Local factors mediate the response of biodiversity to land use on two African mountains

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Abstract

Land-use change is the single biggest driver of biodiversity loss in the tropics. Biodiversity models can be useful tools to inform policymakers and conservationists of the likely response of species to anthropogenic pressures, including land-use change. However, such models generalize biodiversity responses across wide areas and many taxa, potentially missing important characteristics of particular sites or clades. Comparisons of biodiversity models with independently collected field data can help us understand the local factors that mediate broad-scale responses. We collected independent bird occurrence and abundance data along two elevational transects in Mount Kilimanjaro, Tanzania and the Taita Hills, Kenya. We estimated the local response to land use and compared our estimates with modelled local responses based on a large database of many different taxa across Africa. To identify the local factors mediating responses to land use, we compared environmental and species assemblage information between sites in the independent and African-wide datasets. Bird species richness and abundance responses to land use in the independent data followed similar trends as suggested by the African-wide biodiversity model, however the land-use classification was too coarse to capture fully the variability introduced by local agricultural management practices. A comparison of assemblage characteristics showed that the sites on Kilimanjaro and the Taita Hills had higher proportions of forest specialists in croplands compared to the Africa-wide average. Local human population density, forest cover and vegetation greenness also differed significantly between the independent and Africa-wide datasets. Biodiversity models including those variables performed better, particularly in croplands, but still could not accurately predict the magnitude of local species responses to most land uses, probably because local features of the land management are still missed. Overall, our study demonstrates that local factors mediate biodiversity responses to land use and cautions against applying biodiversity models to local contexts without prior knowledge of which factors are locally relevant.

Introduction

Humanity drives global biodiversity decline in many different ways (Butchart *et al.*, 2010). Among the different pressures, anthropogenic land-use change has been shown to have the most severe impact on terrestrial biodiversity (Foley *et al.*, 2005; Jetz, Wilcove & Dobson, 2007; Gibson *et al.*, 2011). A change in land use might greatly reduce the amount or quality of habitat available to species, or contribute to landscape fragmentation resulting in declining species abundance and/or local extinctions (Brooks *et al.*, 2002). Therefore, it is of particular interest to understand how

assemblages of species respond to land use, and if they can persist in human-modified landscapes (Gardner *et al.*, 2007). Statistical biodiversity models are increasingly applied over broad extents to predict the response of species assemblages to land use (Loh *et al.*, 2005; Scholes & Biggs, 2005; Alkemade *et al.*, 2009; Newbold *et al.*, 2014*a*, 2015). Such models can be based on data from many different taxonomic groups, and can inform policymakers about biodiversity trends and influence ongoing international debates about relevant mitigation schemes (Pereira *et al.*, 2010; CBD 2014; Leadley *et al.*, 2014). However, in generalizing across a wide area, such models likely miss local factors that mediate species' response to land use.

Most biodiversity models employ a coarse land-use classification scheme (e.g. Scholes & Biggs, 2005; Alkemade *et al.*, 2009; Newbold *et al.*, 2014*a*, 2015) that cannot capture the full variability of local land-use systems, often missing important land-use categories such as agroforestry (Scholes & Biggs, 2005; Newbold *et al.*, 2015). Others ignore the differential responses of taxonomic groups (Alkemade *et al.*, 2009), which can be important (e.g. Gibson *et al.*, 2011; Murphy & Romanuk, 2014; Newbold *et al.*, 2014*a*). Some biodiversity models of local species richness and abundance have found environmental variables such as land-use intensity, human population density and metrics derived from vegetation greenness data to be influential (Newbold *et al.*, 2014*a*; De Palma *et al.*, 2015). It is however unclear if the inclusion of these variables is relevant in understanding how the local environment mediates biodiversity responses to land use. Similarly it has been shown that functional characteristics can help explain species' varying responses to land use on a broad scale (Owens & Bennett, 2000; Flynn *et al.*, 2009; Newbold *et al.*, 2013; De Palma *et al.*, 2015), but to our knowledge no previous studies have evaluated whether those responses are consistent in a local context. Comparing estimates derived from biodiversity models with local independent data, where the detailed environmental conditions are known and taken into account, could help to identify some of the important local factors that mediate biodiversity responses to land use and ultimately provide insight on how to improve the applicability of biodiversity models.

Addressing the question of how biodiversity responds to land use is especially important in sub-Saharan Africa, where the congruent and patchy distribution of both biodiversity and human population leads to a high risk of biodiversity loss (Balmford *et al.*, 2001; Burgess *et al.*, 2007*a*; Pfeifer *et al.*, 2012). In this study, we investigated biodiversity responses to land use in two study areas in east Africa each with different geological, evolutionary and land-use history. We explicitly test if (1) the response of avian diversity to land use is different in those study areas compared to a taxonomically and geographically broad Africa-wide model of local biodiversity responses to land use, (2) investigate potential explanations for any mismatches using remote-sensed data and information on species' ecological characteristics and threat status, to identify the local factors that mediate the local response of biodiversity to land use and (3)

make recommendations for additional factors to be included in biodiversity models and sampling choices for biodiversity surveys.

