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CAMBRIDGE
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Cropland can support high bird diversity in heterogeneous rural tropical landscapes

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Summary

Land-use change for crop production is one of the key drivers of habitat loss and fragmentation and consequently biodiversity loss and change in tropical regions. This may impact biodiversity-regulated ecosystem services; birds are important to crop health regulating services (e.g. seed dispersal, pest control) and disservices (e.g. seed predation, grain herbivory). However, knowledge is limited on how birds use heterogeneous agricultural landscapes and the consequences for spatial distribution and flow of services and disservices. We studied crop and non-crop–habitat associations of birds in forest–agricultural landscapes of the Kilombero Valley, Tanzania. We focused on dietary preference as a key trait impacting bird responses to land-use change, services, and disservices to crops. We surveyed birds across four main habitat types using repeated point counts, recording a total of 148 species. We found that crop habitats supported higher species richness and larger communities of potentially beneficial species to crop health, whereby 34.5% of invertebrate-feeding species were recorded in cropland. We found that habitat heterogeneity within the landscape supports bird functional diversity and that each habitat type supported unique communities of species. Furthermore, the number of species unique to forest habitats increased with increasing forest canopy closure. Our findings suggest that management strategies for maintaining trees and shrubs, and enhancing tree cover within the crop production landscape, can be effective approaches for maintaining bird diversity and services. However, in-depth studies on trade-offs with disservices need further exploration to mitigate negative impacts of birds on crop yields.

Introduction

Tropical landscapes have undergone increased levels of anthropogenic land-use change, largely due to agricultural expansion to meet increased food demands from human population growth (de Lima et al. 2013; Laurance et al. 2014). This has caused habitat loss and fragmentation for many wildlife species, culminating in declines in habitat quality and biodiversity (Hatfield et al. 2020). Changes to habitat extent and quality (e.g. declining structure, function, and connectivity in the landscape) can have negative consequences for species richness and abundance (Şekercioğlu 2011).

Biodiversity responses to structural and quality changes in their habitats are complex and highly variable across taxa (Pfeifer et al. 2017). Species may exhibit either positive or negative responses to habitat fragmentation, and the ability of habitat fragments to support stable populations of species depends on both the quality of the habitat patch and the quality of the matrix in which the patch is embedded (Smith et al. 2011). It also depends on species' habitat requirements, i.e. types of habitats within the landscape that fit the species' requirements for resource acquisition and species' mobility (Cagnolo et al. 2009). Edges between habitat types created by habitat fragmentation, and the edge effects emanating from these, can result in significant alterations in species composition (Pfeifer et al. 2017). This subsequently is expected to alter ways in which species of different traits utilise habitats in the wider landscape. For example, forest specialist species may vanish from edges along forest patches, but these edges also create the opportunity for spill-over of some species into surrounding habitats (Boesing et al. 2018).

The focus on birds and changes in their functional composition is justified when looking at the challenges faced by farming systems in the rural tropics, including small-scale subsistence farmers and commercial producers. Agricultural expansion to meet global needs for food,

bioenergy, and animal feed (Laurance et al. 2014) is posing a biodiversity threat (Taubert et al. 2018). Birds are often used as indicators of biodiversity responses to land-use changes as they are diverse, well-studied, and cost-effective to sample (Gardner et al. 2008). Several studies have found that diet and ecological special-isation drive bird declines, particularly in forest–agricultural land-scapes (Şekercioğlu et al. 2019). Birds with specialised diets are likely to have greater dependence on their habitats and will there-fore be more negatively affected by habitat fragmentation (Walker 2007; Sekercioglu 2011). Conversely, species with generalist traits, including broad diets and higher levels of sociality, have shown greater levels of adaptability to changes in their environments (Callaghan et al. 2019) This is important in the context of the ecosystem services that birds provide (Şekercioğlu et al. 2019), i.e. pest control and pollination, but also disservices, i.e. seed pre-dation (Imboma et al. 2020; Morante-Filho and Faria 2017; Wenny et al. 2011; Zhang et al. 2007).

Understanding and predicting how bird communities and their services and disservices are changing in response to pervasive land-use changes are important, specifically for discussions on synergies and trade-offs that may apply on the biodiversity–food–energy nexus and for decision-making on the allocation of land to restor-ation. In this study, we explore the habitat dependency and func-tional role of birds in a fragmented crop production landscape typical of the rural tropics. Using a case study region in Tanzania, we firstly explore habitat dependency of birds in the landscape. We examine variation in bird species occurrence within and across the main habitat types, and quantify bird species responses to continu-ous environmental gradients such as percentage of forest cover and distances from forest habitats. Secondly, we assess relationships between bird foraging and habitat dependencies. Specifically, we focus on services and disservices provided by bird species to

agricultural landscapes with a focus on the maintenance of crop health through pest control (i.e. invertebrate-feeding species). Thirdly, we quantify the effects of anthropogenic disturbance (measured as distance to human settlements and roads) on bird species and their abundance distribution in the landscape. Finally, we propose management actions to enhance services provided by bird species but also support the maintenance of bird diversity within the landscape.

