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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 policy-makers 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 data sets.

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

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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.

Keywords:

Biodiversity model; Birds; Eastern Arc Mountains; Homegardens; Kilimanjaro; PREDICTS; Taita Hills;

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 et al. 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 a human-modified landscape (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 and Biggs 2005; Alkemade et al. 2009; Newbold et al. 2014a; Newbold et al. 2015). Such models can be based on data from many different taxonomic groups, and can inform policy-makers about biodiversity trends and influence ongoing international debates about relevant mitigation schemes (Pereira et al. 2010; Leadley et al. 2014; CBD 2014). However, in generalising 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 (eg. Scholes and Biggs 2005; Alkemade et al. 2009; Newbold et al. 2014a; Newbold et al. 2015) that cannot capture the full variability of local land-use systems, often missing important land-use categories such as agroforestry (Scholes and 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 and Romanuk 2014; Newbold et al. 2014a). 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. 2014a; 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 and 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. 2007a; 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.

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 **P**rojecting **R**esponses of **E**cological **D**iversity **I**n **C**hanging **T**errestrial **S**ystems (**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 28/07/2014, see Table SI 1) 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 (SI Table 2; 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 (Figure 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 mil. years for Taita compared to ~2 mil. years for Kilimanjaro, see Platts et al. 2011), and each has different sets of endemic species (Hemp 2006a; Burgess et al. 2007b). Data on bird species richness and abundance were collected visually and audibly using standardized 10-minute 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 et al. 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 (Figure 1, Figure S4-D). Our survey captured local diversity with total sampling effort comparable to similar studies in the African-wide dataset (24 hours on Kilimanjaro and 25 hours 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 and 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); 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 (~100km) 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 three 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 (SRTM) 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 and 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 IUCN threat status. To estimate range size, we calculated the log-transformed total area of bird species' extent-of-occurrence range maps (Birdlife International 2012), after first converting the range map to a 1° grid and restricting it to the continent of Africa. Range size 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 05/11/2014). 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 unique 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-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 $Z = \frac{b_{independent} - b_{broad-scale}}{\sqrt{SEb^2_{independent} + SEb^2_{broad-scale}}}$, where b equals the slope of the modelled effect and *SEb* 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 a 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 (SI Figure 2). All analyses were performed in R (ver. 3.2.2, R Core Team 2014) 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 and 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 (Figure 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 (Figure 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 (SI Figure 3). There was large uncertainty around the means, especially in the African-wide dataset, reflecting a wide range of responses among different studies (SI Figure 1).

There were considerable differences in local environmental conditions between the Africa-wide and independent field datasets (Figure 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 to 4 times higher density than the African-wide average (Figure 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) and species richness (ΔAIC = 4562.48, Δr^2_{GLMM} = 0.02). 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, $\sum AIC_w \approx 1$). Human population density was of high importance for species richness ($\sum AIC_w \approx 1$), but less important for abundance ($\sum AIC_w$ = 0.589). Mean vegetation greenness of the three 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 ($P < 0.001$, Figure S4-B). 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 (Figure 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 (Figure 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 (Figure 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 (Figure 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 (Figure 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 (Figure 2), the total abundance stays fairly stable. However, the African-wide model showed that responses to land use vary substantially among different studies (Figure 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 (Figure S4-C), thus indicating a turnover of species assemblages with elevation. Land use has likely added to this effect and might have 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 (Figure S4-D). 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 (SI Figure 3). 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. 2014a). Birds are highly mobile species, often dependent on various habitats in the surrounding landscape (Haslem and 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 (Newmark 1998; Brooks et al. 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 et al. 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. 2007b; Platts et al. 2011) and the ongoing shift from traditional forms of crop cultivation to monoculture farming (Soini 2005; Hemp 2006b). 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 (Figure 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 hotspot (Burgess et al. 2007b), 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 (Figure 2), emphasizing the importance of natural vegetation for local biodiversity conservation (Brooks et al. 1998; Farwig et al. 2008; Gibson et al. 2011). Overall, our results support evidence (Owens and 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 didn't 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 on 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 2006a; Scales and Marsden 2008; Jose 2009). They can thus contribute to the persistence of species in human-modified landscapes (Bhagwat et al. 2008; Kabir and 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 (Figure 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 (Figure 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 recognising 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. 2014a).

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 data sets 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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Table 1: Best-fit model from among those using all possible combinations of explanatory variables for the African-wide dataset. Pseudo-R² values were computed following (Nakagawa and Schielzeth 2013).

Model terms	**Model**	**K**	**AIC**	**Δ AIC**	**LogLik**	**DF (resid)**	**R² (marginal)**	**R² (conditional)**
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		22	5436.18	1591.91	-2696.09	2224	0.009	0.879
~1		18	5440.37	1596.1	-2702.18			
Land use * Land use intensity + log(Population density) + Vegetation removal + Forest cover + mean Vegetation greenness	Species richness	35	10920.67	0	-5425.34	1984	0.034	0.926
Land use		22	15483.15	4562.48	-7719.58	2834	0.013	0.919
~1		18	15484.08	4563.41	-7724.04			

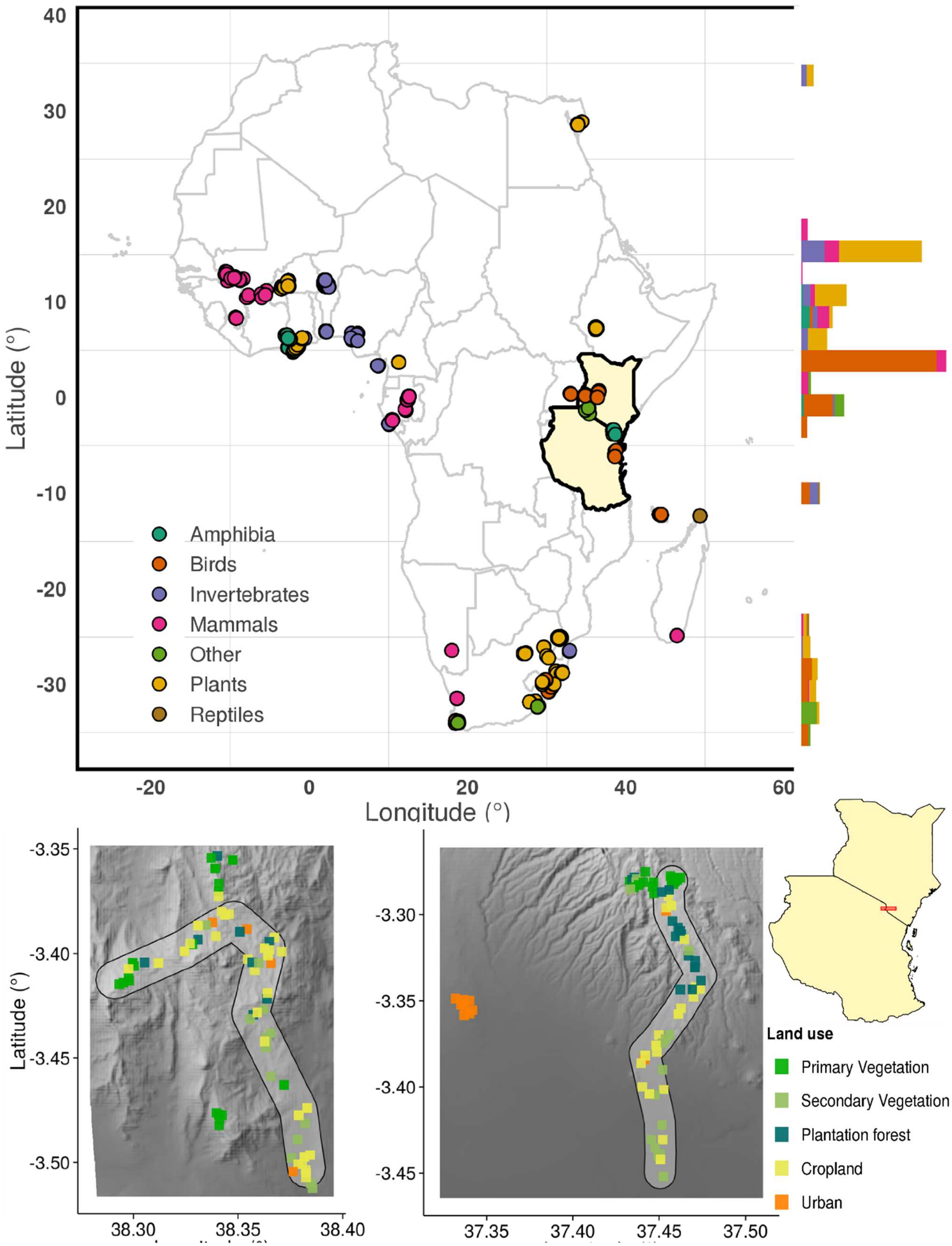

Figure 1: Distribution of studies across Africa coloured by taxonomic group. Bars show the number of sites per latitude coloured by taxonomic group. Highlighted countries indicate the location of the independent field study transects, which consisted of sampling sites along two transects near Mount Kilimanjaro (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 SRTM 90m indicating the topographic relief of the sites.