Materials and methods

Assemblage composition data

To generate African-wide estimates of how local species richness and abundance respond to land use, we used the database of the Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) project (Hudson *et al.*, 2014; www.predicts.org.uk). While these data cover a broad extent, each individual sampling location covered only a small scale (of comparable grain-size to our independent data – see below). We used only the data sources for Africa (extracted 28 July 2014, see Table S1) with land use in each site classified as primary vegetation (1285 sites), secondary vegetation (485), plantation forest (441), cropland (612) and urban (33) habitat (see Hudson *et al.*, 2014 for definitions). Note that 'urban' land use referred to all areas of human settlement, including rural villages. Additionally, we also used the information on land-use intensity according to the classification developed by the PREDICTS Project, which combines information on management intensity and proportion of each site impacted (Table S2; Hudson *et al.*, 2014). This classification was used so that different land uses could be compared across the different studies, both in the African-wide dataset and the independent field data, and necessarily means that some of the variability in land-use systems is omitted.

We collected independent field data for birds (herein called 'independent data') along two transects on the southern slopes of Mount Kilimanjaro, Tanzania and the Taita Hills, Kenya (Fig. 1). Both landscapes are known for their long history of human modification (Conte, 2010; Heckmann *et al.*, 2014), while having a contrasting geological age (~30 Myr for Taita compared to ~2 Myr for Kilimanjaro, see Platts *et al.*, 2011), and each has different sets of endemic species (Hemp, 2006*a*; Burgess *et al.*, 2007*b*). Data on bird species richness and abundance were collected visually and audibly using standardized 10-min fixed time point counts (Bibby *et al.*, 2000), of 50-m radius, along each of the transects. While more accurate estimates of biodiversity can be obtained by taking into account detection probability (Buckland, Marsden & Green, 2008), our sampling methodology was chosen to match the sampling scheme of bird studies in the PREDICTS database. Because detectability is likely to be higher in more open habitats, which are often those with higher human land-use activity, our estimates of the effects of human land use on biodiversity (from both the African-wide and independent datasets) are likely to be conservative. Point counts ($N = 147$) were located along the two transects to represent the land uses in the African-wide dataset, and were visited twice between March and May 2014. Sites were spread across a wide elevational range in both transects (836–2142 m on Taita and 715–1735 m on Kilimanjaro). Some land-use types could only be sampled in particular

elevational ranges. For example, primary vegetation only occurs in high elevations on both transects (Figs. 1, S4d). Our survey captured local diversity with total sampling effort comparable to similar studies in the African-wide dataset [24 h on Kilimanjaro and 25 h on Taita Hills, compared with an average of 35.15 ± 15.92 (SD) sampling hours in the African-wide dataset]. Seasonal changes in the abundance of certain bird species might introduce bias into our field study; however, a resurvey of some of the sites in the Taita Hills in a different climatic season showed similar responses of avian diversity to land use (Norfolk *et al.*, in press). Species identity was determined following commonly used visual taxonomic guides and assisted by audio recordings from freely available bird-sound databases (Stevenson & Fanshawe, 2004; http://www.xeno-canto.org). In total, 172 different bird species were observed at 147 locations in the two study transects. All sites were classified into the same land uses and land-use intensity as in the African-wide dataset: primary vegetation (39 sites), secondary vegetation (31), plantation forest (27), cropland (69) and urban (14) habitat; and within these land uses, minimal, light and intense use intensity. In the analyses, we treated the Kilimanjaro (74 sites) and Taita Hills (73 sites) transects as independent field studies owing to their distance from each other (~100 km) and different geological and evolutionary history.

## Environmental and assemblage structure data

We tested whether site-specific variation in land-use intensity, human population density, forest cover and metrics describing vegetation greenness and vegetation removal mediate local responses to land use in the independent data compared with the African-wide model estimates. We focussed on those variables because previous biodiversity models have highlighted their importance for biodiversity (e.g. Newbold *et al.*, 2014a) and because they are readily available. We extracted forest cover in the year 2000 (the most recent year for which percent forest cover estimates are available at a fine scale) from recently published remote-sensing data at 30-m resolution (Hansen *et al.*, 2013). For vegetation greenness and vegetation removal measures, we extracted data from the moderate resolution imaging spectroradiometer (MODIS) MOD13Q1 product [the normalized difference vegetation index (NDVI)] at 250-m resolution. Vegetation removal was estimated by calculating the area under the curve of a linear interpolation of NDVI over the 3 years prior to and including the year of the study following a method first suggested by Tucker *et al.* (1981), and adjusted for differences in climate seasonality (Newbold *et al.*, 2014a). Mean NDVI over the same time span was used as a measure of average vegetation greenness, to represent continuous gradients of vegetation density not captured by the forest cover dataset. We chose NDVI as our vegetation indicator (rather than, for example, the Enhanced Vegetation Index) for comparability with previous models (Newbold *et al.*, 2014a). For human population, we used Africa-wide high-resolution (100-m)

population density (people per km²) estimates for the year 2010 (adjusted to match UN national estimates) from the www.worldpop.org.uk datasets (Linard *et al.*, 2012). Finally, we included local estimates of elevation from the Shuttle Radar Topography Mission at 90-m resolution (Jarvis *et al.*, 2008).

