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Agricultural expansion in African savannas: effects on diversity and composition of trees and mammals

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Abstract

Land use change (LUC) is the leading cause of biodiversity loss worldwide. However, the global understanding of LUC's impact on biodiversity is mainly based on comparisons of land use endpoints (habitat vs non-habitat) in forest ecosystems. Hence, it may not generalise to savannas, which are ecologically distinct from forests, as they are inherently patchy, and disturbance adapted. Endpoint comparisons also cannot inform the management of intermediate mosaic landscapes. We aim to address these gaps by investigating species- and community-level responses of mammals and trees along a gradient of small scale agricultural expansion in the miombo woodlands of northern Mozambique. Thus, the case study represents the most common pathway of LUC and biodiversity change in the world's largest savanna. Tree abundance, mammal occupancy, and tree- and mammal-species richness showed a non-linear relationship with agricultural expansion (characterised by the Land Division Index, LDI). These occurrence and diversity metrics increased at intermediate LDI (0.3 to 0.7), started decreasing beyond LDI $>$ 0.7, and underwent high levels of decline at extreme levels of agricultural expansion (LDI $>$ 0.9). Despite similarities in species richness responses, the two taxonomic groups showed contrasting β-diversity patterns in response to increasing LDI: increased dissimilarity among tree communities (heterogenisation) and high similarity among mammals (homogenisation). Our analysis along a gradient of landscape-scale land use intensification allows a novel understanding of the impacts of different levels of land conversion, which can help guide land use and restoration policy. Biodiversity loss in this miombo landscape was lower than would be inferred from existing global syntheses of biodiversity-land use relations for Africa or the tropics, probably because such syntheses take a fully converted landscape as the endpoint. As, currently, most African savanna landscapes are a mosaic of savanna habitats and small scale agriculture, biodiversity loss is probably lower than in current global estimates, albeit with a trend towards further conversion. However, at extreme levels of land use change (LDI $>$ 0.9 or $<$ 15% habitat cover) miombo biodiversity appears to be *more* sensitive to LUC than inferred from the meta-analyses. To mitigate the worst effects of land use on biodiversity, our results suggest that miombo landscapes should retain $>$ 25% habitat cover and avoid LDI $>$ 0.75—after which species richness of both groups begin to decline. Our findings indicate that tree diversity may be easier to restore from natural restoration than mammal diversity, which became spatially homogeneous.

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Keywords Miombo woodland · Agriculture expansion · Fragmentation · α-and β-diversity · Occupancy · Mozambique

Introduction

Land conversion to agriculture is the major driver of global biodiversity loss, with consequences for ecosystem functioning and human wellbeing (Haddad et al. 2015; Pfeifer et al. 2017). The expansion of agriculture, and the resulting loss and fragmentation of original habitats, leads to reduced habitat area, increased habitat isolation and novel ecological boundaries (Taubert et al. 2018). These altered landscape characteristics amplify competition, reduce immigration and often increase predation, causing population declines, local species extinctions and changes in species compositions (Fahrig 2010; Pfeifer et al. 2017). However, these effects vary depending on species traits and the spatial structure of the habitat (patch) and the surrounding human-modified landscape (matrix) (Ewers and Didham 2006). The global understanding of the impacts of land use change on biodiversity is mainly based on studies from forest ecosystems comparing binary endpoints (natural forest vs agricultural land; McGill et al. 2015). However, most land cover transformations are a gradual process of landscape-scale intensification, leading to habitat loss and fragmentation. These limitations suggest a potential biogeographical and theoretical knowledge gap. Specifically, it overlooks the possibility that different land use-biodiversity relationships may exist in savannas and ignores the role of heterogeneous landscape mosaics at intermediate land use intensities with varying patch-matrix structures (Franklin and Lindenmayer 2009). While the former is essential for making accurate global biodiversity change projections, the latter is critical for informing local land and biodiversity management. Particularly in African savannas, patchy mosaic agricultural landscapes are widespread and will need to be managed carefully to meet both biodiversity and food security objectives.

Savannas are, even without LUC, heterogeneous systems, conceptually quite different from the simple patch-matrix dichotomy that often underpins habitat change theory (Jules et al. 2016). Savanna landscapes, particularly the miombo woodlands that are our focus here, are socio-ecological systems characterised by age-old human–environment interactions. They comprise a mosaic of land covers—including grass-dominated drainage lines, densely wooded crests, dry forest patches, rocky outcrops and open savannas on hydromorphic soils (Frost and Campbell 1996). On top of this mosaic, there is widespread and long-standing human land use, including permanent agriculture, shifting cultivation, grazing, tree harvesting for timber and energy, and widespread fire (Archibald et al. 2012; McNicol et al. 2018). The miombo supports biodiversity that is globally significant due to high endemicity (Linder et al. 2012) and provides services necessary to the livelihoods of 100 s of millions of rural people (Ryan et al. 2016; Pritchard et al. 2019). Being inherently patchy and a historically human-managed system that has co-evolved with the land-use activities of people, and is characterised by frequent disturbances (Ellis et al. 2010; Ryan et al. 2011), miombo biodiversity might be hypothesised to be resilient to intermediate land-use changes (McNicol et al. 2015), particularly in comparison to other less populated tropical biomes. Resolving this is important because currently, there is a rapid and more complete land cover change underway from mixed farming systems to monoculture farming in several hotspots in Africa. This transformation is notably more prominent on the eastern seaboard and around large cities and associated development corridors