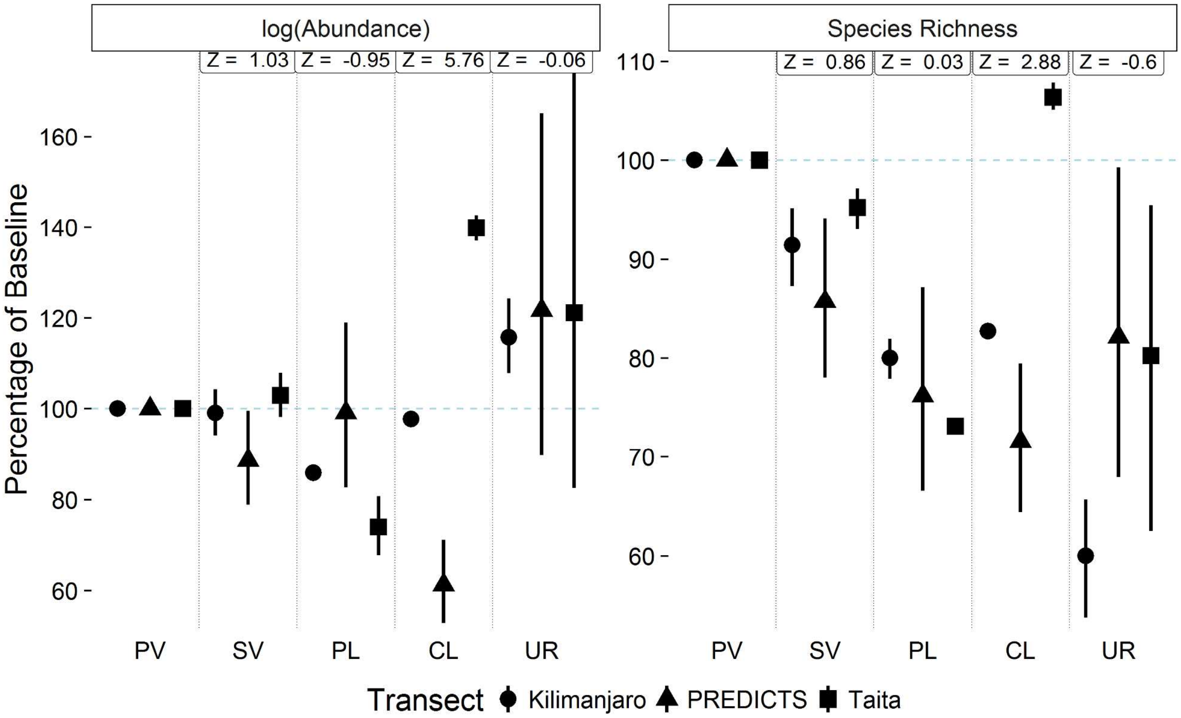

Figure 2: The response of species richness and total abundance to land use, from the Africa-wide model and the independent field data. Land-use categories are primary vegetation (PV), secondary vegetation (SV), plantation forest (PL), cropland (CL) and urban (UR). All coefficients are visualized as proportional 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.

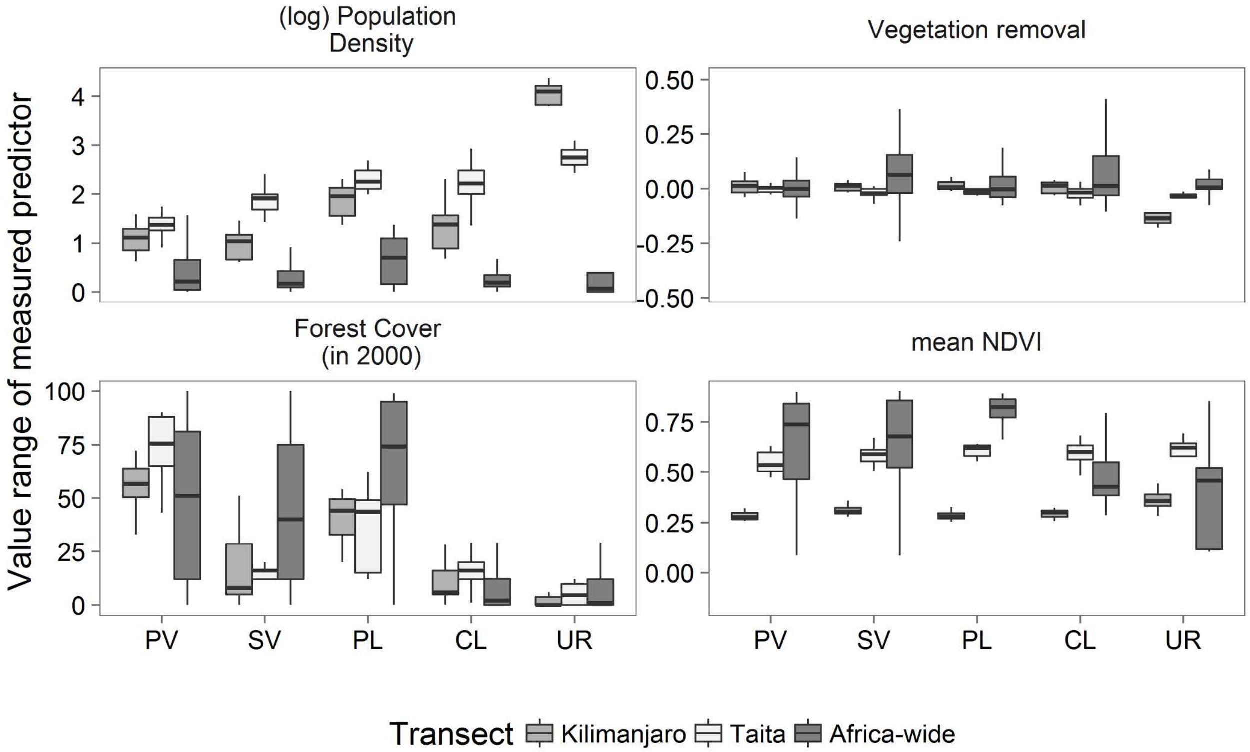

Figure 3: Difference in environmental variables in different land uses, between the Africa-wide and the independent field data ('Kilimanjaro' and 'Taita'). Boxes show the inter-quartile range, while lines show the full range of the data (or 1.5 times the upper and lower quartiles if less extreme). Abbreviations as in Figure 2.

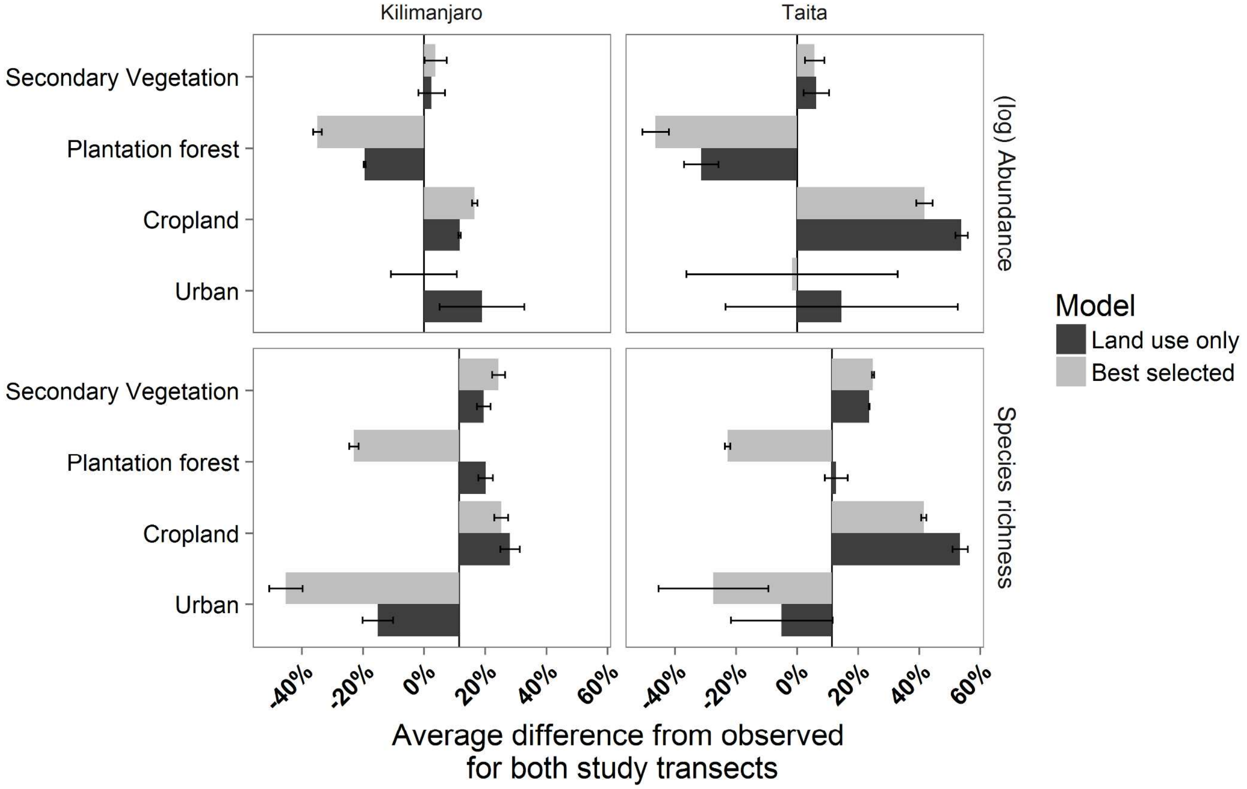

Figure 4: Difference between the relative observed biodiversity values at the field sites, and predicted biodiversity values from the best-selected model and a land-use-only model (see Table 1). Predicted values were obtained by applying the models to the estimated environmental covariates at the field 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 Figure 2.

