 2018; van Toor et al., 2019; Fill et al., 2022). Studies conducted in cacao plantations in Asia (Maas et al., 2013) and South America (Vansynghel et al., 2022) showed that pest suppression by bats and birds increased yield independently of plantation management by 31 % and 114 %, respectively. Also, a study conducted in Africa showed that bats and birds can save farmers an average of \$478 per ha per year through pest consumption—but only when high shade tree cover is maintained (Ferreira et al., 2023a).

Due to bats' flying ability, they can access resources (e.g., roosts and food) spread kilometres apart over the landscape. This makes bats dependent not only on local resources but also on resources that could be spatially rare or temporary (e.g., fruiting trees and insect swarms) (Rainho and Palmeirim, 2011). Since bat guilds have very different ecological habits (ACR, 2019), the distance they cover during foraging are landscape- and guild-specific. For example, some African insectivorous bat species can cover up to three km from their roost to foraging locations (Monadjem et al., 2009; Nkrumah et al., 2016), whereas for some African frugivorous and nectarivorous bat species, the straight-line distance between their roost and the most distant feeding site can be >20 km (Weber et al., 2009; Barclay and Jacobs, 2011; Happold and Happold, 2013; Oleksy et al., 2015). Given that most species of bat are philopatric, meaning they usually return to the same roost after foraging (Lewis, 1995; ACR, 2019), and that flying is energetically costly (Rainho and Palmeirim, 2011), it is vital to consider landscape composition (e.g., amount of forest areas) together with metrics associated with home range size (e.g., distances to foraging sites or urban areas) at different spatial scales to understand the responses of African bat guilds to cacao landscapes.

Several studies have shown that cacao agroforestry systems can support bat diversity comparable to natural forest, with some studies showing that cacao plantations can even contain a higher proportion of forest specialists than secondary forests (Faria et al., 2007; Harvey and González Villalobos, 2007; Pardini et al., 2009; Schroth et al., 2011). Atagana et al. (2021) showed that African cacao plantations can contain similar bat species richness to forest sites, but with distinct species composition. Furthermore, in a recent study from Cameroon, Ferreira et al. (2023b) found that cacao management affected the bat community present in cacao plantations, with insectivorous bats increasing with increasing shade cover and shade tree height, while frugivorous and nectarivorous bats depended on the presence of fruit shade trees. Although these studies highlight the role of local plantation management in increasing the potential value of shaded cacao for bat conservation, little is known about the role of the surrounding landscape on shaping these patterns, especially in Africa. We hypothesise that the landscape is important for African bats as well, because for the other flying vertebrates (birds), abundance and richness in African cacao plantations depends on both local management and landscape context (Jarrett et al., 2021; Sanderson et al., 2022).

Some studies from the Neotropics have already shown that bat communities varied between cacao plantations located within different landscapes contexts, with plantations in landscapes with high forest cover or near forest areas supporting a richer assemblage of bats (Faria et al., 2006, Faria et al., 2007; Ocampo-Ariza et al., 2022). Ocampo-Ariza et al. (2022) showed in Peruvian cacao plantations that responses to surrounding landscape are guild-specific, with insectivorous bats benefitting from the presence of nearby forest while frugivorous bats did not show any association with distance to the forest. Furthermore, Heer et al. (2015) showed in cacao-rubber plantations embedded in a fragmented Brazilian Atlantic Forest that plantations surrounded by secondary forest had higher aerial insectivorous bat diversity than those lacking forest in the vicinity. Even though most studies only focused on the role of forests within cacao landscapes, a study from Brazil showed that the activity of some open-area insectivorous bat species, but not richness, was positively associated with the proportion of pasture at small scales (Falcão et al., 2021). This highlights the importance of considering not only forests but other potential important habitat types (e.g., urban areas and waterbodies) at multiple spatial scales to understand how to properly manage cacao landscapes to benefit all bats guilds and their ecosystems services. Furthermore, because bat communities present in the Neotropics are distinct and independently evolved from the ones present in Africa (Simmons and Cirranello, 2018), it is important to understand if the current evidence from the neotropics is transferrable to this part of the world.

The aim of our study was to investigate how abundance and richness of insectivorous, frugivorous and nectarivorous bats in cacao plantations are influenced by the surrounding landscape characteristics. More specifically, we aimed to understand the distance and scale at which different landscape composition metrics affected the bat communities and to investigate which metrics (composition and distance metrics) were associated with the bat communities present in our plantations. Since our study area was dominated by forest cover, we also wanted to understand which other aspects of the landscape, not usually considered within bat cacao landscape studies, were affecting the community of bats present in our farms (Falcão et al., 2021; Jarrett et al., 2021; Ocampo-Ariza et al., 2022; Sanderson et al., 2022). We predicted that responses of bat communities present in our cacao plantations would be guild-specific as in other areas of the world (Faria et al., 2007; Meyer et al., 2016; Ocampo-Ariza et al., 2022). Specifically, insectivorous bats would be more associated with habitats with high tree density (Atagana et al., 2021; Falcão et al., 2021; Ferreira et al., 2023b), while frugivorous

and nectarivorous bats would be more associated to human modified habitats like human settlements and certain types of plantations due to the higher availability of fruits (Atagana et al., 2021; Egert-Berg et al., 2021). Furthermore, since our bat community is composed by bat species with different needs and home ranges, we predicted that the scale of responses would be dependent not only on the guild but also on each landscape metric. Finally, to translate our results into more practical guidelines, we proposed three different landscape conceptual designs that maximise richness for the different bat guilds.

