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Birds in the matrix: the role of agriculture in avian conservation in the Taita Hills, Kenya

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Abstract

Agricultural conversion of tropical forests is a major driver of biodiversity loss. Slowing rates of deforestation is a conservation priority, but it is also useful to consider how species diversity is retained across the agricultural matrix. Here we assess how bird diversity varies in relation to land use in the Taita Hills, Kenya. We used point counts to survey birds along a land-use gradient that included primary forest, secondary vegetation, agroforest, timber plantation and cropland. We found that the agricultural matrix supports an abundant and diverse bird community with high levels of species turnover, but that forest specialists are confined predominantly to primary forest, with the matrix dominated by forest visitors. Ordination analyses showed that representation of forest specialists decreases with distance from primary forest. With the exception of forest generalists, bird abundance and diversity are lowest in timber plantations. Contrary to expectation, we found feeding guilds at similar abundances in all land-use types. We conclude that while the agricultural matrix, and agroforest in particular, makes a strong contribution to observed bird diversity at the landscape scale, intact primary forest is essential for maintaining this diversity, especially among species of conservation concern.

Introduction

Tropical montane landscapes are undergoing major changes in response to a growing human population, economic development and changing climates (Geist & Lambin, 2002; Lawrence & Vandecar, 2015; Lewis *et al.,* 2015; Platts *et al.*, 2015; Wright, 2005). In particular, deforestation has serious implications for carbon storage (van der Werf *et al.,* 2009) and is a major driver of biodiversity decline (Dirzo & Raven, 2003; Gaston *et al.,* 2003). As such, the protection of remaining stands of tropical montane forest is a conservation priority, but it is also useful to consider how biodiversity is maintained within the surrounding human-modified matrix (Bhagwat *et al.,* 2008; Haslem & Bennett, 2008). Tropical landscapes, especially in Africa, tend to encompass a range of agricultural practices, ranging from traditional agroforestry systems, mixed croplands to monoculture plantations. Understanding how these agricultural systems maintain species diversity at the landscape level is fundamental for informing the complex debate over how to increase food production whilst maintaining biodiversity and ecosystem services in the tropics (Habel *et al*., 2013; Habel *et al.,* 2015; Fischer *et al*., 2014).

Tropical landscapes often support high levels of bird diversity and endemism (Stattersfield *et al*., 1998; Myers *et al.,* 2000) and the conversion of tropical forest to farmland tends to erode both abundance and diversity. The magnitude of this effect can differ considerably between the agricultural systems in question and the spatial configuration of the resulting landscape mosaic (Scales & Marsden, 2008; MacGregor-Fors & Schondube, 2011; Newbold *et al.,* 2012; Gilroy *et al.,* 2015). Tropical agroforestry systems such as homegardens, which contain a mixture of crops and shrubs cultivated beneath a canopy of trees, are often considered in a positive-light with respect to biodiversity conservation (Bhagwat *et al.,* 2008; Jose, 2009). They frequently support high levels of bird diversity, which can equal (Harvey & González Villalobos, 2007; Helbig-Bonitz *et al.,* 2015) or even exceed those associated with primary forest (Van Bael *et al.,* 2007; Mulwa *et al.,* 2012; Buechley *et al.,* 2015). Few studies have assessed the relative contribution of other agricultural practices for tropical bird conservation (but see MacGregor-Fors & Schondube, 2011), although it has been shown that bird diversity tends to decrease with increasing intensification and with reduced tree diversity (Clough *et al.,* 2009; Otieno *et al.,* 2011; Harvey & González Villalobos, 2007; Mulwa *et al.,* 2012). Since mixed agroforestry systems tend to be farmed in conjunction with timber plantations, monoculture croplands and pasture, it is important to consider how bird diversity is maintained across the wider agricultural landscape.

Although agroforests often support high species richness, their communities tend to have a reduced representation of forest specialists thus lowering their conservation value (Naidoo, 2004; Mulwa *et al.,* 2012; Helbig-Bonitz *et al.,* 2015). Birds from different feeding guilds can also show contrasting responses to agriculture, and meta-analyses suggest that large insectivorous and frugivorous forest specialists are most likely to be most at risk following agricultural conversion, whist small insectivores, nectarivores and habitat generalists are more tolerant to these changes (Newbold *et al.,* 2012; Sekercioglu, 2012). Modification of the functional composition of forest bird communities has implications for ecosystem processes such as seed dispersal, pest control and pollination (Bael *et al.,* 2008; Galetti *et al.,* 2013; Maas *et al.,* 2016), so it is useful to consider how tropical agricultural landscapes influence species traits in addition to species diversity.

The Taita Hills in Kenya are the northern-most block of the Eastern Arc Mountains (Fig. 1) and form a highly diverse part of the Eastern Afromontane Biodiversity Hotspot (Mittermeier *et al*., 2004). Historically, the Eastern Arc Mountains have experienced high levels of deforestation (Platts *et al.,* 2011), losing 70-80% of their original forest cover (Newmark, 2002; Hall *et al.,* 2009). In the Taita Hills, less than 2% of the original forest area remains, isolated within a heterogeneous agricultural matrix (Newmark, 1998). The agricultural landscape consists of traditional agroforestry systems (combining crops, shrubs and trees) and monocultures dominated by annual crops such as maize, which tend to have much lower tree coverage. There has also been an expansion of plantation forests, dominated by *Cypress*, *Pinus* and *Eucalyptus* for timber production. Satellite imagery shows that in the past fifty years over half of Taita's indigenous forest was lost due to agricultural conversion, but that total forest cover remained constant due to the expansion of timber plantations on barren land (Pellikka *et al.,* 2009). Timber plantations may perform a role in carbon storage (Christie & Scholes, 1995), but their simplified habitat is associated with a reduction in forest-dependent birds (Farwig *et al.,* 2008).

This study investigates how bird communities vary in response to land use within the Taita Hills and assesses the relative value of different agricultural practices for bird conservation. We compare rates of alpha and beta diversity between primary forest and a range of habitats within the agricultural matrix: agroforests, timber plantations, cropland and secondary vegetation. We also investigate how species responses differ in accordance to their level of forest dependency and feeding guild. Consideration of functional traits in addition to species numbers allows us to assess the wider value of the agricultural matrix in the context of habitat specialists of high conservation concern.

Methods

Study site

The Taita Hills are located in south-eastern Kenya (03°20'S, 38°15'E) and form an isolated mountainous block approximately 640-940 km^2 in area, depending on the inclusion of outlying peaks (Platts *et al*., 2011). The indigenous cloud forest has experienced extensive deforestation and is now restricted to three main fragments, the Chawia, Ngangao and Mbololo forests, totalling 10 km^2 (Brooks *et al.,* 1998; Pellikka *et al.,* 2009). This study extends across the Ngangao massif, which retains the largest fragment of remaining forest, flanked by plantations of *Eucalyptus*, Pine and *Cypress* and traditional homegardens that are farmed in an agroforestry style. At lower elevations agriculture is dominated by annual cropland systems with much sparser tree cover. The 20 km transect utilised in this study extended across the entire massif and ranged from 800 m to 2140 m in elevation, allowing coverage of the full range of agricultural styles practiced in the region (Fig. 1).