Methods

Study area

The study was carried out in the northern part of the Kilombero Valley in southern-central Tanzania located within the Southern Agricultural Growth Corridor of Tanzania (SAGOT) (Gebrekidan et al. 2020) (Figure 1). The study area is bordered to the west by the Udzungwa National Park and to the east by Nyerere National Park (previously the Selous Game Reserve) (Johansson and Abdi 2020). It is a large freshwater floodplain which supports high levels of biodiversity and is considered an important wetland area for bird-life in Tanzania. It is home to several high conservation value endemic species, including newly described *Cisticola* species, i.e. Kilombero Cisticola *C. bakerorum* and White-tailed Cisticola *C. anderseni* (Fjeldså et al. 2021). The landscape has a distinct wet season (December–May), receiving an average annual rainfall of 1,200–1,400 mm. This, coupled with mean temperatures of 20–30° C and fertile soils, has allowed the landscape to be utilised for agriculture and pasturage (Andrew et al. 2015). The landscape encompasses diverse small-scale crop farming for household sub-sistence and cash (hereafter referred to as smallholder farming), high-intensity farming for sugarcane and rice, including a large-
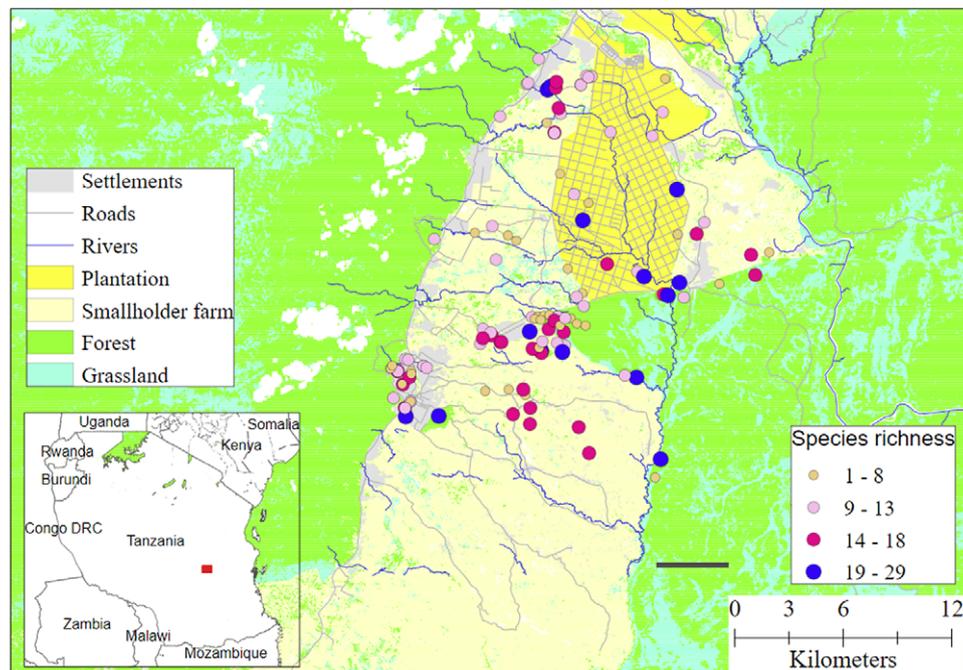

Figure 1. The study landscape and species richness at sampling sites. Using a 2019 Landsat image we mapped the main land-cover classes using random forest models and further separated industry farms from other farms using a digitised boundary file for the sugarcane plantation field. Species richness of birds was calculated from repeated point surveys at each of the 124 sampling sites (December 2019–February 2020) and categorised into five species-richness classes. Species richness varied throughout the landscape with a maximum species richness recording of 29 and minimum of one. The inset map shows the location of the study landscape in Tanzania. Uncategorised areas which were obscured by cloud cover are shown in white

scale sugarcane plantation, the forests of the Magombera Nature Reserve, areas of community-managed forests, and human settlements, of which many run along the western border of the valley adjacent to the Udzungwa Mountains National Park. In this region smallholder farming and large-scale intensive farming has driven land-use changes over decades (Msofe et al. 2019), degrading and fragmenting natural forest, grassland, and wetland habitats within the valley.

Sampling methodology

Repeated point counts (Bibby et al. 2000) were used to survey bird species at 124 sampling locations within the study landscape. These locations were visited twice during each seasonal sampling effort, resulting in each location being surveyed a minimum of four and a maximum of six times. Bird surveys were conducted between 05h00 and 09h00 and 16h00 and 18h00, which coincided with peaks in bird activity. Surveys were not conducted on windy or rainy days and locations were surveyed on non-consecutive days to allow for a broader representation of variability in weather conditions, such as differences in temperature and humidity.

Birds were identified and counted for 10 minutes at each sampling location following an initial two-minute wait period to allow birds to resettle after the arrival of observers. Birds were recorded if seen or if heard within a 60-m radius. Distances from observer to each bird seen were recorded using a rangefinder (Nikon Laser 550AS). Species encountered while moving between sampling points and those which flew over sampling points were not included in the survey records or the analysis but were included in the overall species list for the landscape (Supplementary material Table S1).

Data analysis and modelling

Species data

Data analysis was carried out in R version 4.0.4 of RStudio (RStudio Team 2021). Diet preference data for each bird species observed across survey points during the sampling period were extracted from the Elton Traits database (Wilman et al. 2014). Bird species were grouped into five main diet categories based on percentage intake of food groups from 10 dietary categories (Table S2): plant/seed-based diets, invertebrate diets, frugivorous diets, omnivorous diets, and vertebrate diets, which included scavenger and piscivorous species (Wilman et al. 2014).