### 2. Material and methods

### 2.1. Study area

We carried out the study in 38 cacao plantations in Cameroon, Africa. Cacao plantations were in seven different landscapes: Konye (eight plantations), Bokito (two plantations), Elat (two plantations), Ngoumou (six plantations), Ebolowa (eight plantations), Ayos (eight plantations) and Somalomo (four plantations; Fig. 1). Plantations were always >1.5 ha, separated by at least 544 m and had varying shade cover (22 % to 92 % shade cover and a mean of 66.6 %  $\pm$  25.5 %; see Ferreira et al. (2023b) for more details).

### 2.2. Bat survey

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) in 38 cacao plantations from August 2017 to September 2020, with each field campaign lasting two months We visited each plantation from 2 to 6 times, and all plantations 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)). We

identified, measured, and recorded the echolocation of all captured bats. We used a wing punch to collect a small tissue sample; this procedure has the added benefit of marking bats and thus allowing us to avoid recaptures during the same night. Species identification followed Rosevear (1965), Hayman and Hill (1971), Patterson and Webala (2012), Happold and Happold (2013), and taxonomy followed ACR (2019). Bats were captured and handled in the field following guidelines approved by the American Society of Mammalogists (Sikes et al., 2011). See section 1 in supplementary material for criteria used for bat identification (including echolocation information) and taxonomic grouping.

#### 2.3. Environmental variables

### 2.3.1. Buffer predictors

2.3.1.1. Landscape composition. Landscape variables were obtained from a 10 m raster spatial land cover time series of the world from 2017 to 2020 derived from ESA Sentinel-2 (Karra et al., 2021). In our study areas seven land cover classes occurred: "Bare areas", "Human settlements", "Cropland", "Flooded vegetation", "Rangeland", "Tree cover" and "Water bodies" (see Table S1 for a detailed description). Because the ESA raster showed that most of our landscape was composed by Tree cover and this variable did not distinguish between forest types (e.g., primary and secondary forest) or the presence of agroforestry, we tried to use "Tree height" for 2019 measured by GEDI with a 30 m resolution to account for possible differences in tree structure (Potapov et al., 2021). Values for this variable ranged from 0 to 60 m. See section 2 in supplementary material for more details. Also, to compensate for this lack of power in distinguishing the different types of forest cover, we obtained spatial data from the Interactive Forest Atlas of Cameroon from 2017 to 2020 (Mertens et al., 2012). We used eight shapefiles from this dataset describing roads (unpaved and paved) and different classes of forest management. The eight classes were: 1) "Roads", 2) "Logging



Fig. 1. Location of the 38 cacao plantations in Cameroon, Africa. Each dot represents a cacao plantation on each of the seven different landscape matrices. The number of plantations visited in each landscape is given in brackets. Dja Faunal Reserve is a UNESCO World Heritage Site, the largest protected area in Cameroon, and one of the largest and most biologically diverse protected areas of rainforest in Central Africa. Land cover is represented by the year 2020 of the time series 10 m raster spatial land cover from ESA Sentinel-2. See Table S1 for a detailed description of the different land cover types.

forestry unit", 3) "Annual harvestable area", 4) "Production forests", 5) "Community forests", 6) "Agro-industrial plantations", 7) "Planted areas" and 8) "Area of hunting interest". Due to the low representation of some of the individual classes from the Interactive Forest Atlas of Cameroon, we created two additional classes by merging the four classes associated to logging (2nd to 5th class) into a class called "Combined logging" and the two classes associated to agricultural production (6th and 7th classes) into "Combined plantations" (see Table S1). Hence, we had a total of 17 classes (individual and the clustered) representing the landscape composition of our study area.

To measure how landscape integrity (i.e., forest condition) and human pressures were affecting our bat communities, we used two indexes available for our study area: the "Forest Landscape Integrity Index" (FLII) and the "Congo Basin Human Pressure Index" (HPI). The FLII applies to the 2019 landscape and has a resolution of 300 m (Grantham et al., 2020a). The HPI was for 2015 and had a resolution of 500 m (Grantham et al., 2020b).

2.3.1.2. Landscape scale. Scale-dependence in associations between bat abundance, richness and diversity and variables describing landscape composition were assessed by quantifying compositional metrics within different-sized buffers (500, 1000, 2000, 5000, 10,000, 15,0000 and 20,000 m radius) centred on each of the 38 cacao plantations. These buffer sizes were selected considering the minimum distance between plantations and the home range of some of our common species (Happold and Happold, 2013; ACR, 2019). The area in hectares occupied by each of the seven composition classes from the ESA raster was calculated using the function "lsm c ca" within the R package "landscapemetrics" (Hesselbarth et al., 2019). For the 10 classes of forest management and for the roads obtained from the Forest Atlas, we measured the area in hectares of each class present within the seven buffers. Finally, for both indexes and tree height we measured the mean and sum of the pixel's values within each buffer. Due to an excess of zeros for some classes, we excluded the following habitat classes from further analyses: "Area of hunting interest" (0 ha  $\pm$  0), "Bare areas" (11 ha  $\pm$  50), "Planted areas" (31 ha  $\pm$  153) and "Plantations agro-industrial" (918 ha  $\pm$  2379).