We investigated the range of species' characteristics within assemblages in both the Africa-wide dataset and the independent sites, because these characteristics can influence responses to land use (Owens & Bennett, 2000; Flynn *et al.*, 2009; Newbold *et al.*, 2013; De Palma *et al.*, 2015) and thus might mediate the effect of land use on biodiversity locally. Due to the limited coverage and biased data on non-vertebrate species in publicly available databases, we limited this comparison to avian species in both datasets. The analysis was further restricted to records in the assemblage data that were determined to species level (98.4% of records), and matched to scientific names in the catalogue of life (http://catalogueoflife.org/, see Hudson *et al.*, 2014). In this analysis, we focus on ecological rather than morphological characteristics as for many of the African bird species in our analysis morphological traits are still unavailable. We calculated assemblages' average geographic range size, habitat specialization and threat status defined by the International Union for Conservation of Nature (IUCN). To estimate range size, we calculated the log-transformed total area of bird species' extent of occurrence range maps (Birdlife International, 2015), after first converting the range map to a 1° grid and restricting it to the continent of Africa. Range sizes were log-transformed after visual exploration of the data revealed a strong right-skew of range sizes. The current IUCN threat status for each species was obtained using an automatic query of the IUCN web-api (http://api.iucnredlist.org/; accessed 05 November 2014). We grouped all species with threat categories CR (critically endangered), EN (endangered) and VU (vulnerable) as threatened species, and species currently assessed as NT (near threatened) and LC (least concern) as non-threatened; species classified as NE (not evaluated) or DD (data deficient) were not included further in the analysis. IUCN threat was included owing to its high relevance to policy and decision makers. Finally, we downloaded information on species' habitat preferences from IUCN to assess the percentage of individuals in assemblages that are forest specialists, defined as those species for which any kind of forest habitat is considered to be of major importance. For each site, we calculated, for all occurring bird species: (1) the average log-transformed range size and the proportion of (2) forest specialist species and (3) threatened bird species.

Data analysis

For each site and dataset, we calculated two biodiversity metrics: species richness as the number of uniquely observed taxa and total species abundance as the sum of the abundances of all taxa (corrected where there was varying sampling effort within the published studies, Newbold *et al.*, 2014a). We first modelled the average impact of land use with the African-wide dataset, using generalized linear mixed
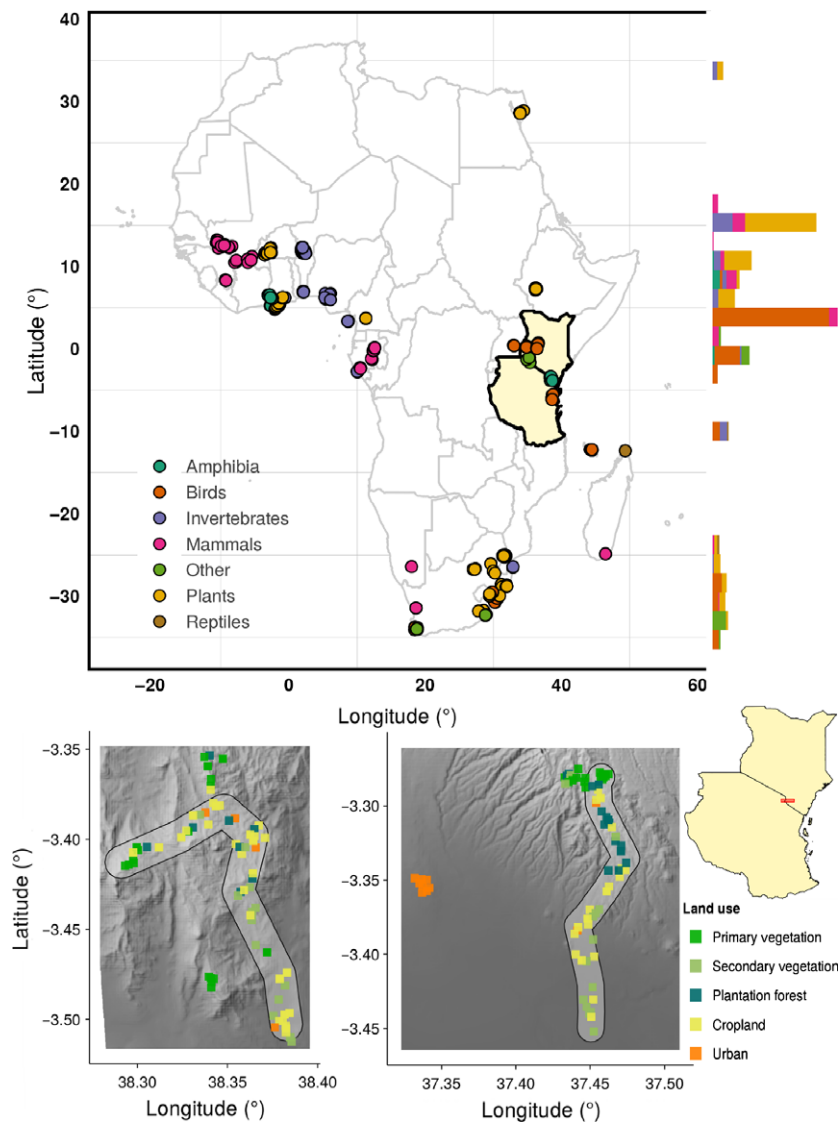
Figure 1 Distribution of studies across Africa coloured by taxonomic group. Bars show the number of sites per latitude coloured by taxonomic group. Highlighted countries indicate the location of the independent field study transects, which consisted of sampling sites along two transects near Mount Kilimanjaro (left) and the Taita Hills (right). All sites are coloured by land use. The background to the panels showing the field transects is a hillshade model derived from Shuttle Radar Topography Mission 90 m indicating the topographic relief of the sites.