The *rgbif* package (Chamberlain et al. 2021) was used to download bird species data for the study area from the Global Biodiversity Information Facility (GBIF). This derived species list was used as a checklist against the bird species recorded during the sampling period to test whether any species may have locally disappeared since the last records acknowledging that birds may have been missed during our surveys and assuming that field sampling carried out was exhaustive. Data on threat status was extracted from the International Union for Conservation of Nature (IUCN) databases using the package *rredlist* (Chamberlain 2020). IUCN Red List status information was used to group species into threatened ("Vulnerable", "Endangered", and "Critically Endangered") and non-threatened ("Least Concern" and "Near Threatened") species. We extracted the type and number of countries, across which the species had been recorded from the IUCN database to identify whether a species was range restricted (*sensu* occurring only in East Africa, namely Zambia, Malawi, Tanzania, Mozambique, Kenya, Burundi, Rwanda, Uganda, South Sudan, Ethiopia, Eritrea, Djibouti, and Somalia), or not. We cross-referenced our species against

the species checklist published for the Eastern Arc Mountains Biodiversity Hotspot (Rovero et al. 2014).

We computed species richness from the species matrix using the average number of individuals per species over the sampling effort and calculated for each sampling location using the "specnumber" function in the *vegan* package (Oksanen et al. 2020). Only species richness was reported and used as the response variable in subsequent modelling approaches.

Habitats, environmental data, and anthropogenic disturbance

We extracted habitat type for each sampling location from land-cover maps developed using ground survey points and Landsat data with random forest models (Pfeifer et al. 2022), corrected by setting cropland pixels in protected areas to grassland and forest pixels in the monoculture plantation to cropland (as these are likely misclassifications). We extracted forest pixels as forest layer and removed isolated forest pixels using clumping algorithms looking across three neighbouring pixels. To characterise the seven environmental drivers, we extracted for each location, percentage forest cover in a 250-m window, forest canopy closure (at point and as average within a 150-m buffer window), distance to nearest forest (m), distance to nearest river (m), and distance to sugarcane plantation (intensive agriculture) as well as smallholder farms (m). We extracted distance to human settlement (m) and distance to roads (m) to each sampling location to capture anthropogenic disturbance. We downloaded digitised road vector data from the Open Street Map database (2019). We manually digitised human settlements, water bodies, and the boundary of the sugarcane plantations using Google Earth Pro (2020). We used QGIS 3.0 (QGIS Development Team 2021) to rasterise roads and settlements and to create presence maps for forests, sugarcane plantations, and smallholder farms. The "proximity tool" in QGIS 3.0 was used to extract information on distances to each variable. The *raster* (Hijmans 2020) and *rgdal* (Bivand et al. 2021) packages were then used to extract environmental and anthropogenic disturbance values from the maps on to each of the sampling locations.

Analysing the functional diversity of birds within the landscape

We constructed Venn diagrams using the *VennDiagram* package (Chen 2021) to visualise unique and shared habitat associations of birds across the survey points. We separately computed the number of unique and shared species between habitat types for (1) all species, and (2) sub-sets of species in each dietary category (i.e. plant/seed-based diets, invertebrate diets, fruit- and/or nectar-based diets, omnivorous diets, and vertebrate diets). We subsequently quantified the percentage of birds for each diet category in the different habitat types.

Bird species richness, habitat dependencies, and anthropogenic disturbances

We tested for significant differences in species richness between habitat types using the non-parametric pairwise Wilcoxon signed-rank test with Bonferroni adjustment (Klopper 2018), because assumptions of normal distribution and variance homogeneity were violated. We then tested for significance in single predictor relationships between environmental drivers and overall species richness, as well as species richness of invertebrate feeders and species richness of plant/seed feeders. In the same way we tested for significance in single predictor relationships between anthropogenic disturbance drivers and overall species richness, species richness of invertebrate feeders, and species richness of plant/seed feeders. This was achieved using Generalised Linear Models

(GLMs) with a Poisson error distribution due to the nature of the bird count data. We subsequently focus on reporting results for significant relationships only.

The resulting model diagnostics were examined for each model, specifically a visual inspection of the residual versus the fitted values, to help identify if there are curvilinear trends in the data and to check for the normal distribution of residuals using Normal Q-Q plot. Log transformations were applied to species richness to investigate whether this improved model performance or model diagnostics. Models were systematically compared using analysis of deviance to determine which model best fit the data and the amount of deviance explained by the model was calculated using the "Dsquared" function (D^2) (see Supplementary material).

We used the *glmulti* package (Calcagno 2020) to compute multiple predictor models explaining variation in total species richness and number of invertebrate-eating species as well as plant/seed and vertebrate-feeding species from combinations of environmental and anthropogenic disturbance variables including interaction effects between human settlement and distance to smallholder farms, distance to plantations, and distance to forest. All predictive variables were checked for intercorrelation using the "corr.test" function with "pearson" in the *psych* package. We excluded highly intercorrelated variables ($R > 0.7$) in the formulation of the full model. We then used the "glmulti" function to identify a final model of the most important predictor variables for each biodiversity metrics, with models ranked using the Akaike Information Criterion (AIC). Finally, we checked for spatial autocorrelation in the final model using Moran's I test for residual spatial autocorrelation in the *spdep* package (Bivand and Wong 2018).

