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Bats are Not Birds – Different Responses to Human Land-use on a Tropical Mountain

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ABSTRACT

Land-use intensification has consequences for biodiversity and ecosystem functioning, with various taxonomic groups differing widely in their sensitivity. As land-use intensification alters habitat structure and resource availability, both factors may contribute to explaining differences in animal species diversity. Within the local animal assemblages the flying vertebrates, bats and birds, provide important and partly complementary ecosystem functions. We tested how bats and birds respond to land-use intensification and compared abundance, species richness, and community composition across a land-use gradient including forest, traditional agroforests (home garden), coffee plantations and grasslands on Mount Kilimanjaro, Tanzania. Furthermore, we asked how sensitive different habitat and feeding guilds of bats and birds react to land-use intensification and the associated alterations in vegetation structure and food resource availability. In contrast to our expectations, land-use intensification had no negative effect on species richness and abundance of all birds and bats. However, some habitat and feeding guilds, in particular forest specialist and frugivorous birds, were highly sensitive to land-use intensification. Although the habitat guilds of both, birds and bats, depended on a certain degree of vegetation structure, total bat and bird abundance was mediated primarily by the availability of the respective food resources. Even though the highly structured southern slopes of Mount Kilimanjaro are able to maintain diverse bat and bird assemblages, the sensitivity of avian forest specialists against land-use intensification and the dependence of the bat and bird habitat guilds on a certain vegetation structure demonstrate that conservation plans should place special emphasis on these guilds.

Key words: Africa; agriculture; biodiversity conservation; community ecology; driving factors; Kilimanjaro; landscape management.

LAND-USE CHANGE IS A CONSEQUENCE OF THE PRODUCTION OF FOOD, fiber and shelter for the growing human population (Ellis *et al.* 2010, Keinan & Clark 2012), but it also has profound consequences for natural ecosystems (Brooks *et al.* 2002, Foley *et al.* 2005). The percentage of natural areas converted for human needs has increased over the past three centuries from 5 percent to 55 percent (Ellis *et al.* 2010). Consequently, 'most of the world's "natural" ecosystems are embedded within lands already modified through land-use' (Ellis & Ramankutty 2008). Currently, 17 out of 34 biodiversity hotspots, most of them in the tropics (Myers *et al.* 2000, Mittermeier *et al.* 2004), are located in areas with above-average population densities and population growth rates (Cincotta *et al.* 2000) and therefore are highly threatened by further land conversion.

In general, land-use intensification changes diversity and composition of many species assemblages (Tscharntke *et al.* 2005, Barlow *et al.* 2007, Flynn *et al.* 2009). The two flying vertebrate taxa, bats and birds, respond largely in a similar way to land-use intensification with decreasing species richness toward disturbed habitats (Medellín *et al.* 2000, Daily *et al.* 2001, Waltert *et al.* 2004, Farwig *et al.* 2008, Williams-Guillén & Perfecto 2010). However, these taxa are not uniform and discrete subsets of species with distinct foraging strategies seem to respond differently to land-use intensification. Bats foraging in dense vegetation or gleaning insects from surfaces are negatively affected by land-use, whereas, aerial hawking insectivore bats that depend on open air space may even benefit from land-use intensification (Medellín *et al.* 2000, Williams-Guillén & Perfecto 2011). Similarly, birds associated with forests are often negatively influenced by increased land-use, whereas, shrubland or open country birds may show positive responses (Farwig *et al.* 2008, Mulwa *et al.* 2012a). While frugivorous and insectivorous birds tend to be negatively affected by habitat disturbance or land-use intensification, avian granivores and omnivores generally increase in abundance and species richness in agricultural areas (Waltert *et al.* 2004, Gray *et al.* 2007, Lefevre 2008, Williams-Guillén & Perfecto 2011, Mulwa *et al.* 2012a).

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Both bats and birds perform important ecosystem functions such as seed dispersal, pollination and arthropod predation (Whelan *et al.* 2008, Kunz *et al.* 2011), and thereby often provide significant economic benefits to farmers (*e.g.,* Kellermann *et al.* 2008, Boyles *et al.* 2011, Ferger *et al.* 2013). Negative responses of bats and birds to habitat alteration are therefore likely to have considerable negative impact on ecosystem functioning. In order to develop sound conservation strategies, it is critical to identify the environmental factors that drive the changes in abundance, species richness and community composition of bat and bird assemblages. Land-use intensification modifies the vegetation structure, the amount of forest cover and the number of woody plant species, which in turn may affect bats (Caras & Korine 2009, Dodd *et al.* 2012, Jung *et al.* 2012) and birds (Heikkinen *et al.* 2004, Laube *et al.* 2008). In addition, the availability of food resources for bats and birds, *e.g.,* insects or fruits, is often negatively influenced by land-use intensification (Vickery *et al.* 2001, Wickramasinghe *et al.* 2004, Tscharntke *et al.* 2005, Dodd *et al.* 2012).

Bats and birds are rarely studied simultaneously within a land-use context (but see Faria *et al.* 2006, 2007, Harvey & González Villalobos 2007) and, therefore, differences in the respective responses of bat and bird communities to land-use changes are only little known. To address this gap, we studied the impact of land-use intensification on both bats and birds on Mount Kilimanjaro, an ecosystem highly threatened by land-use intensification (Maro 1988, Balmford *et al.* 2001, Soini 2005, Hemp 2009). First, we tested how bat and bird abundance, species richness and community composition changed with land-use intensification. We hypothesized that abundance and species richness of both taxa decline and community composition changes with land-use intensification. Second, we asked which land-use-related factors mediate the impact of land-use intensification on species communities. We hypothesized that land-use induced changes in bat and bird abundance, species richness and composition can be explained by differences in vegetation structure as well as in food resource availability.

