# The present and future of tropical grassland and savanna ecosystems in Africa under land-use change

Tim Newbold[1], Elizabeth H. Boakes[1], Samantha L. L. Hill[2,3], Michael B. J. Harfoot[2], Ben Collen[1]

[1]Centre for Biodiversity and Environment Research, Department of Genetics, Evolution and Environment, University College London, London WC1E 6BT, UK.
[2]United Nations Environment Programme World Conservation Monitoring Centre, Cambridge CB3 0DL, UK.
[3]Department of Life Sciences, Natural History Museum, Cromwell Road, London SW7 5BD, UK.

Corresponding author: Tim Newbold (t.newbold@ucl.ac.uk)

ORCID IDs:

Tim Newbold: 0000-0001-7361-0051

Elizabeth Boakes: 0000-0003-3609-4259

Ben Collen: 0000-0003-2564-4243

## Abstract

The world is currently experiencing a period of rapid, human-driven biodiversity loss. Over the past decade, numerous metrics for biodiversity have been used to create indicators to track change in biodiversity. However, our ability to predict future changes has been limited. In this study, we use two very different models to predict the status and possible futures for ecological assemblages in African tropical grasslands and savannas. We show that local biodiversity often responds more to land use in African grasslands and savannas than in other biomes. We estimate that average losses of biodiversity are already between 9.7 and 42.0%, depending on the model and measure of biodiversity used. If current socio-economic trajectories continue ('business-as-usual'), the likely associated land-use changes are predicted to lead to a further 5.6-12.3% loss of biodiversity. In contrast, a scenario that assumes more efficient use of agricultural areas (thus requiring a smaller total area) could be associated with a partial reversal – of as much as 3.2% – of past losses of biodiversity. While the agriculture that causes the majority of land-use change is an important source of economic growth, projections of the effect of land-use change on biodiversity can allow for more informed decisions.

## Introduction

Biodiversity is declining globally, under increasing pressure from a number of different human activities (Tittensor et al. 2014). Among the pressures affecting biodiversity, land-use and land-cover change (henceforth referred to as ‘land-use change’) have had the most profound impacts, at least at a global scale (Green et al. 2005). There is an increasing interest in understanding changes in the biodiversity of ecological assemblages and ecosystems at a local scale, because the land-use interventions that can slow and reverse biodiversity loss operate at this scale. Understanding changes in local-scale biodiversity is also likely to be important when considering the functioning of ecosystems (Hooper et al. 2012, Dornelas et al. 2014, Newbold et al. 2016a).

Broad-scale models can help to understand how land use affects the biodiversity of ecosystems, and to predict future changes. While these inevitably have uncertainties caused by generalizing over wide domains, they are an important tool for understanding and predicting biodiversity change. Most such models have so far been statistical, based on collections of data on biodiversity from the published literature (Alkemade et al. 2009, Gibson et al. 2011, Newbold et al. 2015, Visconti et al. 2016). Global-scale statistical models suggest that local ecological assemblages have lost on average nearly 14% of the species and nearly 11% of the individual organisms that would have been present in the absence of major human land-use change (Newbold et al. 2015). A limitation of statistical models is that they rely predominantly on data available in the published literature. These data are typically biased spatially and taxonomically, and even databases that were collated so as to be as representative as possible have residual biases (e.g. Baillie et al. 2008, Collen et al. 2009, Hudson et al. 2014; Table 1). Furthermore, the data often consist of spatial comparisons and lack a time component, precluding a consideration of the dynamics of biodiversity change and how this relates to transitions between particular combinations of land use.

Recently, mechanistic models of the dynamics of ecological assemblages and their ecosystems (Cramer et al. 2004, Caron-Lormier et al. 2009, Evans et al. 2013, Purves et al. 2013, Harfoot et al. 2014b) have been developed. These models are based on a mathematical representation of underlying ecological processes. As such, their data requirements are smaller (only needing data to parameterise the ecological processes) and they can represent organisms and ecosystems for which little or no data exist.(Cramer et al. 2004, Bondeau et al. 2007)(Purves et al. 2013, Harfoot et al. 2014b) While attempts to develop mechanistic models of ecosystems have had reasonable success in capturing observed properties of ecosystems in the absence of human impacts (Harfoot et al. 2014b), their use for understanding human impacts on ecosystems remains limited to small spatial scales (Caron-Lormier et al. 2009, Bartlett et al. 2016), at least in the terrestrial environment.

Tropical grassy biomes (grasslands and savannas) present an interesting case study for understanding human land-use impacts on ecosystems. Globally, they are estimated to have experienced a much greater extent of conversion from natural to human land uses compared to tropical forests, and indeed most other biomes (Boakes et al. 2010, Ellis 2011), although there is uncertainty over the distinction between grazed natural grassland and true pasture in these estimates (see below). Future conversion to agriculture is likely to be an important pressure on biodiversity in African grasslands and savannas, given that this area is estimated to contain 60% of remaining cultivable land (Roxburgh et al. 2010). Moreover, tropical grassy biomes are relatively poorly represented in global biodiversity databases (e.g. Collen et al. 2009, Hudson et al. 2014), and are much less often considered in ecology and conservation than are tropical forests (Bond and Parr 2010). Global statistical models of biodiversity’s response to land use (e.g. Alkemade et al. 2009, Newbold et al. 2015) assume that the response is the same everywhere. However, the sensitivity of ecological assemblages to land use varies across space (Cowlishaw et al. 2009, Fritz et al. 2009, Newbold et al. 2016b). It is unclear whether the assemblages in tropical grassy biomes respond more or less to land use than those in other biomes. On one hand, their biodiversity has interacted with humans for millennia (at least in Africa; e.g. Sinclair and Norton-Griffiths

1979). On the other hand, the onset of intensive, industrialized agriculture is likely to present conditions not typical of the small-scale agriculture practised in the past, and tropical grasslands and savannas are known to be comprised of a distinct set of species with a high degree of endemism (Bond and Parr 2010).