### 2.3.2. Distance predictors

To assess the effect of Euclidean distance to resources and potential threats in the landscape (e.g., the size of a water body or artificial light may not be relevant for several bat species, while the distance to it may condition its use; Ancillotto et al., 2019), we measured the distance in metres between our 38 cacao plantations and the closest pixel/polygon of each of the 17 classes representing the composition of our study area. Due to excess of zeros for the class "Tree cover" ( $0.14 \text{ m} \pm 1$ ) and the lack of representativeness of the class "Planted areas", we did not use distance predictors for these classes in our analyses. In the final analysis, we used 16 buffer predictors and 15 distance predictors (Table S1). All landscape analyses were performed using R software (Version 4.0.3; R Core Team, 2020).

### 2.4. Statistical analysis

### 2.4.1. Scale of response of bats to cacao landscape composition

To understand the scale (i.e., buffer area and buffer radius) that best explained responses of bats, we started by calculating univariate models for each of the 16 buffer predictors and their respective seven buffer scales. We built 112 univariate models (16 predictors multiplied by seven scales) for each of the eight response variables: abundance and richness of insectivorous, frugivorous and all bats, abundance of nectarivorous bats, and Shannon-Wiener diversity index. Nectarivorous bats were composed of just one species in our study area, *Megaloglossus woermanni*, thus we used only abundance for this guild. We used Generalized Linear Mixed Models (GLMMs) with a Poisson distribution. However, when data were overdispersed, we used a Negative Binomial or Generalized Poisson depending on goodness-of-fit (Yadav et al., 2021). The exception to this was for the Shannon-wiener model, where we used a linear mixed-effects models (LMM) with a Gaussian distribution after checking for normality and homoscedasticity. The fit of models was investigated visually and statistically using a simulationbased approach in the package "DHARMa" (Hartig and Hartig, 2017). To account for the management differences between plantations and repeated visits in our models, we included a random effect of plantation (38 plantations) and another for field campaign (6 campaigns). In addition, we included an offset of the mist-net hours to account for any differences in sampling effort (log number of mist net hours; 1 mist net hour [mnh] equals one 12-m net open for 1 h). Finally, we retained for each buffer predictor and response variable the univariate model with the lowest AICc between the seven buffer scales models and considered that scale as the best to explain the patterns observed for that predictor and response variable (Smeraldo et al., 2021; Levin et al., 2024).

### 2.4.2. Effect of cacao landscape composition and distance on bat communities

To observe the effects of the landscape surrounding our cacao plantations on bat communities, we built multivariate GLMMs separately for the buffer (using only the selected scale based on the univariates models) and distance sets of predictors. Since distance predictors are more associated to the access to resources (e.g., roosts and water) and disturbances, and buffer predictors are more associated to the environmental carrying capacity, (i.e., what are the landscape characteristics that explain the presence of a species/community) (Rainho and Palmeirim, 2011), we ran the models separately for the two sets of predictors to better understand the influence of the different ecological drivers. Prior to the analysis, we standardized all predictors to a mean of zero and a standard deviation of one. We calculated the Spearman's rank correlation coefficient and variance inflation factors (VIF) to test for multicollinearity (Dormann et al., 2013), whereby we considered variables with VIF  $\geq$  10 and/or with a Spearman correlation >0.7 to be collinear, justifying their exclusion from the analysis. Due to buffer scales selected for each of the buffer predictors being specific for each of the eight response variables, we excluded correlated predictors separately for each buffer multivariate model (Fig. S1–5). These procedures reduced the buffer predictors in the multivariate models to 14, ranging from 9 to 13, and the distance predictors to 12 (see Table S2 for predictors included in each full model).

The distance and buffer GLMMs contained a similar structure as the univariate models, with the same distribution for the eight response variables, plantation and field campaign as random effects, and effort as an offset. We ran all possible combinations of predictors included in the full model (see Table S2) with the "MuMIn" package (Barton, 2015) and selected the best-fit models using Akaike's information criterion corrected for small sample sizes (AICc). Models were retained as best-fit models when  $\Delta$ AICc  $\leq 2$ , i.e., when the difference from the best model was  $\leq 2$  (Burnham and Anderson, 2002). Finally, we calculated estimates and confidence intervals by conducting model averaging of the coefficients of best-fit models. We fitted all univariate and full models using the package "glmmTMB" (Brooks et al., 2017). See Fig. S6 for a diagram illustrating the statistical analysis pipeline.

To address the issue of potential spatial autocorrelation, we inspected the residuals of our full and best-fit models using the Moran's I test. Most of the models had no spatial autocorrelation (Table S2), with only six models out of 32 being significantly spatially autocorrelated. Also, we checked if the minimum distance between our 38 plantations was related with our responses variables, with results being non-significant. This indicates that autocorrelation may not contribute to biases in our results. Nevertheless, we included a random effect for plantation to address possible autocorrelation problems and to our knowledge we never had any recaptures between plantations within the same season.