Detectability

Detection efficiency is often an issue that arises when conducting bird surveys, as birds are highly variable in their detection probability (Sanz-Pérez et al. 2020). A simple test was conducted to estimate whether the number of species recorded at each sampling site was underestimated. This was achieved by computing species richness for each sampling location for two separate surveys that were chosen at random for comparability. We quantified the difference in species richness between the two surveys for each survey point and habitat type. A Wilcoxon signed-rank test with Bonferroni adjustment for pairwise comparisons was used to test for

significant differences in richness from survey one to two between habitat types, as a simple measure for detectability differences due to habitat types.

Results

During the sampling period 148 different bird species from 53 families were recorded across the sampling locations. Common Bulbul *Pycnonotus barbatus* and Zanzibar Red Bishop *Euplectes nigroventris* were the most widespread species, recorded in 93 and 76 sampling locations, respectively. Red-chested Cuckoo *Cuculus solitarus* and Black-throated Wattle-eye *Platysteira peltata* were the rarest species in the landscape. *C. solitarus* was recorded only once at a single location in smallholder farmland and *P. peltata* was seen once at a single location in forest habitat. Two threatened species were recorded: Martial Eagle *Polemaetus bellicosus* recorded in smallholder farmland and Kilombero Weaver *Ploceus burnieri*, a range-restricted species endemic to the Kilombero region, which was recorded in smallholder farmland, plantation, and forest habitats.

An additional five range-restricted species were recorded at the sampling sites. Of these, Yellow-rumped Seedeater *Crithagra xanthopygia*, Blue-mantled Crested Flycatcher *Trochocercus cyanomelas*, and Stripe-cheeked Bulbul *Arizelocichla milanjensis*, an Eastern Arc regional endemic species, were recorded solely within smallholder farmland. Zanzibar Red Bishop was recorded in multiple habitat types, including forest habitat, while Fisher's Greenbul *Phyllastrephus fischeri* was recorded in plantations and natural grassland habitats (Table S1). The downloaded GBIF species list for the study area showed a total of 576 bird species, of which we recorded 131 species. An additional 17 bird species that were not found on the GBIF species list were recorded during the sampling period (Table S7).

Of the 148 species recorded, species feeding on invertebrates were most common (45% of all species), and 34.5% of these were recorded at sampling points within smallholder farms (Table 1). Plant/seed-feeding species accounted for 21.6% of all species, with 18.9% of these recorded within smallholder farms. Fruit-eating species and omnivorous species were less common, accounting for 10.1% and 10.8% of total species, respectively, similarly to invertebrate and plant/seed-feeding species they were also most

Table 1. Distribution of species within the landscape. The table shows the total number of species recorded in each habitat type and the total species recorded in the landscape. Percentages of each dietary type were calculated as a percentage of total species recorded in the landscape (148 species). Minimum, median, and maximum values of species richness are also shown

| Land use	Smallholder farm	Forest	Grassland	Plantation	Total landscape
Number of species	121	97	47	69	148
Number of sampling locations	74	31	6	13	
Invertebrate	34.5%	26.3%	15.5%	20.3%	45.0%
Plant/seed	18.9%	15.5%	8.7%	13.5%	21.6%
Frugivore	8.1%	8.1%	1.3%	2.7%	10.1%
Omnivore	8.1%	7.4%	3.3%	2.0%	10.8%
Vertebrate/ scavenger	8.1%	4.0%	1.3%	4.0%	8.7%
Mean species richness	12	10	12	11	11.7
Maximum species richness	22	29	21	19	29
Minimum species richness	1	2	5	5	1
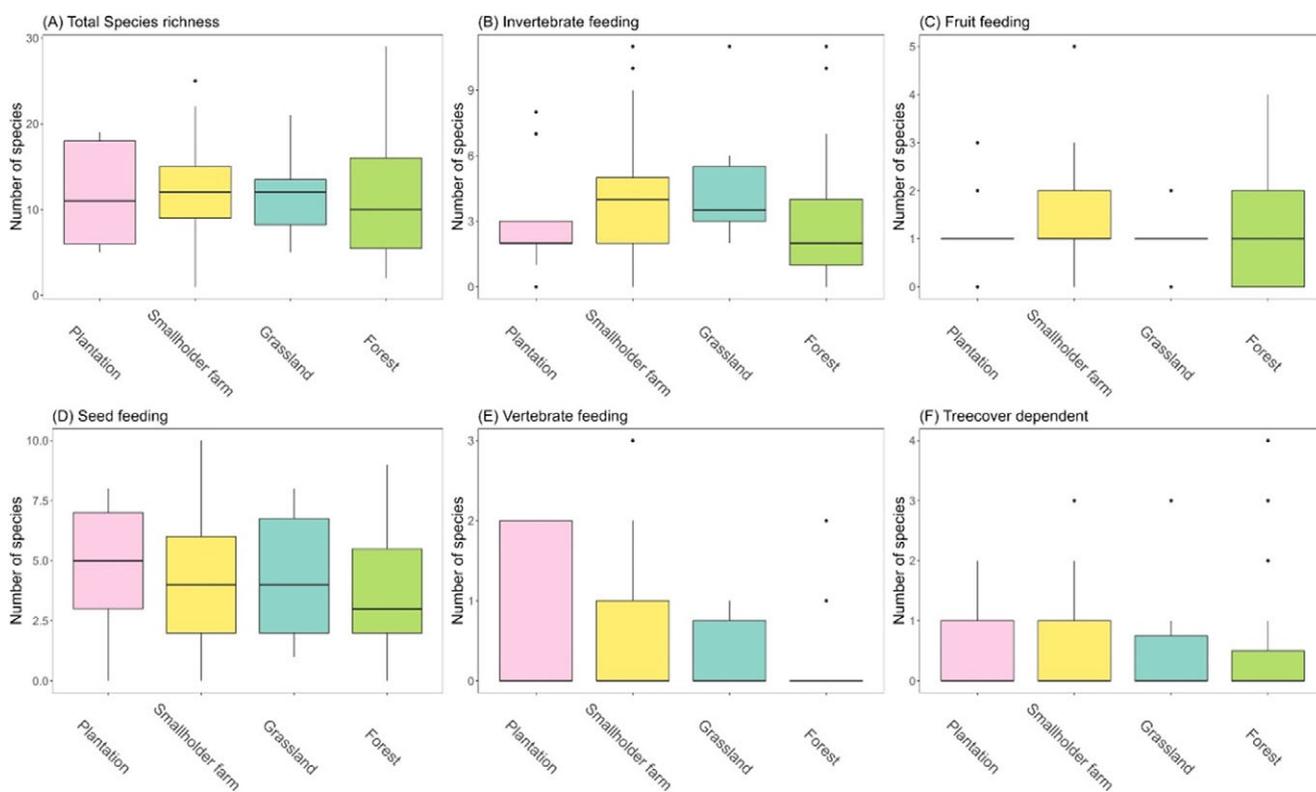
Figure 2. Habitat dependencies of bird species richness. Boxplots showing species richness across the four main habitat types for (A) all species, (B) invertebrate-feeding species, (C) fruit-feeding species, (D) plant/seed-feeding species, and (E) vertebrate-feeding/scavenging species; (F) the number of tree cover-dependent species as listed by IUCN. No pairwise significant differences were detected (non-parametric pairwise Wilcoxon rank-sum test with Bonferroni adjustment). When testing for differences in detection efficiency across the habitat types no pairwise significant differences were found (non-parametric pairwise Wilcoxon rank-sum test with Bonferroni adjustment) (Table S6).