In this study, we assess the effect of land use on the local diversity of ecological assemblages in African tropical grassy biomes, using both a data-driven statistical model and a mechanistic ecosystem model (Supplementary Figure 1).(Cramer et al. 2001) (Oliver and Morecroft 2014) We ask: 1) to what extent the assemblages of Africa's tropical grassy biomes respond to land use, and whether this response is different to the global average response; 2) what the impact of past land use has been on the diversity of ecological assemblages; 3) what future changes to ecological assemblages might be under contrasting scenarios of land-use change; and 4) whether the two different models generate similar predictions of land-use impacts.

## Methods

### *The Statistical Model*

The statistical model was based on the database of the PREDICTS (Projecting Responses of Ecological Diversity in Changing Terrestrial Systems) Project (Hudson et al. 2017; full details are given in the supplementary material). These data were drawn from published studies, each of which describe the abundance (or for 17% of records only occurrence) of species sampled at different levels of human pressure (generally different land uses or land-use intensities). In the data from African grassy biomes (a subset of the global dataset), all measures of abundance were of individuals or groups (even for plants). Land use was classified based on the description of the habitat given in the source paper or provided by the authors of the source paper (Supplementary Table 1). Land use was classified as primary vegetation (natural vegetation with no recorded past destruction of the habitat), secondary vegetation (recovering natural habitat after past destruction), cropland or pasture (too few plantation-forest or urban sites were available to include in the models presented here). This land-use classification is coarse, but was selected so that the models could be generalized over large areas, and for correspondence with available land-use projections. Importantly for this study, pasture describes sites regularly or permanently grazed; whereas sites with irregular grazing, insufficient to substantially alter the habitat architecture, were classified as primary or secondary vegetation. Sites where fire occurs at natural frequency were classified as primary vegetation. In order to understand the effects of slight, small-scale human disturbances – such as irregular grazing or altered fire regimes – within natural (primary and secondary) habitat, we distinguished between minimally and substantially used natural vegetation.(Hudson et al. 2014) The baseline for the models and projections – minimally used primary vegetation – does not preclude some human disturbances, of small extent and magnitude; indeed, there are unlikely to be any areas in African grassy biomes that have experienced no human influence of any kind, which will make our estimates of biodiversity change conservative. Furthermore, primary vegetation does not have to be the potential climax vegetation, if vegetation is maintained in a non-climax state through natural disturbances, such as fire or herbivory. This coarse abstraction of land use, and a degree of subjectivity in the classification, will mean that some potentially important details are lost (land-use classification is particularly challenging for grasslands); but this abstraction is necessary in order to develop broad-scale models.

We developed a model of sampled species richness and sampled total abundance (of all species sought by a given study), as a function of land use (this model does not consider the effects of climate change), using data from the tropical grassy biomes of Africa. These data comprised 170,878 records, for 1,830 uniquely named taxa (374 plants, 919 invertebrates and 537 vertebrates), from 922 sites. The sites were distributed very patchily (representing only 4 of the 26 ecoregions in African tropical grassy biomes; Figure 1a; Supplementary Figure 2a), but showed a reasonable representation of land uses (231 in minimally used primary vegetation, 50 in substantially used primary vegetation, 36 in minimally used secondary vegetation, 33 in substantially used secondary vegetation, 378 in cropland, and 194 in pasture). We fitted generalized linear mixed-effects models with land use as a single categorical fixed effect, and random effects representing the identity of the source study – to capture the wide heterogeneity in sampled taxa, and in the sampling methods and effort among studies – and the spatial blocking structure of sites within studies. To assess whether biodiversity in tropical grassland biomes is responding to land use differently to biodiversity globally, we also developed models using the global data across all biomes (2.8 million records, for over 45,000 uniquely named taxa, from 17,064 sites; Supplementary Figure 2b).

To project the models of species richness and total abundance onto estimates of current and future land-use patterns, we followed the methods in Newbold et al. (2015). Mapped estimates of land use were taken from the harmonized land-use data associated with the Representative Concentration Pathways scenarios (Hurtt et al. 2011). These data describe the proportion of each half-degree grid cell occupied by the six above-named land-use classes. The model-estimated intactness of biodiversity in each land use was applied, and then values averaged across the land uses in each grid cell, weighted by proportional area. For details of the land-use projections used, see ‘Land-use Scenarios’ below.