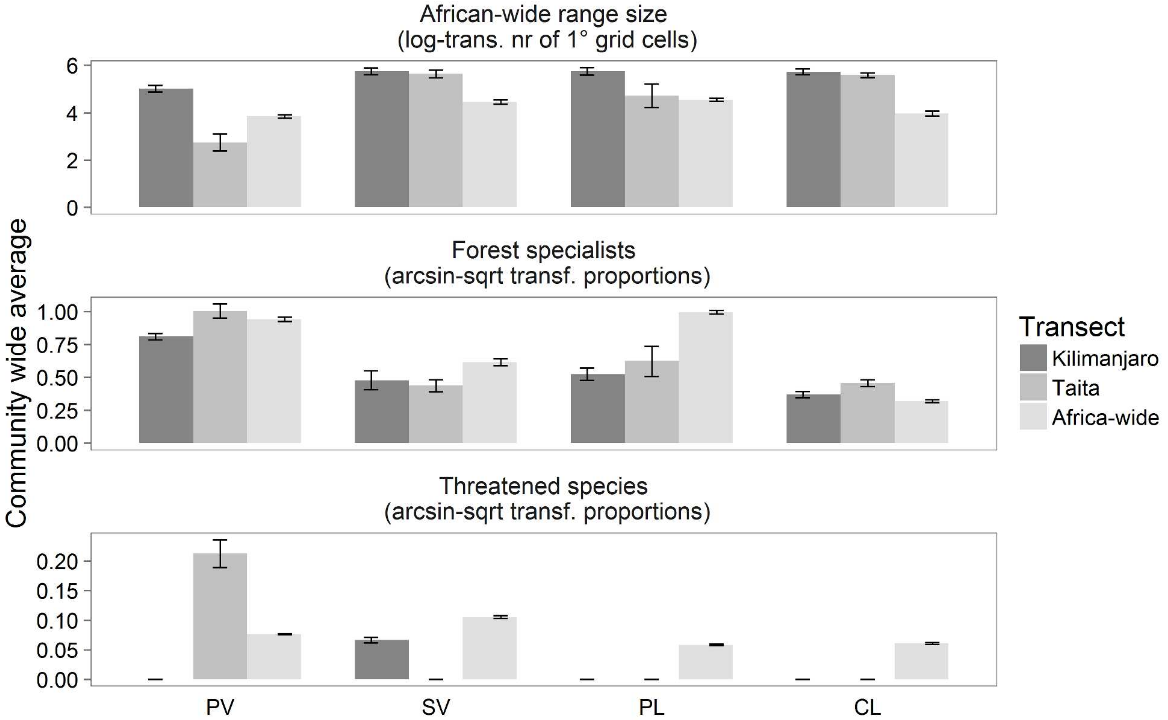

Figure 5: Average assemblage structure in terms of bird species' characteristics, for the Africa-wide and the independent ('Taita' and 'Kilimanjaro') datasets, in different land uses. Range size was measured as the average (log-transformed) extent of occurrence across Africa of all bird species recorded 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 arcsin-squareroot transformed to better highlight differences. Error bars show the standard error of the mean.

Supporting information

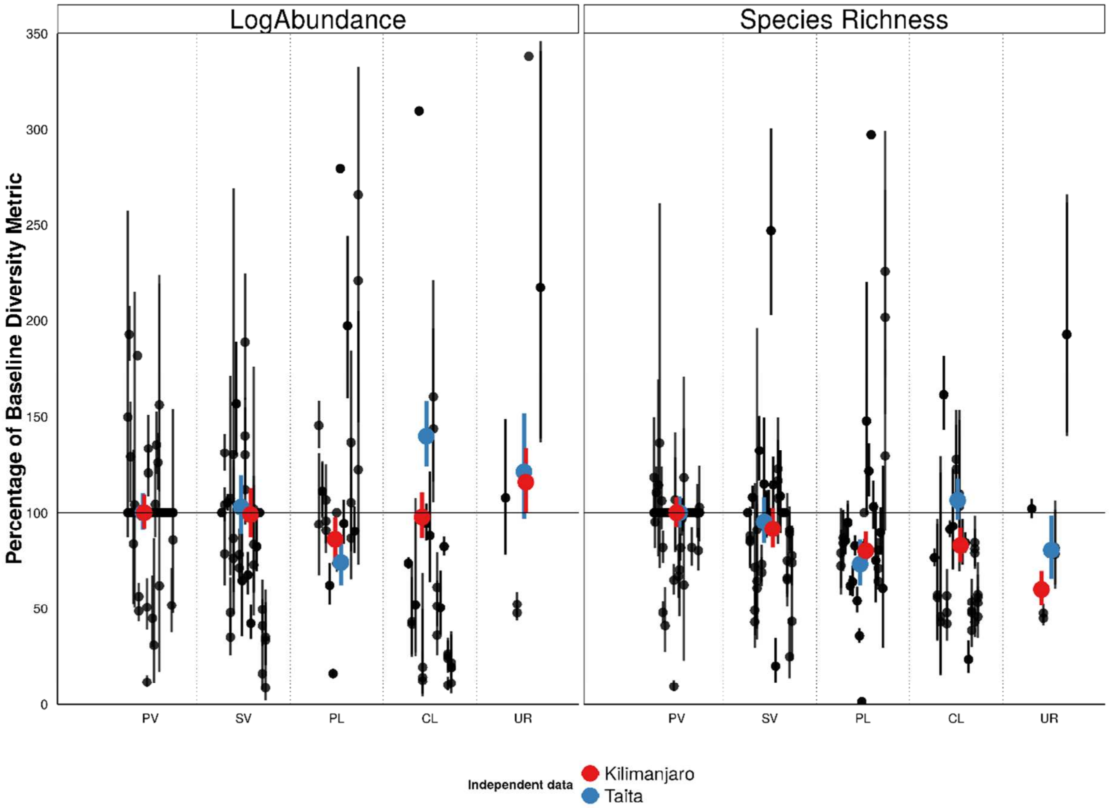

Figure S1: For the broad-scale dataset (black points) and the field sites (coloured points), the relative species richness and abundance values (compared to primary vegetation as a baseline) of all land uses for each individual study. The figure shows that our field-study estimates are always within the range of modelled study-level estimates in the broad-scale dataset. Land-use categories are primary vegetation (PV), secondary vegetation (SV), plantation forest (PL), cropland (CL) and urban (UR).

Table S1: Full list and description of studies in the broad-scale dataset. Studies that looked at multiple taxonomic groups were split into individual studies for the analysis.

First author	Year	Journal title	DOI	NrSites	Land use classes	Taxon	SpeciesRichnes
Naidoo	2004	Animal Conservation	10.1017/S1367943003001185	96	Primary Vegetation,Secondary Vegetation,Cropland	Birds	94
Davis	2005	Environmental Entomology	10.1603/0046-225x(2005)034[1081:eodoas]2.0.co;2	12	Primary Vegetation,Plantation forest	Invertebrates	34
Hoffmann	2005	Belgian Journal of Zoology		2	Secondary Vegetation	Mammals	9
O'Connor	2005	Journal of Applied Ecology	10.1111/j.1365-2664.2005.01065.x	11	Primary Vegetation,Cropland	Plants	220
Scott	2006	Biological Conservation	10.1016/j.biocon.2005.07.014	22	Cropland,Secondary Vegetation,Primary Vegetation	Reptiles,Mammals	17
Lachat	2006	Biodiversity and Conservation	10.1007/s10531-004-1234-6	36	Primary Vegetation,Secondary Vegetation,Plantation forest	Invertebrates	1
Bouyer	2007	Biological Conservation	10.1016/j.biocon.2007.04.001	184	Primary Vegetation,Secondary Vegetation,Cropland	Plants,Invertebrates	67
Basset	2008	Conservation Biology	10.1111/j.1523-1739.2008.01017.x	12	Secondary Vegetation,Urban	Invertebrates	3
Graeme Shannon	2008	Journal of Tropical Ecology	10.1017/S0266467408004951	20	Primary Vegetation	Plants	44
Farwig	2008	Forest Ecology & Management	10.1016/j.foreco.2008.03.042	15	Plantation forest,Primary Vegetation,Secondary Vegetation	Birds	114
Henschel	2008	PhD Thesis		86	Primary Vegetation	Mammals	27
Munyekenye	2008	Ostrich	10.2989/OSTRICH.2008.79.1.4.361	272	Secondary Vegetation,Primary Vegetation,Plantation forest	Birds	129
Oke	2009	African Scientist		5	Primary Vegetation,Plantation forest,Secondary Vegetation	Invertebrates	26
Devineau	2009	Biodiversity and Conservation	10.1007/s10531-008-9574-2	211	Cropland,Primary Vegetation	Plants	329
Hylander	2009	Conservation Biology	10.1111/j.1523-1739.2008.01097.x	167	Plantation forest,Primary Vegetation	Plants	224
Hayward	2009	South African Journal of Wildlife Research	10.3957/056.039.0108	84	Primary Vegetation	Other	48
Lehouck	2009	Oikos	10.1111/j.1600-0706.2009.17300.x	204	Primary Vegetation	Other,Birds	39
Nicolas	2009	Biodiversity and Conservation	10.1007/s10531-008-9572-4	24	Secondary Vegetation,Cropland,Primary Vegetation	Mammals	11
Dures	2010	Biological Conservation	10.1016/j.biocon.2009.12.019	39	Primary Vegetation	Birds	81
Jacobs	2010	Journal of Insect Conservation	10.1007/s10841-010-9270-x	6	Primary Vegetation	Invertebrates	46
Haarmeyer	2010	Biological Conservation	10.1016/j.biocon.2009.11.008	17	Secondary Vegetation	Plants	131

