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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,

1 it is important to consider how bird diversity is maintained across the wider agricultural
2 landscape.

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

14 The Taita Hills in Kenya are the northern-most block of the Eastern Arc Mountains
15 (Fig. 1) and form a highly diverse part of the Eastern Afromontane Biodiversity Hotspot
16 (Mittermeier *et al.*, 2004). Historically, the Eastern Arc Mountains have experienced high
17 levels of deforestation (Platts *et al.*, 2011), losing 70-80% of their original forest cover
18 (Newmark, 2002; Hall *et al.*, 2009). In the Taita Hills, less than 2% of the original forest area
19 remains, isolated within a heterogeneous agricultural matrix (Newmark, 1998). The
20 agricultural landscape consists of traditional agroforestry systems (combining crops, shrubs
21 and trees) and monocultures dominated by annual crops such as maize, which tend to have
22 much lower tree coverage. There has also been an expansion of plantation forests, dominated
23 by *Cypress*, *Pinus* and *Eucalyptus* for timber production. Satellite imagery shows that in the
24 past fifty years over half of Taita's indigenous forest was lost due to agricultural conversion,
25 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 km² 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 km² (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 (qD), whereby parameter q indicates the weight given towards rare or common species. 0D (species richness) is insensitive to relative frequencies, and is therefore weighted towards rare species, 1D (exponential of Shannon) is weighted towards common species, and 2D (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: $\chi^2=22.70$, $df=4$, $P<0.001$, $R^2_{GLMM}=0.11$) 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 : $\chi^2=9.50$, $df=4$, $P=0.049$; 1D : $\chi^2=11.09$, $df=4$, $P=0.026$; 2D : $\chi^2=8.62$, $df=4$, $P=0.071$), 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: $\chi^2=84.53$, $df=4$, $P<0.001$, $R^2_{GLMM}=0.45$), 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: $\chi^2=64.04$, $df=4$, $P<0.001$, $R^2_{GLMM}=0.33$), 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: $\chi^2=38.82$, $df=4$, $P<0.001$, $R^2_{GLMM}=0.19$), 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

1 matrix, supporting 80% of all observed bird species at higher overall abundance than primary
2 forest. This study did not consider how detectability varied between land-use types, but dense
3 vegetation (such as that associated with primary forest) can decrease the likelihood of
4 observing a species by approximately 15% (Anderson *et al.*, 2015). Detectability may have
5 been reduced within forest, but we observed mean bird abundance increasing by more than
6 100% within agroforest plots and changes of this order of magnitude are most likely to reflect
7 genuine changes in underlying bird abundance associated with the surveyed habitats.

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

20 Timber plantations in the Taita Hills supported an impoverished bird community, with
21 less than half the abundance and a quarter of the diversity associated with agroforestry
22 systems and annual croplands. Plantations are dominated by exotic timber species such as
23 *Cypress*, *Pinus* and *Eucalyptus*, and the lack of fruiting forest trees is likely to be limiting the
24 availability of resources for birds in the region. Other studies have noted the inhospitality of
25 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 km²; 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