(Ahrends et al. 2010; McNicol et al. 2018). In future, the expansion of agriculture to meet the growing demands of local and commercial markets may lead to the transformation of the intermediate heterogeneous savanna landscapes to more agriculture-dominated homogenous landscapes where food production will trade-off strongly against biodiversity (Molotoks et al. 2018).

Mitigating biodiversity loss in such landscapes requires a nuanced understanding of how the mosaic of non-agricultural land facilitates biodiversity (Seppelt et al. 2019). Most biodiversity-land use studies overlook the distinctions and complexities of gradual landscape-scale land use intensification; thus, they do not provide the information required to understand the trade-offs between food production and conservation. We study a gradient of agricultural land-use intensity (Baumert et al. 2019), evaluating the organisation of tree and mammal communities. The overall aim is to provide information about how much land should be spared and at what levels of fragmentation to maintain biodiversity above safe levels in agricultural miombo landscapes.

Our first goal was to examine how local species richness changes along an agricultural fragmentation gradient. We expected that the mean local species richness loss in the miombo would be lower than the average losses reported from the overall wet tropics (−18.3%; Murphy and Romanuk 2014) and also from dry tropics in Africa (−21.6%; Newbold et al. 2017). This is because, as mentioned above, the majority of biodiversity-land use studies in the global literature compare land use endpoints (e.g. national park versus farmlands)—ignoring that most African savanna landscapes are predominantly intermediate mosaics and have not yet transitioned to the extreme levels of land use change (Murphy et al. 2016).

Our second goal was to compare the α- and β-diversity responses of trees and mammals to understand taxonomic group differences in response to agricultural expansion. We expected that the impact of land use would differ between tree and mammal communities for the following reasons: clearing for small-scale farming is the primary land use change in our study area, and individual trees are not selectively removed, at least within the miombo woodland cover. Therefore, population declines of tree species are more likely to be random i.e., more abundant and common tree species will be harvested first—in other words, local species decline will be ordered by abundance and ubiquity. This would cause reduced richness but increased dissimilarity among tree communities—subtractive heterogenisation, a pattern driven by random local extinctions (Segre et al. 2014; Socolar et al. 2016). On the other hand, mammal communities are more likely to be structured systematically on the basis of species' traits, dispersibility, and degree of habitat specialisation (Ewers and Didham 2006). Habitat specialists are thus likely to decline due to isolation and reduction in the size of habitat fragments (Jamoneau et al. 2012), whilst habitat generalists, more mobile, and non-forest species may proliferate in the patch-matrix mosaic (Cordeiro et al. 2015). Based on this information, we expected that mammals would undergo loss of species richness and reduced spatial species dissimilarity among mammal communities, i.e., a decline in α β-diversity at high levels of agricultural expansion—subtractive heterogenisation.

We expect the results to be useful for landscape planning and management aimed at biodiversity conservation and the sustainance of local livelihoods. The two taxonomic groups studied are essential for provisioning ecosystem services in the region: trees for fruit, fodder and timber (Frost and Campbell 1996; Sileshi et al. 2007) and mammals for food (mainly medium to small-sized species; Caro, 2001; Linzey and Kesner 1997).

Material and methods

We conducted a 'space-for-time' study along a gradient of miombo landscapes, from low levels of agriculture through to almost complete conversion of the landscape. We collected occurrence data (counts for trees and incidence for mammals) in these landscapes and analysed multi-species occurrence using hierarchical meta-community occupancy models (Dorazio and Royle 2005) in a Bayesian regression modelling framework.

Study area

We carried out this study from April to July 2016 in Posto Administrativo Lioma, in the district of Gurué, located in the northern part of Zambézia, the second-most populous province in Mozambique (Fig. 1). The site has a mean temperature of 22.7 ºC and precipitation of 1030 mm year^{-1}, with most rainfall from November to April (INE 2014). It is primarily a miombo landscape dominated by trees of genus *Brachystegia* and grasses of the genera *Hyparrhenia* and *Andropogon* (Frost 1996). Typical crops include maize, cassava and beans, and cash crops such as pigeon pea, soya, cowpea, sunflower and sesame (INE 2014). Small farms of 1–2 ha in size cover about 90% of the agricultural land (Hanlon and Smart 2012). The commercial farming of soya, which was first introduced in the 1980s by Brazilian companies, stopped due to the civil war (1977–92) and was reinstated in 2002 (Matteo and Otsuki 2016). Since then, small scale commercial farming—mainly driven by the national demand for soya—has been steadily growing, now equalling 2.8% of agricultural land (Matteo and Otsuki 2016; Baumert et al. 2019).