## 2.5. Designing cacao landscape scenarios to promote bat diversity and ecosystem services

To be able to manage cacao landscapes that aim at maximising richness of the three different bat guilds and their ecosystems services, we designed three landscape scenarios based on the marginal means (predicted values) of our final models for each of the eight response variables (models containing all the predictors retained in the best-fit models; Table S2). We calculated predicted values using the package "ggeffects" by varying each buffer and distance predictors that showed significant or marginally significant (p-value <.10) results on the model averaging and by holding all other predictors constant (Lüdecke, 2018). For the buffer predictors associated with habitat composition we converted hectares into percentage of the habitat type present within the buffer scale selected for that predictor. Finally, based on the maximum predicted values (i.e., highest values for abundance, richness and diversity predicted in our models) we used Inkscape (Project Inkscape, 2020) to create three conceptual designs that maximised the abundance and richness of all guilds (all bats and Shannon-Wiener models), the presence of insectivorous bats and their pest suppression services (insectivorous bats models), and the presence of frugivorous and nectarivorous bats and their pollination and seed dispersal services (frugivores and nectarivores bats models). Since we used several buffer scales in our analyses, our conceptual designs gave priority to the smallest scale (500 m) and progressed until the largest scale (20,000 m) due to the management of smaller scales being less costly and more feasible. Finally, we only considered distances metrics if they would fall within any of our buffer scales since our scenarios only propose management recommendations until 20,000 km from the farms. Due to the difficulty of proposing management scenarios associated with average tree height, and disturbances and integrity indices, we did not use those variables.

### 3. Results

During this study, we sampled 108 nights (13,133 mnh) and captured 1514 bats belonging to 34 species/taxa (Table S3). Insectivorous bats composed 64 % of all captures and were represented by 24 different species, with *Hipposideros ruber* and *Rhinolophus alcyone* being the most common. We captured nine species of frugivorous bats, with *Epomops franqueti* representing 46 % of all captures within this guild. The single nectarivorous bat species captured, *Megaloglossus woermanni*, represented 8 % of all captures.

### 3.1. Scale of response of bats to cacao landscape composition

Overall, bats were influenced by composition predictors on larger scales buffers, with buffer radii of 2000 m or below impacting measures of bat richness, abundance, or diversity only in 29 models out of 89 (Fig. 2 and Table S4). Guild responses to each predictor were scale-dependent, with the size of the scale varying between the different composition predictors and bat guilds. We did not observe clear differences between the buffer area of responses to predictors associated with human activity (e.g., Human settlements and Roads) and natural habitats (e.g., Tree cover and Flooded vegetation). See Table S4 for more details on univariate models.

### 3.2. Effect of cacao landscape composition and configuration on bat communities

Responses to landscape predictors (buffer and distance predictors) varied between the three different guilds and diversity index (Fig. 3 and Table S5). Bat abundance for all species combined was positively associated with the amount of tree cover in the landscape and increased with increasing distance to logging forestry units. However, bat species richness was not associated with any predictor. The analysis of the Shannon-Wiener index showed the opposite pattern, with a negative



**Fig. 2.** Best buffer size (i.e., buffer area and radius) selected for each composition predictor and bat group based on smallest AIC from univariate models. Size and colour of the circle denote buffer size, and a missing circle indicates a predictor that was not included due to a strong correlation with another predictor (Fig. S1–5). See Table S1 for the description of predictors and Table S4 for more details on univariate models.

association to the amount of tree cover in the landscape. Also, bat richness was positively associated with increasing indices of human pressure and positively associated with the distance to areas of hunting interest, and to combined and agro-industrial plantations.

For insectivorous bats, patterns between abundance and richness were quite distinct (Fig. 3 and Table S5). Richness of insectivorous bats was only associated with distance predictors, being positively associated with distance to combined/agro-industrial plantations and rangeland. Abundance for this guild was associated to four buffers and two distance predictors: positively to the amount of tree cover, flooded vegetation and rangeland in the landscape; but negatively associated with the amount of combined logging. Finally, similarly to richness, abundance of this guild was also positively associated with increasing distance to agro-industrial plantations and rangelands.

Frugivorous bats were associated with both buffer and distance predictors (Fig. 3 and Table S5). Abundance of frugivores was associated with two distance predictors and three buffer predictors. For distance predictors, frugivores were more abundant far from logging forestry units and nearby roads; while for buffer predictors they were positively associated to the amount of flooded vegetation and community forests, and negatively to mean tree height. Richness of this guild was associated positively with three buffer predictors (human settlements, flooded vegetation and water bodies). It was also negatively associated with increasing distance to agro-industrial plantations and roads, and positively associated with distance to human settlements. Finally, nectarivorous bats were associated positively to the buffer predictor roads in the landscape and to increasing distance to cropland, but negatively associated with increasing distance to roads (Fig. 3 and Table S5).

### 3.3. Designing cacao landscape scenarios to promote bat diversity and ecosystem services

To manage cacao landscape considering all guilds as a whole, we needed to optimize the abundance, richness, and diversity of all species (i.e., maximum values for all bats and Shannon-Wiener models). Based on our results, to optimize abundance of all bats, we needed to keep >95



**Fig. 3.** Regression coefficients for the effects of buffer and distance predictors on the abundance and richness of all species, insectivores, frugivores and nectarivores, and on bat diversity in 38 cacao plantations in Cameroon, Africa. Points represent estimates obtained from model averaging of the coefficients of best-fit models. Error bars represent 95 % confidence intervals. Significant results are indicated as \*\*\* p < .001, \*\* p < .01, and \* p < .05, while marginal results as (\*) p < .1. Black circles show results associated with abundance, orange circles with richness and blue with diversity. See Tables S2 and S5 for additional modelling information.