Marsh	2010	Biological Conservation	10.1016/j.biocon.2010.03.010	90	Primary Vegetation,Secondary Vegetation,Plantation forest	Invertebrates,Birds	62
Gaigher	2010	Journal of Insect Conservation	10.1007/s10841-010-9286-2	10	Primary Vegetation,Plantation forest	Other	22
Safian	2011	Journal of Insect Conservation	10.1007/s10841-010-9343-x	7	Primary Vegetation,Secondary Vegetation,Plantation forest	Invertebrates	113
Neuschulz	2011	Oikos	10.1111/j.1600-0706.2011.19097.x	36	Primary Vegetation,Cropland,Secondary Vegetation	Birds	90
Schumann	2011	Biological Conservation	10.1016/j.biocon.2011.06.018	166	Cropland,Primary Vegetation	Plants	1
Phalan	2011	Science	10.1126/science.1208742	32	Primary Vegetation,Plantation forest	Birds,Plants	330
Granjon	2011	Mammalian Biology	10.1016/j.mambio.2011.06.003	119	Primary Vegetation,Urban,Cropland	Mammals	21
D'Cruze	2011	Animal Conservation	10.1111/j.1469-1795.2011.00459.x	9	Primary Vegetation,Secondary Vegetation,Plantation forest	Reptiles	11
Muchane	2012	International Journal of Biodiversity and Conservation	10.5897/ijbc12.030	12	Primary Vegetation,Cropland	Other	3
Siebert	2012	Plant Ecology and Evolution	10.5091/plecevo.2011.501	92	Primary Vegetation,Secondary Vegetation,Plantation forest,Urban,Cropland	Plants	799
Wiafe	2012	Journal Of Ecology and Natural Environment	10.5897/JENE11.144	64	Primary Vegetation	Mammals	4
Malonza	2012	Herpetotropicos		13	Primary Vegetation,Plantation forest	Amphibia	8
Norfolk	2012	Agriculture, Ecosystems and Environment	10.1016/j.agee.2012.08.007	30	Primary Vegetation,Cropland	Invertebrates	20
Ofori-Boateng	2013	Biotropica	10.1111/j.1744-7429.2012.00887.x	6	Primary Vegetation,Secondary Vegetation	Amphibia	16
Oke	2013	African Journal of Ecology	10.1111/aje.12029	5	Secondary Vegetation,Primary Vegetation	Invertebrates	30
Adum	2013	Conservation Biology	10.1111/cobi.12006	48	Primary Vegetation,Plantation forest	Amphibia	24
Nakashima	2013	African Zoology	10.3377/004.048.0212	5	Secondary Vegetation,Primary Vegetation	Mammals	3
Ndang'ang'a	2013	Ostrich	10.2989/00306525.2013.860929	333	Cropland,Secondary Vegetation	Birds	74
Reynolds	2013	African Zoology	10.3377/004.048.0217	56	Secondary Vegetation	Birds	78
Hassan	2013	British Journal of Applied Science & Technology	10.9734/BJAST/2014/2200	32	Primary Vegetation	Birds	90
CIFOR	2013	www.cifor.org/mla		100	Plantation forest,Secondary Vegetation,Cropland	Plants	500
Norfolk	2013	Basic and Applied Ecology	10.1016/j.baae.2013.10.004	36	Primary Vegetation,Plantation forest,Urban	Plants	84
Bösing	2014	Journal of Arid Environments	10.1016/j.jaridenv.2014.02.011	6	Primary Vegetation	Mammals	11
Wronski	2014	Journal of Molluscan Studies	10.1093/mollus/eyu008	37	Primary Vegetation,Secondary Vegetation	Invertebrates	55

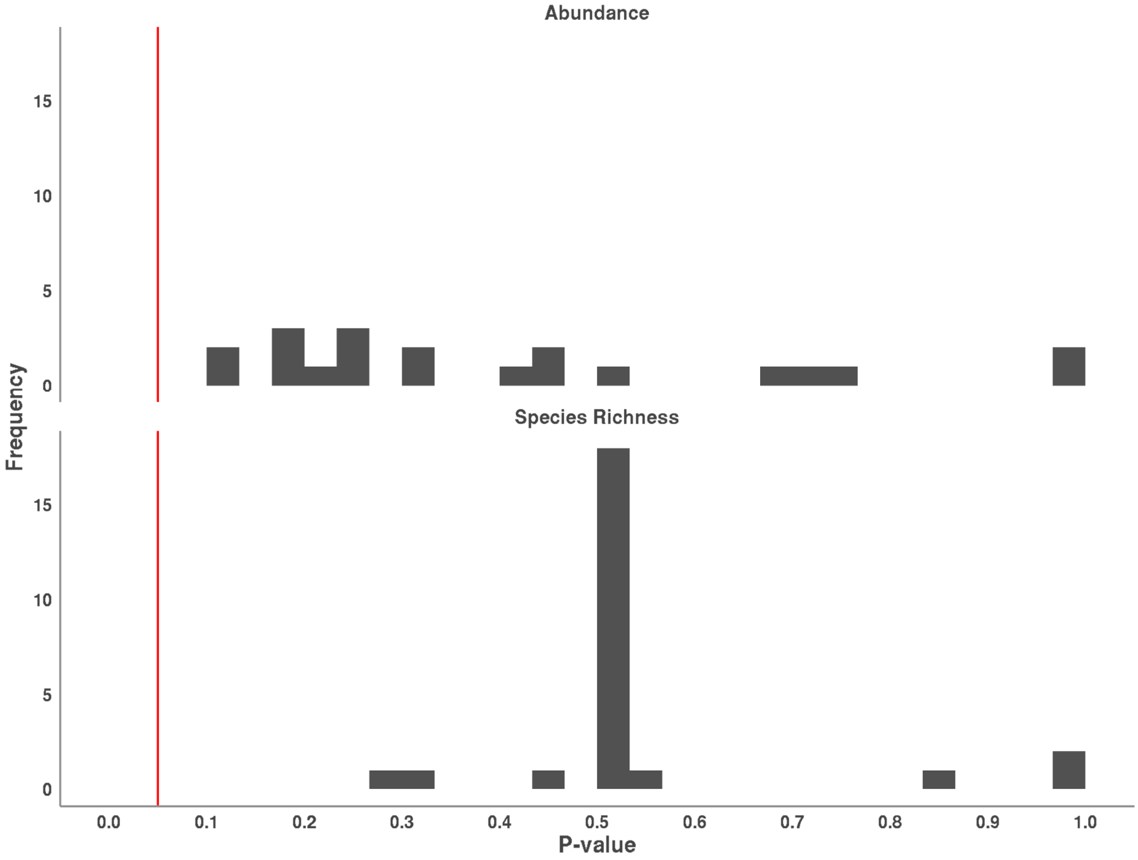

Figure S2: Tests for spatial autocorrelation within the model residuals, showing the distribution of P-values from sets of Moran's tests on the residuals associated with each individual study. Significant autocorrelation ($P < 0.05$) is indicated by the vertical red line.

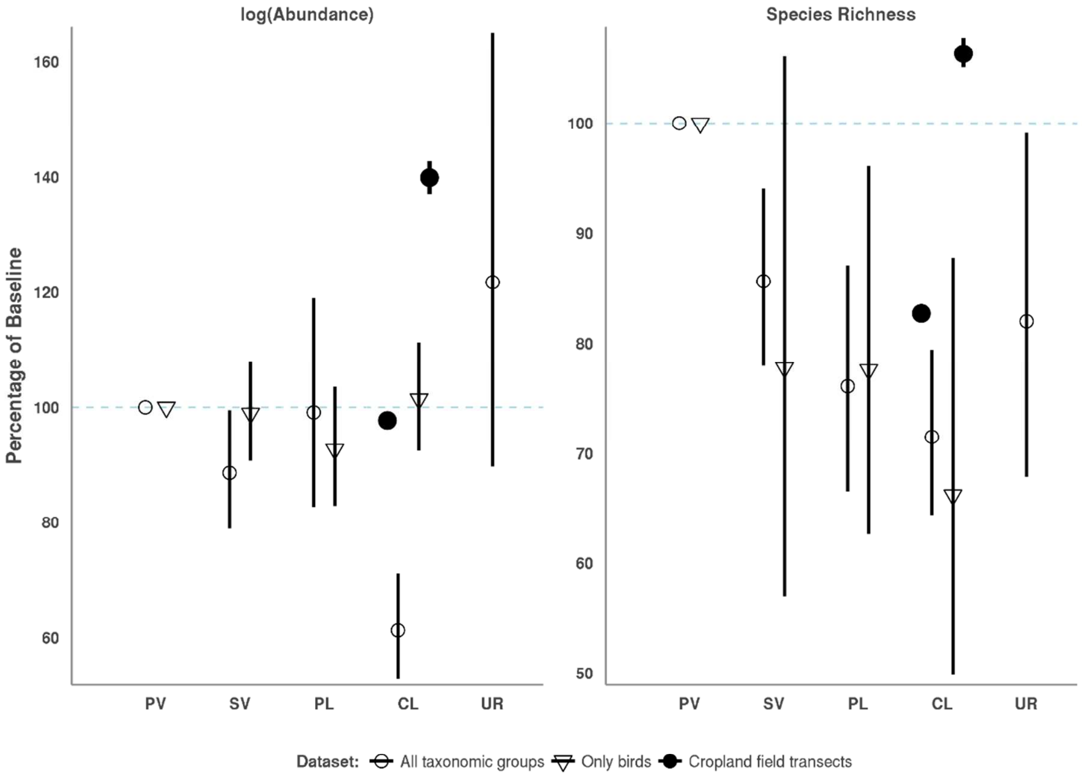

Figure S3: The response of species richness and total abundance to land use, from the Africa-wide model (open symbols) and the independent field data for cropland (closed symbols). Here, the Africa-wide models are shown for all taxonomic groups (open circles) and for birds only (open triangles). Land-use categories are primary vegetation (PV), secondary vegetation (SV), plantation forest (PL) and cropland (CL). There is no urban category (UR) for comparison as there were insufficient numbers of urban sites in the broad scale dataset for birds. All values are expressed as the percentage of the baseline values in primary vegetation. Error bars show one standard error.