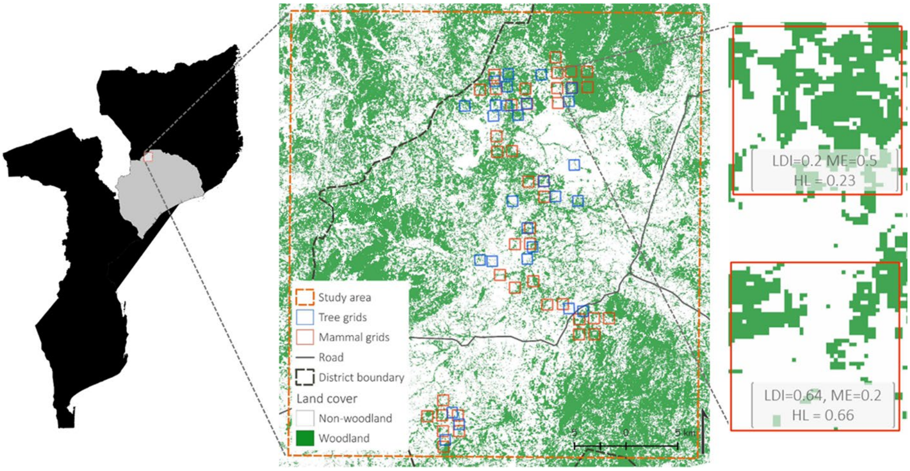

Fig. 1 Study area in Zambézia province in north-central Mozambique. We selected landscape sampling units (1 km^2 grids) within which we collected incidence data of mammal (red boxes) and count data of tree species (blue boxes) and computed land division index (LDI), total woodland cover (ME) and woodland cover loss between 2007 and 2014 (HL). Camera trap locations for mammal sampling were at least 2 km away from each other; this provides independent observations for most mammal species observed in this study

Measures of agricultural expansion

We used indicators of fragmentation and changes in miombo cover to measure the intensity of agricultural expansion in the miombo ecosystem. To map these changes, we made above-ground woody biomass maps for 2007 and 2014 using images obtained by the Phased Array L-band Synthetic Aperture Radar sensor on the Advanced Land Observing Satellite following the methods described in Ryan et al. (2012). We classified all pixels above 15 tC ha^{-1} as wooded miombo and all pixels below this value as non-wooded following other studies in the region (Ryan et al. 2012, 2014). We divided the study area into grids of 1 km^2, representing landscape-scale sampling units (LSU). To ensure that the LSUs represent miombo, we excluded LSUs with a mean elevation of $>$ 800 m ASL (Shirima et al. 2011). In each LSU, we estimated three land cover variables:

(i) Land Division Index (LDI), a measure of fragmentation defined as the probability that two randomly selected points in the landscape are situated in two different patches of the habitat (Jaeger 2000; Mcgarigal 2015)
(ii) Miombo extent (ME), the proportion of the LSU covered by wooded miombo in 2014, a measure of habitat quantity.
(iii) Habitat loss (HL) between 2007 and 2014, the area that was converted from wooded to non-wooded, as a % of the 2007 miombo extent.

Habitat quantity (ME) and habitat loss (HL) are in most cases negatively correlated, but a landscape can naturally have lower habitat quantities without undergoing habitat loss, so the latter was also included to take into account this inherent variation.

LDI can help differentiate between fragmentation and habitat quantity effects as it is more sensitive to dissection than shrinkage and, therefore, is a robust measure of fragmentation (Jaeger 2000). We also examined the relationship between diversity and other environmental variables—soil type (ISRIC 2013), accessibility—proximity to the nearest paved road (CIESIN, ITOS 2013), and mean annual temperature (MAT) and precipitation (MAP) (Hijmans et al. 2005). MAP was significantly related to diversity and was thus used as one of the explanatory variables for occupancy and diversity. Further, ME and HL were correlated with LDI (correlation coefficient $r = 0.9$ and 0.25, respectively; correlation plot in supporting information: SI Fig. 1). Hence, to reduce multicollinearity, we used their residuals (i.e. the amount of variation not explained by LDI) as variables following the concept of sequential regression (Dormann et al. 2013) in the order LDI, ME, and HL. Hereafter, HL_{resid}, and ME_{resid} refer to the residuals of "$HL \sim LDI$", and "$ME \sim LDI + HL_{resid}$", respectively. We considered fragmentation to be the primary driver of biodiversity (Pfeifer et al. 2017), followed by habitat quantity and intensity of habitat loss, hence the order LDI, ME and HL.