METHODS

STUDY SITE.—Our study was conducted on the southern slope of Mount Kilimanjaro, Tanzania (2°45′–3°25′ S, and 37°00′–37°43′ E), within the framework of the DFG research group Kilimanjaro (https://www.kilimanjaro.biozentrum.uni-wuerzburg.de/). The study encompassed 19 permanently marked 0.25 ha study plots (50 m × 50 m in size) over a land-use gradient ranging from natural lower montane forest (hereafter: forest; four plots), to an agroforestry system (hereafter: home gardens; five plots), coffee plantations with shade trees (hereafter: coffee plantations; five plots) and grasslands (five plots) (Fig. 1) in low to middle elevations (1400–2000 m asl). While the natural habitat type in this elevational belt is forest, the Chagga people partly converted the forests into extensive home gardens for their traditional agricultural subsistence (Hemp 2006). These gardens consist of a mix of natural forest vegetation in the form of large shade trees and agriculturally used plants (*e.g.,* coffee, banana, taro, sweet potato). The more industrialized coffee production resulted in large, mainly shaded coffee plantations. The shade trees are either invasive or traditional forest trees. Where the original forest cover was completely logged and removed, the Chagga cultivate grasslands that are frequently cut to feed their livestock. Study plots were chosen in areas dominated by the same land-use type, ensuring that the vegetation structure of the plot vicinity was similar to the study plots. Mean temperature for the year 2011 was 17.5°C at 1692 m asl (Nkweseko station 3°11′5.80″ S and 37°14′26.92″ E, T. Appelhans & T. Nauss, unpubl. data). Precipitation varied seasonally on Mount Kilimanjaro with a long wet season from March to June and a short wet season between November and December. We collected data during the two dry seasons from December 2010 to March 2011 and June to September 2011.

ACOUSTIC MONITORING AND SOUND ANALYSIS OF BATS.—For methodological reasons we focussed on the more speciose aerial insectivorous bat species and omitted the few species of non-echolocating fruit bats. We started the monitoring of bats after sunset and finished at the latest at 2200 h. We recorded echolocation calls of insectivorous bats at the four corners of each study plot per season using a point-stop method (Estrada-Villegas *et al.* 2010, Jung *et al.* 2012). During one recording round, every point was sampled for 5 min. We conducted four recording rounds during one night, resulting in maximum recording duration of 80 min per plot per night (4 × 4 × 5 min). We recorded all passing bats, using a manually triggered real time ultrasound recording device (D1000×; Pettersson Elektronik AB, Uppsala, Sweden) at a sampling rate of 384 kHz and a ten second recording duration (5 sec each before and after a triggering event). Visual observations of bat releases during the day indicate maximum detection distances of ~ 20 m for our recording setup.

We generated spectrograms through an FFT – analysis with 512 or 1024 samples FFT length and an overlap of 93.75 percent, using a flat top window in AviSoft-SASLab Pro (v. 5.1.05, Berlin, Germany). For analysis, we counted bat passes following Estrada-Villegas *et al.* (2010). Bat passes with very faint and therefore low quality calls were excluded from the analysis (13.9% of 7162 passes), to prevent a misleading identification. These faint passes are mainly a result of bats passing further away from the recording device and occurred evenly across all study sites, thus we suggest that our conclusion and discussion is not affected by their exclusion. We measured start and terminal frequency, peak frequency, call duration and interpulse interval. Using literature data and available reference calls, we classified bat passes into 19 different sonotypes (Table S1). However, due to the current lack of reference calls for many African bat species, assignation of sonotypes to distinct species was not possible in every case. As an approximation for species richness, we therefore used sonotype richness. With acoustic methods it is not possible to identify individuals, but our recording scheme, where we changed our location every 5 min, minimizes the possibility to record the same bat multiple times. Furthermore, as bat passes

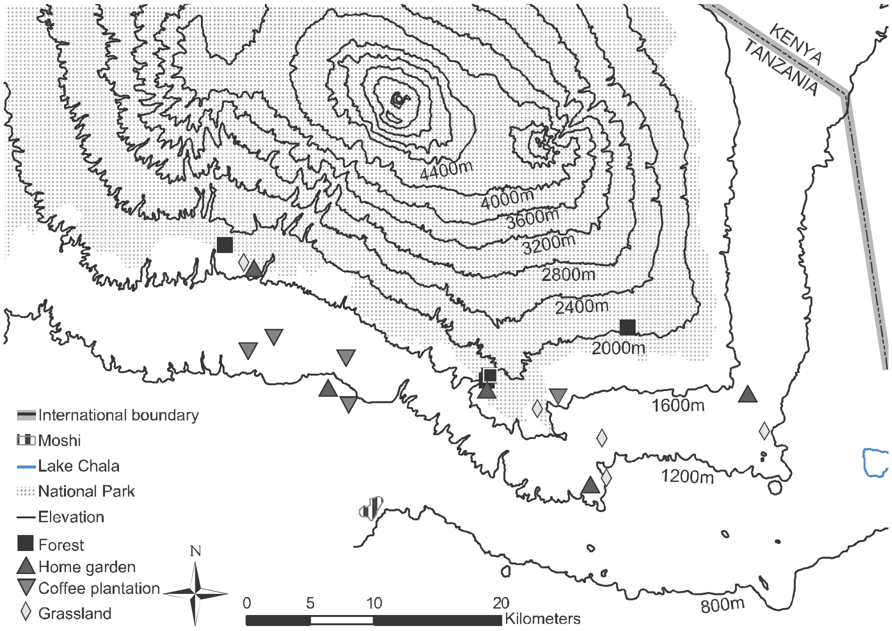

FIGURE 1. Map of the study area showing the distribution of 19 study sites (forest "■" [4], home garden "▲" [5], coffee plantation "▼" [5] and grassland "◊" [5]) along the southern slopes of Mount Kilimanjaro, Tanzania.

should not be equated with bat individuals we used occurrence from one study plot as an approximate measure for total abundance (Estrada-Villegas *et al.* 2010, Jung *et al.* 2012). Occurrence for each sonotype per plot per night was therefore calculated by adding presence-only data from all 5-min point-stop recordings. The maximal possible value per sonotype therefore was 16.

Bat sonotypes were classified to habitat guilds based on literature and call characteristics (Schnitzler & Kalko 2001). We distinguished bats: (1) hunting in open space or above the canopy, *i.e.,* uncluttered space bats; (2) foraging in edge or gap-like situations, *i.e.,* background cluttered space bats and (3) flying mostly in dense vegetation, *i.e.,* highly cluttered space bats. A list of bat sonotypes, their occurrence and functional group is given in Table S2.