effects models (GLMMs: Bolker *et al.*, 2009), with a Gaussian distribution of errors for log-transformed abundance values and a Poisson distribution for species richness. The use of GLMMs was necessary to account for differences among studies (e.g. differences in sampling methods, sampling effort and taxonomic group sampled). These differences were accounted for by including the study identity as a random intercept. We tested if inclusion of taxonomic grouping as a random intercept improved the model [lower Akaike's information criterion (AIC)], it did not. We also tested whether two other random terms improved model fit: (1) any spatial block of sampled sites, such as point counts along transects, and (2) land use as a random slope nested within study. For

both models, the best random effects structure (lowest AIC) contained a random slope of land use nested within study, and a random intercept for study identity. Initial models were constructed using the recorded land-use category as a single explanatory variable. Average species richness and total abundance in different land uses in the independent data were then compared with the coefficients of the land-use-only biodiversity model, with correspondence assessed using Z statistics (Cohen *et al.*, 2013), defined as $Z = \frac{b_{\text{independent}} - b_{\text{broad-scale}}}{\sqrt{\text{SE}b^2_{\text{independent}} + \text{SE}b^2_{\text{broad-scale}}}}$, where b equals the slope of the modelled effect and $\text{SE}b$ its standard error. A z score is a standardized measurement that quantifies the offset of one

value from a normally distributed mean with values smaller than 1.96 generally indicating non-significant deviations (Cohen *et al.*, 2013). Because of study-level methodological differences we could only calculate relative biodiversity values. We used primary vegetation as a baseline for both datasets and calculated the percentage difference in each other land-use category. Some of the differences between the African-wide model and independent data might be because the independent data focused only on birds. To assess the extent to which this was the case, we also developed an African-wide model with the same structure but only containing bird data from the African-wide dataset (1090 sites).

To test whether the addition of more environmental information than just land use could improve the correspondence between the independent data and the African-wide biodiversity model, we developed a second set of GLMMs of species richness and total abundance using the African-wide dataset. In these models we again fitted land use, but this time also land-use intensity (including in interaction with land use) and all continuous environmental variables (see above). We subjected this model to a model-selection process, by fitting models with all possible additive combinations of explanatory variables and selecting the model with the lowest AIC value. The goodness of fit (AIC and R^2, assessed against the model-training data) of the new model and the land-use-only model were compared, and we assessed the importance of the included covariates by summing the AIC weights of all models containing each variable (Burnham & Anderson, 2002). To assess the change in correspondence with the independent data both the best-performing model and a land-use-only model were used to predict abundance and species richness at the independent field study sites, using the environmental variables.

We tested the residuals of both the land-use-only and the overall best-fitting model for spatial autocorrelation using a Moran's *I* test. None of the individual studies showed significant autocorrelation within our models (Fig. S2). All analyses were performed in R (ver. 3.2.2, R Core Team, 2015) mainly using lme4 (ver. 1.10, Bolker *et al.*, 2009; Bates *et al.*, 2014) for model fitting, AICcmodavg for model selection (ver. 2.0.3, Mazerolle, 2015), spdep for spatial autocorrelation tests (ver. 0.5-88, Bivand & Piras, 2015) and MODISTools (ver. 0.94.6, Tuck *et al.*, 2014) for obtaining NDVI data.

Results

Responses to land use of both biodiversity metrics were largely consistent between the modelled African-wide estimates and the independent data, although there were large discrepancies for some land uses (Fig. 2; log-abundance: median absolute $Z = 0.991$, range = 0.06–5.76; species richness: median absolute $Z = 0.728$, range = 0.037–2.877). The biggest discrepancy between the independent data and the African-wide biodiversity model was for cropland sites: the independent sites (especially in the Taita Hills transect) had much higher total abundance and species richness than predicted from the Africa-wide dataset (Fig. 2). This discrepancy became smaller for abundance if the African-wide model was based only on bird data, but this was not the case for the species richness model (Fig. S3). There was large uncertainty around the means, especially in the African-wide dataset, reflecting a wide range of responses among different studies (Fig. S1).