Species sampling

We collected species occurrence data within a sample of 1 km^2 LSUs: abundance for trees using 20 m radius circular plots and incidence for mammals using camera traps (Fig. 1). For trees, we made a post-hoc selection of existing inventory data by selecting 27 LSUs with a mean elevation of $\leq$ 800 m ASL, each containing ~ 3 tree plots. Within each plot, the diameter at breast height (DBH) of all tree stems $>$ 5 cm DBH was measured, and the stems were identified by their local names, with the help of local experts. Stems unidentified in the field were collected and identified later by reference to Palgrave, (2002). Tree identification was corroborated by botanists at the University of Eduardo Mondlane in Maputo. The 42 individuals (2% of total stems) that could not be identified were grouped into distinct unknown species (n = 13) based on morphological characteristics.

To sample mammal communities, we used a stratified sample of 40 LSUs representing a gradient of fragmentation from low to high. Within each LSU, we placed one camera trap within 100 m of the centre, at the best camera trapping location, chosen as an open and frequently used pathway, to maximise detection (O'Connell et al. 2011). The cameras were visited every week to download images and check functioning. Each LSU was considered as a site, and every day-night period of the camera trap a sampling occasion. Camera traps were supposed to be operated for 60–65 days; however, due to camera thefts ($n = 3$; excluded from the analysis), disturbance by people, and inclement weather conditions, not all cameras recorded an equal number of camera-days. The camera-days ranged from 8 to 65 and had a mean of 45 days. Mammals in camera trap images were identified to the species level where possible, by reference to field guides (Liebenberg 2000; Kingdon 2001; Stuart and Stuart 2007; Gutteridge and Liebenberg 2013). Where species identification could not be made ($n = 5$, 0.5% of all mammal occurrences), the morphologically distinct individuals were classified to the lowest possible taxonomic group (genus, family or order) and given unique identification codes. Three domestic species in our dataset (dog, cat and pig) were removed from the analysis.

Statistical analysis

Our objective in this study was to test relationships between species and community level attributes (detailed in Table 1) and landcover variables (LDI, ME_{resid} and HL_{resid}). To do this we built species- and community-level hierarchical mixed-effects models (Dorazio and Royle 2005) for both taxonomic groups with landcover variables as predictors in additive combination.

Since the effects of fragmentation can be non-linear (Andrén 1994; Ewers and Didham 2006), we included quadratic and cubic terms of LDI (LDI^2 and LDI^3) as predictors, and compared models with and without these terms using penalised deviance ($\widehat{D}$) as a measure of model fit (Van Der Linde 2005). $\widehat{D}$ is given by $\widehat{D}$= DIC—2 pD, where DIC = Deviance Information Criterion (DIC), and pD = posterior mean of the deviance. The values of DIC and pD increase with model complexity, and hence,$\widehat{D}$, which incorporates a degree of penalty for complexity, was used as a measure of model fitness (Van Der Linde 2005). Details of the models, model structures, and parameters values are provided in supporting information (SI: SI models and SI Table 1 and 2). The goodness of fit table is provided in the result section.

We specified the models using BUGS (Kéry 2010; Kéry and Schaub 2012) and executed simulations using three Markov chains, with 75,000 iterations for each chain (the first 25,000 iterations of which were discarded as burn-in), and set the thinning rate to 50, yielding 3000 samples from the posterior distributions. We checked all the models for convergence using the Gelman-Rubin convergence diagnostic, with potential scale reduction factor values approaching 1 considered acceptable (Gelman and Rubin 1992). We use the % deviation of the standardised beta-coefficients from the intercept as the standard effect size (± standard deviation) with posterior probabilities (Pp) as a measure of confidence in

Table 1 The response variables used to characterise the way that fragmentation impacts biodiversity

Response level	Taxa	Quantity	Units	Method	Model
1. Species	Tree	Abundance	Number of individuals per 20 m radius plot	Tree counts modelled as a Poisson distribution accounting for variation between plots	Dorazio/Royle/Yamaura model of abundance (Yamaura et al. 2012)
2. Species	Mammals	Occupancy	Probability of occupancy of the 1 km square	Mammal incidence modelled as Bernoulli trial accounting for variability in detection	Dorazio/Royle model of occupancy (Dorazio and Royle 2005)
3. Community	Tree & mammals	Richness	Number of species per 1 km square	Detection-corrected estimate of species richness	Community state parameters computed from the detection-corrected estimates of species occurrences from the first two models
4. Community	Tree & mammals	Turnover	Unitless (0–1)	Simpson dissimilarity	
5. Community	Tree & mammals	Nestedness	Unitless (0–1)	Difference between Sorenson and Simpson dissimilarity (Baselga 2010)	

Table 2 Model goodness of fit, as estimated by the penalised deviance ($\widehat{D}$)

Models	Predictors		
	LDI	*LDI + LDI²*	*LDI + LDI² + LDI³*
Mammal occupancy	1285	1290	**1270**
Mammal community—richness and turnover	*– 165*	*– 163*	***– 159***
Tree abundance	1090	**755**	2376
Tree community—richness and turnover	*– 78*	***– 81***	*– 90*

The values in bold correspond to the models that were selected in this study. Note that the community models are based on the outputs from occurrence (occupancy and abundance) models. As well as the LDI predictors shown here, each model also includes residuals of *ME* Miombo extent, *HL* habitat loss, *MAP* mean annual precipitation

The italics indicate short form initials of predictor variables in the model

the posterior estimates. Where more than one species is mentioned together, we provide the mean *Pp* of all species concerned.