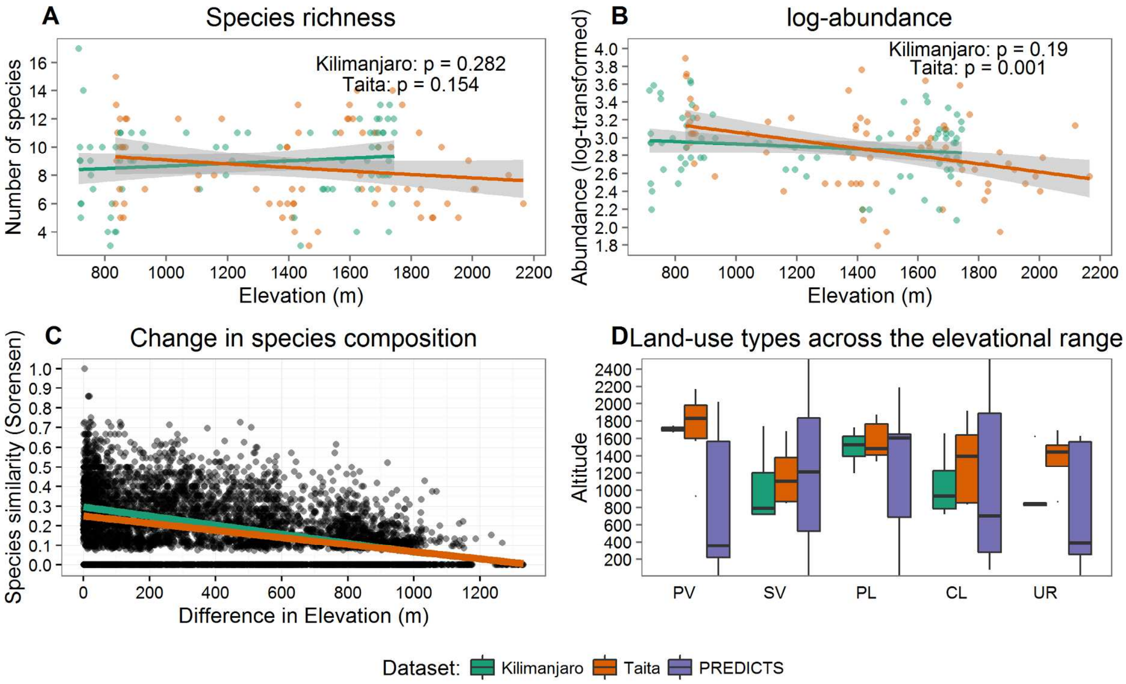

Figure S4: Effect of elevation (in m) on species richness, log-abundance and species composition for our independent field sites at Taita and Kilimanjaro. Generalized linear model with Poisson errors (for Species richness) and Gaussian errors (for log-abundance) were fitted independently for each transect. Changes in composition were assessed as Sorensen similarity index between all pairs of sites and fitted against the absolute difference in elevation between sites using generalized linear models with Gaussian errors. (**A**) There was no significant effect of elevation on species richness for either transect, but there was a significant effect for log-abundance in the Taita Hills (**B**). (**C**) Species assemblage similarity decreases with elevational differences between sites. (**D**) Distribution of the land-use classes of our independent sites across the elevational range of both study transects. Land use abbreviations as in Figure S1.

Table S2: The 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.

	Minimal use	Light use	Intense use
Primary forest (forest composed of native vegetation, which is not known to have been destroyed during historical times)	Any threats identified are very minor (e.g., very light use) or very limited in the scope of their effect (e.g., hunting of a particular species of limted ecological importance).	One or more threats of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem.	One or more threats that is severe enough to markedly change the nature of the ecosystem (e.g., clear-felling).
Primary Non-Forest (native vegetation, which has not been destroyed recently enough for there to be any discernible impact on vegetation architecture)	Any threats identified are very minor (e.g., very light use) or very limited in the scope of their effect (e.g., hunting of a particular species of limted ecological importance).	One or more threats of moderate intensity (e.g., selective logging) or breadth of impact (e.g., bushmeat extraction), which are not severe enough to markedly change the nature of the ecosystem.	One or more threats that is severe enough to markedly change the nature of the ecosystem (e.g., clear-felling).
Mature Secondary Vegetation (previously destroyed vegetation recovering to natural state rather than being managed to maintain it in a non-natural state; architecture, if not diversity, approaching original complexity)	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
Intermediate Secondary Vegetation (previously destroyed vegetation recovering to natural state rather than being managed to maintain it in a non-natural state; mixed architecture or mid-successional stage of recovery)	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
Young Secondary Vegetation (previously destroyed vegetation recovering	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use

to natural state rather than being managed to maintain it in a non-natural state; mainly ruderal species and simple architecture; early-successional stage)			
Secondary Vegetation (indeterminate age) (previously destroyed vegetation recovering to natural state rather than being managed to maintain it in a non-natural state; age indeterminate)	As for Primary Vegetation-Minimal use	As for Primary Vegetation-Light use	As for Primary Vegetation-Intense use
Plantation forest	Extensively managed or mixed timber, fruit/coffee, oil-palm or rubber plantations in which native understorey and/or other native tree species are tolerated, which are not treated with pesticide or fertiliser, and which are not clear-felled.	Monoculture fruit/coffee/rubber plantations with limited pesticide input, or mixed species plantations with significant inputs. Monoculture timber plantations of mixed age with no clear-felling. Monoculture oil-palm plantations with no clear-felling.	Monoculture fruit/coffee/rubber plantations with significant pesticide input. Monoculture timber plantations with similarly aged trees or timber/oil-palm plantations with extensive clear-felling.
Cropland	Low-intensity farms, typically with small fields, mixed crops, crop rotation, little or no inorganic fertiliser use, little or no pesticide use, little or no ploughing, little or no irrigation, little or no mechanisation.	Medium intensity farming, typically showing some but not many of the following: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, no crop rotation, mechanisation, monoculture crop. Organic farms in developed countries often fall within this category, as may high-intensity farming in developing countries.	High-intensity monoculture farming, typically showing many of the following features: large fields, annual ploughing, inorganic fertiliser application, pesticide application, irrigation, mechanisation, no crop rotation.
Pasture	Pasture with minimal input of fertiliser and pesticide, and with low stock density	Pasture either with significant input of fertiliser or pesticide, or with high stock density	Pasture with significant input of fertiliser or pesticide, *and* with high stock density (high enough to cause significant

	(*not* high enough to cause significant disturbance or to stop regeneration of vegetation).	(high enough to cause significant disturbance or to stop regeneration of vegetation).	disturbance or to stop regeneration of vegetation).
Urban	Extensive managed green spaces; villages.	Suburban (e.g. gardens), or small managed green spaces in cities.	Fully urban with no significant green spaces.

Table S3: Full model selection table for (log-transformed) abundance. All possible combinations of land use (PREDICTS.LU), land-use intensity (PREDICTS.LUI) Land use/Land-use intensity interaction (LUInter), log-transformed human population density (logpop), forest cover (FC2000), elevation (elev), mean NDVI (meanNDVI) and vegetation offtake (yield.ndvi.corr) were fitted. Shown are the model covariates, the parameter count (K), AIC, delta AIC, the Model likelihood (ModelLik), AIC weights (AICWt), log-likelihood (LL) and cumulative AIC weights (Cum.Wt). ModelLik and AICwt are rounded to the fifth decimal for visual display.

Model covariates	K	AIC	Delta AIC	ModelLik	AICWt	LL	Cum.Wt
LUInter + logpop + yield.ndvi.corr + meanNDVI	34	3844.269	0	1.00000	0.29457	-1888.13	0.294573
LUInter + yield.ndvi.corr + meanNDVI	33	3845.503	1.234303	0.53948	0.15892	-1889.75	0.453489
LUInter + logpop + yield.ndvi.corr + meanNDVI + elev	35	3846.001	1.732176	0.42059	0.12390	-1888	0.577384
LUInter + yield.ndvi.corr + FC2000 + meanNDVI	34	3846.449	2.17982	0.33625	0.09905	-1889.22	0.676434
LUInter + logpop + yield.ndvi.corr + FC2000 + meanNDVI	35	3846.626	2.357402	0.30768	0.09063	-1888.31	0.767067
LUInter + yield.ndvi.corr + meanNDVI + elev	34	3846.748	2.479162	0.28951	0.08528	-1889.37	0.852348
LUInter + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	36	3847.765	3.496445	0.17408	0.05128	-1887.88	0.903628
LUInter + yield.ndvi.corr + FC2000 + meanNDVI + elev	35	3848.256	3.987263	0.13620	0.04012	-1889.13	0.943749
LUInter + yield.ndvi.corr	32	3850.436	6.167005	0.04580	0.01349	-1893.22	0.95724
LUInter + logpop + yield.ndvi.corr	33	3850.454	6.185683	0.04537	0.01337	-1892.23	0.970605
LUInter + logpop + yield.ndvi.corr + FC2000	34	3851.611	7.342244	0.02545	0.00750	-1891.81	0.978102
LUInter + yield.ndvi.corr + FC2000	33	3851.969	7.700208	0.02128	0.00627	-1892.98	0.984369
LUInter + logpop + yield.ndvi.corr + elev	34	3852.429	8.160732	0.01690	0.00498	-1892.21	0.989348
LUInter + yield.ndvi.corr + elev	33	3852.431	8.162312	0.01689	0.00497	-1893.22	0.994323
LUInter + logpop + yield.ndvi.corr + FC2000 + elev	35	3853.589	9.319884	0.00947	0.00279	-1891.79	0.997111
LUInter + yield.ndvi.corr + FC2000 + elev	34	3853.966	9.697042	0.00784	0.00231	-1892.98	0.999421

PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI	27	3859.728	15.45902	0.00044	0.00013	-1902.86	0.99955
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + meanNDVI	26	3860.643	16.37373	0.00028	0.00008	-1904.32	0.999632
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI + elev	28	3861.481	17.2122	0.00018	0.00005	-1902.74	0.999686
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI	28	3861.597	17.32805	0.00017	0.00005	-1902.8	0.999737
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI	27	3862.253	17.98379	0.00012	0.00004	-1904.13	0.999774
PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI	23	3862.341	18.07208	0.00012	0.00004	-1908.17	0.999809
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + meanNDVI + elev	27	3862.545	18.27588	0.00011	0.00003	-1904.27	0.999841
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	29	3863.326	19.05705	0.00007	0.00002	-1902.66	0.999862
PREDICTS.LUI + yield.ndvi.corr + meanNDVI	22	3863.473	19.2043	0.00007	0.00002	-1909.74	0.999882
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI + elev	28	3864.119	19.85003	0.00005	0.00001	-1904.06	0.999896
PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI + elev	24	3864.234	19.96501	0.00005	0.00001	-1908.12	0.99991
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI	24	3864.25	19.9814	0.00005	0.00001	-1908.13	0.999923
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr	26	3864.83	20.56122	0.00003	0.00001	-1906.41	0.999934
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr	25	3864.874	20.60512	0.00003	0.00001	-1907.44	0.999943
PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI	23	3865.166	20.89678	0.00003	0.00001	-1909.58	0.999952
PREDICTS.LUI + yield.ndvi.corr + meanNDVI + elev	23	3865.441	21.17186	0.00003	0.00001	-1909.72	0.999959
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000	27	3866.031	21.76258	0.00002	0.00001	-1906.02	0.999965
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	25	3866.128	21.85887	0.00002	0.00001	-1908.06	0.99997

PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000	26	3866.494	22.22537	0.00001	0.00000	-1907.25	0.999975
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + elev	27	3866.822	22.55307	0.00001	0.00000	-1906.41	0.999978
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + elev	26	3866.874	22.60495	0.00001	0.00000	-1907.44	0.999982
PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI + elev	24	3867.113	22.84442	0.00001	0.00000	-1909.56	0.999985
PREDICTS.LUI + logpop + yield.ndvi.corr	22	3867.314	23.04509	0.00001	0.00000	-1911.66	0.999988
PREDICTS.LUI + yield.ndvi.corr	21	3867.667	23.39856	0.00001	0.00000	-1912.83	0.999991
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + elev	28	3868.021	23.75271	0.00001	0.00000	-1906.01	0.999993
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000	23	3868.45	24.181	0.00001	0.00000	-1911.22	0.999994
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000 + elev	27	3868.494	24.22498	0.00001	0.00000	-1907.25	0.999996
PREDICTS.LUI + yield.ndvi.corr + FC2000	22	3869.212	24.94299	0.00000	0.00000	-1912.61	0.999997
PREDICTS.LUI + logpop + yield.ndvi.corr + elev	23	3869.314	25.04508	0.00000	0.00000	-1911.66	0.999998
PREDICTS.LUI + yield.ndvi.corr + elev	22	3869.659	25.38994	0.00000	0.00000	-1912.83	0.999999
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + elev	24	3870.449	26.18066	0.00000	0.00000	-1911.22	1
PREDICTS.LUI + yield.ndvi.corr + FC2000 + elev	23	3871.2	26.93107	0.00000	0.00000	-1912.6	1
LUInter + logpop + meanNDVI	33	4104.084	259.8153	0.00000	0.00000	-2019.04	1
LUInter + meanNDVI	32	4104.626	260.3575	0.00000	0.00000	-2020.31	1
LUInter + logpop + meanNDVI + elev	34	4104.875	260.6064	0.00000	0.00000	-2018.44	1
LUInter + meanNDVI + elev	33	4105.689	261.4202	0.00000	0.00000	-2019.84	1
LUInter + logpop + FC2000 + meanNDVI	34	4106.072	261.8027	0.00000	0.00000	-	1

						2019.04	
LUInter + FC2000 + meanNDVI	33	4106.525	262.2567	0.00000	0.00000	-2020.26	1
LUInter + logpop + FC2000 + meanNDVI + elev	35	4106.836	262.5672	0.00000	0.00000	-2018.42	1
LUInter + FC2000 + meanNDVI + elev	34	4107.525	263.256	0.00000	0.00000	-2019.76	1
PREDICTS.LU + PREDICTS.LUI + logpop + meanNDVI	26	4115.069	270.8006	0.00000	0.00000	-2031.53	1
PREDICTS.LU + PREDICTS.LUI + logpop + meanNDVI + elev	27	4116.165	271.8961	0.00000	0.00000	-2031.08	1
PREDICTS.LU + PREDICTS.LUI + meanNDVI	25	4116.171	271.9019	0.00000	0.00000	-2033.09	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000 + meanNDVI	27	4117.069	272.8005	0.00000	0.00000	-2031.53	1
PREDICTS.LU + PREDICTS.LUI + meanNDVI + elev	26	4117.528	273.2592	0.00000	0.00000	-2032.76	1
PREDICTS.LUI + logpop + meanNDVI	22	4117.746	273.4771	0.00000	0.00000	-2036.87	1
PREDICTS.LU + PREDICTS.LUI + FC2000 + meanNDVI	26	4118.117	273.8479	0.00000	0.00000	-2033.06	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000 + meanNDVI + elev	28	4118.16	273.8911	0.00000	0.00000	-2031.08	1
PREDICTS.LUI + logpop + meanNDVI + elev	23	4118.978	274.7094	0.00000	0.00000	-2036.49	1
PREDICTS.LUI + meanNDVI	21	4119.061	274.7927	0.00000	0.00000	-2038.53	1
PREDICTS.LU + PREDICTS.LUI + FC2000 + meanNDVI + elev	27	4119.43	275.1616	0.00000	0.00000	-2032.72	1
PREDICTS.LUI + logpop + FC2000 + meanNDVI	23	4119.745	275.476	0.00000	0.00000	-2036.87	1
PREDICTS.LUI + meanNDVI + elev	22	4120.508	276.2392	0.00000	0.00000	-2038.25	1
PREDICTS.LUI + logpop + FC2000 + meanNDVI + elev	24	4120.976	276.707	0.00000	0.00000	-2036.49	1
PREDICTS.LUI + FC2000 + meanNDVI	22	4121.021	276.752	0.00000	0.00000	-	1

						2038.51	
PREDICTS.LUI + FC2000 + meanNDVI + elev	23	4122.429	278.1605	0.00000	0.00000	-2038.21	1
LUInter	31	4225.365	381.0963	0.00000	0.00000	-2081.68	1
LUInter + logpop	32	4225.82	381.5512	0.00000	0.00000	-2080.91	1
LUInter + logpop + elev	33	4226.453	382.1839	0.00000	0.00000	-2080.23	1
LUInter + elev	32	4226.827	382.558	0.00000	0.00000	-2081.41	1
LUInter + logpop + FC2000	33	4226.911	382.6424	0.00000	0.00000	-2080.46	1
LUInter + FC2000	32	4227.284	383.0152	0.00000	0.00000	-2081.64	1
LUInter + logpop + FC2000 + elev	34	4228.217	383.9483	0.00000	0.00000	-2080.11	1
LUInter + FC2000 + elev	33	4228.751	384.482	0.00000	0.00000	-2081.38	1
PREDICTS.LU + PREDICTS.LUI + logpop	25	4235.15	390.8816	0.00000	0.00000	-2092.58	1
PREDICTS.LU + PREDICTS.LUI	24	4235.861	391.5927	0.00000	0.00000	-2093.93	1
PREDICTS.LU + PREDICTS.LUI + logpop + elev	26	4236.647	392.3783	0.00000	0.00000	-2092.32	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000	26	4236.832	392.5627	0.00000	0.00000	-2092.42	1
PREDICTS.LU + PREDICTS.LUI + elev	25	4237.493	393.224	0.00000	0.00000	-2093.75	1
PREDICTS.LU + PREDICTS.LUI + FC2000	25	4237.756	393.4871	0.00000	0.00000	-2093.88	1
PREDICTS.LUI + logpop	21	4238.026	393.7577	0.00000	0.00000	-2098.01	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000 + elev	27	4238.336	394.0672	0.00000	0.00000	-2092.17	1
PREDICTS.LUI	20	4239.075	394.8065	0.00000	0.00000	-	1

						2099.54	
PREDICTS.LU + PREDICTS.LUI + FC2000 + elev	26	4239.396	395.1272	0.00000	0.00000	-2093.7	1
PREDICTS.LUI + logpop + elev	22	4239.561	395.2922	0.00000	0.00000	-2097.78	1
PREDICTS.LUI + logpop + FC2000	22	4239.69	395.4208	0.00000	0.00000	-2097.84	1
PREDICTS.LUI + elev	21	4240.732	396.4633	0.00000	0.00000	-2099.37	1
PREDICTS.LUI + FC2000	21	4240.955	396.6866	0.00000	0.00000	-2099.48	1
PREDICTS.LUI + logpop + FC2000 + elev	23	4241.24	396.9717	0.00000	0.00000	-2097.62	1
PREDICTS.LUI + FC2000 + elev	22	4242.624	398.3557	0.00000	0.00000	-2099.31	1
PREDICTS.LU + logpop + yield.ndvi.corr	24	5044.166	1199.898	0.00000	0.00000	-2498.08	1
PREDICTS.LU + logpop + yield.ndvi.corr + elev	25	5044.487	1200.219	0.00000	0.00000	-2497.24	1
PREDICTS.LU + logpop + yield.ndvi.corr + meanNDVI + elev	26	5044.706	1200.437	0.00000	0.00000	-2496.35	1
PREDICTS.LU + logpop + yield.ndvi.corr + meanNDVI	25	5044.963	1200.694	0.00000	0.00000	-2497.48	1
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000 + meanNDVI	26	5045.708	1201.439	0.00000	0.00000	-2496.85	1
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	27	5045.857	1201.589	0.00000	0.00000	-2495.93	1
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000	25	5046.105	1201.836	0.00000	0.00000	-2498.05	1
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000 + elev	26	5046.487	1202.218	0.00000	0.00000	-2497.24	1
PREDICTS.LU + yield.ndvi.corr + meanNDVI + elev	25	5050.417	1206.148	0.00000	0.00000	-2500.21	1
PREDICTS.LU + yield.ndvi.corr + elev	24	5050.672	1206.403	0.00000	0.00000	-2501.34	1
PREDICTS.LU + yield.ndvi.corr	23	5051.06	1206.791	0.00000	0.00000	-2502.53	1