### *The Mechanistic Ecosystem Model*

As an alternative way of understanding human land-use impacts on ecosystems, we used the Madingley general ecosystem model, which represents all photoautotrophic organisms and all heterotrophic organisms with body masses larger than 10 µg. This model is described in detail elsewhere (Harfoot et al. 2014b). Briefly, organisms are divided into functional groups: on land, divisions are made between trophic levels (autotrophs, herbivores, omnivores and carnivores), between endotherms and ectotherms, and between semelparous and iteroparous reproductive strategies. Organisms are also characterized by their body mass (juvenile, adult and current body masses).Purves et al. 2013)

The dynamics of plants are modelled using a terrestrial carbon model, where ecological processes are modelled, directly or indirectly, as a function of climate (Smith et al. 2013b). The plant model was chosen because future projections of the driving climate variables are readily available. Non-climatic factors important in shaping grassland/savanna plant dynamics, such as fire, are captured implicitly to the extent that they correlate with climatic variables (Smith et al. 2013b). However, explicit representation of these processes in future might allow better predictions for grasslands and savannas Scheiter and Higgins 2009.

The model has been shown to capture observed properties of individual organisms and the coarse structure of ecosystems reasonably well under environmental conditions without human impact, especially in grassland ecosystems (Harfoot et al. 2014b). To simulate land-use impacts in the model, we removed from the model plant biomass calculated as a certain proportion of net primary production, following the Human Appropriation of Net Primary Production (HANPP) paradigm (Haberl et al. 2007). We used published data on HANPP for the year 2000, compiled based on statistics on permanent agriculture and forestry (excluding wood-fuel harvesting), and estimates of global spatial patterns of land use and soil degradation, excluding the effects of shifting cultivation and vegetation loss from fire (important limitations in the application of these estimates to grassland/savanna systems) (Haberl et al. 2007). To project HANPP estimates, we developed simple spatial models as a function of the total areas of cropland, pasture and urban land use within each cell – using the same HYDE land-use data (Hurtt et al. 2011) as described above – and UN subregion (to control for some of the socio-economic factors that might drive spatial differences in human use of the land). These models explained a substantial proportion of the estimated spatial variation in HANPP ($R^2$ values were 0.42 for land-use losses and 0.53 for harvest losses). The spatial models of HANPP were then applied to the current and future land-use projections (for details, see ‘Land-use Scenarios’ below).

*Land-use Scenarios*

At a global scale, the availability of land-use scenarios is limited. The most consistent scenarios are those produced by the Integrated Assessment Models (Hurtt et al. 2011). For reconstructions of historical land use, the two principal reconstructions are HYDE (e.g. Klein Goldewijk et al. 2011) and KK10 (e.g. Kaplan et al. 2011). We use the results from HYDE because these results form part of the harmonized land-use database describing both past and future changes (Hurtt et al. 2011). By 2005, the HYDE scenario estimates that there had been substantial losses of natural vegetation in African tropical grasslands (Supplementary Figure 3a), with replacement by human-dominated land uses (Supplementary Figure 3d). Consequently, a substantial biomass of vegetation was removed from ecosystems (Supplementary Figure 3g), which we assume becomes unavailable for herbivores.

There are a greater number of future projections of land use available. Here we use the projections associated with the Representative Concentration Pathways (RCP) scenarios, because they provide the most commonly used set of land-use estimates that are consistent across broad spatial scales and multiple socio-economic scenarios (Hurtt et al. 2011). Among the future scenarios, we focus on the MESSAGE and MINICAM projections as opposite extremes of land-use change, and thus of expected changes to biodiversity. The MESSAGE scenario is often assumed to be the outcome of a ‘business-as-usual’ trajectory (Burrows et al. 2014, Newbold et al. 2015), and is most consistent with a continuation of current trends in emissions (Oldfield and Steffen 2014). This scenario is associated with a growth of the human population to 12 billion by 2100, a large degree of conversion of natural habitats to agricultural uses (Supplementary Figure 3c,f), and a global average temperature rise of approximately 4°C by 2100 (Hurtt et al. 2011). Our spatial models (see above) estimate that the predicted land-use change in this scenario will lead to a substantial reduction in plant biomass available to herbivores (Supplementary Figure 3i). Globally, this scenario is expected to have the most negative impact on biodiversity of the RCP scenarios for biodiversity (Newbold et al. 2015). In contrast, the MINICAM scenario assumes a slower growth in the human population (8.7 billion by 2095), and more efficient use of agricultural land (thus requiring a smaller area) (Hurtt et al. 2011), leading to the decreases in human-dominated land uses (Supplementary Figure 3e). Our spatial models (see above) estimate that the decrease in the area of human land uses will lead to a decline in the average plant biomass extracted by humans from ecosystems. The MINICAM scenario is associated with a 1.75°C rise in global average temperatures by 2100 (Hurtt et al. 2011) and is expected to have more positive outcomes for biodiversity than the MESSAGE scenario, at least in terms of land-use impacts (Newbold et al. 2015).