There were considerable differences in local environmental conditions between the Africa-wide and independent field
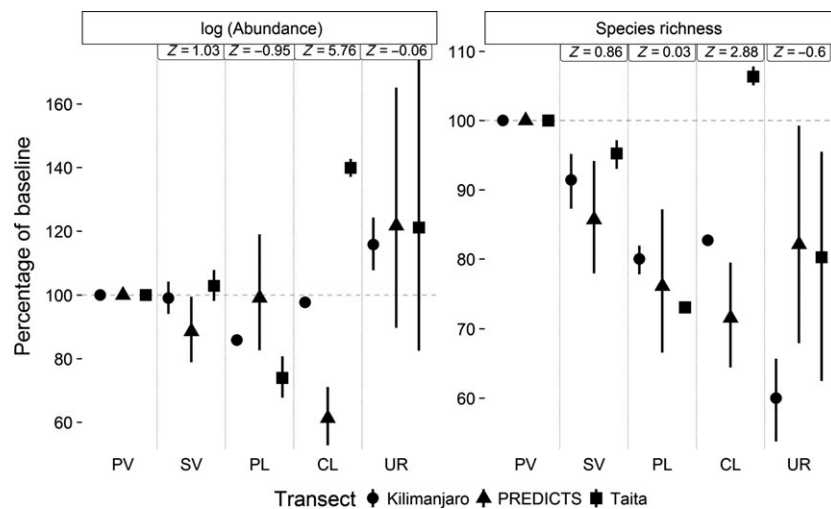
Figure 2 The response of species richness and total abundance to land use, from the Africa-wide model and the independent field data. Land-use categories are primary vegetation (PV), secondary vegetation (SV), plantation forest (PL), cropland (CL) and urban (UR). All coefficients are visualized as proportional difference to primary vegetation (PV), which was set at a baseline of 100%. Error bars show one standard error. Labels on top show the *Z* statistic, which quantifies the distance between the independent data and the African-wide modelled estimates, taking into account the uncertainty in both cases. *Z* statistics further from zero indicate greater mismatch.

datasets (Fig. 3). Mean vegetation greenness (NDVI) of independent sites in primary vegetation, secondary vegetation and plantation forest were lower than the average African site, whereas the opposite was true for cropland and urban sites in the Taita Hills. Forest cover was higher in primary vegetation and cropland at sites on both independent transects. Independent sites had a higher human population density than the average African sites in all land-use categories, especially urban sites, which had up to 2.5–4 times higher density than the African-wide average (Fig. 3).

The full model based on the African-wide dataset, and including all environmental variables as explanatory variables, showed a better fit to the data for both total abundance (ΔAIC = 1591.91, Δr^2_{GLMM} = 0.08, Table 1) and species richness (ΔAIC = 4562.48, Δr^2_{GLMM} = 0.02, Table 1). However, these models still only explained a low proportion of the observed variation in total abundance (marginal r^2_{GLMM} = 0.09) and species richness (r^2_{GLMM} = 0.03). Across all candidate models, land use, land-use intensity, their interaction and vegetation removal were of the greatest relative importance for explaining abundance and species richness (for each of these variables, summed AIC weights, $\sum$AIC$_w$ ≈ 1). Human population density was of high importance for species richness ($\sum$AIC$_w$ ≈ 1), but less important for abundance ($\sum$AIC$_w$ = 0.589). Mean vegetation greenness of the 3 years before the sampling was more important for abundance ($\sum$AIC$_w$ = 0.944) than for species richness ($\sum$AIC$_w$ = 0.506). Elevation was not selected among the explanatory variables in the best model, and was of lower importance for both species richness ($\sum$AIC$_w$ = 0.270) and abundance ($\sum$AIC$_w$ = 0.316). Furthermore, elevation did not show a significant correlation with species richness ($P > 0.05$) at the independent field sites. However, the abundance of bird species in the Taita Hills decreased significantly with increasing elevation ($P < 0.001$, Fig. S4b). We found the difference between model-predicted values and

observed values in the independent data to be quite mixed depending on the model used, the biodiversity metric considered and the land use in question (Fig. 4). For abundance the land-use-only model (average absolute difference = 19.81%) performed slightly worse in predicting relative abundance compared to the best-selected model (average absolute difference = 18.83%), while for species richness the land-use-only model predictions were closer to the observed (average absolute difference = 15.47%) than those from the best-selected model (average absolute difference = 27.44%). A notable exception was cropland, for which the predictions made by the full model with all environmental factors were substantially better than those made by the land-use only model (Fig. 4).

Bird species at our independent sites were on average more wide-ranged species compared to bird species at sites in the African-wide dataset (Fig. 5), with the exception of primary forests in the Taita Hills, where significantly more narrow-ranged species were found. Sites in the independent dataset had similar or lower proportions of forest specialist species than the sites in the African-wide dataset, with the exception of primary vegetation and cropland in the Taita Hills where the proportion of forest specialist birds was higher (Fig. 5). Our independent sites had similar proportions of threatened bird species as the average site in the African-wide dataset, but higher proportions in primary vegetation in the Taita Hills study area (Fig. 5).