We classified land use into five discrete categories: primary forest, secondary vegetation, agroforest, timber plantation and cropland. We define primary forest as uncultivated land dominated by wild tree species (typically we observed *Macadamia, Persea, Syzygium* and *Xymalos* spp.), whereas uncultivated land with visible disturbance to forest and lower tree cover is classified as secondary vegetation. Agroforests include homegardens and small plots that contain cultivated plants grown amongst trees (100-200 trees per hectare). Typically we observed banana, maize or potatoes, with dominant tree genera including *Ficus, Eucalyptus, Kigelia, Prunus* and *Xymalos.* Timber plantations are areas cultivated specifically for timber and are dominated by *Cypress, Pinus* or *Eucalyptus.* Croplands are areas cultivated for the production of annual crops such as maize, cassava and sugar cane and typically have much lower levels of tree coverage than agroforests (<40 trees/hectare).

Survey methods

We surveyed birds using 10 minute fixed-radius point counts following the methodology described in Bibby *et al.* (2000). All visually or audibly detectable birds occurring within an approximately 50 m radius to the observer were counted. We conducted counts only if conditions were suitable (no heavy rain or fog) and only between 0600 h and 1100 h.

In 2014, we conducted point counts at 67 plots picked semi-randomly across the land-use gradient in order to cover the full range of land-use practices present (Fig. 1). Plots encompassed natural forest (N=15), agroforest (N=18), timber plantation (N=8), secondary vegetation (N=17) and cropland (N=9). We sampled each of these plots twice, between March and April 2014. We resampled 20 of these plots in December 2014 and April 2015 (Fig. 1): within each plot, five point counts were conducted at 100 m intervals, using a random start point. In this second sampling round, plots included natural forest (N=4), agroforest (N=11), secondary vegetation (N=4) and cropland (N=1).

Nomenclature followed the 4th edition of the Checklist of the Birds of Kenya, which is the latest version revised by the Bird Committee of East African Natural History of Society and Stevenson *et al.* (2004). We excluded from further analyses those bird species that could not be determined to species level (N=6). All bird species were classified by their level of forest dependence and feeding guild. We determined forest dependency using the established classification of East African forest birds (Bennun *et al.,* 1996), which categorises species as forest specialists (FF), forest generalists (F) or forest visitors (f). We assigned feeding guilds based on primary diet, grouping species as insectivores, granivores, frugivores, nectarivores, piscivores, raptors or scavengers, as described by Şekercioğlu *et al.* (2004).

Environmental variables

We conducted tree surveys in the subset of 20 plots shown in Fig. 1. We identified to species level all woody stems with a diameter at breast height (dbh) ≥ 10 cm. Where necessary, we collected voucher specimens for later identification at the East African Herbarium (National Museums of Kenya). Using these data, we calculated stem density and tree species richness per 1 ha plot.

In order to consider the effect of isolation from natural forest, we calculated the Euclidean distance from each sampling point to the nearest patch of primary forest using land cover data that was created using supervised classification of SPOT satellite imagery for the year 2011 (Heikinheimo, 2015).

Statistical analyses

Statistical analyses were conducted in R version 3.2 (R Core Team, 2015) using the vegan package (Oksanen *et al.,* 2012). Utilisation of the point-count method precluded the calculation of detection probabilities, so we performed statistical analyses using raw abundance data. We estimated species richness per land-use type using Chao's species richness estimator, first using the full data set, and second by subsampling 15 points counts from the total pool available within each land-use category (to account for differences in sampling effort), and recording the mean richness estimators across these points. We used Sørensen's similarity index to compare the pairwise similarity of all species that occurred in each land-use type.

We calculated alpha diversity for each point count using Hill's numbers (Hill, 1973). Hill's numbers are defined to the order of q (${}^{q}D$), whereby parameter q indicates the weight given towards rare or common species. ${}^{0}D$ (species richness) is insensitive to relative frequencies, and is therefore weighted towards rare species, ${}^{1}D$ (exponential of Shannon) is weighted towards common species, and ${}^{2}D$ (inverse Simpson) is weighted towards abundant species. These diversity indices are particularly useful because they are scalable and can provide insight into the representation of rare, common and abundant species within different land-use types (Jost, 2006; Tuomisto, 2010; Chao *et al.,* 2012). We calculated beta diversity for each land-use type, determined as the multiple-community dissimilarity between points. Dissimilarity was also weighted by the aforementioned q, with q=0 calculated as the Sørensen dissimilarity index (insensitive to species abundance), q=1 as the Horn index and q=2 as the Morisita index (Chao *et al.,* 2012). This combination of metrics provides insight into not only the proportion of species shared, but the relative abundances of those shared species. We calculated beta diversity indices using the SpadeR package (Chao *et al*., 2015).

We used linear mixed effect models to test for the impact of land use on bird abundance and all three measures of Hill's diversity using the lme4 package (Bates, 2005). We log-transformed response variables to normalise the data and improve model fit. We included land use as a fixed effect, and observer as a random intercept to account for the different sampling methods that were used in the first and second sampling rounds and to account for any potential observer bias. We also included plot nested within elevational zone as a random effect, to account for spatial autocorrelation along the altitudinal gradient. We assessed the strength of the fixed effect (land use) using marginal R^2 values calculated using the MuMIn package (Barton, 2014), and significance by comparing the fit of models (with and without land use) using Chi-squared tests (Zuur *et al.,* 2009). Equivalent models were also run for bird abundance within the forest dependency and feeding guild categories. Details of model fit are included in Table S1.

In order to assess how community composition was affected by land use, we performed non-metric multidimensional scaling (NDMS) with the Bray-Curtis dissimilarity function. This unconstrained ordination technique was used to collapse the species data into two dimensions so that differences between land-use categories could be detected. Because it relies upon rank-orders (rather than absolute abundance) it can accommodate non-linear species responses, allowing the detection of underlying responses to environmental change (Oksanen *et al.,* 2012). The NDMS environmental variables (land use, tree density, tree species richness, and distance from primary forest) were imposed onto the plot using the *envfit* function with the significance of these environmental variables determined using permutation tests (999 permutations).

Results

The impact of land use on bird abundance and diversity

A total of 5351 birds were recorded across the land-use gradient, representing 202 species from 57 families (see Table S2 for full species list). Of these species, 44 (22%) were unique to agroforest, nine to primary forest (5%), 17 to secondary vegetation (8%) and five to cropland (2%). Sampling had not reached species saturation (Fig. S1) and Chao's estimated species richness was 242 (± 14). Eighty percent of observed species were present in agroforests, which supported higher levels of estimated species richness than the other land-use categories, even when the estimations were controlled for the varying sample sizes (Fig. 2). Secondary vegetation supported the second highest number of species, followed by cropland, primary forest and plantation. Pairwise Sørensen's similarity estimates showed that species overlap was highest between primary forest, secondary vegetation and agroforest, with approximately two thirds of species shared (Table 1). Cropland shared more species with agroforest and secondary vegetation than with primary forest or plantation. Plantations showed overall low levels of species similarity with all other land-use types.