Like all broad-scale land-use scenarios, those associated with the RCPs have limitations (Harfoot et al. 2014a). An important limitation for studies of grasslands and savannas is the distinction between natural grassland and pasture. The harmonized land-use scenarios that were used in this study to estimate human land-use impacts on ecosystems suggest that there is a large expanse of pasture in Africa in the present day. The estimates of the Human Appropriation of Net Primary Production (HANPP; Haberl et al. 2007), which were used as the basis for estimating land-use impacts in the mechanistic ecosystem model, also predict a large loss of vegetation to humans in some (but not all) of the same places. It is likely that some of these places represent areas of natural vegetation with low levels of grazing (classified in the models as primary/secondary vegetation). This is a key uncertainty in the projections made by all broad-scale biodiversity models.

### *Model Outputs*

Each of the two models is able to produce a different suite of output metrics, reflecting their different strengths. For the statistical model, we made estimates of the intactness of ecological assemblages in terms of species richness and total abundance. For the mechanistic general ecosystem model, we made estimates of the intactness of the total abundance (density of individuals) of heterotrophic organisms (plant abundance cannot be estimated because plants are modelled as stocks of biomass rather than individual organisms) and total biomass of all organisms (including plants). Because the general ecosystem model is based on broad functional types, it cannot yet make predictions about species richness. While the total abundance of a community is not particularly informative for conservation, it is a useful (and practical) proxy measure when considering changes in ecosystem function (Steffen et al. 2015). We mapped projections for each of these metrics across all tropical grassy biomes within Africa.

### *Data and Code Availability*

The data underlying the statistical model of biodiversity are publicly available from the Natural History Museum's data portal at http://dx.doi.org/10.5519/0066354 (Hudson et al. 2016). The code for the Madingley Model can be downloaded from https://github.com/Madingley/C-sharp-version-of-Madingley.

## Results

### *Do the Ecological Assemblages of Tropical Grasslands Respond More to Land Use Than Those in Other Biomes?*

The statistical models suggest a stronger response of abundance to land use in tropical grasslands compared with the average across all biomes. An exception to this pattern was seen for natural vegetation (primary and secondary) subject to substantial human use. In African tropical grassy biomes, natural vegetation used substantially by humans contained greater total community abundance than minimally used natural vegetation (Figure 1b). The response of species richness to land use was similar in tropical grasslands and worldwide, except in pasture, to which the biodiversity of tropical grassy biomes was shown to be disproportionately sensitive (Figure 1c).

*The current status of African tropical grasslands*

We estimate that by 2005 there had been substantial changes to the diversity of ecosystems in African tropical grassy biomes, as a result of land-use change (Figure 2). The statistical model of biodiversity responses to land use suggests that these biomes had lost on average 21.6% of species richness and 42.0% of the total abundance of organisms. Change has been fairly consistent over time, but if anything steepest in recent decades (Supplementary Figure 4). The magnitude of changes predicted by the general ecosystem model was much smaller. Specifically, the model predicted that ecosystems had lost on average 9.7% of the total abundance of animal organisms and 15.4% of the total biomass of all organisms (including plants). The projections made by the two models were spatially similar in broad terms, but the congruence was only moderate (Figure 2). Notable areas of disagreement were in the Horn of Africa and northern Namibia/southern Angola.

*Potential futures for African tropical grasslands*

A continuation of current socio-economic trajectories (‘business as usual’), leading to land-use changes corresponding most closely to the MESSAGE scenario, is predicted to lead to further changes in the biodiversity of ecological assemblages and ecosystems under both models (Figure 3). The statistical model of biodiversity predicts further losses of 5.6% of species richness and 12.3% of the total abundance of organisms by 2100, at a similar rate of loss to recent decades (Supplementary Figure 4). The general ecosystem model predicts a further 6.8% loss of abundance and a 10.5% loss of biomass. In contrast, under the

MINICAM scenario, a slowing in the rate of loss of primary vegetation and a rapid increase in recovered natural (secondary) vegetation in African tropical grassy biomes is projected, through more efficient agriculture and thus abandonment of cropland and pasture (Thomson et al. 2011). In African tropical grasslands/savannas, this leads to a 1% increase in species richness and a 3.2% increase in total abundance according to the statistical model (Figure 4; Supplementary Figure 4), and increases of 2.2% of total abundance and 2.8% of total biomass according to the general ecosystem model (Figure 3). As with the predictions of current status, the future projections made by the two models showed broad congruence, but with significant areas of disagreement (Figure 3).

## Discussion

Our results suggest that human land-use change has strongly influenced the local biodiversity of ecosystems in Africa's tropical grassy biomes.(Cramer et al. 2004, Bondeau et al. 2007) and restricted to small spatial scales Caron-Lormier et al. 2009, Bartlett et al. 2016) However, while biodiversity has declined overall, human land use has in some cases had a positive effect, depending on its nature and intensity (Figure 1). The 6% decline in abundance since 1970 predicted by our statistical model was much smaller than the 19% decline of vertebrates estimated by the Living Planet Index for the Afrotropics (WWF 2014), although the latter estimate measures species’ population trends not community abundance, and covers not only grassy biomes but also forests. The increasing influence of humans in future is likely to cause further overall declines in biodiversity. We show that the ecological assemblages of African tropical grassy biomes in many cases respond more to land use compared with other biomes, especially when considering changes in organism abundance. These differences could be due both to differences in the sensitivity of the biota and differences in the characteristics of different land-use systems among biomes.