recorded in smallholder farmland. Vertebrate-feeding species and scavengers were least common in the landscape (8.7% of all species) and again were mostly recorded in smallholder farmland (8.1%).

Species richness recorded at each sampling site varied across sampling locations and ranged from between one and seven species to between 21 and 29 species (Figure 1). Small variations in species richness between sampling sites in different habitat types were noted. Sampling sites located in forest habitats showed the highest variation of species richness in the landscape with values ranging from two to 29 species. On average sampling sites in forest recorded 10 species. Sampling sites located in plantations showed the least variation in species richness with values ranging from five to 19 and a median value of 11 (Table 1). However, species richness recorded at sampling sites within the different habitat types did not differ significantly (Bonferroni-adjusted pairwise Wilcoxon test, $P > 0.05$) (Figure 2A). The number of invertebrate-feeding species did not differ between the four habitat types, nor did that of seed/plant, fruit, or vertebrate-feeding species. Similarly, there was no difference in tree cover-dependent species richness between the habitat types (Figure 2B–F).

Most species recorded in the landscape were found in smallholder farms ($N = 121$) and 34 of these were solely found in this land-use type. Similarly, forest habitats supported many species ($N = 97$) and 14 of these were unique to forest habitat. In plantations and grassland habitats only four unique species were recorded for each (Figure 3A). Invertebrate-feeding species were the most widely distributed across the habitat types with each habitat type supporting several unique species. Sixteen unique species were found within smallholder farms while only three species were found to

be unique to plantations and grassland (Figure 3B). In contrast, fruit-eating species had a narrower distribution, with only two unique species recorded within smallholder farms and no unique fruit-eating species were found within plantations (Figure 3C).

Following log transformations of response metrics model diagnostics did not improve, subsequently we report only the results for untransformed variables. Single predictor analysis revealed that the percentage of canopy closure within a 150-m window was the most important environmental driver that explained the patterns of species richness in the landscape, with overall species richness declining with increasing canopy closure (coefficient: -0.004, P <0.001) (Figure 4A). However, separating between species only found on croplands and those only found in forests, showed that species richness patterns with forest canopy closure were masked (Figure 4B and C). Specifically, the number of forest species increased with increasing canopy closure and the number of cropland species declined. Similarly, the number of invertebrate-feeding species declined with canopy closure estimated as average within 150-m buffer windows (coefficient: -0.005, P <0.05, $D^2 = 0.02$), with only those found in forests increasing (coefficient: 0.061, P <0.001, $D^2 = 0.36$), and only those found in cropland declining (coefficient: -0.064, P <0.05, $D^2 = 0.14$) (Figure 5A–C).