Sampling and guild classification of birds.—We used audio-visual point counts to sample birds in eight subplots per study plot and season. The centers of four subplots were identical to the points used for the bat recordings and the remaining four were located with a minimum distance of 40 m to the former to avoid overlap of subplots. As detection bias increases with distance, we deliberately designed subplots in a way that ensured appropriate detectability of birds across all habitat types (Mulwa *et al.* 2012a,b). We established circular subplots with 20 m radius around each point in densely vegetated habitats (forest, home garden, coffee plantation) and square subplots (35.5 m × 35.5 m) at grassland plots, covering the same sampling area in all land-use types (Laube *et al.* 2008). Size of the subplots indicates a maximum distance between observer and bird of 50 m. Within the eight subplots we counted all seen or heard birds for 10 min and identified them to species level using Zimmerman *et al.* (1999). Counting started at the first subplot at civil twilight and finished at the latest at 0900 h. We used the total number of birds counted across all eight subplots as a measure of abundance, and the number of identified species as species richness. We classified bird species to the following habitat guilds, following Bennun *et al.* (1996): forest specialists (*i.e.,* occurring in the interior of undisturbed forest), forest generalists (*i.e.,* occurring in undisturbed forest but also found at forest stripes, edges and gaps) or forest visitors (*i.e.,* may be recorded in forests, but are more common in non-forest habitats). Species not classified by Bennun *et al.* (1996) were defined as open country birds, which included species restricted to open habitats, low shrubs and cultivated areas (Zimmerman *et al.* 1999). We further classified bird species into the following feeding guilds based on their major food items (Kissling *et al.* 2007): frugivores (feeding on fruits only, or on fruits and other plant material), granivores (feeding on seeds only or on seeds and non-fruit plant material), insectivores (feeding on invertebrates only), carnivores (feeding on vertebrates only or on vertebrates and invertebrates) and omnivores (feeding on a larger variety of animal and plant resources). A list of all encountered bird species along with their abundance, habitat and feeding guild classification is presented in Table S3.

Sampling of vegetation structure and food resources.—Canopy height, canopy closure and foliage cover were quantified for each subplot. To evaluate the data separately for bat and bird assemblages we used either four or eight subplots per season for our analysis (Table S4). We assessed maximum canopy height with a laser range finder (Zeiss Victory 10 × 45 T*RF, Carl Zeiss, Germany) and canopy closure with a spherical crown densiometer (Forestry Suppliers, Jackson, Mississippi, U.S.A.). Foliage cover was estimated as percentage of foliage cover in eight strata (0 m, 1 m, 2 m, 4 m, 8 m, 16 m, 32 m and 64 m aboveground) (Farwig *et al.* 2008) to the nearest 5 percent. Subsequently, the mean number of strata with > 0 percent foliage cover was calculated (Meyer & Kalko 2008) as vertical vegetation heterogeneity. To take into account horizontal vegetation heterogeneity across subplots, we determined the coefficient of variation in the mean number of strata across the subplots (Raman & Sukumar 2002). In addition, data on tree density (number of trees >10 dbh per hectare) were available for each study plot (G. Rutten, A. Enßlin, A. Hemp and M. Fischer, unpubl. data).

Finally, an index of vegetation structure was calculated, using the scores of the study plots along the first axis of a non-metric multidimensional scaling analysis (NMDS). The NMDS was calculated (four subplots for bats final stress: 0.01147; eight subplots for birds: final stress = 0.00945) based on normalized Euclidean distances of mean canopy height (log transformed), mean canopy closure (arcsine transformed), mean number of strata (log transformed), the coefficient of variation in the mean number of strata (log transformed), and tree density (log transformed) (metaMDS, (Oksanen *et al.* 2012), Table S4). Again, depending on whether the data were used for bat or bird assemblages, the analysis was based on either four or eight subplots.

As an approximation for the availability of food resources, we assessed nocturnal insect biomass for bats and diurnal insect biomass as well as fruit and flower abundance for birds (Table S4). Nocturnal insects per plot and season were sampled with a custom-made light trap with a superactinic light tube (6 watt, Fritz Weber Entomologiebedarf, Stuttgart, Germany) that was operated on the study plot for 20 min after each bat recording round. Acoustic sampling of bats and nocturnal insect trapping was alternated to avoid mutual interference. To sample diurnal insects per plot and season, 100 sweeps with a 30 cm diameter sweep net were conducted along two 50 m transects. Total fresh biomass of nocturnal and diurnal insects >1 mm was determined with a precision scale (precision ± 0.002 g, CM 50-C2N, Kern & Sohn GmbH, Balingen-Frommern, Germany). For fruit and flower abundance, the number of fruits and flowers were estimated for each fruiting or flowering tree within the four or eight subplots, respectively, on a logarithmic scale (0-10, >10–100, >100–1000, >1000–10,000, >10,000–100,000, >100,000–1,000,000 fruits or flowers, respectively) and summed over the study plot.

STATISTICAL DATA ANALYSIS.—To calculate inventory completeness (as percentage of observed in relation to estimated species richness) we used the software package EstimateS (Colwell 2009). We chose richness estimators for bat sonotype richness (Michaelis-Menten) or bird species richness (first order jackknife) following the framework of Brose and Martinez (2004).

If not stated differently all following statistical tests were performed in R v. 2.15.1 (R Development Core Team 2012, Vienna, Austria). To test whether observed occurrence/abundance of all bats/birds as well as habitat and feeding guilds differed among land-use types, we fitted generalized linear mixed effects models (GLMM) with a Poisson error distribution and integrated plots and elevation as random effects using a Penalized Quasi-Likelihood approach (glmmPQL, MASS package, Venables & Ripley 2002). Plots were used as random effect to control for the repeated measures per plot across season and elevation to correct for an unbalanced distribution of study plots over the elevational range of our study area (Fig. 1). A Tukey *post-hoc* test was used to test for significant differences among land-use types. We tested whether sonotype or species composition of bat and bird assemblages differed among land-use types with an analysis of similarity (anosim, vegan package, Oksanen *et al.* 2012) that is analogous to an analysis of variance and tests for differences between *a priori*-defined groups of community samples (here land-use type) based on a (dis)similarity matrix (Clarke 1993).