Calculations and analysis were undertaken using the statistical software R version 3.4.2 (R Core Team 2017). We used the *vegan* package (Oksanen et al. 2016) to compute species richness, *iNEXT* (Hsieh et al. 2016) for sample-based rarefied species richness, accumulation and survey completeness, and *adespatial* (Dray et al. 2016) for species β-diversities. To fit the Bayesian models, we used the *jagsUI* package (Kellner 2015). We followed the R scripts in Kéry and Royle (2016) for constructing the metacommunity models. Figures were drawn using *ggplot2* (Wickham 2009).

Results

Survey effort and model selection

We measured a total of 1215 tree stems and recorded 864 mammal occurrences (from 1693 trap-nights) belonging to 88 and 21 species, respectively. Sample-based species accumulation showed that mammals reached a clear asymptote while trees did not, although both taxonomic groups attained significant survey completeness > 95% (SI Fig. 4).

All models obtained sufficient convergence and had low Monte Carlo error (Gelman and Rubin 1992). For mammal occupancy, the model with quadratic and cubic terms of LDI ($\text{LDI} + \text{LDI}^2 + \text{LDI}^3$) produced the lowest $\widehat{D}$ (Table 2) and was selected as the best model. For tree abundance, the 2nd-degree model ($\text{LDI} + \text{LDI}^2$) without LDI^3 had the lowest $\widehat{D}$ and hence was selected as the more plausible model. In the case of the community models for both trees and mammals, the model selection was unclear as there were only minor differences between the three model structures as estimated by $\widehat{D}$ (Table 2). For simplicity's sake, we thus selected the community model structure of trees and mammals based on whichever model structure was agreed by their respective occurrence models because the community models use the outputs from the occurrence models (see Table 1). So, if the quadratic abundance model is preferred for tree abundance (model 1), it makes sense to use quadratic models for tree community attributes (richness etc.; models 3–5); likewise, the 3rd-degree model was selected for mammal community attributes as it was the best model for mammal occupancy.

Effects of land use change on α- and β-diversity

The overall effects of LUC on species and community level diversity metrics were non-linear and there were some differences between taxonomic groups. The species richness of both trees and mammals showed a non-linear relationship with LDI: increasing from low (<0.3) to moderate (0.3–0.7) and declining at high LDI values (>0.7, $Pp=0.9$; Figs. 2 and 3). For trees, the species richness began to decrease at lower LDI than that of mammals (0.6 vs 0.75).

The nestedness of tree communities reduced ($Pp=0.99$) at low LDI, stabilised at moderate LDI, and declined again at high LDI. This was matched with a decline and an increase in tree species turnover at low and high LDI values ($Pp=0.89$). On the other hand, mammals had reduced turnover ($Pp=0.95$) and increasing nestedness ($Pp=0.72$) in response to LDI.

The predictors of diversity other than LDI had varied effects: tree species richness showed a positive response to HL_{resid} ($Pp=0.85$) and had a negative association with ME_{resid} ($Pp=0.95$) and MAP ($Pp=0.97$). Tree species turnover increased with ME_{resid} ($Pp=0.87$) and MAP ($Pp=0.98$) and decreased with HL_{resid} ($Pp=0.95$). In mammals, ME_{resid}, HL_{resid} and MAP were negatively associated with species richness ($Pp=0.86$) and positively related to turnover ($Pp=0.81$). The species richness, turnover and nestedness of mammals and trees and their model residuals had weak and statistically non-significant spatial autocorrelation (Moran's $I=0.05$ and 0.09, $p>0.1$ for mammals and trees, respectively).

Overall, the picture is clear. At high LDI, tree communities lost species richness but increased in within-site dissimilarity, i.e., subtractive heterogenisation. In contrast, at

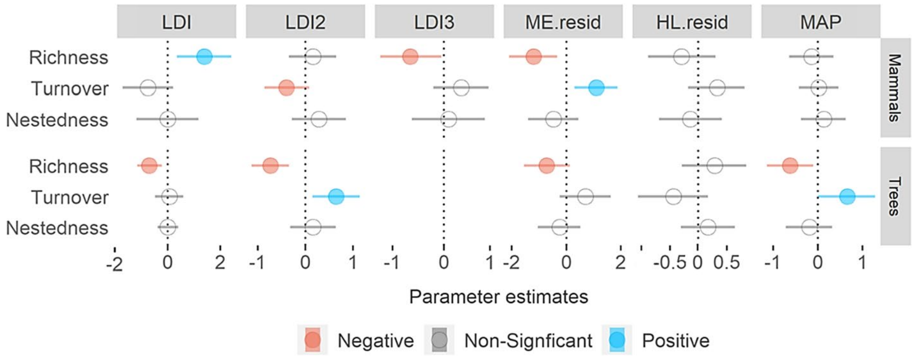

Fig. 2 The effect size of the predictors of community diversity metrics., Circle positions represent scaled coefficients (proportion of deviation from the intercept), horizontal lines on the circles indicating 95% CI, and colours showing the direction of the effect. Increasing LDI was associated with reduced species richness of trees and mammal species, reduced mammal turnover and increased tree species turnover. *LDI* Land Division Index, *ME* Miombo extent i.e., habitat quantity, *HL* habitat loss, *MAP* mean annual precipitation. For HL and ME, the residuals of an LDI ~ ME and LDI ~ HL model are used to account for the correlation between these predictors