Discussion

Our results show that independently observed local biodiversity responses to land use are mostly consistent with an African-wide model estimates. While species richness consistently declines with increasing levels of human land use in most cases (Fig. 2), the total abundance stays fairly stable. However, the African-wide model showed that
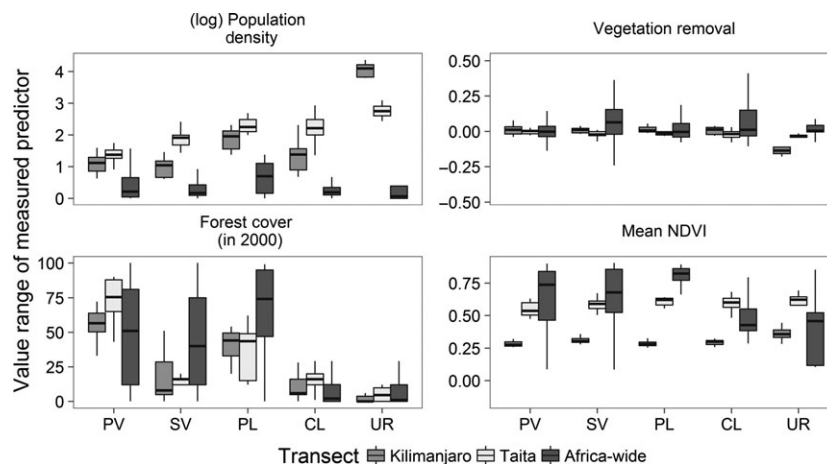
Figure 3 Difference in environmental variables in different land uses, between the Africa-wide and the independent field data ('Kilimanjaro' and 'Taita'). Boxes show the inter-quartile range, while lines show the full range of the data (or 1.5 times the upper and lower quartiles if less extreme). Abbreviations as in Fig. 2.
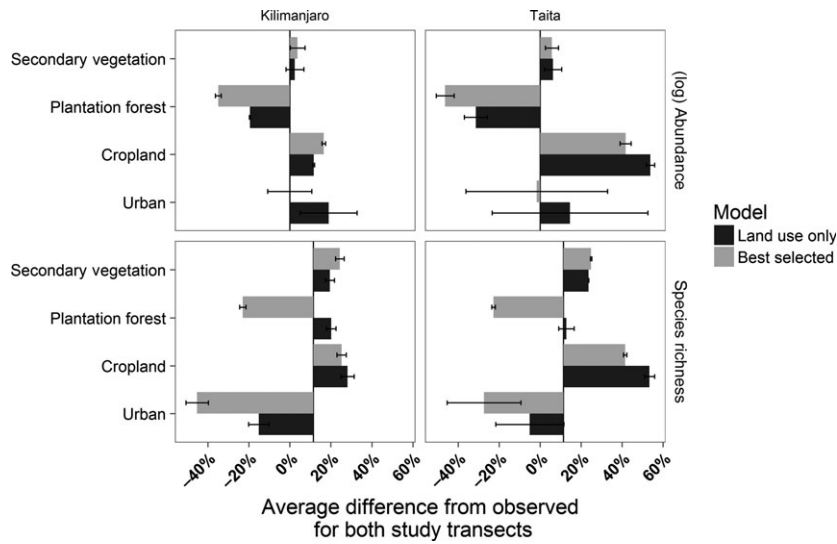
Figure 4 Difference between the relative observed biodiversity values at the field sites, and predicted biodiversity values from the best-selected model and a land-use-only model (see Table 1). Predicted values were obtained by applying the models to the estimated environmental covariates at the field study sites. The predicted model estimates were subtracted from the observed field values. Thus, positive values indicate a model predicting lower biodiversity than was observed with overall smaller bars indicating better fit to the observed. Primary vegetation was used as the baseline and abbreviations are as in Fig. 2.

Table 1 Best-fit model from among those using all possible combinations of explanatory variables for the African-wide dataset

Response	Model terms	Model	K	AIC	ΔAIC	LogLik	d.f. (resid.)	R^2 (marginal)	R^2 (conditional)
Log-abundance									
Best-performing model	Land use × Land-use intensity + Log(population density) + Vegetation removal + Mean vegetation greenness	Log-abundance	34	3844.27	0	−1888.13	1515	0.088	0.876
Land use only	Land use		22	5436.18	1591.91	−2696.09	2224	0.009	0.879
Null model	~1		18	5440.37	1596.1	−2702.18			
Species richness									
Best-performing model	Land use × Land-use intensity + Log(population density) + Vegetation removal + Forest cover + Mean vegetation greenness	Species richness	35	10 920.67	0	−5425.34	1984	0.034	0.926
Land use only	Land use		22	15 483.15	4562.48	−7719.58	2834	0.013	0.919
Null model	~1		18	15 484.08	4563.41	−7724.04			

Pseudo-R^2 values were computed following (Nakagawa & Schielzeth, 2013).

responses to land use vary substantially among different studies (Fig. S1); this heterogeneity is especially apparent in urban sites, perhaps because local factors, such as vegetation greenness and proximity to nearby forests, mediate responses. It should be noted, however, that there are only few urban studies in Africa in the database, indicating that there is a need for further research on the effect of urbanization on biodiversity in this continent. We could not detect any influence of elevation on species richness in either of