% of the composition of the landscape as tree cover in a 20,000 m buffer around the cacao plantation (Fig. S7). However, to optimize the diversity levels in our plantations we needed to keep the tree cover percentage below 47 % in a buffer of 5000 m (Fig. S7). Thus, to maximise both abundance and diversity we kept a maximum of 47 % of tree cover within a 5000 m buffer and increased the value of tree cover to 98.3 % for the remaining area of 20,000 m buffer to compensate for the loss of tree cover in the 5000 buffer (Fig. 4 and S11). All distance variables that had an effect at >20 km from the plantations were excluded from the landscape design, namely, Plantations Agro-industrial, Combined plantations, Logging forestry units and Areas of Hunting Interest. We decided to proceed in this way because our scenarios only aimed to manage a landscape until 20,000 km from the plantations (our largest buffer scale). Since in our predictive models not all area of the buffers was allocated to a specific landscape composition, empty areas where management can be done more freely were left in the conceptual design (53 % of the 5000-buffer area). However, these areas have some limitation associated to the distance variables. More specifically, Plantations Agro-industrial, Combined plantations, Logging forestry units and Areas of Hunting Interest should not be used within these areas.

To maximise abundance and richness of insectivorous bats in cacao landscapes, based on our results, we needed to keep at least 40 % of the composition of the landscape as rangeland in a 1000 m buffer around the cacao plantation, at least 20 % of flooded vegetation and a maximum of 1 % of combined logging areas in a buffer of 5000 m (Fig. S8). However, we needed also to maintain at least 97 % of the landscape as tree cover in a buffer of 20,000 m around the plantation (Fig. S8). Hence, to maximise abundance, we kept in the 1000 m buffer a maximum of 60 % of tree cover, in the 5000 m buffer a maximum 79 % of tree cover, and in the 20,000 m buffer we increased the tree cover to 98.5 % to compensate the losses in the smaller buffers (loss of 21 % of forest cover in a 5000 m buffer represents only 1.5 % of a 20,000 m buffer area; Fig. 4 and S12). To maximise abundance and richness, there should not be human activities associated with agriculture (i.e., agro-industrial plantations and combined plantations) within the 20,000 m buffer around the cacao plantation and rangeland should be at least at >5300 m from the plantation (Fig. 4, S8 and S12). Empty areas for the insectivorous bats comprised only 1.6 % of the 20,000-buffer area and had limitations that could not be used within these areas.

To maintain abundance and richness of frugivorous and nectarivorous bats in cacao landscapes at optimum levels (i.e., maximise the values for these guilds) and maintain potential seed dispersal and pollination services, based on our results, we kept at least 17 % of the landcover as flooded vegetation in a 1000 m buffer around the cacao plantations, at least 13 % of flooded vegetation and 10 % of roads in a 2000 m buffer, at least 8 % of community forest and 5 % of human settlements in a 15,000 m buffer, and at least 0.5 % of water bodies in a 20,000 m buffer (Fig. 4, S9–10 and S13). However, roads (unpaved) should be passing at least 40 m from the plantation and human settlements (not including small villages in the surrounding of plantations) should be kept as far as 2200 m. Finally, agro-industrial plantations should be placed no further than 6300 m from the plantations, while logging forest units and croplands should be maintained outside of the



**Fig. 4.** Conceptual designs illustrating a suggestion on how to manage a cacao landscape within a 20,000 m buffer area to promote the abundance, richness, and diversity of all guilds together, insectivores, and frugivores and nectarivores. To see in more detail the conceptual designs see Fig. S11–13. See last section of results for specific values associated to the conceptual designs. The different sized circles denote the scale of responses (1000, 2000, 5000, 10,000, 15,000 or 20,000 m) at which results were significant. Design was based on the results from the predictive models (Fig. S7–10).

20,000 m buffer (Fig. 4, S9–10 and S13). Empty areas for the noninsectivorous bats comprised 92 % of the 20,000-buffer area and had limitations associated with Logging forestry units and Cropland (human planted crops not at tree height; see Table S1 for more details).

In the three conceptual designs, empty areas remained available where freedom is given to policymakers to manage the landscape. However, these empty areas in a specific design should prioritize landscape compositions that positively influenced bats in one of the other designs (Fig. 3). For example, tree cover should be used in part of the empty areas of non-insectivorous bats' design to guarantee that insectivores can still use the landscape. On the other hand, habitats that support high abundance of fruits should be used in empty areas of insectivorous bats' design to guarantee that frugivores and nectarivores will still use the landscape. Also, these empty areas can prioritize landscape compositions that facilitate farmers access to their plantations (e.g., roads) and their livelihoods (e.g., settlements).

### 4. Discussion

We investigated for the first time how the landscape around cacao plantations shaped the community of African bats. For this, we used a large group of predictors, classified into two categories: buffer and distance predictors. We found that each guild responded differently to the amount and distance of the different land use types, with the scale of response being habitat-dependent. Tree cover and flooded vegetation affected the abundance and diversity of all bats, insectivorous bats and frugivorous bats, whereas other natural habitat types like rangeland and water bodies were important to insectivores and frugivores, respectively. We also found that only non-insectivorous bats were positively associated to human infrastructures and other agroforestry activities; however, overall diversity (insectivorous and non-insectivorous species) increased with human pressure at large scales. Although the association between diversity and human pressure at large scales was an unexpected result, this may be driven by the positive associations we found between non-insectivores and human activities and pressures. Since the ShannonWiener Index takes into account both species richness and evenness, and frugivores\nectarivores were more evenly distributed in terms of abundance when compared with insectivores, this may have inflated the diversity score towards non-insectivorous bats. However, since the abundance model for all bats showed patterns more similar to insectivorous bats, we made a compromise between the two models in the management scenario to maintain the abundance, richness and diversity of all guilds.