To test for the influence of vegetation structure and food resources on bat and bird sonotype/species richness and occurrence/abundance, an information-theoretic model selection approach was employed using a set of Poisson GLMMs (Table S5; glmer, lme4 package, Bates *et al.* 2012), with plots and elevation as random effects. We restricted inference to a subset of plausible models selected *a priori* (see Table S5). The Akaike's information criterion, corrected for small sample size (AICc) following Burnham and Anderson (2002), was calculated for each model. Subsequently we calculated the Akaike difference (Δ_{AICc}) to the model with the minimum AICc. Models with $\Delta_{AICc} < 2$ are considered to have substantial support (Burnham & Anderson 2002). In addition, we calculated the Akaike weights (w_i) for each candidate model, which provide approximate probabilities that model i is the actual best model in the set of candidate models (Burnham & Anderson 2002).

Similarly, we assessed whether bat or bird community composition could be explained by vegetation structure or food resources. For bat or bird community composition we first calculated a NMDS based on Bray-Curtis dissimilarities of bat occurrence and bird abundance of each plot visit (metaMDS, vegan package (Oksanen *et al.* 2012); bats: final stress = 0.171, birds: final stress = 0.181). The scores of both NMDS axes were analyzed as bat or bird community composition using an information-theoretic model selection approach based on normal distributed LMMs (Table S5; lmer, lme4 package, Bates *et al.* 2012), with plots and elevation as random effect.

To investigate how the composition of bat and bird assemblages changed across land-use types, a NMDS based on Bray-Curtis dissimilarities of mean bat occurrence and mean bird abundance was performed (metaMDS, vegan package, Oksanen *et al.* 2012). To evaluate how vegetation structure and food resources were correlated with the NMDS ordination, we applied a vector-fitting approach (envfit, vegan package, Oksanen *et al.* 2012) and further performed linear models to test for correlation with both NMDS axes. As ordination techniques react sensitive to rare species, only bat sonotypes and bird species with an occurrence/abundance of >1 were included.

RESULTS

BAT OCCURRENCE, RICHNESS AND SONOTYPE COMPOSITION.—Overall, 6169 bat passes were acoustically registered, resulting in 1307 occurrences of 19 insectivorous bat sonotypes, belonging to seven families (Table S1; Table S2). Observed sonotype richness nearly reached the estimated values, with a total inventory completeness of 99.8 percent (Table 1). Occurrence and sonotype richness of all bats differed significantly between land-use types, with highest values in coffee plantations and lower values in home gardens, forest and grasslands (GLMM: occurrence: $F_{3,34} = 14.08$, $P < 0.001$, Fig. 2A; sonotype richness: $F_{3,34} = 11{,}81$, $P < 0.001$; Fig. 3A). Within the habitat guilds we found significant differences in occurrence and sonotype richness among land-use types for uncluttered space bats (GLMM: occurrence: $F_{3,34} = 12.20$, $P < 0.001$; sonotype richness: $F_{3,34} = 11.89$, $P < 0.001$) and background cluttered space bats (GLMM: occurrence: $F_{3,34} = 9.13$, $P < 0.001$; sonotype richness: $F_{3,34} = 4.006$, $P < 0.05$). For both bat habitat guilds occurrence and sonotype richness were highest in coffee plantations. While for uncluttered space bats lowest occurrence and sonotype richness were recorded in forest sites, background cluttered space bats showed lowest occurrences and number of sonotypes in grasslands. An analysis of similarity revealed significant differences in species composition among land-use types (analysis of similarity: statistic $R = 0.4403$, $P = 0.001$, for details see Table S2).

BIRD ABUNDANCE, RICHNESS AND SPECIES COMPOSITION.—Overall, 2404 birds belonging to 124 species and 38 families were recorded (Table S3). Total inventory completeness based on species accumulation curves reached 75.7 percent (Table 1). Different land-use types resembled one another in overall bird abundance (GLMM: $F_{3,34} = 0.26$, $P = 0.856$, Fig. 2B), whereas, within each of the four habitat guilds the abundance of birds differed significantly among land-use types (GLMM: forest specialists species: $F_{3,34} = 24.22$, $P < 0.001$; forest generalists: $F_{3,34} = 9.60$, $P < 0.001$, forest visitors: $F_{3,34} = 5.58$, $P = 0.003$; open country birds: $F_{3,34} = 5.81$, $P = 0.003$; Fig. 2B). Forest specialists and generalists were highly abundant at forest sites and decreased with human land-use intensity, while abundance of non-forest birds was lowest in forests and home gardens and increased with land-use intensity (Fig. 2B). There were no significant differences in bird species richness among land-use types (GLMM: $F_{3,34} = 0.163$, $P = 0.921$, Fig. 3B). In contrast, significant differences were found in species richness among land-use types for all four habitat guilds (GLMM: forest specialists: $F_{3,34} = 68.47$, $P < 0.001$; forest generalists: $F_{3,34} = 15.79$, $P < 0.001$; forest visitors: $F_{3,34} = 12.18$, $P = 0.003$; open country birds: $F_{3,34} = 8.012$, $P = 0.003$). While species richness of forest specialists and generalists decreased with land-use intensification, species richness of forest visitors and non-forest birds increased with land-use intensification (Fig. 3B). Species composition differed significantly among land-use types (analysis of similarity: statistic $R = 0.6599$, $P = 0.001$, for detailed differences see Table S3).

Frugivorous bird significantly differed in abundance among land-use types (GLMM: $F_{3,34} = 4.495$, $P = 0.009$, Fig. 2C). Significant differences were also found in species richness of frugivorous (GLMM: $F_{3,34} = 7.599$, $P < 0.001$, Fig. 3C) and granivorous species (GLMM: $F_{3,34} = 4.818$, $P = 0.007$, Fig. 3C). Although numbers of frugivorous species were significantly lower in grassland sites, granivorous birds showed significantly higher species richness in grasslands and coffee plantations.