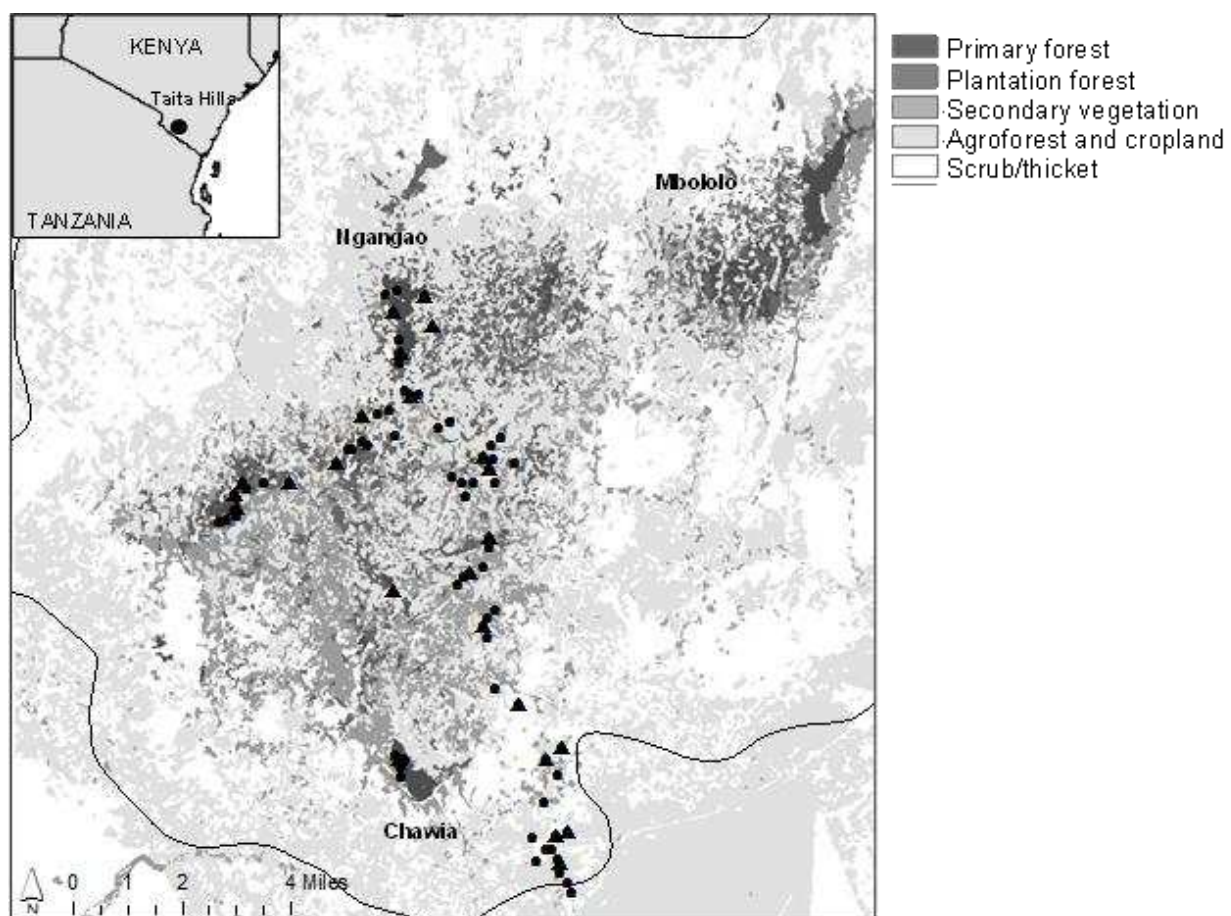


FIG 2

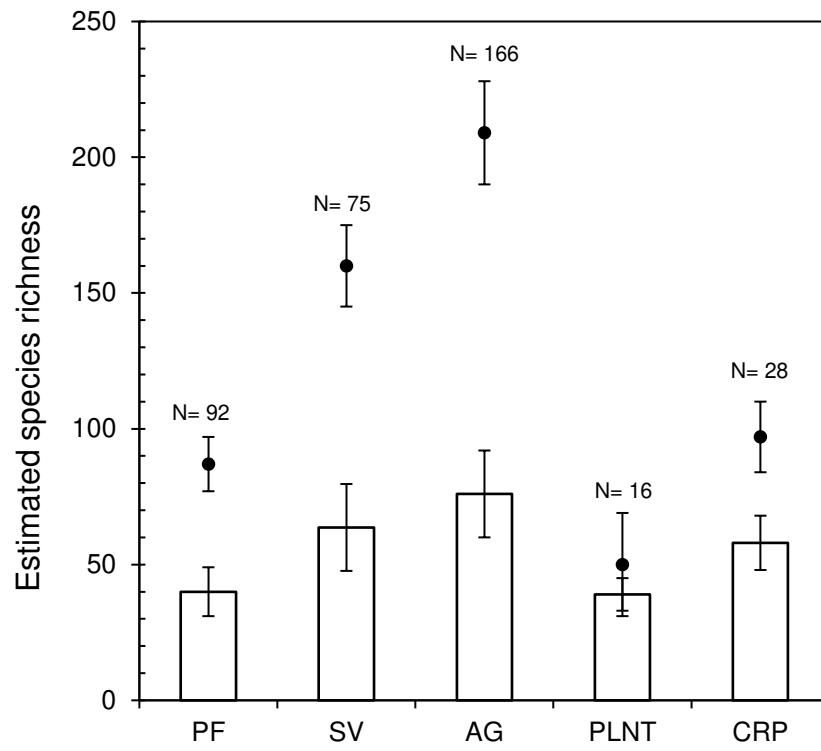


Fig 3

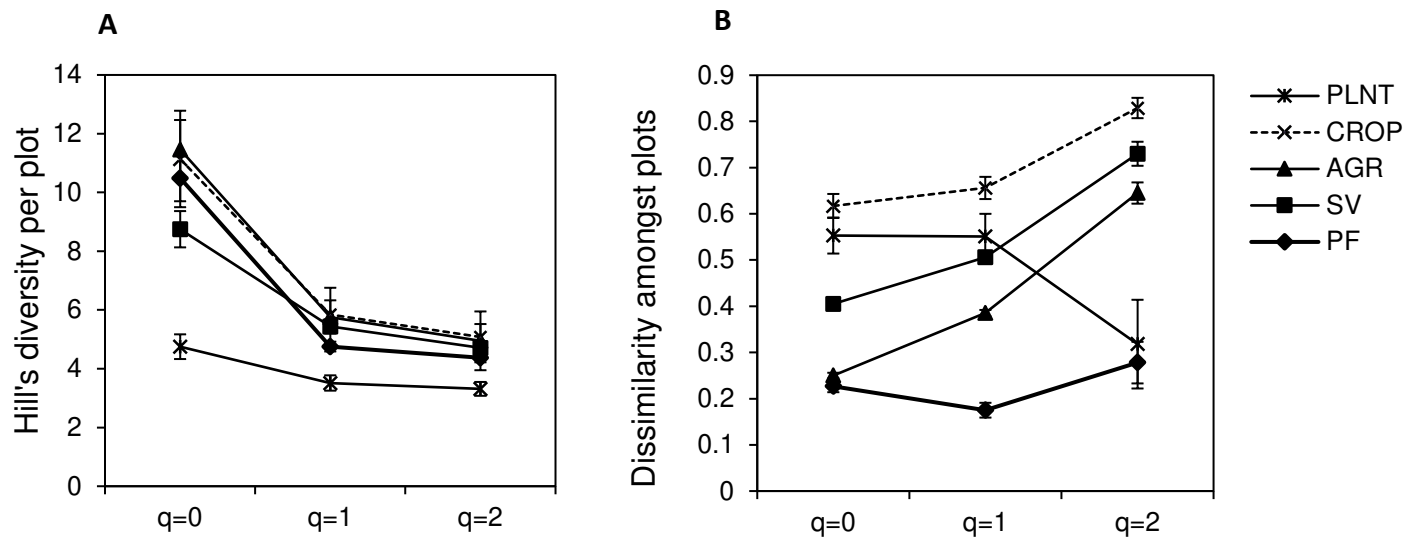


FIG 4

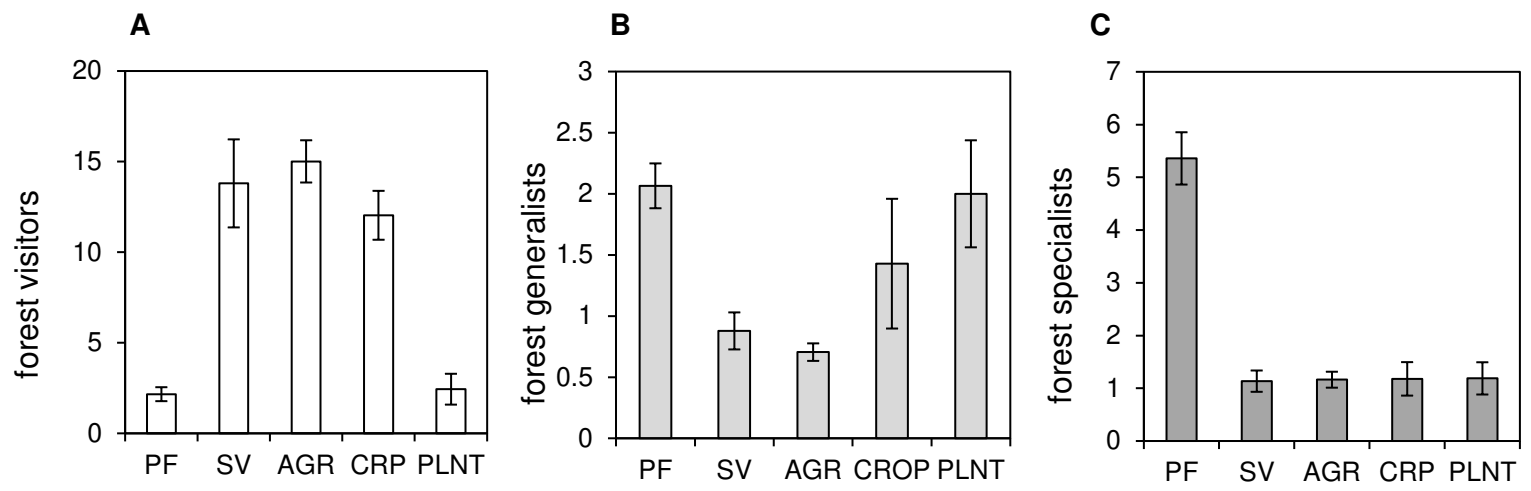
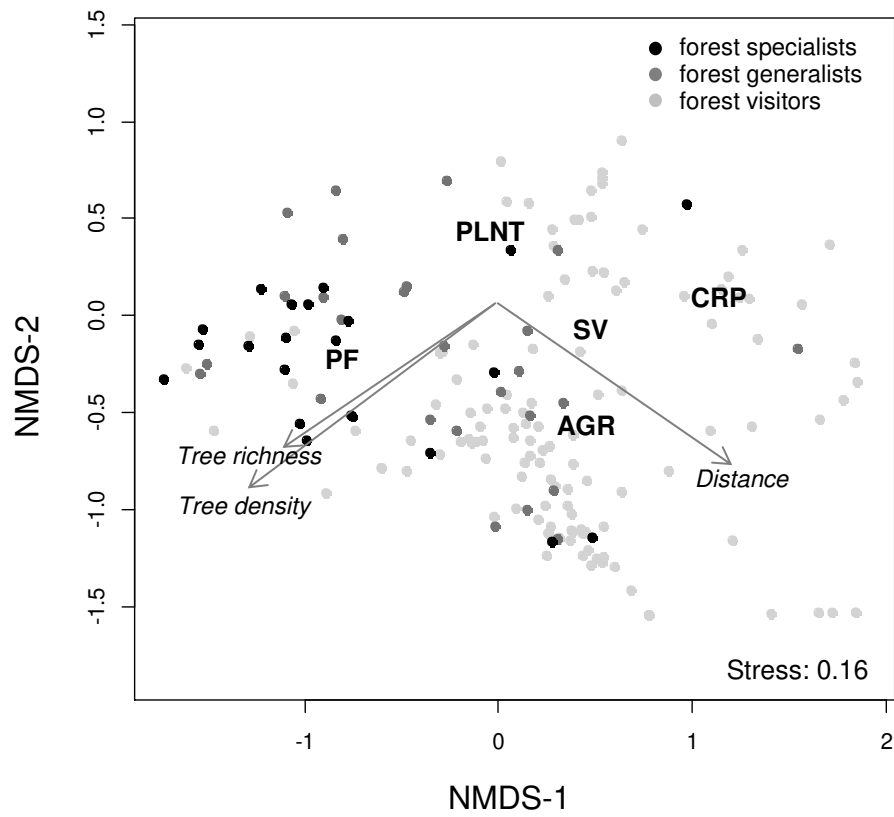


FIG 5



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
⁰ D	1.29	-293.33	9	0.03
¹ D	-10.8	-105.09	9	0.04
² D	-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.

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

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

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

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

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

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

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