PREDICTS.LU + yield.ndvi.corr + meanNDVI	24	5051.557	1207.288	0.00000	0.00000	-2501.78	1
PREDICTS.LU + yield.ndvi.corr + FC2000 + meanNDVI + elev	26	5052.229	1207.961	0.00000	0.00000	-2500.11	1
PREDICTS.LU + yield.ndvi.corr + FC2000 + elev	25	5052.411	1208.142	0.00000	0.00000	-2501.21	1
PREDICTS.LU + yield.ndvi.corr + FC2000	24	5053.017	1208.748	0.00000	0.00000	-2502.51	1
PREDICTS.LU + yield.ndvi.corr + FC2000 + meanNDVI	25	5053.148	1208.879	0.00000	0.00000	-2501.57	1
yield.ndvi.corr	19	5055.335	1211.067	0.00000	0.00000	-2508.67	1
PREDICTS.LU + logpop + meanNDVI	24	5307.316	1463.047	0.00000	0.00000	-2629.66	1
PREDICTS.LU + logpop + meanNDVI + elev	25	5308.63	1464.361	0.00000	0.00000	-2629.31	1
PREDICTS.LU + logpop + FC2000 + meanNDVI	25	5308.73	1464.461	0.00000	0.00000	-2629.36	1
PREDICTS.LU + logpop + FC2000 + meanNDVI + elev	26	5310.204	1465.936	0.00000	0.00000	-2629.1	1
PREDICTS.LU + meanNDVI	23	5312.902	1468.634	0.00000	0.00000	-2633.45	1
PREDICTS.LU + meanNDVI + elev	24	5313.982	1469.714	0.00000	0.00000	-2632.99	1
PREDICTS.LU + FC2000 + meanNDVI	24	5314.777	1470.508	0.00000	0.00000	-2633.39	1
PREDICTS.LU + FC2000 + meanNDVI + elev	25	5315.931	1471.662	0.00000	0.00000	-2632.97	1
meanNDVI	19	5316.582	1472.313	0.00000	0.00000	-2639.29	1
PREDICTS.LU + logpop + FC2000 + elev	25	5434.084	1589.816	0.00000	0.00000	-2692.04	1
PREDICTS.LU + FC2000 + elev	24	5439.595	1595.326	0.00000	0.00000	-2695.8	1
PREDICTS.LU + logpop + elev	24	5432.11	1587.842	0.00000	0.00000	-2692.06	1
PREDICTS.LU + logpop + FC2000	24	5432.402	1588.133	0.00000	0.00000	-2692.2	1
PREDICTS.LU + elev	23	5437.656	1593.387	0.00000	0.00000	-	1

						2695.83	
PREDICTS.LU + FC2000	23	5438.17	1593.901	0.00000	0.00000	-2696.08	1
PREDICTS.LU + logpop	23	5430.475	1586.206	0.00000	0.00000	-2692.24	1
elev	19	5441.679	1597.41	0.00000	0.00000	-2701.84	1
FC2000	19	5442.255	1597.986	0.00000	0.00000	-2702.13	1
logpop	19	5435.91	1591.641	0.00000	0.00000	-2698.96	1
PREDICTS.LU	22	5436.183	1591.915	0.00000	0.00000	-2696.09	1

Table S4: Full model selection table for species richness. All possible combinations of land use (PREDICTS.LU), land-use intensity (PREDICTS.LUI) Land use/Land-use intensity interaction (LUInter), log-transformed human population density (logpop), forest cover (FC2000), elevation (elev), mean NDVI (meanNDVI) and vegetation offtake (yield.ndvi.corr) were fitted. Shown are the model covariates, the parameter count (K), AIC, delta AIC, the model likelihood (ModelLik), AIC weights, log-likelihood (LL) and cumulative AIC weights (Cum.Wt). ModelLik and AICwt are rounded to the fifth decimal for visual display

Model covariates	**K**	**AIC**	**Delta AIC**	**ModelLik**	**AICWt**	**LL**	**Cum.Wt**
LUInter + logpop + yield.ndvi.corr + FC2000 + meanNDVI	35	10920.67	0	1.00000	0.22634	-5425.34	0.226343
LUInter + logpop + yield.ndvi.corr	33	10920.71	0.034688	0.98281	0.22245	-5427.35	0.448794
LUInter + logpop + yield.ndvi.corr + meanNDVI	34	10921.62	0.952034	0.62125	0.14062	-5426.81	0.589411
LUInter + logpop + yield.ndvi.corr + FC2000	34	10921.71	1.038024	0.59511	0.13470	-5426.85	0.724109
LUInter + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	36	10922.65	1.975058	0.37250	0.08431	-5425.32	0.808421
LUInter + logpop + yield.ndvi.corr + elev	34	10922.7	2.025582	0.36320	0.08221	-5427.35	0.89063
LUInter + logpop + yield.ndvi.corr + meanNDVI + elev	35	10923.62	2.951892	0.22856	0.05173	-5426.81	0.942363
LUInter + logpop + yield.ndvi.corr + FC2000 + elev	35	10923.7	3.032539	0.21953	0.04969	-5426.85	0.992052
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr	26	10931.15	10.48308	0.00529	0.00120	-	0.99325

					5439.58	
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI	28	10931.56	10.89099	0.00432	0.00098	-5437.78	0.994227
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000	27	10931.95	11.27773	0.00356	0.00081	-5438.97	0.995032
PREDICTS.LUI + logpop + yield.ndvi.corr	22	10932.3	11.63023	0.00298	0.00067	-5444.15	0.995707
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI	24	10932.45	11.78284	0.00276	0.00063	-5442.23	0.996332
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI	27	10932.5	11.82845	0.00270	0.00061	-5439.25	0.996944
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000	23	10932.57	11.89915	0.00261	0.00059	-5443.28	0.997534
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + elev	27	10933.14	12.4702	0.00196	0.00044	-5439.57	0.997977
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	29	10933.55	12.88052	0.00160	0.00036	-5437.78	0.998338
PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI	23	10933.74	13.06877	0.00145	0.00033	-5443.87	0.998667
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + elev	28	10933.94	13.27108	0.00131	0.00030	-5438.97	0.998964
PREDICTS.LUI + logpop + yield.ndvi.corr + elev	23	10934.3	13.62841	0.00110	0.00025	-5444.15	0.999213
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	25	10934.47	13.79464	0.00101	0.00023	-5442.23	0.999442
PREDICTS.LU + PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI + elev	28	10934.5	13.82666	0.00099	0.00023	-5439.25	0.999667
PREDICTS.LUI + logpop + yield.ndvi.corr + FC2000 + elev	24	10934.61	13.94325	0.00094	0.00021	-5443.31	0.999879
PREDICTS.LUI + logpop + yield.ndvi.corr + meanNDVI + elev	24	10935.74	15.0676	0.00053	0.00012	-5443.87	1
LUInter + yield.ndvi.corr + meanNDVI + elev	34	11404.4	483.7311	0.00000	0.00000	-5668.2	1
LUInter + yield.ndvi.corr + elev	33	11404.63	483.962	0.00000	0.00000	-5669.32	1
LUInter + yield.ndvi.corr + FC2000 + meanNDVI + elev	35	11404.68	484.0101	0.00000	0.00000	-5667.34	1

LUInter + yield.ndvi.corr + meanNDVI	33	11405.08	484.4091	0.00000	0.00000	-5669.54	1
LUInter + yield.ndvi.corr	32	11405.1	484.4339	0.00000	0.00000	-5670.55	1
LUInter + yield.ndvi.corr + FC2000 + meanNDVI	34	11405.59	484.9176	0.00000	0.00000	-5668.79	1
LUInter + yield.ndvi.corr + FC2000 + elev	34	11406.44	485.772	0.00000	0.00000	-5669.22	1
LUInter + yield.ndvi.corr + FC2000	33	11406.95	486.2824	0.00000	0.00000	-5670.48	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + elev	26	11418.47	497.7985	0.00000	0.00000	-5683.23	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr	25	11418.7	498.0322	0.00000	0.00000	-5684.35	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + meanNDVI + elev	27	11418.73	498.0565	0.00000	0.00000	-5682.36	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI + elev	28	11418.88	498.2072	0.00000	0.00000	-5681.44	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + meanNDVI	26	11419.12	498.446	0.00000	0.00000	-5683.56	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI	27	11419.5	498.8267	0.00000	0.00000	-5682.75	1
PREDICTS.LUI + yield.ndvi.corr + elev	22	11419.7	499.0331	0.00000	0.00000	-5687.85	1
PREDICTS.LUI + yield.ndvi.corr + meanNDVI + elev	23	11419.82	499.1495	0.00000	0.00000	-5686.91	1
PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI + elev	24	11419.84	499.1689	0.00000	0.00000	-5685.92	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000 + elev	27	11420.16	499.4901	0.00000	0.00000	-5683.08	1
PREDICTS.LU + PREDICTS.LUI + yield.ndvi.corr + FC2000	26	11420.45	499.7748	0.00000	0.00000	-5684.22	1
PREDICTS.LUI + yield.ndvi.corr	21	11420.6	499.9254	0.00000	0.00000	-5689.3	1
PREDICTS.LUI + yield.ndvi.corr + FC2000	22	11420.8	500.1341	0.00000	0.00000	-5688.4	1
PREDICTS.LUI + yield.ndvi.corr + meanNDVI	22	11420.97	500.3002	0.00000	0.00000	-5688.49	1