Mean bird abundance per plot differed significantly according to land use (lmer: χ^2= 22.70, df= 4, P<0.001, R^2_{GLMM}=0.11) and was highest in agroforest, secondary vegetation and cropland, which supported approximately twice the numbers associated with primary forest (PF: 8 ± 0.5, SV: 16 ± 2.4, AGR: 17 ± 1.1, CRP: 15 ± 1.5, PLNT: 7 ± 0.7). Bird abundance was lowest in timber plantations. Mean alpha diversity per plot was also affected by land use (Fig. 3A) with agroforest and cropland supporting slightly higher levels of diversity than secondary vegetation and primary forest, and timber plantation the lowest. The strength of this effect decreased with the order of q, and was only significant at levels q=0 and q=1 (^0D: χ^2=9.50, df=4, P=0.049; ^1D: χ^2=11.09, df=4, P=0.026; ^2D: χ^2=8.62, df=4, P=0.071), suggesting that the effective numbers of rare and common species were more strongly affected by land use than were abundant species.

Partitioning beta diversity between plots showed that spatial turnover differed amongst the land-use categories (Fig. 3B). Species turnover was extremely low between primary forest plots with low dissimilarity at all levels of q, which suggests high spatial homogeneity across our forest plots. Agroforest plots showed relatively low levels of dissimilarity at q=0, but dissimilarity increased sharply at levels q=1 and q=2 suggesting high turnover in the identities of common and abundant species. Levels of turnover were higher still in secondary vegetation and cropland, which also showed a sharp increase in dissimilarity with the order of q, suggesting high spatial heterogeneity in both the identity and relative abundance of species. Conversely, timber plantations showed a decrease in dissimilarity with the order of q, suggesting that dominant species were more likely to be shared between plots than were rarer species.

Response of functional guilds to land use

Out of the total species pool, 152 species were classified as forest visitors, 30 as forest generalists and 23 as forest specialists. In terms of abundance, the vast majority of birds were forest visitors (77% of all individuals), followed by forest specialists (15%) and forest generalists (8%). Forest specialists included several bird species of high conservation importance, such as the endemic Taita Thrush (*Turdus helleri*, Critically Endangered) and Taita Apalis (*Apalis fuscigularis*, Critically Endangered), with many others pending assessment for the IUCN Red List (www.iucnredlist.org, accessed November 2015).

All three forest guilds showed significant responses to land use, but the direction and strength of these responses differed in accordance to their level of forest dependency (Fig. 4A-C). Forest visitors responded strongly to land use (Fig. 4A: χ^2=84.53, df=4, P<0.001, R^2_{GLMM}=0.45), occurring at low abundance and low species richness within primary forest and plantation, and at high abundance in agroforest where their numbers increased 12-fold. Forest specialists were also highly sensitive to land use (Fig. 4C: χ^2=64.04, df=4, P<0.001, R^2_{GLMM}=0.33), occurring at the highest abundance within the primary forest, with numbers dropping sharply in all other land-use types (Fig 4C). Forest generalists showed a weaker response than specialists (Fig. 4B: χ^2=38.82, df=4, P<0.001, R^2_{GLMM}=0.19), and though they also occurred at highest numbers in primary forest, their numbers did not decrease as sharply in other land-use types.

In total eight feeding guilds were recorded, with all guilds represented in each land-use type. Insectivores were the most abundant guild (35% of individuals from 93 species), followed by granivores (28%, 42 species), frugivores (20%, 25 species) and nectarivores (12%, nine species). The other three feeding guilds (raptors, piscivores and scavengers) made up less than 5% of the total abundance between them. None of the feeding guilds exhibiting a significant response to land use (all P>0.05; Appendix Table 1).

Community analysis

Community composition as determined using NDMS ordination showed significant differences between land-use types (Fig 5: R^2=0.44, P=0.001) and could be significantly fitted by vectors that represented tree density and tree species richness (density: R^2=0.69, P=0.001; richness: R^2=3.6, P=0.030). The distance from nearest patch of natural forest also explained a significant proportion of variation in the ordination (distance: R^2=0.37, P=0.006).

The NDMS ordination plot (Fig. 5) clearly separates forest specialists, forest generalists and forest visitors along axis-1. Forest specialists tended to have negative loadings and were associated with primary forest and higher tree density and species richness. Forest visitors tended to have positive loadings along axis-1 and were associated with the other land-use types. There was a strong clustering of species in the middle of the plot in association with agroforest habitat.

Discussion

The impact of land use on bird abundance and diversity

Bird abundance varied considerably along the land-use gradient in the Taita Hills, with the agricultural matrix supporting twice the abundance associated with primary forest. Traditional agroforestry systems were a particularly species richness component of the matrix, supporting 80% of all observed bird species at higher overall abundance than primary forest. This study did not consider how detectability varied between land-use types, but dense vegetation (such as that associated with primary forest) can decrease the likelihood of observing a species by approximately 15% (Anderson *et al.,* 2015). Detectability may have been reduced within forest, but we observed mean bird abundance increasing by more than 100% within agroforest plots and changes of this order of magnitude are most likely to reflect genuine changes in underlying bird abundance associated with the surveyed habitats.

Overall species richness was highest within agroforests and croplands, but at a plot-level alpha diversity was equivalent to that observed in primary forest. This can be attributed to the higher levels of species turnover associated with the agricultural plots as compared to forest plots. The homogeneity of primary forest contrasts with results observed in Brazil where beta diversity was considerably higher in forest as compared to agricultural landscapes (Morante-Filho *et al.,* 2016). This result is likely to reflect differences in scale between the two studies. Within the Taita Hills, primary forest only remains at high elevations whilst agricultural land spans a wider elevational range with more varied environmental conditions. Considering beta diversity at a wider scale would undoubtedly reveal that the Eastern Arc montane forest as a whole is more diverse that agricultural land (Stattersfield *et al.,* 1998), but given the existing matrix within the Taita Hills, low intensity agriculture makes an important contribution towards the maintenance of landscape-level diversity within this study site.

Timber plantations in the Taita Hills supported an impoverished bird community, with less than half the abundance and a quarter of the diversity associated with agroforestry systems and annual croplands. Plantations are dominated by exotic timber species such as *Cypress*, *Pinus* and *Eucalyptus*, and the lack of fruiting forest trees is likely to be limiting the availability of resources for birds in the region. Other studies have noted the inhospitality of plantations for birdlife; in western Kenya bird species richness decreased by one third in sugarcane plantations as compared to structurally heterogeneous smallholdings (Mulwa *et al.,* 2012), and the abundance and species richness of forest specialists declined in transition from natural forest to exotic timber plantations (Farwig *et al.,* 2008). In Costa Rica, plantain monocultures have been shown to support less than 15% of the species observed in banana and cacao agroforests (Harvey & González Villalobos, 2007). The loss of shade trees within agroforestry systems themselves can also lead to a reduction in bird diversity (Clough *et al.,* 2009), with the simplification of agroforests reducing their conservation value. In the Taita Hills, the conversion of structurally diverse agroforests into monoculture timber plantations is likely to have equivalent negative effects, and should be strongly discouraged from a conservation perspective. The current timber plantations were introduced in the late 1950s in a bid to increase forest cover and provide local people with timber jobs and fuel wood (Pellikka *et al.,* 2009). Any future expansion of timber plantations would threaten bird conservation, with plantations supporting far lower levels of bird diversity than secondary regrowth, agroforests and annual croplands.