Overall species richness also declined with the percentage of forest pixels within a 250-m window (coefficient: - 0.005, P <0.05, $D^2 = 0.02$) and with percentage canopy closure at sampling point (coefficient: -0.003, P <0.05, $D^2 = 0.02$). The number of invertebrate-feeding species declined with canopy closure at the sampling point (coefficient: -0.004, P <0.05). No significant relationships were observed between total species richness,

Figure 3. Shared and unique species between habitat types. Venn diagrams are used to visualise differences and similarities between the four habitat types in terms of species found. In all instances, cropland habitats (here separated between smallholder farms and plantations) supported the largest numbers of shared and unique species. (A) All species; (B) invertebrate-feeding species; C) fruit-eating species; (D) plant/seed-eating species.
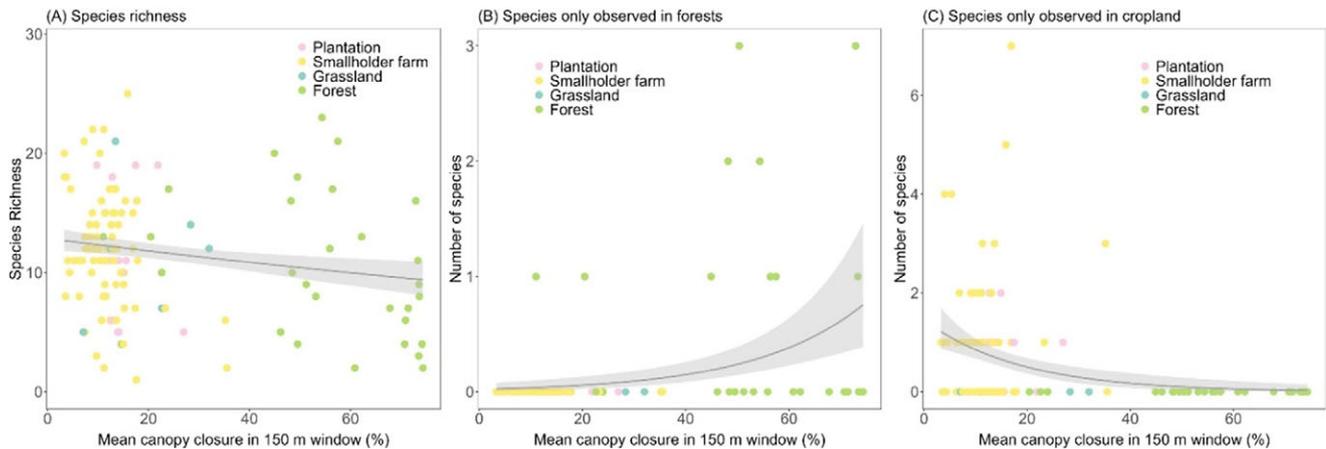

Figure 4. Species richness response to percentage canopy closure. Canopy closure was estimated as mean canopy closure (%) within a 150-m buffer around a given sampling point. (A) Total species richness declined with increasing forest canopy closure (coefficient = -0.004, SE = 0.001, D^2 = 0.03, df =122, P <0.001). Separating between species only found in forests (B) and species only found in croplands (C) indicated that increasing canopy closure had a positive effect on forest species (coefficient = 0.047, SE = 0.010, D^2 = 0.28, df = 122, P <0.01) and a negative effect on cropland species (coefficient = -0.053, SE = 0.014, D^2 = 0.17, df = 122, P <0.001). df = degrees of freedom; SE = standard error.

invertebrate-feeding species richness, and seed-eating species richness, and any other environmental drivers.

The number of plant/seed-eating species increased very weakly with distance from human settlements (coefficient: 1.72E-04, P <0.001, D^2 = 0.02) and the number of vertebrate-feeding species increased with distance to the nearest forest (coefficient: 0.001, P <0.05, D^2 = 0.04). No further significant patterns with anthropogenic drivers of disturbance were found in our study landscape (Table S3).

As expected from single predictor models, multi-predictor models explaining total species richness (AIC = 774, null deviance: 3,664 on 123 degrees of freedom (df), residual deviance: 3,548.8 on 122 df), and number of invertebrate-feeding species (AIC = 583, null deviance: 775.55 on 123 df, residual deviance: 760.66 on 122 df) within the landscape retained only percentage canopy closure in a 150-m buffer as an important predictor variable. Models that explained the number of seed/plant-feeding species (AIC = 601) or fruit-feeding species (AIC = 376) in the landscape retained only distance from human settlements, and models explaining the number of vertebrate-feeding species retained only distance from the nearest forest (AIC = 270).
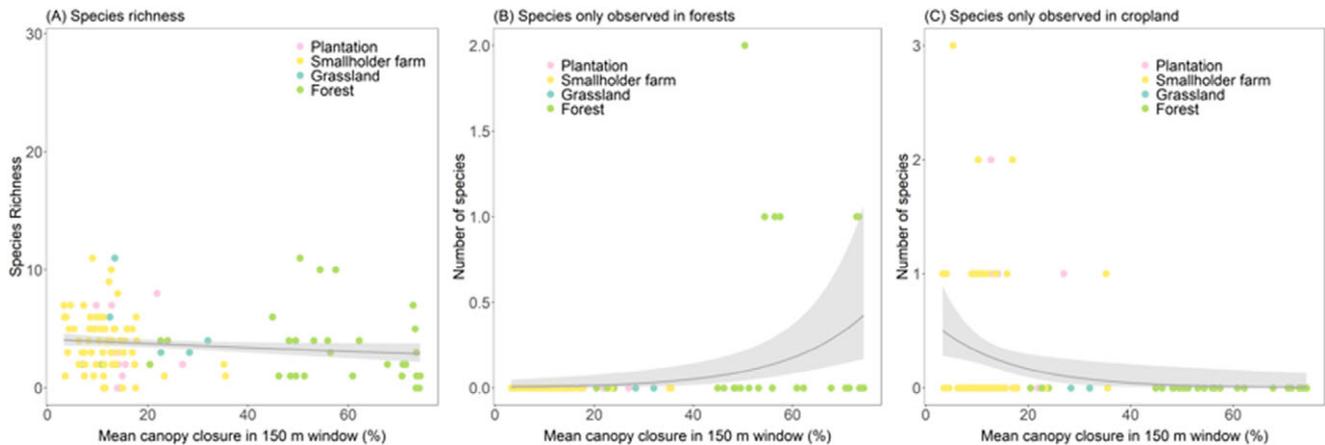
Figure 5. Invertebrate-feeding species richness response to percentage canopy closure. Canopy closure was estimated as mean canopy closure (%) within a 150-m buffer around a given sampling point. (A) Total invertebrate-feeding species richness declined with increasing forest canopy closure (coefficient = -0.005, SE = 0.002, D^2 = 0.02, df = 122, P <0.05). (B) Increasing canopy closure had a positive effect on invertebrate-feeding species unique to forest (coefficient = 0.061, SE = 0.018, D^2 = 0.36, df = 122, P <0.001). (C) A negative effect on invertebrate-feeding species unique to cropland was observed (coefficient = -0.064, SE = 0.027, D^2 = 0.14, df = 122, P <0.01). df = degrees of freedom; SE = standard error.