VEGETATION STRUCTURE AND FOOD RESOURCES AS EXPLAINING FACTORS FOR BAT AND BIRD RESPONSES.—Generalized linear models that included nocturnal insect biomass provided the best fit for explaining bat occurrence (Table 2). However, there was no difference between models including only biomass of nocturnal insects and those comprising insect biomass together with vegetation structure. Bat sonotype richness was best explained by models that only included either insect biomass or vegetation structure, albeit neither of both factors was significant (Table 2). Vector fitting of vegetation structure and food resources onto an NMDS ordination (final stress = 0.123) revealed a significant correlation of sonotype composition with vegetation structure only (Fig. 4A, $R^2 = 0.3537$, $P = 0.031$). Vegetation structure was significantly correlated with NMDS axis 1 (linear model: $F_{1,17} = 9.222$, $P < 0.008$), which corresponds to the land-use gradient of our study plots from natural forest sites to intensively used grasslands. Bat habitat guilds separated along NMDS axis 1, indicating that uncluttered space bats were more abundant in grasslands with low vegetation structure, and some of the highly cluttered space bats occurred more frequently in forest plots with high vegetation structure. Differences in sonotype composition best corresponds to the linear mixed effect model including only vegetation structure (Table 2).

Total bird abundance was best explained by the model including all three food resources (insect biomass, fruit and flower abundance; Table 2). The best fitting model for bird species richness included only vegetation structure, albeit its effect was not significant (Table 2). Differences in bird species composition among study plots were significantly correlated with differences in vegetation structure in the best fitting model (Table 2). Accordingly, the composition of bird communities as represented

TABLE 1. *Bat and bird observed sonotype/species richness (S_{obs}), estimated sonotype/species richness (S_{est}, based on the Michaelis-Menten estimator for bats and first-order jackknife for birds) and inventory completeness (IC) in the different land-use types, with* N *sampling nights/days.*

		Bats			Birds		
	N	S_{obs}	S_{est}	IC (%)	S_{obs}	S_{est}	IC (%)
Forest	8	13	14.1	82.8	42	58.6	71.6
Home garden	10	13	13.7	93.4	46	62.2	74
Coffee plantation	10	17	18.7	95.9	60	85.2	70.4
Grassland	10	11	11.6	92.1	58	84.1	69
Total	38	19	19	99.8	124	164	75.7

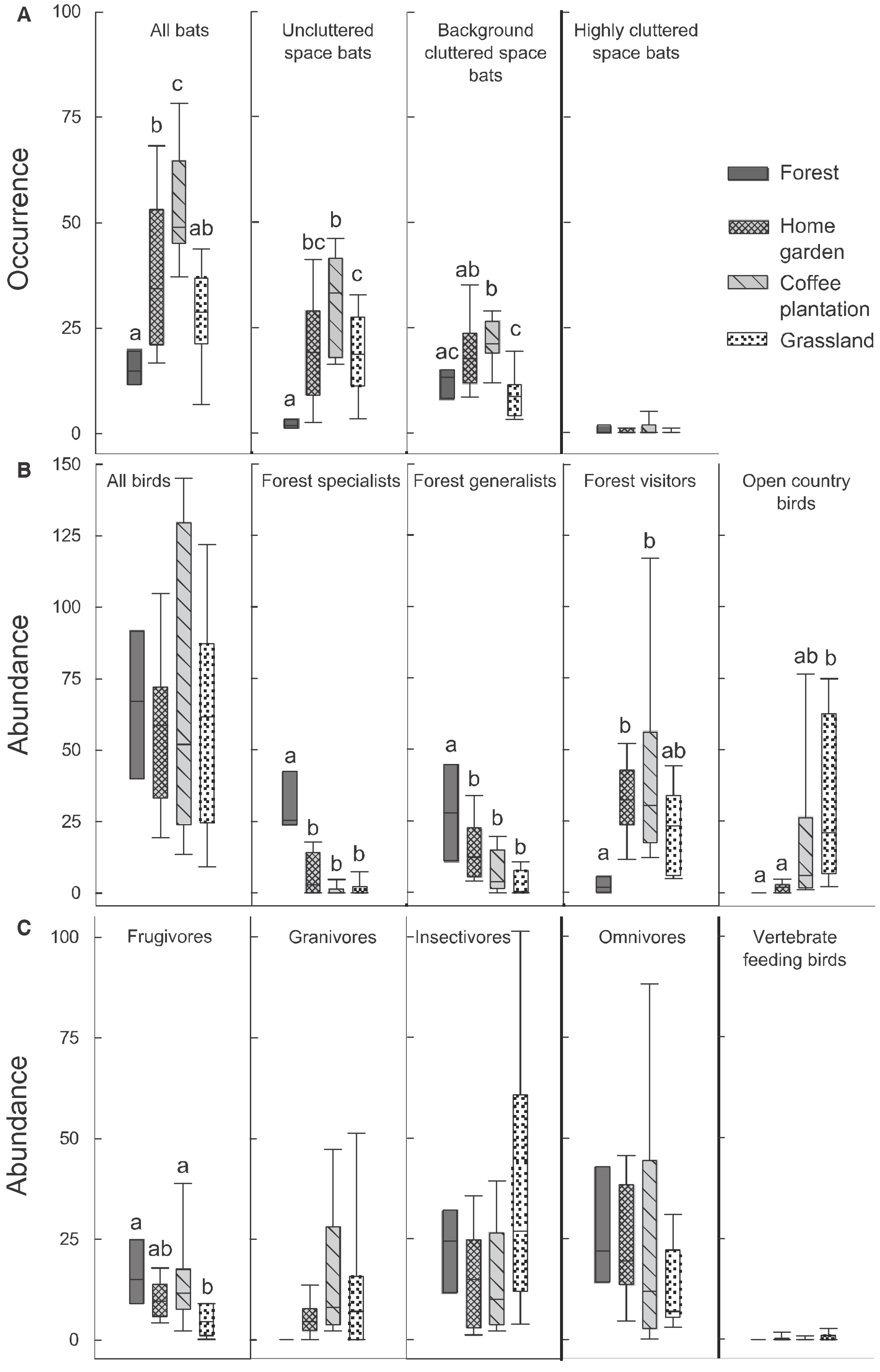

FIGURE 2. Differences in median occurrence of bats or their respective habitat guilds (A) and total abundance of birds or their respective habitat (B) or feeding guilds (C) across land-use types (forest, home gardens, coffee plantations and grasslands). Boxes represent 25th and 75th percentiles; whiskers represent 10th and 90th percentiles. Significant differences among land-use type (*post-hoc* Tukey test, $P < 0.05$) are indicated by different letters.

in the NMDS ordination (final stress = 0.148) was significantly fitted by vectors representing vegetation structure ($R^2 = 0.6972$, $P = 0.001$) and fruit abundance ($R^2 = 0.3726$, $P = 0.021$). The NMDS ordination (Fig. 4B) reflects a separation of forest specialists and generalists, which were more abundant in forest plots, from forest visitors and open country birds, which were more frequently found in plots with human utilization (home gardens, coffee plantations and grasslands). This separation occurred primarily along the 1st NMDS axis, which was correlated with vegetation structure (linear model: $F_{1,17} = 22.06$, $P < 0.001$). In contrast to habitat guilds, different feeding guilds showed no distinct grouping in the NMDS (Fig. 4C).