### 4.1. Effect of cacao landscape structure on insectivorous bats

Elsewhere in the tropics, most species of insectivorous bats are associated positively with tree cover and respond negatively to human pressures (e.g., logging) and the presence of anthropogenic habitats (Meyer et al., 2016; Williams-Guillén et al., 2016; Ocampo-Ariza et al., 2022). We found similar patens to these in our study in Cameroon, with the abundance of insectivores at very large scales increasing with the amount of tree cover, and with richness and abundance decreasing with the presence of neighbouring intensively managed plantations (like agro-industrial plantations) (Figs. 2 and 3). Our results support the idea that forest areas are ecologically irreplaceable by serving as source populations for insectivorous bats to plantations, contrary to modified habitats (Tscharntke et al., 2012). However, in our study we could not distinguish between the different types of tree cover, meaning the tree cover in our landscape could be associated with secondary forests or other types of habitats like agroforests. Nevertheless, studies conducted in agroforestry systems with high level of tree cover or in areas dominated by secondary forests showed that these systems still have the potential to maintain high levels of insectivorous bat diversity (Heer et al., 2015; Ferreira et al., 2023b). In our study, forest cover only influenced the abundance of insectivores at large scales (20,000 m), which could indicate that despite some potential for cacao plantations and nearby forest to harbour insectivorous bats, they may still lack sufficient roosting sites. Most of the insectivorous bat species captured in our study tend to roost in old-growth trees or caves (ACR, 2019) that may not be as available or of the same quality in disturbed habitats compared with undisturbed forests areas (Faria et al., 2007; Ferreira et al., 2023b). Thus, these bats may be only using cacao plantations as foraging areas or to commute between feeding and roosting sites (Faria et al., 2007). Nevertheless, the presence of forest cover adjacent to cacao plantations may facilitate the access of bats to the food sources present in cacao plantations (insects/pest outburst; (Maas et al., 2016; Puig-Montserrat et al., 2020; Ferreira et al., 2023a)) and potentialize their pest suppression services in these plantations (Tscharntke et al., 2007, 2012).

The abundance of insectivorous bats was also positively correlated with the amount of Flooded vegetation and Rangeland at small scales (Figs. 2 and 3). Several studies have shown that flooded habitats can be of extreme importance to bats due to their availability of arthropods and water, being usually positively associated with increasing bat activity, richness and diversity (Blakey et al., 2017; Mas et al., 2021). Even though the abundance of insectivores depended mostly on forest cover at large scales, at small scales the presence of flooded vegetation can provide bats with foraging areas containing a high concentration of insects and water availability that may be lacking in cacao plantations (Mas et al., 2021). Rangeland in Cameroon was characterized mainly by open habitats like pastures and savannahs (Table S1). Although pastures with scattered trees and small corridors in cacao landscape can be positively associated with the foraging activity of open-area insectivorous bats (Falcão et al., 2021), the richness and abundance of this guild in our study area decreased with the presence of nearby rangelands. A study conducted in West Africa showed that the most commonly captured bat in our study area, Hipposideros ruber, used open habitats like wooded savannas but rarely used grass savannahs, showing that only rangelands with some sparse tree cover may be beneficial to these bats (Nkrumah et al., 2016). However, our landscape cover data did not distinguish between different types of open habitat, making it impossible to discriminate if there is a type of rangeland driving these negative patterns with distance but not with overall cover amount. Hence, it is important for future studies to disentangle these patterns by trying to distinguish the different types of rangelands within cacao landscapes.

It is important to highlight that when compared to other big cacao exporters like Ivory Coast or Ghana (Asare et al., 2014; Barima et al., 2016; Kalischek et al., 2023), Cameroon still contains a lot of forested areas. Thus, human disturbances are likely to be present in Cameroon to a much lesser degree or intensity than in those countries, allowing the possibility of sustaining a diverse bat community that includes many insectivores. The role of forest for the conservation of forest specialist bat species is irreplaceable (Meyer et al., 2016).

### 4.2. Effect of cacao landscape structure on frugivorous and nectarivorous bats

Contrary to insectivorous bats, frugivorous and nectarivorous bats were associated with anthropogenic habitats like human settlements and roads (Figs. 2 and 3). More specifically, the richness of frugivores increased with increasing area of human settlements at large scales. The presence of urban areas is usually associated with a higher density and diversity of native/exotic fruit trees due to farming and irrigation, benefiting many frugivorous species (del Vaglio et al., 2011; Jung and Threlfall, 2016; Berthon et al., 2021; Egert-Berg et al., 2021). Indeed, many frugivorous species present in our study occur in urban areas and take benefit from this more stable year-round source of fruits (Happold and Happold, 2013; Atagana et al., 2021; Egert-Berg et al., 2021). Nevertheless, we found that the richness of frugivores decreased when human settlements were nearby the plantations. Although frugivores can benefit from urban areas, some species may only use them to forage and still roost in other type of habitats (Happold and Happold, 2013). Some studies conducted with bat species that use caves or similar structures as day-roost (like two of our nine species) showed that bats commute kilometres at night from roosts in rural/natural sites to feeding sites in urban areas or plantations (Syafiq et al., 2016; Egert-Berg et al., 2021). Like nectarivores, the abundance and richness of frugivores increased when roads were nearby the cacao plantations, with the number of roads at small scales also increasing the abundance of nectarivores. Roads can have negative impacts on bats by creating barrier effects and causing high mortality rates due direct kills associated with traffic (Altringham and Kerth, 2016). However, these patterns are usually associated to paved roads and most of the roads in our study area are small unpaved roads with reduced traffic (Cameroon has only 10% of its Road Network paved; Logistics Capacity Assessments, 2019). Azhar et al. (2015) found similar patterns with richness of fruit bats increasing with the proximity to unpaved roads in agroforestry oil palm plantations in Malaysia. This could be related with a higher fruit availability next to roads due to farmers using accessible areas along roads to plant other commercial crops (like banana) (Weber et al., 2009; Azhar et al., 2015). Also, frugivorous and nectarivorous bats in Africa do not echolocate (ACR, 2019) and thus may benefit from the presence of uncluttered tracks like small roads as flyways between roosting and feeding areas (Monadjem et al., 2010; Medinas et al., 2019). Indeed, the small scale of responses to the number of roads (2000 m) and the positive association with roads nearby plantations seems to indicate unpaved roads are important for these guilds to access cacao plantations.