We found that there were differences in detectability efficiency between habitat types. Yet, none of these differences were significant (Bonferroni-adjusted pairwise Wilcoxon test) (Table S6).

Discussion

Understanding and managing the ability of tropical forest–agricultural landscapes to support diverse bird communities is crucial for conservation, ecosystem health, and food security. In this context, assessing habitat dependencies of birds and identifying land management and land use-related environmental variables that can affect bird occurrence across habitats within the landscape is important. Using biodiversity indicators such as total species richness, species richness of different diet type, and the number of species per diet type, our results clearly show that smallholder croplands under present-day management regimes can be considered valuable habitats. We suggest that smallholder farms, which in our landscape are often diverse in composition and integrated with trees, are used by many bird species including those providing services to farmers. The highest numbers of unique invertebrate and vertebrate-eating bird species, for example, which potentially provide pest control services, were found on smallholder farms, and most remaining species were shared between smallholder farms and other habitat types. It is worth highlighting that species feeding on fruits and seeds, and thus potentially acting as pests, are also found in high numbers on smallholder farms. Continuous landscape metrics added limited value in allowing us to understand species distributions. Overall species richness declined with tree canopy closure, which was driven by species adapted to crop habitat types as opposed to those species solely found in forests that showed opposite trends. Yet, distance to forests had no discernible effect on observed species numbers, perhaps a consequence of species mobility in this highly heterogeneous landscape. We suggest that retaining diversity in croplands and including areas of forest and interspersed trees in the landscape, whether within village boundaries or in the agricultural matrix, remains important, particularly in areas of the agricultural matrix that are devoid of tree cover, as many species found in crop habitats were also observed in forests and/or grassland. This perhaps supports calls for the adoption of agroforestry practices to achieve biodiversity outcomes in crop production landscapes as it remains unclear how the removal of natural habitats would impact these species.

Diverse cropland habitats can support high numbers of bird species. Mulwa et al. (2012) and Morelli (2013), for example, found species richness was higher within the structurally complex agricultural systems of western Kenya and central Italy respectively, and Şekercioğlu et al. (2019) highlighted the importance of tree cover within Costa Rican farming landscapes for enhanced species diversity. Landscape complexity is likely maintaining biodiversity and may explain the deviation from previous observations that bird species were more abundant in forest habitats compared with agricultural habitats (Hodda et al. 1998; Naidoo, 2004). This is further supported by the recent meta-analysis conducted by Estrada-Carmona et al. (2022), which concluded that complex agricultural landscapes sustained higher levels of biodiversity and supported greater numbers of species that could be considered advantageous to agriculture. Small-scale subsistence farms in the Kilombero Valley, like many other subsistence farming areas in the tropics, are generally made up of a variety of different crop types and are often interspersed with trees, grasslands, and shrubs (Johansson and Abdi 2020). The heterogeneity of these subsistence plots can provide a diversity of habitat niches thus facilitating high levels of species richness (Mulwa et al. 2012; Lindenmayer, 2019).

The likely effect of land use and farming type on bird richness is important in the context of debates on optimal approaches to restoration of farmed landscapes assumed to be primarily forested in the past. Whilst smallholder farming and habitat complexity can support higher bird species richness, we find that large-scale intensive farming, sugarcane in our case, is less effective in maintaining birds by themselves, instead requiring the accessibility of other natural areas in the vicinity. Homogenisation of habitat structure for commercial crop production may have adverse effects on habitat availability for bird species. The industry farm also uses chemical control of insects potentially altering food availability for birds causing them to shift foraging to surrounding land. Yet, there is limited evidence from our studies to demonstrate significant impacts on overall species numbers observed in the sugarcane plantation.