our independent sites or the African-wide dataset. However, bird abundance decreased with elevation in the Taita Hills, which could be explained by the fact that the low elevation areas receive many nutrients and water, thus increasing resources and diversity of land cover available for many bird species. Similarity of species composition decreased with increasing elevational distance between sites (Fig. S4c), thus indicating a turnover of species assemblages with elevation. Land use has likely added to this effect and might have
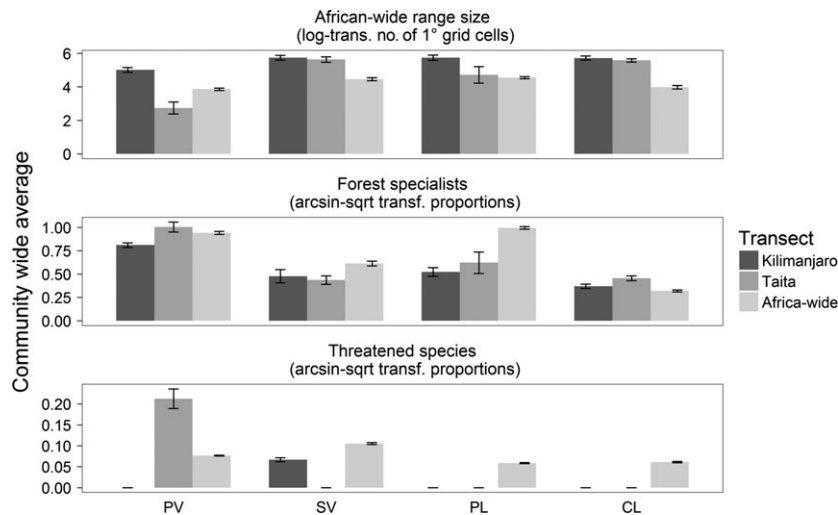
Figure 5 Average assemblage structure in terms of bird species' characteristics, for the Africa-wide and the independent ('Taita' and 'Kilimanjaro') datasets, in different land uses. Range size was measured as the average (log-transformed) extent of occurrence across Africa of all bird species recorded at each site, forest specialism was classified based on the IUCN classification of habitat preference, and threat status was from the IUCN Red List (species classified as critically endangered, endangered or vulnerable were considered to be 'threatened'). For each sites, we calculated the average proportions of species classified as forest specialist or as threatened. Proportions of forest specialist and threatened species was arcsine-square root transformed to better highlight differences. Error bars show the standard error of the mean.

altered the natural elevational gradient in species richness (McCain, 2009). The interaction between elevation and land use, however, could not be tested with confidence as land use in both study transects is not spread equally across elevations (Fig. S4d). In particular, primary vegetation sites are significantly higher in elevation than other land uses (see next section for possible implications of this for the results). The biggest discrepancy between the biodiversity estimates was for cropland: the independent data had higher values of both biodiversity metrics than predicted from the Africa-wide dataset. This might partly reflect the fact that the field survey sampled only birds: bird-only models of the African-wide datasets decreased the mismatch within cropland, at least for abundance (Fig. S3). Previous research has shown that taxonomic groups can show different responses to land use (Lawton *et al.*, 1998; Schulze *et al.*, 2004; Newbold *et al.*, 2014*a*). Birds are highly mobile species, often dependent on various habitats in the surrounding landscape (Haslem & Bennett, 2008) and show seasonal fluctuations of activity. Therefore, our independent field data will reflect neither the whole assemblage present in the study area nor the general effect of land use on biodiversity. The discrepancy emphasizes the need to collect field data for a set of taxonomic groups that are as representative as possible. In addition to real taxonomic differences in responses to land use, it is likely also that surveying of different taxonomic groups is done at different spatial scales, which could also cause apparent differences in responses among taxa (note, however, that a previous study using the same dataset found little effect of sampling scale on relative differences in diversity among land uses; Newbold *et al.*, 2015). On the other hand, the African-wide model omits several aspects of the local

environmental and ecological conditions, which we discuss in the following sections.

Impoverished species pool

One explanation for the difference in biodiversity between cropland sites on the Taita Hills and the average cropland site in the Africa-wide model could be that the primary vegetation in Taita Hills has already suffered more biodiversity loss than the average primary vegetation site in the African-wide dataset. The Taita Hills have a high degree of habitat fragmentation and the lowest overall forest cover in all of the Eastern Arc Mountains (Newmark, 1998; Platts *et al.*, 2011), reflecting the long history of human modification and disturbance in the area (Brooks *et al.*, 1998; Newmark, 1998; Heckmann *et al.*, 2014). Such conditions might have influenced the response of species richness to land use by leaving assemblages that are impoverished and relatively insensitive to further land-use disturbance (Filippi-Codaccioni *et al.*, 2010); the resulting biota might also show different associations between species characteristics and sensitivity than seen in newly impacted regions (Fritz, Bininda-Emonds & Purvis, 2009).

The greater Kilimanjaro area and the Taita Hills have been used by humans for many centuries (Heckmann *et al.*, 2014). Expeditions undertaken by German missionaries visiting Mount Kilimanjaro noted that the land was already extensively used in the 19th century (Börjeson, 2009) and similar evidence suggests that the agricultural terraces of the Taita Hills are centuries old (Conte, 2010). These sources indicate that both landscapes have experienced human influence for many centuries. The loss of natural vegetation

seems to have accelerated in the last century owing to increasing human population density, colonial forestry operations (Brooks *et al.*, 1998; Hemp, 2005; Burgess *et al.*, 2007*b*; Platts *et al.*, 2011) and the ongoing shift from traditional forms of crop cultivation to monoculture farming (Soini, 2005; Hemp, 2006*b*). Biodiversity models would benefit from incorporating estimates of land-use history, but the currently available data (e.g. Klein Goldewijk *et al.*, 2011) are too coarsely resolved to be very useful.