Although frugivores responded mainly to anthropogenic habitats, two natural habitats were also associated positively with this guild (Fig. 3). Their richness and abundance increased with the amount of flooded vegetation at small scales, and their richness increased with water bodies at larger scales. The association of this guild with habitats containing water is in accordance with other studies that showed that water availability is an important factor for the distribution of frugivorous species (Lucan et al., 2016; Manga Mongombe et al., 2019). Also, our most common frugivorous bat species, *Epomops franqueti*  (representing >45 % of frugivorous captures; Table S3), roosts often in dense foliage of large trees near or over water, indicating that the relationship to flooded vegetation at small scales may be driven mostly by this species (Happold and Happold, 2013).

The presence of other crops (like agro-industrial oil palm and rubber plantations; Table S1) nearby our plantations benefited frugivorous bats, while nectarivorous bats were less abundant in farms that were closer to cropland to cropland (Fig. 3). Cropland was composed mainly by non-tree crops (like cereals; Table S1) and thus this habitat type may offer very limited food (i.e., flowers) and roost resources to *Megaloglossus woermanni*, our only nectarivorous species (Weber et al., 2009). Similar to cacao, agro-industrial oil palm and rubber plantations can support ecologically important frugivorous species by offering a constant and reliable fruit supply and roosting alternatives, contributing to increase the richness of this guild within cacao plantations (e.g., mangoes and bananas; Azhar et al., 2015; Syafiq et al., 2016; Waghiiwimbom et al., 2020; Atagana et al., 2021; Tanalgo et al., 2021).

Finally, community forests were also associated positively with the abundance of frugivores. Although no studies have investigated the relationship between bats and forests exclusively protected and managed by village communities, some studies have shown that if managed properly the flora and fauna status can improve under this type of forest management (Brown et al., 2002; Odera, 2004; Duguma et al., 2018). Nevertheless, these types of forest still seem dominated by animals more adapted to anthropogenic habitats (Akouehou et al., 2010). This may explain why this forest type was not associated with insectivores and only with the abundance of frugivores, which in general are not rare or sensitive species. Contrary to studies from the Neotropics and Asia (Castro and Michalski, 2014; Meyer et al., 2016), the abundance of frugivores increased with the distance to logging forestry units, indicating a negative relation with logging. Although these logging units can also be within community forests, it seems that logging outside of these forests may be more intensive and thus depleting this habitat of important trees that frugivorous may use to feed and roost. However, because our data did not allow us to distinguish the anthropogenic activities associated with these community forests, future studies should investigate the logging intensity in these areas and the role of community forests for the conservation of bats.

### **4.3.** Landscape management scenarios that promote bat diversity and services in cacao

To conserve biodiversity properly, some authors suggested that management scenarios should be implemented at landscape and not patch scale, with amount of forest cover always as a top priority (Arroyo-Rodríguez et al., 2020). Also, some authors highlight that preserving at least 30 % to 40 % of forest may reduce extinction risk by 50 % and ensure the persistence of most forest species (Arroyo-Rodríguez et al., 2020; Hannah et al., 2020). However, our conceptual designs showed that 40 % of forest cover would not to be enough to maximise insectivorous bat diversity, while to maximise frugivore and nectarivore diversity other habitats would be more important than forest cover. This supports the idea that standard figures of forest cover can lead to problematic outcomes due to thresholds varying between study areas and animal groups (Banks-Leite et al., 2021). Also, because cacao agroforestry is usually planted under a multi-strata of canopy trees it is hard to discriminate cacao from forest with enough confidence using satellite imagery (Numbisi et al., 2019). Future designs should try to consider this distinction to understand how much cacao agroforestry can be included in the landscape and how far these plantations need to be from each other without affecting the community of bats.

We showed that a conceptual design with high amounts of natural habitat types (e.g., forest and rangeland) and reduced human pressures (e.g., logging and intensive agriculture) can maximise richness and abundance of insectivores. Research has shown that these in turn can result in increased pest suppression services within cacao plantations (Maas et al., 2016). However, we also showed that to maximise richness and abundance of frugivores and nectarivores we needed a landscape that included higher amounts of anthropogenic habitats (e.g., dense villages and unpaved roads) with the presence of some natural habitats (e.g., flooded vegetation). In countries like Ivory Coast or Ghana where large areas of forest have already been cleared (Kalischek et al., 2023), frugivorous bats may be more successful and thus require less management (i.e., increased human alteration) than in the relatively more forested country of Cameroon.