Landscape disturbance can lead to the biotic homogenisation of bird communities (Devictor *et al.,* 2008), resulting in habitats that are dominated by a few, highly abundant species. There was no evidence of biotic homogenisation within agroforests, secondary vegetation or croplands, where abundant species showed high levels of turnover between plots. However in plantation forests, abundant bird species showed the lowest levels of turnover, indicating that plots tended to be dominated by a few abundant species. Previous studies of frugivorous birds within the Taita Hills noted high turnover in the relative abundance of species between forest fragments, which was attributed to variation in the fruit resources available in fragments (Githiru *et al.,* 2002). It is likely that the heterogeneity of trees and crops cultivated within agroforests and cropland contributes towards the high turnover of bird species in this landscape. When more complex habitats are converted into simplified plantation forest or monoculture cropland, these beneficial effects to biodiversity appear to be lost.

Detrimental impact of agriculture on forest specialists

It is becoming increasingly recognised that agroforestry systems have the potential to support high levels of bird diversity and numerous studies elsewhere in East Africa and in South America have observed higher species richness in multi-strata agroforestry systems than in primary forest (Harvey & González Villalobos, 2007; Van Bael *et al.,* 2007; Mulwa *et al.,* 2012; Buechley *et al.,* 2015). Other studies have reported equal (Waltert *et al.,* 2005; Harvey & González Villalobos, 2007; Helbig-Bonitz *et al.,* 2015) or lower species richness than primary forest (Naidoo, 2004; Waltert *et al.,* 2004), but a consistent pattern is that the relative abundance of forest specialists tends to decrease when moving from natural forest into agricultural land. We observed a dramatic decline in the abundance of forest specialists in all agricultural land-use types as compared to primary forest, and though agroforests were able to support high numbers of species, the majority of these were forest visitors.

In our study the presence of forest specialists was positively associated with the higher tree density and tree species richness found in primary forests, a trend which has also been observed in Western Kenya (Mulwa *et al.,* 2012), Tanzania (Helbig-Bonitz *et al.,* 2015) and Uganda (Naidoo, 2004). Simulations using Ugandan data have suggested that densely forested agroforestry programmes do not raise tree densities to levels required to support forest bird communities (Naidoo, 2004), suggesting that in isolation agroforestry systems cannot maintain populations of forest specialists. Conserving existing stands of primary forest within the agricultural matrix should be the priority for conserving threatened forest specialists, such as the locally endemic and globally threatened Taita Thrush and Taita Apalis

(Critically Endangered B2ab: area of occupancy <10 km^2; severely fragmented and continued decline in habitat and numbers; http://www.iucnredlist.org).

Ordination analysis showed that the number of forest specialist and generalist species declined with increasing distance from primary forest, suggesting that the agricultural matrix alone is unable to support the full range of species present within the Taita Hills. Other studies have also found that landscape configuration influences the composition of tropical bird communities, with increasing distance from primary forest leading to a decrease in forest specialists in Indonesian cacao agroforests (Clough *et al.,* 2009) and a decline in range-restricted birds with low foraging plasticity in a Columbian forest-agricultural matrix (Gilroy *et al.,* 2015).

The impact of land use on feeding guilds

Feeding guild analyses can provide important insight into the ecological functioning of bird communities (Sekercioglu, 2012), and a pan-tropical meta-analysis has shown that frugivorous and insectivorous birds tend to be the most sensitive to agricultural disturbance in tropical landscapes (Newbold *et al.,* 2012). In our study feeding guild proved a much poorer indicator of species' responses to land use than forest dependency, with all land-use types supporting equivalent numbers of insectivores, frugivores and granivores. Similarly a recent assessment of trait predictors suggests that feeding guild is a weak predictor of bird responses to land-use change (Gilroy *et al.,* 2015).

Conclusions and implications

This study demonstrates the importance of intact forest patches for conserving threatened forest specialists. Though the heterogeneous agricultural matrix makes a strong contribution to overall bird diversity, agricultural plots exhibit reduced representation of forest specialists so cannot act as a substitute for primary forest. Within the agricultural matrix, traditional agroforestry systems support the most diverse and heterogeneous bird communities, whilst in monoculture timber plantations diversity is notably low and communities dominated by a few highly abundant species. The continued protection of remaining primary forest must be a priority in order to conserve threatened forest specialists, but the further expansion of timber plantations within the agricultural matrix could also pose a threat to landscape-level diversity.

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TABLE 1 Sørensen's similarity between land-use categories

	Secondary forest	Agroforest	Cropland	Plantation
Primary forest	0.67	0.62	0.43	0.35
Secondary forest		0.70	0.60	0.33
Agroforest			0.60	0.27
Cropland				0.28

Fig1 Location of plots within the Taita Hills, Kenya with land cover derived from SPOT satellite imagery for 2011. Black circles represent plots sampled in March to April 2014, and black triangles represent plots which were also resampled in December 2014 and April 2015.

Fig 2 Estimated Chao species richness in the different land-use categories. White bars represent standardised estimates of species richness, which were calculated as the mean estimated richness per 15 point counts with standard errors of the mean. Black points represent estimated species richness and standard errors calculated from the full dataset, with the sample size within each land-use category indicated above each point.

Fig 3 The impact of land use on (A) alpha diversity (measured as Hill's numbers) and (B) beta diversity (dissimilarity between plots) of bird communities within the Taita Hills. Both measures are weighted to the order of q, which reflects the sensitivity of the indices to the relative abundance of species: q=0 is sensitive to rare species, q=1 is sensitive to common species and q=2 is sensitive to highly abundant species.

Fig 4 The impact of land-use on bird abundance within the forest-dependency guilds; (A) forest visitors, (B) forest generalists and (C) forest specialists. Bars represent mean abundance per 15 minute point count with SEM. Land use categories: PF = primary forest, SV = secondary vegetation, AGR= agroforest, CRP= cropland, PLNT = timber plantation.

Fig 5 Non-metric multidimensional scaling plot illustrating bird community structure in relation to land use. Circles represent bird species, with forest visitors in light grey, forest generalists in dark grey and forest specialists in black. Vector arrows represent landscape variables. Land-use categories: PF= primary forest, SV= secondary vegetation, AGR = agroforest, CRP = cropland and PLNT= timber plantation.