Our study sites had on average a similar proportion of forest-dependent species in primary vegetation, but a smaller proportion in plantation forest sites than in the African-wide dataset (Fig. 5). However, the average number of narrow-ranged and threatened bird species was higher on the Taita Hills compared to sites across Africa, which reflects the high conservation value of large continuous forest in this global biodiversity hot-spot (Burgess *et al.*, 2007*b*), and suggests that not all sensitive species have yet been lost from assemblages at the Taita Hills. It has been suggested that plantation forests could support conservation efforts if appropriately managed (Brockerhoff *et al.*, 2008). However, this does not seem to be the case for our field sites: plantation forests, such as *Eucalyptus*, pine and *Cypress* stands on Taita Hills had lower abundance and species richness than either primary or secondary vegetation (Fig. 2), emphasizing the importance of natural vegetation for local biodiversity conservation (Brooks *et al.*, 1998; Farwig, Sajita & Böhning-Gaese, 2008; Gibson *et al.*, 2011). Overall, our results support evidence (Owens & Bennett, 2000; Flynn *et al.*, 2009; Newbold *et al.*, 2013; De Palma *et al.*, 2015) that accounting for functional characteristics can add precision to African-wide biodiversity models for certain well-studied taxonomic groups.

It is also possible that the species pool appears impoverished because the reference primary vegetation sites were located at high elevations, which are probably less diverse naturally. However, this is unlikely to explain our results entirely for three reasons. First, cropland had relatively high biodiversity even when compared with secondary vegetation, which like cropland was found at lower elevations in our field study areas. Second, other human land uses did not have as high biodiversity as cropland despite also being found at low elevations. Third, the observed mismatch in biodiversity in croplands can be best explained by the occurrence of low-intensity agroforestry systems (known locally as *homegardens*), which were located at higher elevations than more intensively used croplands.

High-diversity cropland

Cropland sites in our independent dataset had relatively high diversity and a possible reason could be the management mode, since the majority of these sites were tropical agroforestry systems known locally as *homegardens*, which occur in mid-high elevational ranges. Tropical homegardens, such as the Chagga homegardens in Kilimanjaro, have many biodiversity-beneficial characteristics of agroforestry systems such as higher indigenous tree density and permanent or semi-permanent cultivation cycles, thus ensuring consistent vegetation cover and provision of valuable microhabitats

(Hemp, 2006*a*; Scales & Marsden, 2008; Jose, 2009). They can thus contribute to the persistence of species in human-modified landscapes (Bhagwat *et al.*, 2008; Kabir & Webb, 2008; Gardner *et al.*, 2009), a conclusion which our study supports. The landscape context and proximity to nearby remaining forest fragments could also have led to an increase in species richness.

We show that the cropland sites in our independent dataset have slightly higher forest cover and mean vegetation greenness than the typical cropland site in Africa (Fig. 3). These environmental factors might help explain the discrepancies in estimated avian diversity, and led to better predictions of bird diversity in croplands when included in the models (Fig. 4). We suggest that more research on broad-scale environmental variables that are locally relevant is needed to improve models of biodiversity responses to land use. In addition to differences in environmental variables, along both independent study transects, cropland sites were composed of slightly more forest-dependent species than the average cropland site in Africa, showing that the local environmental features of cropland are associated with retention of at least some forest species. We suggest that agricultural management practices and land-use dynamics are important factors to consider in biodiversity models, either by considering the intensity of human land use (Newbold *et al.*, 2015), explicitly recognizing agroforestry as distinct land-use type (Alkemade *et al.*, 2009), or by including remote-sensed information on vegetation greenness or tree cover in cropland (Pettorelli *et al.*, 2005; Hansen *et al.*, 2013; Newbold *et al.*, 2014*a*).

Conclusion

We identified important local factors that mediate biodiversity's response to land use. Biodiversity models might be inaccurate if used to predict land-use impacts on biodiversity at local scales if local conditions do not conform to the average conditions seen in the African-wide dataset. This highlights the importance of local surveys that identify the local conditions and influencing variables before applying generalized biodiversity models in a local context. On the other hand, field datasets need to consider a wide, representative set of taxa in order to be representative of biodiversity's response to land use. The inclusion of local land management information, vegetation data from remote sensing and species characteristics information can make biodiversity models more applicable to local settings. However, more research is needed to identify which variables are locally relevant.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Figure S1. For the broad-scale dataset (black points) and the field sites (coloured points), the relative species richness and abundance values (compared to primary vegetation as a baseline) of all land uses for each individual study.

Figure S2. Tests for spatial autocorrelation within the model residuals, showing the distribution of *P*-values from sets of Moran's tests on the residuals associated with each individual study.

Figure S3. The response of species richness and total abundance to land use, from the Africa-wide model (open symbols) and the independent field data for cropland (closed symbols).

Figure S4. Effect of elevation (in m) on species richness, log-abundance and species composition for our independent field sites at Taita and Kilimanjaro.

Table S1. Full list and description of studies in the broad-scale dataset.

Table S2. The Projecting Responses of Ecological Diversity In Changing Terrestrial Systems (PREDICTS) project (Hudson *et al.*, 2014, www.predicts.org.uk) land use and land-use intensity matrix to which all study sites have been classified.

Table S3. Full model selection table for (log-transformed) abundance.

Table S4. Full model selection table for species richness.