The loss of individuals, species and biomass from ecosystems might lead to the impairment of certain ecosystem functions (such as productivity, pollination and nutrient cycling) and the resilience of these ecosystem functions (Isbell et al. 2011, Hooper et al. 2012, Oliver et al. 2015, Steffen et al. 2015), although evidence for this comes only from experimental low-diversity grassland communities, not real high-diversity communities. The future of African grassland ecosystems depends upon the human socio-economic pathway adopted. A continuation of ‘business as usual’ in tropical grasslands, although potentially important for economic growth in the region, will likely lead to further declines in biodiversity, while scenarios with mitigation of land-use changes could lead to a partial offsetting of past losses. A similar pattern has already been demonstrated globally with statistical models of biodiversity’s response to land use (Newbold et al. 2015). Here we show that the same pattern holds for tropical grassy biomes in Africa, using two very different models of the effect of land use.

The spatial patterns predicted by both models were broadly similar. Both estimated large declines in biodiversity in the past, and continued declines in the future under the MESSAGE scenario, for the Sahel region and in southern Africa. Under the MESSAGE scenario, conversion of natural habitats to agricultural land use is predicted to be very widespread across Africa’s grasslands; an area that comprises 60% of the world’s uncultivated land (Roxburgh et al. 2010). Under the MINICAM scenario, which assumes a slower growth in the human population, and more efficient use of agricultural land leading to decreased areas of cropland and pasture in western African grasslands and in parts of the Sahel region (Supplementary Figure 3), both models predict that past losses might be reversed to some extent. This scenario assumes technological improvements will allow for more efficient use of agricultural land (thus requiring a smaller total area), leading to a rapid restoration of natural (secondary) vegetation. On the other hand, the climate mitigation achieved in the MINICAM scenario is assumed largely to be achieved through afforestation (Hurtt et al. 2011), which could have a strong negative effect on biodiversity. Afforestation for carbon storage is predicted to become a major pressure on Africa's tropical grassy biomes

(Parr et al. 2014), but the land-use projections used here do not adequately represent this. The relative value of afforested grasslands for biodiversity is an important topic for further study. We did not have enough data to consider intensity of use of agricultural areas. Understanding at a broad scale the optimal balance between high-intensity agriculture over a small area and low-intensity agriculture over a wider area also requires further study (Seppelt et al. 2016).

Morin and Thuiller 2009)Although there was broad agreement between the models, there were also notable areas of disagreement, particularly in northern Namibia/southern Angola and in the Horn of Africa. Such differences are important for guiding the future development of broad-scale models, which otherwise can miss important details and processes. Much of the disagreement can be ascribed to the different assumptions about pasture made by each of the models. The average removal of vegetation biomass from pastures under each scenario is much smaller than from cropland (Supplementary Figure 5). Since vegetation removal is the only way that land use impacts ecosystems in the general ecosystem model, estimated changes in areas dominated by pasture were relatively small. In contrast, the statistical model of the response of biodiversity to land use shows pastures to have relatively low species richness and abundance, especially in tropical grassy biomes (Supplementary Figure 3). There are many ways that human land use can affect ecological systems beyond the simple removal of vegetation, such as changes to the architecture of the vegetation, the impact of livestock beyond their grazing, chemical inputs, and pressures associated with land use such as road development and bushmeat hunting. There is a need for future general ecosystem models to account better for these other indirect effects of land use. On the other hand, the projections of land use may overestimate the extent of regularly grazed pasture at the expense of occasionally grazed natural habitat. This latter land-use type was classified as primary vegetation in our statistical model, and was shown to have similar, sometimes higher, biodiversity than ungrazed natural vegetation (Figure 1). This distinction is important for biodiversity and should be considered more carefully in future land-use models.

There were two further key differences between the predictions made by the two models. First, the magnitude of the changes (especially past changes) predicted by the general ecosystem model were smaller than for the statistical model. This is likely partly owing to the differences discussed in the previous paragraph, but there are other differences between the models that might also contribute. Importantly, while the database used in the statistical models is broadly representative of the taxa found in terrestrial ecosystems, including plants, invertebrates and vertebrates (Hudson et al. 2014), there is a bias toward larger-sized species. In contrast, the general ecosystem model simulates all plants and all animals larger than 10 μg. There is some evidence that larger-sized animals respond more strongly to human activities than smaller animals (Gardner et al. 2008, Flynn et al. 2009, Newbold et al. 2013, Birkhofer et al. 2015; but see e.g. Newbold et al. 2015), in which case statistical models based on biodiversity databases biased towards larger species may over-estimate effects of land use. More generally, there is a lack of data on land-use impacts on biodiversity in grasslands and savannas, compared with forests. Gathering a greater number of data, with more even spatial coverage, will allow us to reduce the uncertainty in broad-scale biodiversity models to some extent. The second key difference between the predictions made by the two models is that estimates of changes in total abundance by the general ecosystem model were much more spatially variable than the estimates made by the statistical model. This is probably because the general ecosystem model is a dynamic model capturing feeding interactions among organisms, whereas the statistical model is based on a database of snapshot samples of ecological assemblages. Furthermore, the general ecosystem model captures more representatively the smallest organisms within ecosystems, which have exponentially higher variance in population sizes over time (Cohen et al. 2012).