FIG 1

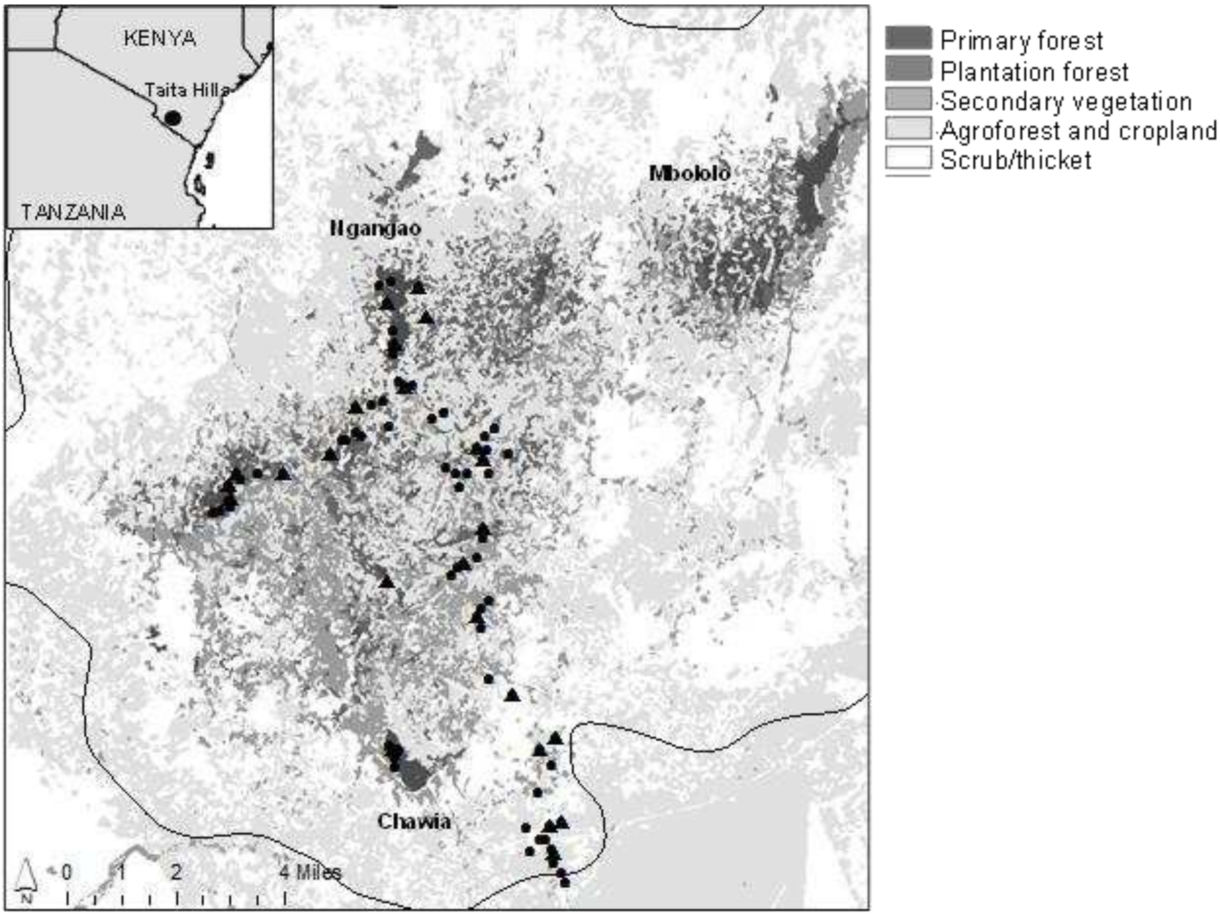
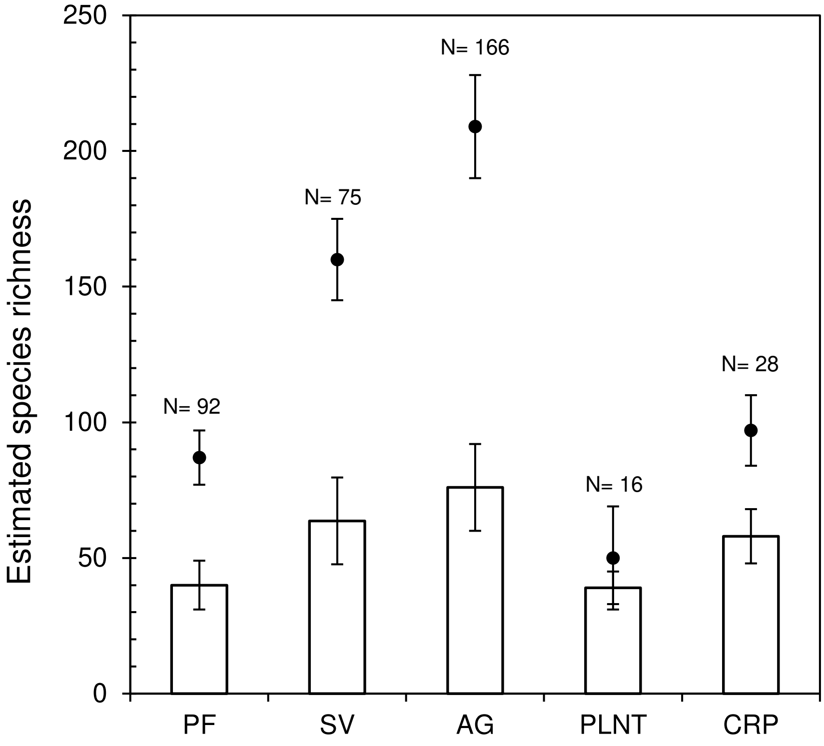

KENYA
Taita Hills
TANZANIA
Ngangao
Mbololo
Chawia
0
1
2
4 Miles
N
Primary forest
Plantation forest
Secondary vegetation
Agroforest and cropland
Scrub/thicket

FIG 2



Estimated species richness
250
200
150
100
50
0
N= 166
N= 75
N= 92
N= 28
N= 16
PF
SV
AG
PLNT
CRP

Fig 3

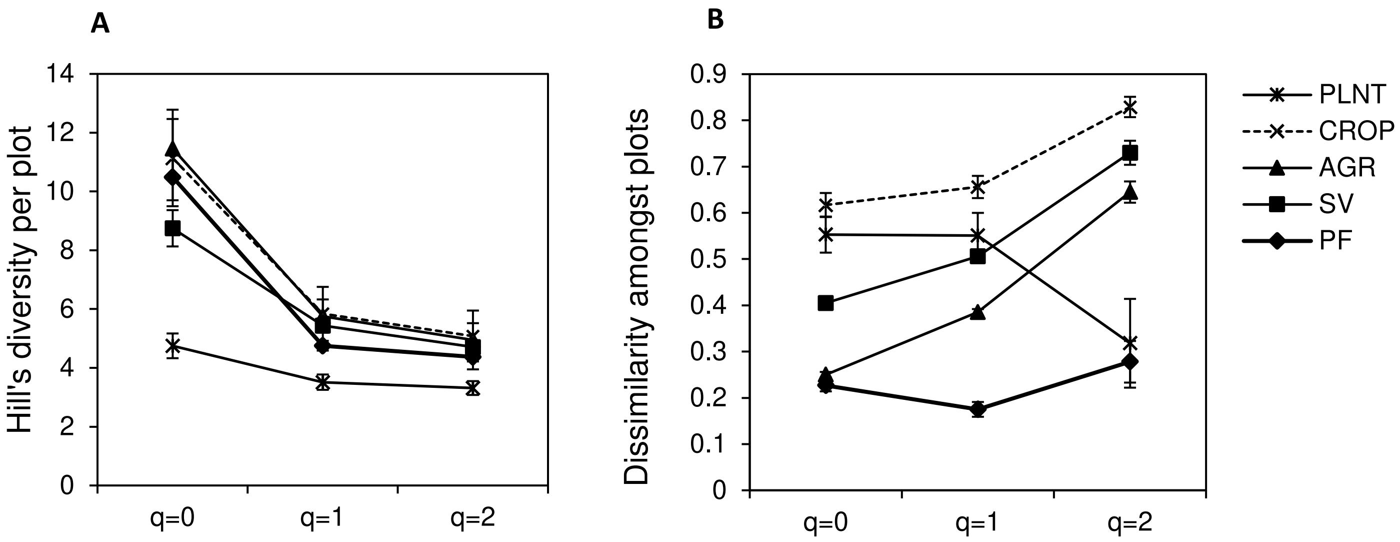

A
B
Hill's diversity per plot
14
12
10
8
6
4
2
0
q=0
q=1
q=2
Dissimilarity amongst plots
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
PLNT
CROP
AGR
SV
PF