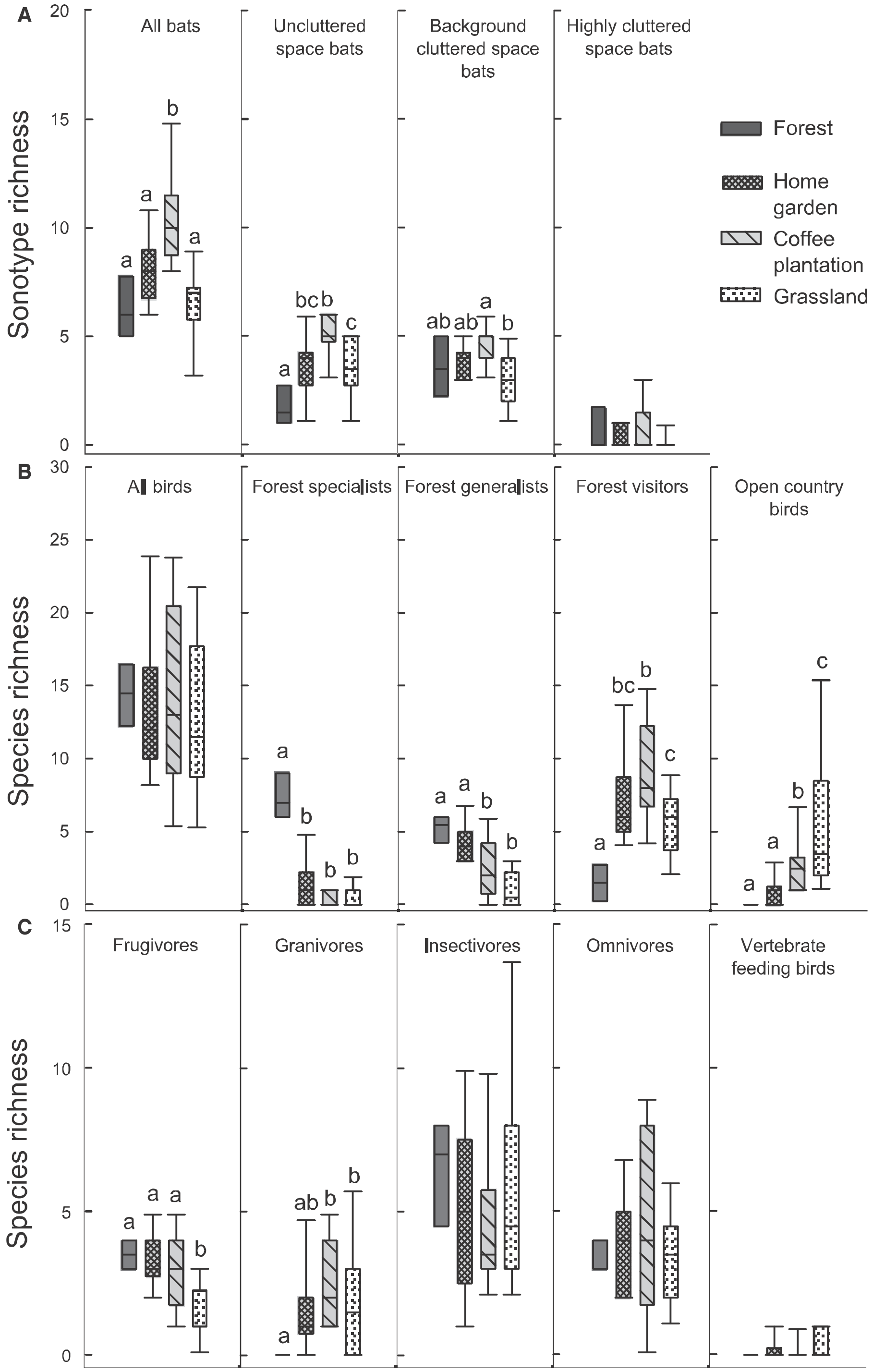

FIGURE 3. Differences in the median sonotype richness of bats or their respective habitat guilds (A) and species richness of birds or their respective habitat or feeding guilds (B, C) between land-use types (forest, home gardens, coffee plantations and grasslands). Boxes represent 25th and 75th percentiles; whiskers represent 10th and 90th percentiles. Significant differences among land-use type (*post-hoc* Tukey test, $P < 0.05$) are indicated by different letters.

DISCUSSION

Land-use intensification has distinctly negative effects for ecosystem functioning and is one of the most important drivers for biodiversity loss (Sala *et al.* 2000, Thuiller 2007). As nocturnal and diurnal predators, seed dispersers and pollinators, bats and birds contribute essentially to ecosystem functioning (Whelan *et al.* 2008, Kunz *et al.* 2011). Consequently, understanding the differences between the responses of bats and birds to land-use intensification and knowing the underlying

TABLE 2. *Best fitting generalized linear mixed model (GLMM; Akaike difference $\Delta_{AICc} < 2$), explaining associations between occurrence/abundance or sonotype/species richness of bats and birds, respectively, and vegetation structure and food resources (A). Best fitting linear mixed effect model (LMM; Akaike difference $\Delta_{AICc} < 2$), explaining associations between bat or bird community composition and vegetation structure and food resources (B). See Table S5 for complete modeling results.*

(A)