In this study, we focus on alpha (local) measures of biodiversity. Local diversity is likely to be important for understanding changes in ecosystem function (Hooper et al. 2012), but other measures reflecting the global endangerment of species may be required to gain a full picture of the conservation implications of land-use change. (e.g. Staver et al. 2011) We also focus only on the effects of land use. Tropical grassland biomes also face other pressures, which could add to or interact with the effects of land use. First, climate change is likely to become an increasingly important driver of biodiversity change in the coming decades(Cramer et al. 2001, Scheiter and Higgins 2009) (refs). Tropical grasslands are predicted to experience a relatively high level of absolute temperature increase in future, and soon to experience temperatures beyond the range of recent variability (Mora et al. 2013). Moreover, the C4 grasses that dominate tropical grasslands are predicted to be disproportionately impacted by rising $CO_2$ (Cramer et al. 2001, Midgley and Bond 2015). Consequently, models (restricted to well-known species groups) that consider both land use and climate suggest that tropical grasslands will experience relatively high losses of biodiversity in future (Visconti et al. 2016). Second, fire is an important process in shaping the structure of grassland ecosystems (Knapp et al. 2004), and human activities are altering fire regimes (Reid and Ellis 1995, Fuhlendorf and Engle 2001), which may have important effects on ecological assemblages (Smith et al. 2013a, Kelly et al. 2015). Future climate and land-use change are likely to exacerbate changes to fire regimes. Furthermore, changes in ecosystem structure might influence fire regimes through changes in herbivory levels, but global data currently do not permit a good understanding of this interaction (Lehmann et al. 2014). Models like the general ecosystem model used here, as well as dynamic global vegetation models (e.g. Scheiter and Higgins 2009), present an opportunity to fill this gap. The effect of fire is captured to some extent in the general ecosystem model in that climate-determined fire frequency affects the mortality of plants (Smith et al. 2013b). However, the effects of fire will be much more diverse than this, and the model does not yet capture the interaction between land use and fire frequency. Finally, hunting is an important driver of biodiversity decline in African grasslands and savannas (Lindsey et al. 2013), which was captured only implicitly to the extent that it correlates with land use.(Newbold et al. 2015)(Laurance et al. 2014)

*Conclusions*

We show that human land use has had large effects on the biodiversity of tropical grasslands in Africa (although the distinction between grazed natural vegetation and pasture is a key uncertainty in the projections). Future changes to tropical grasslands will depend on the socio-economic pathways adopted. Regardless of the model type employed, business as usual scenarios are predicted to be accompanied by substantial further changes to ecosystems, while more efficient use of land for agriculture offers the potential of a partial offsetting of past changes. Clearly there are challenges to be faced in selecting pathways of future development and protection, not least because habitat change can have positive consequences for local human communities, and agriculture is a strong source of economic growth. Predictions of the future impacts of these changes will help policy-makers make informed decisions.

## Acknowledgements

We thank Georgina Mace, Neil Burgess and Andy Purvis for their contributions to the ideas behind this paper. This work was supported by a Leverhulme Trust Research Project grant (TN and BC). TN and SLLH were also supported by a grant from the UK Natural Environment Research Council (grant number: NE/J011193/2). TN is also funded by a Royal Society University Research Fellowship.

## References

Alkemade, R. et al. 2009. GLOBIO3: a framework to investigate options for reducing global terrestrial biodiversity loss. - Ecosystems 12: 374–390.

Baillie, J. E. M. et al. 2008. Toward monitoring global biodiversity. - Conserv. Lett. 1: 18–26.

Bartlett, L. J. et al. 2016. Synergistic impacts of habitat loss and fragmentation on model ecosystems. - Proc. R. Soc. London Ser. B, Biol. Sci. 283: 20161027.

Birkhofer, K. et al. 2015. Land-use effects on the functional distinctness of arthropod communities. - Ecography 38: 889–900.

Boakes, E. H. et al. 2010. Extreme contagion in global habitat clearance. - Proc. R. Soc. London Ser. B, Biol. Sci. 277: 1081–1085.

Bond, W. J. and Parr, C. L. 2010. Beyond the forest edge: Ecology, diversity and conservation of the grassy biomes. - Biol. Conserv. 143: 2395–2404.

Bondeau, A. et al. 2007. Modelling the role of agriculture for the 20th century global terrestrial carbon balance. - Glob. Chang. Biol. 13: 679–706.

Burrows, M. T. et al. 2014. Geographical limits to species-range shifts are suggested by climate velocity. - Nature 507: 492–495.

Caron-Lormier, G. et al. 2009. How might we model an ecosystem? - Ecol. Modell. 220: 1935–1949.

Cohen, J. E. et al. 2012. Allometric scaling of population variance with mean body size is predicted from Taylor's law and density-mass allometry. - Proc. Natl. Acad. Sci. U. S. A. 109: 15829–15834.

Collen, B. et al. 2009. Monitoring change in vertebrate abundance: the Living Planet Index. - Conserv. Biol. 23: 317–327.

Cowlishaw, G. et al. 2009. High variability in patterns of population decline: the importance of local processes in species extinctions. - Proc. R. Soc. London Ser. B, Biol. Sci. 276: 63–69.