FIG 4

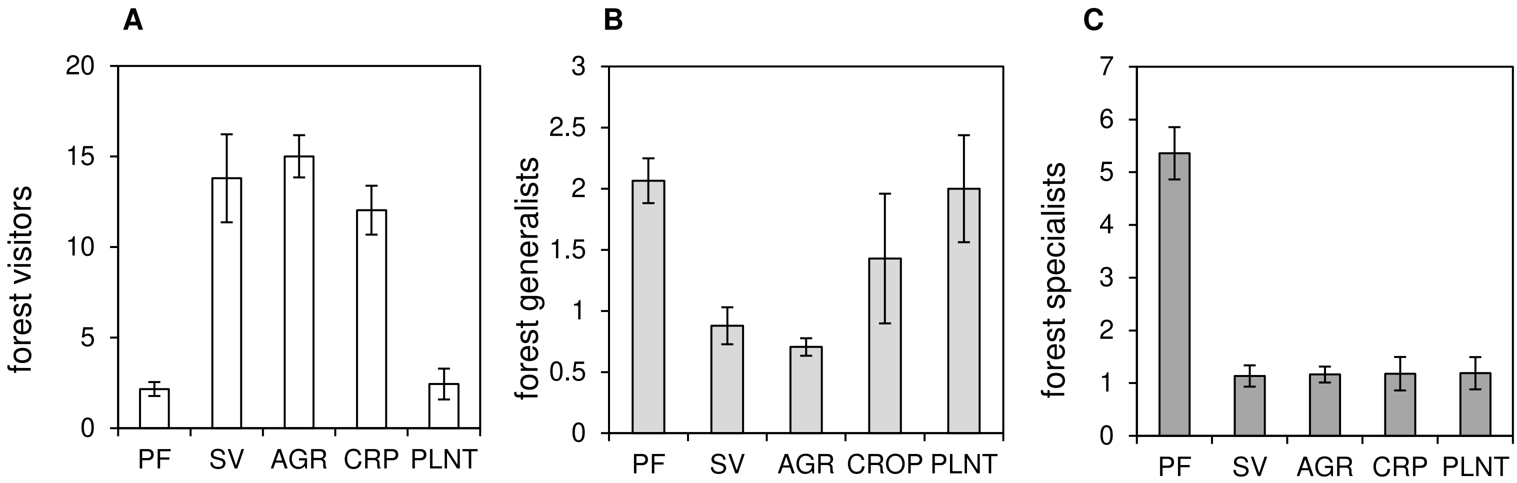
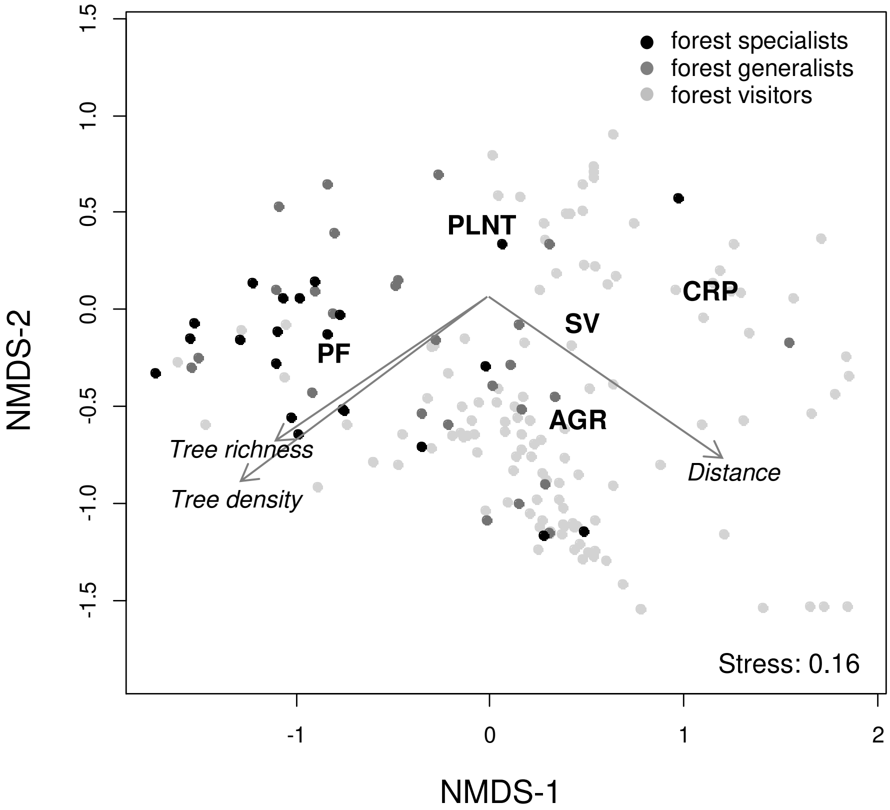

A
B
C
20
15
10
5
0
forest visitors
PF
SV
AGR
CRP
PLNT
3
2.5
2
1.5
1
0.5
0
forest generalists
PF
SV
AGR
CROP
PLNT
7
6
5
4
3
2
1
0
forest specialists
PF
SV
AGR
CRP
PLNT

FIG 5



forest specialists
forest generalists
forest visitors
PLNT
CRP
SV
PF
AGR
Tree richness
Tree density
Distance
Stress: 0.16
1.5
1.0
0.5
0.0
-0.5
-1.0
-1.5
NMDS-2
-1
0
1
2
NMDS-1

SUPPLEMENTARY MATERIAL

Table S1 Results from linear mixed effect models testing for an impact of land use on bird abundance and diversity. Delta AIC represents the change in AIC between models with and without land use, and R^2 represents the strength of the effect of land use.

	Delta AIC	LogLik	df	R^2
Abundance	9.4	-291.53	9	0.11
^0D	1.29	-293.33	9	0.03
^1D	-10.8	-105.09	9	0.04
^2D	-13.5	-125.55	9	0.03
Forest specialists	47.6	-321.35	9	0.33
Forest generalists	22.2	-275.76	9	0.19
Forest visitors	70.05	-375.63	9	0.45
Insectivores	-13.29	-352.47	9	0.01
Frugivores	-12.21	-351.53	9	0.02
Granivores	-10.78	-507.04	9	0.01
Nectarivores	-12.21	-330.70	9	0.02

Table S2 Full species list with functional guilds.