PREDICTS.LUI + yield.ndvi.corr + FC2000 + meanNDVI	23	11421.28	500.6133	0.00000	0.00000	-5687.64	1
PREDICTS.LUI + yield.ndvi.corr + FC2000 + elev	23	11421.38	500.707	0.00000	0.00000	-5687.69	1
LUInter + logpop + FC2000 + meanNDVI	34	12226.23	1305.556	0.00000	0.00000	-6079.11	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000 + meanNDVI	27	12226.74	1306.072	0.00000	0.00000	-6086.37	1
PREDICTS.LUI + logpop + FC2000 + meanNDVI	23	12226.8	1306.13	0.00000	0.00000	-6090.4	1
LUInter + logpop + meanNDVI	33	12227.66	1306.987	0.00000	0.00000	-6080.83	1
LUInter + logpop + FC2000 + meanNDVI + elev	35	12228.07	1307.399	0.00000	0.00000	-6079.03	1
PREDICTS.LU + PREDICTS.LUI + logpop + meanNDVI	26	12228.26	1307.591	0.00000	0.00000	-6088.13	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000 + meanNDVI + elev	28	12228.63	1307.955	0.00000	0.00000	-6086.31	1
PREDICTS.LUI + logpop + meanNDVI	22	12228.68	1308.011	0.00000	0.00000	-6092.34	1
PREDICTS.LUI + logpop + FC2000 + meanNDVI + elev	24	12228.75	1308.077	0.00000	0.00000	-6090.37	1
LUInter + logpop + meanNDVI + elev	34	12229.59	1308.917	0.00000	0.00000	-6080.79	1
PREDICTS.LU + PREDICTS.LUI + logpop + meanNDVI + elev	27	12230.22	1309.546	0.00000	0.00000	-6088.11	1
PREDICTS.LUI + logpop + meanNDVI + elev	23	12230.67	1310.003	0.00000	0.00000	-6092.34	1
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000 + meanNDVI + elev	27	13336.61	2415.942	0.00000	0.00000	-6641.31	1
PREDICTS.LU + yield.ndvi.corr + FC2000 + meanNDVI + elev	26	13801.11	2880.439	0.00000	0.00000	-6874.55	1
PREDICTS.LU + logpop + FC2000 + meanNDVI + elev	26	14733.83	3813.157	0.00000	0.00000	-7340.91	1
PREDICTS.LU + logpop + yield.ndvi.corr + meanNDVI + elev	26	13336.11	2415.439	0.00000	0.00000	-6642.05	1
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000 +	26	13334.96	2414.288	0.00000	0.00000	-	1

elev						6641.48	
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000 + meanNDVI	26	13334.97	2414.301	0.00000	0.00000	-6641.49	1
LUInter + FC2000 + meanNDVI + elev	34	12712.74	1792.066	0.00000	0.00000	-6322.37	1
LUInter + logpop + FC2000 + elev	34	12507.21	1586.54	0.00000	0.00000	-6219.61	1
PREDICTS.LU + PREDICTS.LUI + FC2000 + meanNDVI + elev	27	12710.92	1790.252	0.00000	0.00000	-6328.46	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000 + elev	27	12506.67	1585.998	0.00000	0.00000	-6226.33	1
PREDICTS.LUI + FC2000 + meanNDVI + elev	23	12713.04	1792.369	0.00000	0.00000	-6333.52	1
PREDICTS.LUI + logpop + FC2000 + elev	23	12506.89	1586.223	0.00000	0.00000	-6230.45	1
PREDICTS.LU + FC2000 + meanNDVI + elev	25	15196.37	4275.702	0.00000	0.00000	-7573.19	1
PREDICTS.LU + yield.ndvi.corr + meanNDVI + elev	25	13800.42	2879.748	0.00000	0.00000	-6875.21	1
PREDICTS.LU + yield.ndvi.corr + FC2000 + elev	25	13799.38	2878.709	0.00000	0.00000	-6874.69	1
PREDICTS.LU + yield.ndvi.corr + FC2000 + meanNDVI	25	13801.49	2880.816	0.00000	0.00000	-6875.74	1
PREDICTS.LU + logpop + meanNDVI + elev	25	14733.24	3812.567	0.00000	0.00000	-7341.62	1
PREDICTS.LU + logpop + FC2000 + elev	25	15022.37	4101.702	0.00000	0.00000	-7486.19	1
PREDICTS.LU + logpop + FC2000 + meanNDVI	25	14732.41	3811.744	0.00000	0.00000	-7341.21	1
PREDICTS.LU + logpop + yield.ndvi.corr + elev	25	13334.12	2413.448	0.00000	0.00000	-6642.06	1
PREDICTS.LU + logpop + yield.ndvi.corr + meanNDVI	25	13334.33	2413.657	0.00000	0.00000	-6642.16	1
PREDICTS.LU + logpop + yield.ndvi.corr + FC2000	25	13333.33	2412.661	0.00000	0.00000	-6641.67	1
LUInter + meanNDVI + elev	33	12713.08	1792.414	0.00000	0.00000	-	1

						6323.54	
LUInter + FC2000 + elev	33	12991.25	2070.58	0.00000	0.00000	-6462.63	1
LUInter + FC2000 + meanNDVI	33	12712.49	1791.819	0.00000	0.00000	-6323.24	1
LUInter + logpop + elev	33	12507.03	1586.36	0.00000	0.00000	-6220.52	1
LUInter + logpop + FC2000	33	12505.21	1584.541	0.00000	0.00000	-6219.61	1
PREDICTS.LU + PREDICTS.LUI + meanNDVI + elev	26	12711.19	1790.52	0.00000	0.00000	-6329.6	1
PREDICTS.LU + PREDICTS.LUI + FC2000 + elev	26	12989.29	2068.618	0.00000	0.00000	-6468.64	1
PREDICTS.LU + PREDICTS.LUI + FC2000 + meanNDVI	26	12710.82	1790.154	0.00000	0.00000	-6329.41	1
PREDICTS.LU + PREDICTS.LUI + logpop + elev	26	12506.79	1586.124	0.00000	0.00000	-6227.4	1
PREDICTS.LU + PREDICTS.LUI + logpop + FC2000	26	12504.67	1584.001	0.00000	0.00000	-6226.34	1
PREDICTS.LUI + meanNDVI + elev	22	12713.32	1792.65	0.00000	0.00000	-6334.66	1
PREDICTS.LUI + FC2000 + elev	22	12991	2070.331	0.00000	0.00000	-6473.5	1
PREDICTS.LUI + FC2000 + meanNDVI	22	12711.88	1791.211	0.00000	0.00000	-6333.94	1
PREDICTS.LUI + logpop + elev	22	12507.38	1586.705	0.00000	0.00000	-6231.69	1
PREDICTS.LUI + logpop + FC2000	22	12504.9	1584.226	0.00000	0.00000	-6230.45	1
PREDICTS.LU + meanNDVI + elev	24	15195.45	4274.784	0.00000	0.00000	-7573.73	1
PREDICTS.LU + FC2000 + elev	24	15484.83	4564.155	0.00000	0.00000	-7718.41	1
PREDICTS.LU + FC2000 + meanNDVI	24	15196.4	4275.727	0.00000	0.00000	-7574.2	1
PREDICTS.LU + yield.ndvi.corr + elev	24	13798.43	2877.761	0.00000	0.00000	-6875.22	1
PREDICTS.LU + yield.ndvi.corr + meanNDVI	24	13800.48	2879.805	0.00000	0.00000	-6876.24	1
PREDICTS.LU + yield.ndvi.corr + FC2000	24	13799.83	2879.156	0.00000	0.00000	-	1

						6875.91	
PREDICTS.LU + logpop + elev	24	15021.23	4100.56	0.00000	0.00000	-7486.62	1
PREDICTS.LU + logpop + meanNDVI	24	14731.66	3810.987	0.00000	0.00000	-7341.83	1
PREDICTS.LU + logpop + FC2000	24	15020.81	4100.139	0.00000	0.00000	-7486.4	1
PREDICTS.LU + logpop + yield.ndvi.corr	24	13332.33	2411.659	0.00000	0.00000	-6642.16	1
LUInter + elev	32	12990.03	2069.356	0.00000	0.00000	-6463.01	1
LUInter + meanNDVI	32	12717.09	1796.419	0.00000	0.00000	-6326.54	1
LUInter + FC2000	32	12990.54	2069.865	0.00000	0.00000	-6463.27	1
LUInter + logpop	32	12505.03	1584.36	0.00000	0.00000	-6220.52	1
PREDICTS.LU + PREDICTS.LUI + elev	25	12988.17	2067.496	0.00000	0.00000	-6469.08	1
PREDICTS.LU + PREDICTS.LUI + meanNDVI	25	12710.87	1790.197	0.00000	0.00000	-6330.43	1
PREDICTS.LU + PREDICTS.LUI + FC2000	25	12988.73	2068.064	0.00000	0.00000	-6469.37	1
PREDICTS.LU + PREDICTS.LUI + logpop	25	12504.8	1584.125	0.00000	0.00000	-6227.4	1
PREDICTS.LUI + elev	21	12990.2	2069.529	0.00000	0.00000	-6474.1	1
PREDICTS.LUI + meanNDVI	21	12712.1	1791.428	0.00000	0.00000	-6335.05	1
PREDICTS.LUI + FC2000	21	12989.59	2068.921	0.00000	0.00000	-6473.8	1
PREDICTS.LUI + logpop	21	12505.38	1584.713	0.00000	0.00000	-6231.69	1
PREDICTS.LU + elev	23	15483.53	4562.863	0.00000	0.00000	-7718.77	1
PREDICTS.LU + meanNDVI	23	15195.21	4274.539	0.00000	0.00000	-7574.6	1
PREDICTS.LU + FC2000	23	15484.67	4564.004	0.00000	0.00000	-7719.34	1
PREDICTS.LU + yield.ndvi.corr	23	13798.48	2877.807	0.00000	0.00000	-6876.24	1

PREDICTS.LU + logpop	23	15019.67	4098.996	0.00000	0.00000	-7486.83	1
PREDICTS.LU + PREDICTS.LUI	24	12987.55	2066.878	0.00000	0.00000	-6469.77	1
elev	19	15485.01	4564.34	0.00000	0.00000	-7723.51	1
meanNDVI	19	15195.93	4275.261	0.00000	0.00000	-7578.97	1
FC2000	19	15485.48	4564.81	0.00000	0.00000	-7723.74	1
yield.ndvi.corr	19	13798.94	2878.275	0.00000	0.00000	-6880.47	1
logpop	19	15024.02	4103.345	0.00000	0.00000	-7493.01	1
LUInter	31	12989.25	2068.584	0.00000	0.00000	-6463.63	1
PREDICTS.LUI	20	12988.61	2067.938	0.00000	0.00000	-6474.3	1
PREDICTS.LU	22	15483.15	4562.482	0.00000	0.00000	-7719.58	1