Cramer, W. et al. 2001. Global response of terrestrial ecosystem structure and function to $CO_2$ and climate change: results from six dynamic global vegetation models. - Glob. Chang. Biol. 7: 357–373.

Cramer, W. et al. 2004. Tropical forests and the global carbon cycle: impacts of atmospheric carbon dioxide, climate change and rate of deforestation. - Philos. Trans. R. Soc. London Ser. B, Biol. Sci. 359: 331–343.

Dornelas, M. et al. 2014. Assemblage time series reveal biodiversity change but not systematic loss. - Science 344: 296–9.

Ellis, E. C. 2011. Anthropogenic transformation of the terrestrial biosphere. - Philos. Trans. R. Soc. London Ser. A, Math. Phys. Eng. Sci. 369: 1010–1035.

Evans, M. R. et al. 2013. Predictive systems ecology. - Proc. R. Soc. London Ser. B, Biol. Sci. 280: 20131452.

Flynn, D. F. B. et al. 2009. Loss of functional diversity under land use intensification across multiple taxa. - Ecol. Lett. 12: 22–33.

Fritz, S. A. et al. 2009. Geographical variation in predictors of mammalian extinction risk: big is bad, but only in the tropics. - Ecol. Lett. 12: 538–549.

Fuhlendorf, S. D. and Engle, D. M. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns. - Bioscience 51: 625.

Gardner, T. A. et al. 2008. Understanding the biodiversity consequences of habitat change: the value of secondary and plantation forests for neotropical dung beetles. - J. Appl. Ecol. 45: 883–893.

Gibson, L. et al. 2011. Primary forests are irreplaceable for sustaining tropical biodiversity. - Nature 478: 378–381.

Green, R. E. et al. 2005. Farming and the fate of wild nature. - Science 307: 550–555.

Haberl, H. et al. 2007. Quantifying and mapping the human appropriation of net primary production in earth’s terrestrial ecosystems. - Proc. Natl. Acad. Sci. U. S. A. 104: 12942–12947.

Harfoot, M. et al. 2014a. Integrated assessment models for ecologists: the present and the future. - Glob. Ecol. Biogeogr. 23: 124–143.

Harfoot, M. B. J. et al. 2014b. Emergent global patterns of ecosystem structure and function from a mechanistic general ecosystem model. - PLoS Biol. 12: e1001841.

Hooper, D. U. et al. 2012. A global synthesis reveals biodiversity loss as a major driver of ecosystem change. - Nature 486: 105–108.

Hudson, L. N. et al. 2014. The PREDICTS database: a global database of how local terrestrial biodiversity responds to human impacts. - Ecol. Evol. 4: 4701–4735.

Hudson, L. N. et al. 2016. Dataset: The 2016 release of the PREDICTS database. in press.

Hudson, L. N. et al. 2017. The database of the PREDICTS (Projecting Responses of Ecological Diversity In Changing Terrestrial Systems) project. - Ecol. Evol. 7: 145–188.

Hurtt, G. C. et al. 2011. Harmonization of land-use scenarios for the period 1500–2100: 600 years of global gridded annual land-use transitions, wood harvest, and resulting secondary lands. - Clim. Change 109: 117–161.

Isbell, F. et al. 2011. High plant diversity is needed to maintain ecosystem services. - Nature 477: 199–202.

Kaplan, J. O. et al. 2011. Holocene carbon emissions as a result of anthropogenic land cover change. - The Holocene 21: 775–791.

Kelly, L. T. et al. 2015. Optimal fire histories for biodiversity conservation. - Conserv. Biol. 29: 473–481.

Klein Goldewijk, K. et al. 2011. The HYDE 3.1 spatially explicit database of human-induced global land-use change over the past 12,000 years. - Glob. Ecol. Biogeogr. 20: 73–86.

Knapp, A. K. et al. 2004. Generality in ecology: testing North American grassland rules in South African savannas. - Front. Ecol. Environ. 2: 483–491.

Laurance, W. F. et al. 2014. Agricultural expansion and its impacts on tropical nature. - Trends Ecol. Evol. 29: 107–116.

Lehmann, C. E. R. et al. 2014. Savanna vegetation-fire-climate relationships differ among continents. - Science 343: 548–552.

Lindsey, P. A. et al. 2013. The bushmeat trade in African savannas: impacts, drivers, and possible solutions. - Biol. Conserv. 160: 80–96.

Midgley, G. F. and Bond, W. J. 2015. Future of African terrestrial biodiversity and ecosystems under anthropogenic climate change. - Nat. Clim. Chang. 5: 823–829.

Mora, C. et al. 2013. The projected timing of climate departure from recent variability. - Nature 502: 183–187.

Morin, X. and Thuiller, W. 2009. Comparing niche- and process-based models to reduce prediction uncertainty in species range shifts under climate change. - Ecology 90: 1301–13.

Newbold, T. et al. 2013. Ecological traits affect the response of tropical forest bird species to land-use intensity. - Proc. R. Soc. London Ser. B, Biol. Sci. 280: 20122131.

Newbold, T. et al. 2015. Global effects of land use on local terrestrial biodiversity. - Nature 520: 45–50.

Newbold, T. et al. 2016a. Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. - Science 353: 288–291.