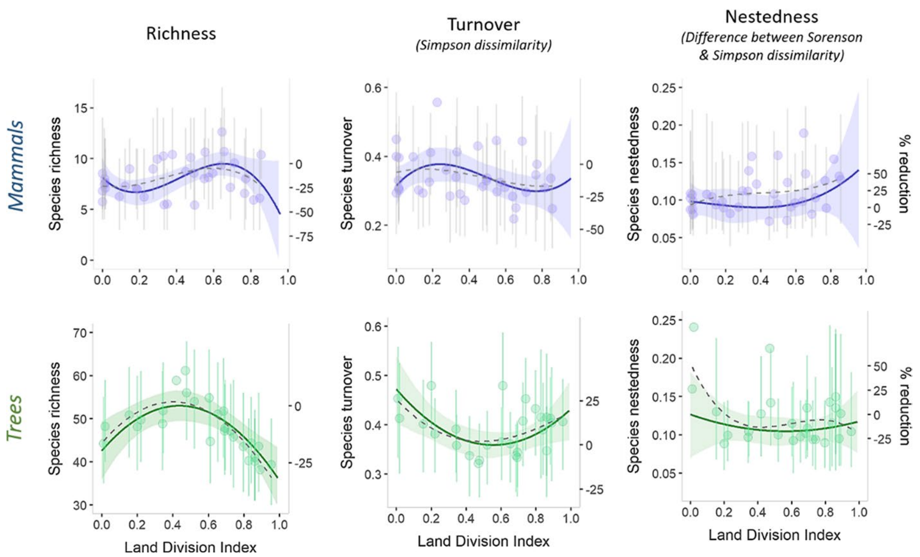

Fig. 3 Community-level responses of trees and mammals to agricultural expansion (represented by the Land Division Index). The circles denote point estimates with 95% CRIs (vertical lines) from the meta-community occupancy models. The dashed line is a spline smooth based on those point estimates. The blue and green lines are predicted species diversity responses—richness, turnover and nestedness, from the regression model that considers the estimation error (posterior standard deviations) of the point estimates from the meta-community occupancy models. The shaded area represents the 95% CRI of the model-predicted species diversity responses. Land Division Index is associated with declining species richness of both trees and mammals and has different effects on β-diversity—compositional drift in trees and biotic homogenisation in mammals at high LDI values

high levels of LDI, mammals lost species richness and became more similar in species composition—subtractive homogenisation.

Effects on species occurrence

At the species-level, the effect of agricultural expansion on tree communities was largely negative as most tree species had reduced abundance at higher levels of LDI. The negatively affected tree species included dominant miombo species such as *Brachystegia spiciformis* and *B. boehmii,* and non-dominants such as *Pterocarpus angolensis*, *Sclerocarya birrea*, *Combretum apiculatum* and *Albizia adianthifolia*. Increasers included *Annona senegalensis* (prized for its edible fruit), *Mangifera indica* (planted mainly by humans), *Terminalia sericea,* and *Piliostigma thonningii* (a rapidly growing species that colonises clearings and fallow; SI-Fig. 6). For mammals, the probability of occupancy of all species responded non-linearly: it increased at low to intermediate LDI and reduced after high LDI. The species which had significantly higher occupancy at intermediate LDI consisted of elephant shrews, murids (African spiny mouse, *Acomys sp.*, and thicket rat, *Grammomys* sp.) and species that are known to survive well in human-influenced, disturbed and fragmented landscapes (lesser bushbaby, *Galago moholi*, and rusty-spotted genet, *Genetta maculata*). On the other hand, species such as the African giant rat *(Cricetomys gambianus*), Bush hyrax *(Heterohyrax brucei),* and South African hedgehog *(Atelerix frontalis),* in addition to the previously mentioned African spiny mouse, showed a significant negative reduction in occupancy at high LDI (see species level coefficient plots in SI-Fig. 7).

In summary, LDI was associated with the reduced abundance of a majority of tree species and lower occupancy of all mammal species, thus creating more species losers than winners. The effect of the other predictor variables was minor, and HL_{resid} and MAP had poor posterior probabilities ($Pp < 0.6$) and were associated with an almost equal number of species winners and losers; ME_{resid} had a significant negative association with most mammal species. Plots of species-level model coefficients with 95% CI of trees and mammals are provided in the SI.