The absence of effects from distance to forests, rivers or anthropogenic sources of disturbances is perhaps surprising. However, settlements and roads within the landscape are mostly located

at the edges of forested areas and interspersed within diverse smallholder cropland making it difficult to detect disturbance signals emanating from these structures. We do note that we found no significant interaction effects in our statistical models between the drivers tested. Analyses focusing on changes in abundance of indicator species may perhaps provide more in-depth insights. Further consideration and perhaps testing for potential alternative food sources that birds may find within village boundaries or along road verges, including the presence of semi-natural habitat features, may also be beneficial. Human settlements may prove to be valuable foraging sites for some birds (Tryjanowski et al. 2020). For example, species that are primarily opportunistic scavengers such as Pied Crow *Corvus albus* are known to forage near to human settlements and roads where there is generally a supply of resources such as discarded food scraps and roadkill (Cunningham et al. 2016).

Benefits of birds that relate to their feeding behaviour include pest control, pollination, the control of disease, and the dispersal of seed (Imboma et al. 2020; Wenny et al. 2011). We found diet to have effects on the distribution of bird species within the landscape. For example, the most abundant species recorded in each habitat type was Common Bulbul, predominantly a frugivore but also known to be an opportunistic feeder that will feed on seeds and invertebrates. Most vertebrate and invertebrate-feeding species are found in more than one habitat type, but patterns emerge with regards to unique species associations for some habitat types, and smallholder farms featured the highest number of unique species found in the wider landscape.

It is important to highlight that several species were found only within forest habitats, indicating the potential of these habitats for providing specific resources required by forest bird communities, which have been shown to have increased sensitivity to the effects of habitat loss (Şekercioğlu et al. 2019). Therefore, retaining areas of forest could be important for the persistence of forest-dependent species in the landscape. Our research, however, also provides further evidence for arguments that agricultural landscapes if managed for habitat complexity can benefit biodiversity as well as ecosystem productivity through biodiversity-regulated ecosystem services (Estrada-Carmona et al. 2022) In agricultural landscapes where tree cover has been preserved and enhanced through agroforestry practices, bridging the gap between naturally forested areas and cropland, greater bird species richness can be maintained (Mendoza et al. 2014) due to increased accessibility of required resources including nesting and perch sites, food resources, and shelter from adverse weather and predation (Douglas et al. 2014). Complex smallholder plots interspersed with small forest fragments may be able to ensure the conservation of forest-dependent, threatened, and regionally endemic species, particularly in the context of providing specialist resources and maintaining habitat connectivity, as forest patches may aid in facilitating the movement of species across the landscape (Berens et al. 2014).

We note that variation in detectability between habitat types exists and can potentially influence results. Largely, issues with detection of avian communities are influenced by habitat vegetation density, and as such, birds in sparse, open habitats will be more easily detected than those in dense forests (Sanz-Pérez et al. 2020). Bird size and/or colour also has an influence on detection, for example, small dull-coloured birds may easily blend into their surroundings and are therefore difficult to spot (Johnston et al. 2014). However, we found no pattern between habitat types and our admittedly simple metric of detectability. To counteract this issue for improved future studies, species richness could be estimated using non-parametric species estimators such as first and second order jack-knifes and a bootstrap (Hellman and Fowler 1999;

Muhamad et al. 2013). Alternatively complementary sampling methods such as use of mist nests could be implemented. An additional limitation of this study is the discrepancy in the distribution of sampling locations between habitat types, with the majority of sampling locations being in cropland. Largely this was due to inconsistencies in land-use classification, particularly between areas of grassland and cropland due to the coarseness of the land-use types. While the map has been visually checked for accuracy, some uncertainties remain. Aside from improvements of land-use maps used in analyses, for enhanced accuracy the number of sampling sites would need to be increased in forest, grassland, and human settlements to even out the sampling design for the landscape.

Conclusions

Our study illustrates the importance of considering habitat dependencies and associations of bird species in complex forest–agricultural landscapes. Our findings lend further support for the importance of habitat complexity within tropical landscapes used for crop production to maintain diverse bird communities. Additionally, our findings do not diminish the importance of maintaining forest patches within the agricultural matrix and retaining areas of natural forest, specifically for their contribution to the conservation of forest-dwelling bird communities. With agricultural expansion increasing in the region, similar to other tropical landscapes elsewhere, there is immense pressure on natural habitats in the landscape altering configuration and quality of remaining natural habitats. Management strategies promoting conservation of species diversity while allowing for continued agricultural production will be the most effective and sustainable, particularly within this landscape that is required to meet food security and livelihood needs of the residing communities. Strategies that increase benefits of birds in agricultural landscapes, which can be advantageous to farming communities and to maintaining ecosystem functionality, should be prioritised. This should include conserving areas of natural habitat, retaining diversity of crops and including patches of trees in agricultural lands, and accessibility of natural habitats like forests and grasslands, which ultimately can be sources of birds venturing into surrounding cropland in search of food. Bird-derived pest control services subsequently can reduce the need for pesticides and rodent control measures in croplands, making them financially more viable, whilst helping to reduce infiltration of chemicals into the environment. Whilst our study did not account for plant species richness across habitat types sampled, we suggest that simple, cost-effective solutions such as conserving and planting indigenous trees, shrubs, and grasses in farmed areas and retaining crop diversity can ensure greater bird diversity, especially in areas of high-intensity crop production.

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