GLMM Model	Structural parameter	Estimate	Error	*Z* value	*P* (|Z|)
Bat occurrence	Intercept	3.310	0.129	25.731	<0.001
AIC$_c$: 124.09	Insects	0.064	0.019	3.375	<0.001
Deviance: 122.6					
Bat occurrence	Intercept	3.310	0.128	25.782	<0.001
AIC$_c$: 125.44	Insects	0.063	0.019	3.384	<0.001
Deviance: 121.8	Vegetation structure	−0.109	0.123	−0.888	0.374
Bat sonotype richness	Intercept	2.036	0.078	26.215	<0.001
AIC$_c$: 35.35	Insects	0.011	0.031	0.342	0.732
Deviance: 26.14					
Bat sonotype richness	Intercept	2.053	0.061	33.69	<0.001
AIC$_c$: 35.37	Vegetation structure	0.019	0.061	0.31	0.756
Deviance: 26.16					
Bird abundance	Intercept	3.777	0.173	21.856	<0.001
AIC$_c$: 370.9	Insects	0.025	0.027	0.913	0.361
Deviance: 356.2	Fruits	0.264	0.034	7.815	<0.001
	Flowers	−0.277	0.041	−6.759	<0.001
Bird species richness	Intercept	2.605	0.069	37.77	<0.001
AIC$_c$: 67.57	Vegetation structure	0.026	0.071	0.36	0.715
Deviance: 58.36					

(B)

LMM Model	Structural parameter	Estimate	Standard Error	χ^2	*P* > (|χ^2|)
Bat community composition	Intercept	−0.013	0.100		
AIC$_c$: 55.38	Vegetation structure	−0.245	0.098	6.185	0.013
Deviance: 37.89					
Bird community composition	Intercept	<0.001	−0.133		
AIC$_c$: 45.69	Vegetation structure	−0.592	−0.133	19.126	<0.001
Deviance: 37.89					

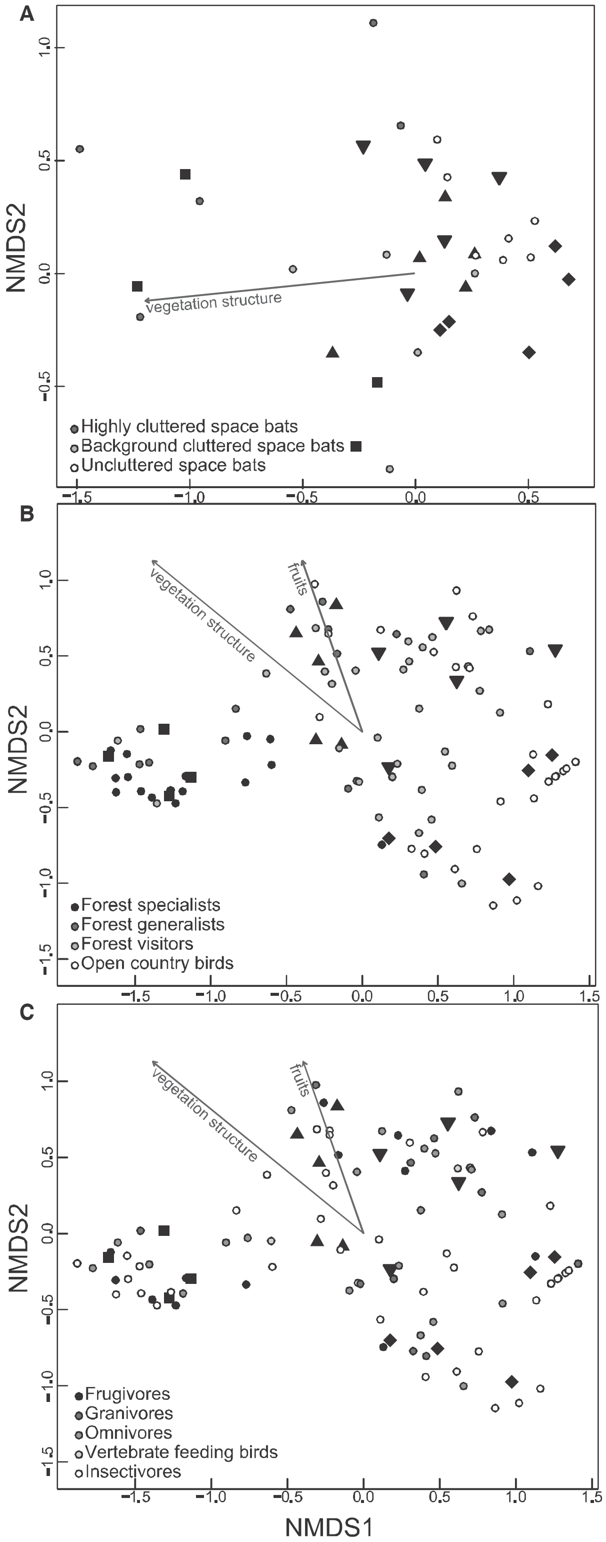

FIGURE 4. Non-metric multidimensional scaling (NMDS) ordination based on Bray-Curtis dissimilarities for the composition of bat habitat guilds (A) and bird habitat (B) or feeding guilds (C) on 19 study sites. Habitat variables (vegetation structure and/or fruits) that were significantly correlated with the NMDS were fitted as vectors onto the ordination. (■) forest, (▲) home garden, (▼) coffee plantation and (◆) grassland.

factors are of paramount interest for a sustainable landscape management.

We hypothesized that both bats and birds should respond negatively to land-use intensification. However, although bats showed highest occurrence and sonotype richness in coffee plantations, bird abundance and species richness did not change across the land-use gradient. These results contrast with a previous study from the Neotropics reporting parallel changes in abundance and richness patterns of bats and birds along a land-use gradient from forest, cacao and banana agroforestry systems to plantain monocultures (Harvey & Gonzâlez Villalobos 2007).