Discussion

Fragmentation: few winners and many losers

Our results underline the disruptive effects of agricultural expansion on species populations and diversity. We found that agricultural expansion was associated with a decrease in population size in 75% of species, indicating the '*more species losers than winners*' paradigm (McKinney and Lockwood 1999). The tree species that declined were primarily miombo dominants and species used by humans for timber and firewood. While the decline of miombo species may be related to the random loss of species through habitat loss, the decline of livelihood-relevant species may be driven by the selective over-harvesting along the edges of habitat patches.

For most mammal species, occupancy was highest at intermediate levels of fragmentation and woodland cover. The species positively associated with the intermediate levels of fragmentation consisted of the rapidly breeding *Elephantulus* species and murids and generalist predators. Assuming that the less divided woodland landscapes are relatively undisturbed by humans, our finding of positive effects of intermediate fragmentation is similar to the results Caro (2001) obtained in miombo woodlands of western Tanzania and studies in other ecosystems (Andrén 1994; Conde y Vera and Rocha 2006; Cusack 2011; Rich et al. 2016). By showing that even after the positive effect of the intermediate disturbance, most mammal /tree species declined in occupancy/abundance at higher levels of land use and associated fragmentation, our results expand upon the existence of non-linear relationships and possible thresholds observed in forests (Andrén 1994; Hill and Caswell 1999; Mönkkönen and Reunanen 1999; Pardini et al. 2010).

Declines in species richness

As expected, the species richness of both trees and mammals reduced with agricultural expansion-led fragmentation. Both groups showed a hump-shaped pattern of species richness in response to fragmentation—species richness increasing at the intermediate levels of fragmentation (30–70%) but declining beyond a fragmentation (~70%) and habitat quantity threshold (~30%). The intermediate disturbance hypothesis could explain the non-linear patterns. The intermediate levels of fragmentation and habitat loss would have created landcover heterogeneity which is associated with an increase in the landscape-wide species pool due to niche complementarity (Pardini et al. 2010; Tscharntke et al. 2012). In the case of tree communities, an increase in diversity at intermediate levels despite loss of miombo trees species is possibly due to colonisation of new species as a result of tree planting or selection by humans (e.g. mango) or regeneration of early-successional species as observed elsewhere (McNicol et al. 2015; Yeboah and Chen 2016). The non-linear response of mammals may be due to their ability to move and exploit resources in multiple fragments when the fragmentation is low and habitat patches are within reach (Pardini et al. 2005). However, as the landscapes become more fragmented and increasingly homogenous, the size of remaining woodland patches and woody cover in the landscapes reduce, leading to increased competition and predation, and a subsequent decline in mammal species richness (Magrach et al. 2014).

At the extreme levels of agriculture expansion, comparable to the land use endpoints used in the global syntheses (Murphy and Romanuk 2014; Newbold et al. 2015, 2017), we found > 40% decline in species richness (− 49 ± 19% after 95% fragmentation). This loss is much higher than the African average of 21.6% in Newbold et al. (2017) and the "tropical average" of 25.6% in Murphy and Romanuk (2014). A possible reason why we found higher biodiversity losses is that our study takes into account the landscape-scale relationships between biodiversity and land use change. In contrast, most studies included in the global syntheses of biodiversity and land use change have focussed on patch-scale observations of biodiversity responses to land use. In these patch-scale observations, biodiversity losses may be influenced and mitigated by landscape heterogeneity and associated source-sink process (Kormann et al. 2018), and hence, underestimated.

The majority of African savanna landscapes, however, have not undergone complete patch-to-matrix transformation (McNicol et al. 2018). A rough indication of the current impact of intermediate transformation is given by combining all our sites above 25% fragmentation. Here, the reduction in species richness was ~ 13 ± 6%. This estimate is just slightly below the global average of 13.6% reduction in local species richness under complete patch-to-matrix conversions suggested by Newbold et al. (2015), and considerably lower than the averages from the global syntheses we discussed above. This study provides a more representative depiction of the current state of biodiversity change in the miombo, which is still at the intermediate stages of land use transformation.

Taxonomic heterogeneity in β-diversity responses

The β-diversity response to agricultural expansion, in contrast to the alpha-diversity response, differed between the two taxonomic groups. Tree communities underwent compositional drift in highly fragmented landscapes, possibly because of contrasting successional pathways following random extinctions due to habitat loss. The ubiquitous miombo woodland dominants declined, and fast-growing secondary vegetation and successional species became more abundant. Such combined effects of turnover and species loss results in *subtractive heterogenisation—loss of species richness with increased dissimilarity between communities* (McGill et al. 2015; Socolar et al. 2016), and is represented in our result by the increase in the turnover and loss of the nestedness component of tree β-diversity. This finding corroborates similar studies from African woodlands (McNicol et al. 2015) and other ecosystems (Laurance et al. 2006; Arroyo-Rodríguez et al. 2013).