Species	Common name	Feeding Guild	Forest Dependency
ACCIPITRIDAE			
Accipiter melanoleucus	Great sparrowhawk	RAPT.	f
Accipiter minullus	Little sparrowhawk	RAPT.	f
Accipiter tachiro	African goshawk	RAPT.	F
Aquila wahlbergi	Wahlberg's eagle	RAPT.	FF
Buteo augur	Augur buzzard	RAPT.	FF
Buteo buteo	Common buzzard	RAPT.	F
Buteo oreophilus	Mountain buzzard	RAPT.	FF
Circaetus cinerascens	Western banded snake eagle	RAPT.	F
Haliaeetus vocifer	African fish eagle	PISC.	f
Kaupifalco monogrammicus	Lizard buzzard	RAPT.	f
Lophaetus occipitalis	Long-crested eagle	RAPT.	F
Milvus migrans	Black kite	GRAN.	f
Polyboroides typus	African harrier-hawk	RAPT.	f
Stephanoaetus coronatus	Crowned eagle	RAPT.	F
ACROCEPHALIDAE			
Acrocephalus baeticatus	African reed warbler	INSECT.	f
ALCEDINIDAE			
Alcedo cristata	Malachite kingfisher	PISC.	f
ANATIDAE			
Alopochen aegyptiaca	Egyptian goose	PISC.	f
Dendrocygna viduata	White-faced whistling duck	PISC.	f
Plectropterus gambensis	Spur-winged goose	PISC.	f
APODIDAE			
Cypsiurus parvus	African palm swift	INSECT.	f
Schoutedenapus myoptilus	Scarce swift	INSECT.	f
Tachymarptis aequatorialis	Mottled swift	INSECT.	f
Apus affinis	Little swift	INSECT.	f
ARDEIDAE			
Ardea cinerea	Grey heron	PISC.	f
Ardea melanocephala	Black-headed heron	PISC.	f
Ardeola ralloides	Squacco heron	PISC.	f
Bubulcus ibis	Cattle egret	INSECT.	f
Mesophoyx intermedia	Intermediate egret	INSECT.	f
BUCEROTIDAE			
Tockus alboterminatus	Crowned hornbill	FRUG.	f
Bycanistes brevis	Silvery-cheeked Hornbill	FRUG.	F
CAPRIMULGIDAE			
Caprimulgus tristigma	Freckled nightjar	INSECT.	f
CERYLIDAE			
Ceryle rudis	Pied kingfisher	PISC.	f
CHARADRIIDAE			
Vanellus spinosus	Spur-winged lapwing	PISC.	f

CICONIIDAE			
Ciconia episcopus	Woolly-necked stork	RAPT.	f
CISTICOLIDAE			
Camaroptera brachyura	Green-backed camaroptera	INSECT.	f
Camaroptera brevicaudata	Grey-backed camaroptera	INSECT.	f
Cisticola cantans	Singing cisticola	INSECT.	f
Cisticola chiniana	Rattling cisticola	INSECT.	f
Cisticola erythrops	Red-faced cisticola	INSECT.	f
Cisticola galactotes	Winding cisticola	INSECT.	f
Prinia subflava	Tawny-flanked prinia	INSECT.	f
Apalis flavida	Yellow-breasted apalis	INSECT.	f
Apalis fuscigularis	Taita apalis	INSECT.	FF
Apalis melanocephala	Black-headed apalis	INSECT.	FF
COLIIDAE			
Colius striatus	Speckled mousebird	FRUG.	f
COLUMBIDAE			
Aplopelia larvata	Lemon dove	FRUG.	FF
Streptopelia capicola	Ring-necked dove	FRUG.	f
Streptopelia semitorquata	Red-eyed dove	FRUG.	f
Streptopelia senegalensis	Laughing dove	FRUG.	f
Turtur chalcospilos	Emerald-spotted wood dove	FRUG.	f
Turtur tympanistria	Tambourine dove	FRUG.	F
CORACIIDAE			
Coracias garrulus	European roller	INSECT.	f
CORVIDAE			
Corvus albicollis	White-necked raven	SCAV.	f
Corvus albus	Pied crow	SCAV.	f
Corvus splendens	House crow	SCAV.	f
CUCULIDAE			
Centropus superciliosus	White-browed coucal	INSECT.	f
Chrysococcyx caprius	Diederik cuckoo	INSECT.	f
Chrysococcyx cupreus	African emerald cuckoo	INSECT.	F
Chrysococcyx klaas	Klaas's cuckoo	INSECT.	f
Cuculus clamosus	Black cuckoo	INSECT.	FF
Cuculus solitarius	Red-chested cuckoo	INSECT.	F
DICRURIDAE			
Dicrurus adsimilis	Fork-tailed drongo	INSECT.	f
EMBERIZIDAE			
Emberiza poliopleura	Somali bunting	GRAN.	f
ESTRILDIDAE			
Amadina fasciata	Cut-throat finch	GRAN.	f
Estrilda astrild	Common waxbill	GRAN.	f
Estrilda rhodopyga	Crimson-rumped waxbill	GRAN.	f
Hypargos niveoguttatus	Red-throated twinspot	GRAN.	F
Lagonosticta rubricata	African firefinch	GRAN.	f
Lagonosticta senegala	Red-billed firefinch	GRAN.	f

Lonchura bicolor	Black-and-white mannikin	GRAN.	f
Lonchura cucullata	Bronze mannikin	GRAN.	f
Mandingoa nitidula	Green-backed twinspot	GRAN.	f
Pytilia melba	Green-winged pytilia	GRAN.	f
Spermestes bicolor	Black-and-white mannikin	GRAN.	f
Lonchura cucullata	Bronze mannikin	GRAN.	f
Uraeginthus bengalus	Red-cheeked cordon-bleu	GRAN.	f
FALCONIDAE			
Falco biarmicus	Lanner falcon	RAPT.	f
FRINGILLIDAE			
Crithagra reichenowi	Reichenow's seedeater	GRAN.	f
Crithagra striolata	Streaky seedeater	GRAN.	f
Crithagra sulphurata	Brimstone canary	GRAN.	f
Crithagra xanthopygius	Yellow-rumped seedeater	GRAN.	f
Linurgus olivaceus	Oriole finch	GRAN.	F
HALCYONIDAE			
Halcyon leucocephala	Grey-headed kingfisher	PISC.	f
HIRUNDINIDAE			
Cecropis abyssinica	Lesser striped swallow	INSECT.	f
Cecropis daurica	Red-rumped swallow	INSECT.	f
Delichon urbicum	Common house martin	INSECT.	f
Hirundo daurica	Red-rumped swallow	INSECT.	f
Hirundo rustica	Barn swallow	INSECT.	f
Psalidoprocne albiceps	White-headed saw-wing	INSECT.	f
Psalidoprocne pristoptera	Black saw-wing	INSECT.	f
Ptyonoprogne fuligula	Rock martin	INSECT.	f
Riparia paludicola	Plain martin	INSECT.	f
INDICATORIDAE			
Indicator exilis	Least honeyguide	INSECT.	FF
Indicator minor	Lesser honeyguide	INSECT.	f
Prodotiscus regulus	Wahlberg's honeybird	INSECT.	f
JACANIDAE			
Actophilornis africanus	African jacana	PISC.	f
LANIIDAE			
Lanius collaris	Common fiscal	INSECT.	f
Lanius collurio	Red-backed shrike	INSECT.	f
Lanius dorsalis	Taita fiscal	INSECT.	f
Lanius humeralis	Northern fiscal	INSECT.	f
Lanius isabellinus	Isabelline shrike	INSECT.	f
Bradypterus lopezi	Evergreen forest warbler	INSECT.	F
LYBIIDAE			
Lybius melanopterus	Brown-breasted barbet	FRUG.	f
Pogoniulus bilineatus	Yellow-rumped tinkerbird	FRUG.	F
Pogoniulus leucomystax	Moustached tinkerbird	FRUG.	F
Pogoniulus pusillus	Red-fronted tinkerbird	FRUG.	f
Trachyphonus darnaudii	D'Arnaud's barbet	FRUG.	f