In our study, food resource availability turned out to be the most important predictor for occurrence of insectivorous bats as well as for overall bird abundance. Thus, we confirm other studies demonstrating the high importance of food availability both for insectivorous bats (Rautenbach *et al.* 1996, Meyer *et al.* 2004) and for birds (Mulwa *et al.* 2012b). Many long-distance flying insectivorous bat species are able to respond positively to high local insect availability (Norberg & Rayner 1987), which could explain their high abundances and sonotype richness in the coffee plantations that represent a high land-use intensity. In contrast, only few bird species are able to track their food resources across habitat boundaries, while many are rather specialized and therefore more restricted to preferred habitat types (Mulwa *et al.* 2012b, Ferger *et al.* 2013, Neuschulz *et al.* 2013). Hence species richness patterns in birds depend primarily on the intensity of land-use and to a weaker degree on food availability.

Vegetation structure was an important factor explaining general differences in bat sonotype as well as bird species composition, as it was correlated with the distribution of both bat and bird habitat guilds among land-use types. Uncluttered and background cluttered space bat guilds differed slightly. For background cluttered space bats we found higher occurrence and species richness in forests, compared to grasslands, while uncluttered space bats showed a reversed pattern. These differences are consistent with a study from the Neotropics that suggests pronounced differences in activity between background cluttered and uncluttered space bats in different land-use types (Williams-Guillén & Perfecto 2011). Analysis of sonotype composition further demonstrated that bats preferring uncluttered habitats were mostly associated with low degree of vegetation structuring, in contrast to background cluttered space bats that preferred high vegetation structuring.

Forest specialized birds showed a distinct affinity to highly structured natural forest and were almost absent from the grassland sites, indicating a high sensitivity to land-use intensification (Neuschulz *et al.* 2013). In contrast, open country birds were almost absent from forest plots. These results are consistent with the different occurrence of bird habitat guilds in different land-use types in Kenya (Farwig *et al.* 2008, Mulwa *et al.* 2012a). Such differences may be caused by different degrees of forest dependence, including also the particular habitat requirements for breeding in bird habitat guilds (Bennun *et al.* 1996).

The weak differences between bat habitat guild responses to land-use patterns in our study are in stark contrast to the strong differences among the bird guilds. More distinct responses to different land-use types in bird than in bat species composition was found also in the Neotropics (Harvey & Gonzâlez Villalobos 2007). The strong differences between bats and birds might be caused by the generally higher species richness in birds (Howard & Moore 1991, Simmons 2005) and the resulting higher niche diversification (Bennun *et al.* 1996, Şekercioğlu *et al.* 2004, Kissling *et al.* 2012). Furthermore, insectivorous bats are able to cover long distances during one night (Norberg & Rayner 1987) and may therefore forage in or pass over several land-use types (Estrada-Villegas *et al.* 2010, Jung & Kalko 2011), whereas, especially insectivorous birds are more restricted in their habitat requirements and therefore to their territory (Lloyd & Marsden 2011, Mulwa *et al.* 2012a, Ferger *et al.* 2013).

By bioacoustic monitoring of bats we were only monitoring aerial insectivorous species, accounting for approximately three quarters of all bat species. When focussing correspondingly also on the insectivorous bird species only, we find no significant differences in species abundance or richness across the land-use types. It is not possible to monitor in the same way gleaning animalivorous bats, *i.e.*, species collecting their prey from plant or other surfaces, respectively, as echolocation calls of these are extremely weak (Schnitzler & Kalko 2001). Bat and bird species from these foraging guilds react very sensitive to habitat disturbances (Meyer & Kalko 2008, Lloyd & Marsden 2011) and might have responded rather differently than aerial insectivorous bats. The omnivorous and vertebrate-feeding bird guilds also occurred with similar species numbers throughout all land-use types, indicating that they are also largely unaffected by land-use intensification. In contrast, frugivorous species declined with increasing land-use intensity, granivores increased, consistent to reports from Gray *et al.* (2007) and Waltert *et al.* (2005). We were also not able to monitor frugivorous bats with our acoustic methods, as most Old World fruit bats do not echolocate (Monadjem *et al.* 2010). However, a mist-netting study at Mount Kilimanjaro indicates that frugivorous bat species mostly occur in home garden habitats (Helbig-Bonitz *et al.* 2014) and decline with further land-use intensification, similar to frugivorous birds.

Along the slopes of Mount Kilimanjaro continuous forest areas can only be found close to or within the Kilimanjaro National Park. Consequently, all other land-use types in our study area are found only at lower elevations outside the National Park. However, in order to control for effects of elevation we are including it as a random factor into our statistical analysis and therefore the encountered differences should be just an effect of land-use intensification.

In conclusion, our study provides a first insight into the responses of bats and birds to land-use within a highly endangered and very unique African ecosystem, the lower slopes of Mount Kilimanjaro. Although our results demonstrate strong differences among the responses of different flying vertebrate guilds to land-use intensification, overall bat and bird responses were not consistently negative. Differences among habitat guilds were less pronounced in aerial insectivorous bats than in birds, and therefore results on guild level might not provide conclusive conservation strategies for both taxa. Hence, for this purpose it may be necessary to focus on species-specific responses, in particular in bats. Furthermore, for future studies it will be essential to include also the Old World fruit bats (Chiroptera: Pteropodidae), as these seem to respond differently to land-use intensification than aerial insectivorous bats (Helbig-Bonitz *et al.* 2014).

Nevertheless, our results suggest that a highly structured landscape, such as that found on the slopes of Mount Kilimanjaro, may support high species richness and functional diversity for bats and in particular for birds. Different bat and bird habitat guilds prefer different degrees of vegetation structure. The slopes of Mount Kilimanjaro harbor a habitat mosaic composed of forests, family-based agroforestry systems (home gardens) and grasslands that together form a structurally diverse landscape that supports many bat and bird species. Considering the ongoing human population growth occurring throughout Africa (Cincotta *et al.* 2000), the need for more agricultural areas clearly threatens the remaining natural forest cover. Forest protection as realized by the Kilimanjaro National Park is thus of high importance to maintain sensitive forest specialists, in particular birds.

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SUPPORTING INFORMATION

Additional Supporting Information may be found with online material:

TABLE S1. *Bat sonotype identification parameters.*

TABLE S2. *List of bat sonotypes and occurrence recorded.*

TABLE S3. *List of bird species and abundance counted.*

TABLE S4. *Variables used for vegetation structure index and food resources.*

TABLE S5. *Details about all generalized linear mixed effect models.*

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