On the other hand, mammal communities became more similar in community composition in landscapes dominated by a agricultural matrix and fragmented woodland patches. Specifically, they underwent niche-based deterministic reduction leading to a strong *subtractive homogenisation—loss of species richness with reduced dissimilarity between communities* (McGill et al. 2015; Socolar et al. 2016). This pattern in mammals is mainly because, as the woodland habitat in the woodland-agriculture mosaic reduced and became fragmented, disturbance-sensitive species with preferences for woodland habitats declined, and a nested subset of ubiquitous disturbance-tolerant species survived in the non-woodland matrix. Also, species such as the African giant rat (*Cricetomys gambianus*), rock hare (*Pronolagus rupestris*) and the common duiker (*Sylvicapra grimmia*) are preferentially hunted using dogs and traps (personal observation and Timberlake et al. 2009), which leads to a loss of these species across all fragmented landscapes.

The contrasting patterns of β-diversity observed in this study will have implications for maintaining biodiversity in these human-modified landscapes. Tree communities which experienced biotic heterogenisation are more likely to recover as species needed for recovery are maintained in the meta-community species pool (Tscharntke et al. 2012). Mammal communities experience more disruptive effects of fragmentation. Therefore, they would require more focused land and conservation management policies to maintain the habitat structure above the thresholds that we will discuss below.

Limitations

It is worth noting that the effect of fragmentation on individual species may be confounded by local contexts (Ewers and Didham 2006). The remaining woodland patches in the undivided landscapes that we studied may have gone through selective harvesting of trees and defaunation due to hunting for bushmeat (Timberlake et al. 2009; Zach et al. 2016), which may explain the lower densities of trees and mammals in these areas. The observed nonlinearity in responses of communities in this study would, in that case, simply be the result of multiple filtration processes: harvesting and hunting causing declines in population size across all species (Reyna-Hurtado and Tanner 2007; Hegerl et al. 2015), and fragmentation leading to selection of smaller mammals, generalists and domesticated species (Jamoneau et al. 2012; Keinath et al. 2016). For a clearer understanding of the effect of fragmentation and habitat loss in the region, the biodiversity of undisturbed, less divided and large miombo woodland patches in similar climatic and topographic conditions should be the reference point for community size and integrity. We excluded the high-elevation landscapes with relatively undisturbed woodland areas, as they were inaccessible and not preferred for farming. But these woodland patches, although mainly non-miombo, maybe the last remaining undisturbed refuges supporting fauna that have migrated from the disturbed and fragmented landscapes. Accounting for the role of these high elevation habitats will be essential to understand and accurately predict biodiversity change in this region.

In terms of model selection, we used $\widehat{D}$ values as an indicator of deviance and model fit, and selected models with the lowest penalised deviance as the most plausible model. For community models, however, the deviance difference among the models was small, indicating that models were similar and that any polynomial model could be valid for community-level metrics. However, since the community-level metrics used in the community models were derived from the occupancy models, we simply selected the community models' structure to match the occupancy models. A strength of the approach here is that we account for heterogeneity in species detection, which is not often done in the land use-biodiversity literature, which primarily estimates diversity (richness and composition) purely based on plot-level observations of diversity.

Lastly, this study is a space-for-time substitution; therefore, generalisation and validation of the results and the thresholds by undertaking multi-season and multi-spatial scale studies should be the focus of future research.

Conclusion

Our study demonstrates that fragmentation and the associated loss of habitat cover due to agricultural expansion in the miombo results in reductions in the diversity, abundance and occupancy of the majority of tree and mammal species. Severe reductions in species richness and population size were observed at the highest levels of fragmentation and habitat loss. However, as most African savanna landscapes are still at the intermediate levels of land use intensification, the extent of local biodiversity loss in the African savanna ecosystems has not reached these highest levels.

We show that different taxonomic groups respond differently to land use intensification. Trees undergo subtractive heterogenisation with a reduction in species richness and increased species dissimilarity. In contrast, mammal communities experience subtractive homogenisation due to decreased species richness combined with a loss of species dissimilarity. Finally, we also show that the effects of fragmentation on biodiversity may be non-linear: beyond ~ 75% fragmentation, the impact of fragmentation switches from positive to negative.

These results underline the ecological importance and conservation value of mosaic landscapes in African savannas, especially those with intermediate fragmentation levels. They also suggest that to maintain savanna biodiversity above safe levels (Hooper et al. 2012), the landscape must contain > 25% habitat cover with < 75% fragmentation. However, this does not mean that the savanna landscapes can be modified to those levels without consequences: the effects on species compositions of both groups—trees and mammals—are noticeable even at low levels of intensification. Furthermore, this study used human-utilised landscapes as a baseline and, therefore, the effects on biodiversity could be much more severe if comparisons are made with less modified landscapes.

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Author contributions HT, CR, and CLP conceived the ideas and designed the methodology. HT collected the mammal data and performed the fragmentation analysis. EW collected the tree data. MC facilitated fieldwork and data collection. CR prepared the biomass maps. HT collated and analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication. The authors declare no conflict of interest.

Data avalability Data and R code used in this study are available from the Git Repository. https://github.com/hgtripathi/2021-GurFrag

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