Tricholaema lacrymosa	Spot-flanked barbet	FRUG.	FF
Tricholaema melanocephala	Black-throated barbet	FRUG.	f
MACROSPHENIDAE			
Sylvietta whytii	Red-faced crombec	INSECT.	f
MALACONOTIDAE			
Chlorophoneus nigrifrons	Black-fronted bushshrike	INSECT.	f
Chlorophoneus sulfureopectus	Orange-breasted bushshrike	INSECT.	f
Chlorophoneus viridis	Gorgeous bushshrike	INSECT.	F
Dryoscopus cubla	Black-backed puffback	INSECT.	f
Laniarius aethiopicus	Tropical boubou	INSECT.	f
Laniarius funebris	Slate-colored boubou	INSECT.	f
Tchagra australis	Brown-crowned tchagra	INSECT.	f
Telophorus nigrifrons	Black-fronted bushshrike	INSECT.	f
MEROPIDAE			
Merops oreobates	Cinnamon-chested bee-eater	INSECT.	F
Merops pusillus	Little bee-eater	INSECT.	f
MONARCHIDAE			
Terpsiphone viridis	African paradise flycatcher	INSECT.	f
Trochocercus cyanomelas	Blue-mantled crested flycatcher	INSECT.	F
MOTACILLIDAE			
Anthus lineiventris	Striped pipit	INSECT.	F
Motacilla aguimp	African pied wagtail	INSECT.	f
Motacilla cinerea	Grey wagtail	INSECT.	f
Motacilla clara	Mountain wagtail	INSECT.	f
MUSCICAPIDAE			
Bradornis microrhynchus	African grey flycatcher	INSECT.	f
Bradornis pallidus	Pale flycatcher	INSECT.	f
Cercotrichas leucophrys	White-browed scrub robin	INSECT.	f
Cossypha caffra	Cape robin-chat	INSECT.	f
Cossypha natalensis	Red-capped robin-chat	INSECT.	F
Cossypha semirufa	Rüppell's robin-chat	INSECT.	F
Melaenornis fischeri	White-eyed slaty flycatcher	INSECT.	f
Melaenornis pammelaina	Southern black flycatcher	INSECT.	F
Muscicapa adusta	African dusky flycatcher	INSECT.	F
Muscicapa caerulescens	Ashy flycatcher	INSECT.	F
Muscicapa striata	Spotted flycatcher	INSECT.	f
Pogonocichla stellata	Muscicapidae	INSECT.	F
Saxicola rubetra	Whinchat	INSECT.	f
Saxicola torquatus	African stonechat	INSECT.	f
MUSOPHAGIDAE			
Tauraco hartlaubi	Hartlaub's turaco	FRUG.	FF
NECTARINIIDAE			
Chalcomitra amethystina	Amethyst sunbird	NECT.	f
Cinnyris mediocris	Eastern double-collared sunbird	NECT.	F
Cinnyris venustus	Variable sunbird	NECT.	f
Cyanomitra olivacea	Olive sunbird	NECT.	FF

Hedydipna collaris	Collared sunbird	NECT.	f
Nectarinia famosa	Malachite sunbird	NECT.	F
Nectarinia kilimensis	Bronzy sunbird	NECT.	f
NUMIDIDAE			
Numida meleagris	Helmeted guineafowl	GRAN.	f
ORIOLIDAE			
Oriolus larvatus	Black-headed oriole	FRUG.	F
PARIDAE			
Parus albiventris	White-bellied tit	INSECT.	f
PASSERIDAE			
Passer domesticus	House sparrow	GRAN.	f
Passer griseus	Northern grey-headed sparrow	GRAN.	f
Passer rufocinctus	Kenya sparrow	GRAN.	f
Petronia pyrgita	Yellow-spotted petronia	GRAN.	f
Plocepasser mahali	White-browed sparrow-weaver	GRAN.	f
PHALACROCORACIDAE			
Phalacrocorax africanus	Reed cormorant	PISC.	f
Phalacrocorax carbo	Great cormorant	PISC.	f
PHOENICULIDAE			
Rhinopomastus cyanomelas	Common scimitarbill	INSECT.	F
PICIDAE			
Campethera nubica	Nubian woodpecker	INSECT.	f
PLATYSTEIRIDAE			
Batis minor	Black-headed batis	INSECT.	FF
Batis molitor	Chinspot batis	INSECT.	f
PLOCEIDAE			
Euplectes albonotatus	White-winged widowbird	GRAN.	f
Euplectes capensis	Yellow bishop	GRAN.	f
Euplectes nigroventris	Zanzibar red bishop	GRAN.	f
Ploceus baglafecht	Baglafecht weaver	GRAN.	f
Ploceus bojeri	Golden palm weaver	GRAN.	f
Ploceus cucullatus	Village weaver	GRAN.	f
Ploceus intermedius	Lesser masked weaver	GRAN.	f
Ploceus ocularis	Spectacled weaver	GRAN.	f
Ploceus spekei	Speke's weaver	GRAN.	f
Ploceus subaureus	Eastern golden weaver	GRAN.	f
Quelea quelea	Red-billed quelea	GRAN.	f
Amblyospiza albifrons	Thick-billed weaver	GRAN.	f
PYCNONOTIDAE			
Chlorocichla flaviventris	Yellow-bellied greenbul	FRUG.	F
Phyllastrephus cabanisi	Cabanis's greenbul	FRUG.	FF
Phyllastrephus strepitans	Northern brownbul	FRUG.	f
Phylloscopus ruficapilla	Yellow-throated woodland warbler	INSECT.	FF
Phylloscopus trochilus	Willow warbler	INSECT.	f
Pycnonotus barbatus	Common bulbul	FRUG.	f
Andropadus importunus	Sombre greenbul	FRUG.	f

Andropadus milanjensis	Stripe-cheeked greenbul	FRUG.	FF
RALLIDAE			
Amaurornis flavirostra	Black crake	PISC.	f
RECURVIROSTRIDAE			
Himantopus himantopus	Black-winged stilt	PISC.	f
SCOLOPACIDAE			
Actitis hypoleucos	Common sandpiper	PISC.	f
Gallinago gallinago	Common snipe	PISC.	f
SCOPIDAE			
Scopus umbretta	Hamerkop	PISC.	f
STURNIDAE			
Cinnyricinclus sharpii	Sharpe's starling	INSECT.	FF
Lamprotornis chalybaeus	Greater blue-eared starling	INSECT.	f
Onychognathus morio	Red-winged starling	INSECT.	f
SYLVIIDAE			
Sylvia atricapilla	Eurasian blackcap	INSECT.	F
THRESKIORNITHIDAE			
Threskiornis aethiopicus	African sacred ibis	PISC.	f
TROGONIDAE			
Apaloderma narina	Narina trogon	INSECT.	FF
TURDIDAE			
Geokichla gurneyi	Orange ground thrush	INSECT.	FF
Turdus helleri	Taita thrush	INSECT.	FF
VIDUIDAE			
Vidua chalybeata	Village indigobird	GRAN.	f
Vidua macroura	Pin-tailed whydah	GRAN.	f
Vidua paradisaea	Eastern paradise whydah	GRAN.	f
ZOSTEROPIDAE			
Zosterops abyssinicus	Abyssinian white-eye	NECT.	f
Zosterops silvanus	Montane white-eye	NECT.	FF

Fig S1 Species accumulation curve within each land-use category.