Here, we also proposed a conceptual design that would be a compromise for maintaining all guilds within cacao landscapes based on the patterns observed for the abundance and diversity of all guilds (Fig. 4). The suggested design dramatically reduced tree cover nearby cacao plantations, but still allowed for high tree cover and space for other important natural and anthropogenic habitats. This scenario should allow for the maintenance of acceptable levels of abundance and richness of all guilds, thus maintaining the important pest suppression services that insectivorous bats provide within cacao plantations. However, this scenario would likely cause the decline of the more forest dependent bat species like Hipposideros fuliginosus (Table S3). This landscape management scenario is a compromise that creates only partial win-win scenarios for the three different bats guilds, with unknown outcomes. Hence, the application of these management recommendations should ideally be accompanied with studies that investigate the positive or negative impacts of the different scenarios on the three bat guilds, and how their ecosystems services and cacao production would be affected by it.

Although these scenarios are based on an intense survey of bats in multiple cacao plantations across four years, their feasibility to balance biodiversity and cacao production was not under study and thus they have their own limitations. For example, cutting down forest around the cocoa plantation to make space for roads is not what this study is proposing. Here, we give the best scenarios to preserve bats if those areas are ever to go under development or agriculture is to be intensified. Protecting native forests should always be the main goal to guarantee that the rarest forest dependent bat species are preserved (Meyer et al., 2016). Since we could not map cacao agroforestry and cacao can be planted under native forest, it is impossible to understand the real impact that these scenarios would have on cocoa production. Furthermore, these scenarios are specific to Cameroon and thus more studies would be needed to understand their value for other areas.

Policymakers should look at the values (amount of landcover and distance) proposed as guidelines and not rules. For example, to find a compromise between the results from the model of all guilds and diversity, we had to balance the amount of tree cover within the area of the 5000 m and 20,000 m buffer. Since to optimize diversity we had to keep a maximum of 47 % of tree cover within a 5000 m, we had to reduce the amount of tree cover in the surroundings of our plantations below what would be expected if we only followed the results from the all-guilds model. This decision could have implications for the insectivorous bats that tend to have smaller home ranges and thus may need tree cover to commute between roosting and feeding areas (Monadjem et al., 2009; Meyer et al., 2016; Nkrumah et al., 2016). Although long-term studies would be needed to understand the real impact of these designs, other potential conceptual designs are possible. For instance, a design that overpasses the proposed tree cover for the 5000 buffer by creating empty areas outside of this buffer area could be more realistic and allow the presence of other types of habitat or infrastructure throughout the 20,000 buffer landscape. These changes would likely affect overall diversity, but since this index is possibly driven by non-insectivorous bats, other measures adapted from the frugivore and nectarivore conceptual design (Fig. 4 and S13) could be implemented to minimise its negative impacts. Our conceptual designs show a way to move forward, but it is of paramount importance that policymakers focus on follow-up studies that try to understand the impacts of the implementation of these guidelines on bat communities, cacao production and human

#### livelihoods.

Our proposed landscape designs aim to optimize bat diversity and abundance in cacao plantations with some conceptual designs being dominated by tree cover. Although Cameroon and our study area still has a high percentage of forested areas (Fig. 1; Kalischek et al., 2023), our designs could hinder farmers' revenues by limiting the plantation of non-tree crops, their access to plantations and infrastructures by limiting the development of road networks, or their overall livelihoods by limiting urbanization around the farms. Balancing biodiversity with agricultural productivity requires integrated approaches that consider both ecological goals and the socio-economic needs of farmers (Camargo et al., 2019). Hence, socio-economic studies and active stakeholder involvement are essential to refine these conceptual designs and ensure the conservation efforts proposed align with the realities of cacao farming, farmers and local communities of the area.

### 5. Conclusions

We showed that the different groups of bats (insectivores, frugivores and nectarivores) responded differently to the cacao landscape, and we proposed three different scenarios that could help cacao farmers and policymakers to maximise the diversity of the different bat groups and their services. However, given that current evidence of ecosystem services in cacao only focusses on insectivorous bats (Maas et al., 2016; Vansynghel et al., 2022; Ferreira et al., 2023a), we highlight the need to also implement strategies that consider frugivorous and nectarivorous bats due to their importance in pollinating fruit trees (e.g., Banana and Mango trees) used as secondary source of income by cacao farmers (Raghuram et al., 2011; Aziz et al., 2021), and their potential contribution in restoring disturbed or deforested natural areas caused by the intensification of cacao production (van Toor et al., 2019; Kalischek et al., 2023). Finally, since cacao is the fastest expanding export-oriented crop across Africa (Ordway et al., 2017), the landscape scenarios proposed in our study may not be able to support the current cacao productivity. Hence, these scenarios should be used by policymakers only as a reference and adapted accordingly to the reality in the field, with adequate monitoring programmes running in parallel to understand if these measures have negative or positive impacts on bat communities and cacao production.

### CRediT authorship contribution statement

**Diogo F. Ferreira:** Writing – review & editing, Writing – original draft, Methodology, Funding acquisition, Formal analysis, Data curation. **Crinan Jarrett:** Writing – review & editing, Methodology, Funding acquisition, Conceptualization. **Patrick Jules Atagana:** Writing – review & editing, Methodology, Investigation. **Andreanna J. Welch:** Writing – review & editing, Funding acquisition, Conceptualization. **Luke L. Powell:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Conceptualization. **Hugo Rebelo:** Writing – review & editing, Supervision, 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.

### Data availability

Data will be made available on request.

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### Appendix A. Supplementary data

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