Newbold, T. et al. 2016b. Global patterns of terrestrial assemblage turnover within and among land uses. - Ecography 39: 1151–1163.

Oldfield, F. and Steffen, W. 2014. Anthropogenic climate change and the nature of Earth System science. - Anthr. Rev. 1: 70–75.

Oliver, T. H. and Morecroft, M. D. 2014. Interactions between climate change and land use change on biodiversity: attribution problems, risks, and opportunities. - WIREs Clim. Chang. 5: 317–335.

Oliver, T. H. et al. 2015. Biodiversity and resilience of ecosystem functions. - Trends Ecol. Evol. 30: 673–684.

Parr, C. L. et al. 2014. Tropical grassy biomes: Misunderstood, neglected, and under threat. - Trends Ecol. Evol. 29: 205–213.

Purves, D. W. et al. 2013. Time to model all life on Earth. - Nature 493: 295–297.

Reid, R. S. and Ellis, J. E. 1995. Impacts of pastoralists on woodlands in South Turkana, Kenya: livestock-mediated tree recruitment. - Ecol. Appl. 5: 978–992.

Roxburgh, C. et al. 2010. Lions on the move: The progress and potential of African economies. McKinsey Global Institute.

Scheiter, S. and Higgins, S. I. 2009. Impacts of climate change on the vegetation of Africa: an adaptive dynamic vegetation modelling approach. - Glob. Chang. Biol. 15: 2224–2246.

Seppelt, R. et al. 2016. Harmonizing biodiversity conservation and productivity in the context of increasing demands on landscapes. - Bioscience 66: 890–896.

Sinclair, A. R. E. and Norton-Griffiths, M. 1979. Serengeti: Dynamics of an Ecosystem. - The

University of Chicago Press.

Smith, M. D. et al. 2013a. Long-term effects of fire frequency and season on herbaceous vegetation in savannas of the Kruger National Park, South Africa. - J. Plant Ecol. 6: 71–83.

Smith, M. J. et al. 2013b. The climate dependence of the terrestrial carbon cycle, including parameter and structural uncertainties. - Biogeosciences 10: 583–606.

Staver, A. C. et al. 2011. The global extent and determinants of savanna and forest as alternative biome states. - Science 334: 230–232.

Steffen, W. et al. 2015. Planetary boundaries: Guiding human development on a changing planet. - Science 347: 1259855.

Thomson, A. M. et al. 2011. RCP4.5: a pathway for stabilization of radiative forcing by 2100. - Clim. Change 109: 77–94.

Tittensor, D. P. et al. 2014. A mid-term analysis of progress toward international biodiversity targets. - Science 346: 241–244.

Visconti, P. et al. 2016. Projecting global biodiversity indicators under future development scenarios. - Conserv. Lett. 9: 5–13.

WWF 2014. Living Planet Report 2014. WWF International.

## Figure and Table Legends

**Figure 1.** (a) Map of sites in Africa's tropical grassy biomes. Sites were very patchily distributed, but showed a reasonable representation of land uses: 281 in primary vegetation, 69 in secondary vegetation, 378 in cropland and 194 in pasture. (b, c) Response to land use of ecological assemblages in tropical grasslands, in terms of total abundance of organisms (a) and species richness (b). Responses for tropical grasslands (shown as opaque symbols) are compared with global responses (translucent symbols). For primary and secondary vegetation, minimally used refers to areas where recorded human disturbances are very minor; substantially used refers to areas where human disturbances are of at least moderate intensity or broad in spatial footprint (see Table S1 for more detail). All values are shown as the % difference relative to the value in primary vegetation.

**Figure 2.** Estimated intactness - given land-use change - of ecological assemblages in 2005, according to a statistical model of biodiversity's response to land use (a and b) and a mechanistic general ecosystem model (c and d). Estimated changes shown are total abundance of organisms (a and c), species richness (b) and total biomass (d).

**Figure 3.** Predicted intactness of ecological assemblages in tropical grasslands by 2100, according to a statistical model of biodiversity's response to land use (a-d) and a mechanistic general ecosystem model (e-h). Predicted changes shown are total abundance of organisms (a-b and e-f), species richness (c-d) and total biomass (g-h). Predictions are shown under two Representative Concentration Pathways scenarios: the MESSAGE scenario (a, c, e, g) and the MINICAM scenario (b, d, f, h). Colours correspond to those in Figure 2 for the same model-metric combinations.

**Table 1.** Comparison of statistical and mechanistic models of the response of biodiversity to land-use change

## Tables

**Table 1**

| **Statistical models of biodiversity response** | **Mechanistic models of biodiversity response** |
|---|---|
| Based on survey/monitoring data from populations and species assemblages | Based on mechanistic relationship among biological, physical and ecological processes |
| Test predictability e.g. using hold-out of a proportion of data used to build model | Test of predictive ability using an ecosystem property that is measured but not reported |
| Correlative - built from association between biodiversity and environment (e.g. land use) variables | Mechanistic - built from basic ecological mechanisms |
| Prediction limited to environmental conditions observed previously | Prediction in novel conditions possible through projection of dynamics |
| Limited in breadth; data are still comparatively rare, and focus on particular species or populations and on particular geographic regions | Limited by computational power and knowledge of the processes and the relationships among the modelled parameters |