

Assessing the impacts of livestock production on biodiversity in rangeland ecosystems

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Biodiversity in rangelands is decreasing, due to intense utilization for livestock production and conversion of rangeland into cropland; yet the outlook of rangeland biodiversity has not been considered in view of future global demand for food. Here we assess the impact of future livestock production on the global rangelands area and their biodiversity. First we formalized existing knowledge about livestock grazing impacts on biodiversity, expressed in mean species abundance (MSA) of the original rangeland native species assemblages, through metaanalysis of peer-reviewed literature. MSA values, ranging from 1 in natural rangelands to 0.3 in man-made grasslands, were entered in the IMAGE-GLOBIO model. This model was used to assess the impact of change in food demand and livestock production on future rangeland biodiversity. The model revealed remarkable regional variation in impact on rangeland area and MSA between two agricultural production scenarios. The area of used rangelands slightly increases globally between 2000 and 2050 in the baseline scenario and reduces under a scenario of enhanced uptake of resource-efficient production technologies increasing production [high levels of agricultural knowledge, science, and technology (high-AKST)], particularly in Africa. Both scenarios suggest a global decrease in MSA for rangelands until 2050. The contribution of livestock grazing to MSA loss is, however, expected to diminish after 2030, in particular in Africa under the high-AKST scenario. Policies fostering agricultural intensification can reduce the overall pressure on rangeland biodiversity, but additional measures, addressing factors such as climate change and infrastructural development, are necessary to totally halt biodiversity loss.

dose-response model | intactness | land use

Habitat degradation and land use change are among the major factors causing biodiversity loss, worldwide (1). Rangelands are no exception as they are under stress from conversion into cropland and pressure from livestock and excessive fire (2, 3). Other important drivers of change include climate change, habitat fragmentation, and the development of infrastructure (4–6). Rangelands, which compose ~25% of the world's land area, include grasslands, scrublands, woodlands, wetlands, and deserts and are found from the Asian steppes to the Andean regions of South America and from the mountains of Western Europe to the African savanna.

Vegetation and wild herbivores coevolved in many rangeland systems and some are among the most species-rich in the world. The scrublands of the Southern African Karoo, for example, support >6,000 different plant species (7), whereas African savannas are reputed for their rich diversity of large mammals. However, losses of wildlife in African rangelands are increasingly attributed to encroachment of agriculture and competition with livestock (8, 9).

Livestock farming is the most widespread human activity and the dominant land use in rangeland ecosystems. Rangelands provide 10% of the global meat supply and support an estimated 200 million pastoralists and the herds of nearly 1 billion camels, cattle, and smaller livestock, in addition to yaks, horses,

reindeer, and other ungulates (10). The effects of grazing on rangeland biodiversity include the removal of biomass, trampling and destruction of root systems, and replacement of wild grazers by livestock (6). The combined effects depend on (i) the extent of rangelands grazed by livestock, (ii) the grazing intensity, (iii) the original type of vegetation (e.g., impacts are greater when forests are cleared for the purpose of grazing), and (iv) land management (e.g., fertilized, planted with exotic species, etc.).

The extent of rangelands has changed over time due to conversion of forested land into man-made grasslands (e.g., ref. 11), the conversion of rangeland into cropland, and the replacement of abandoned rangeland with forests (e.g., ref. 12). As a result of these processes, the extent of grazed rangelands increased by 24,000 km² annually, between 1987 and 2000 (13). The rates of conversion of land and the intensity of rangeland use are likely to continue changing over the next decades as a result of the forecasted increased global demand for food. However, the impact on rangeland biodiversity of such increases in demand for crop and livestock commodities through possible conversion to and from rangeland and changes in the intensity of their use for livestock production remain poorly understood.

Over the last century, increased livestock production has been achieved mainly through a shift from pastoral systems with free-range feeding toward mixed and industrial systems, where a substantial part (>10%) of the feed comes from crops or crop by-products and so-called landless or industrial livestock production systems, where the bulk of the feed (>90%) is produced off farm. Consequences of these shifts are substantial increases in cropland area for feed production and a strong increase in animal population densities outside rangelands (14). Although this change may have released pressure on rangeland systems, it has not avoided expansion of domestic livestock grazing into natural rangelands. This outcome has been the case in most of Africa and in the Brazilian Cerrado and Amazon region, whereas at the same time grazed rangelands in the central south of Brazil were replaced by cropland, such as for soybean and sugarcane production (15, 16).

These trends are expected to continue in the future, as the human population will increase to ~9.3 billion by 2050 (17). This increase, combined with increasing prosperity and a shift in dietary patterns, will lead toward a larger demand for meat and milk. This trend may be enhanced when costs of animal products fall if production shifts from traditional pastoral systems to more energy- and nutrient-efficient production systems (17).

Several approaches are available to quantify impacts of land use on biodiversity (1). A frequently used method is to project

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future species distribution using empirical models describing the relation between environmental variables and individual species (e.g., ref. 18). This approach assumes that the range of species will change with these environmental variables. Other authors use species–area relationships, assuming that the number of species directly relates to the extent of natural area (2, 19). The GLOBIO3 model uses general cause–effect relationships between human impact factors and a generic measure of intactness of biodiversity: the relative mean species abundance (MSA) of originally occurring species in pristine ecosystems (4). It expresses the relative difference between an undisturbed ecosystem and a disturbed or managed ecosystem on a scale from 1 (undisturbed) to 0 (completely destroyed) (20). GLOBIO3 allows the calculation of the effect of grazing within the context of multiple drivers of biodiversity change. The model currently accounts for the following impact factors: land use (including grazing), infrastructural development, habitat fragmentation, nitrogen deposition, and climate change.

Using the GLOBIO3 approach, this paper presents a first attempt to quantify biodiversity impacts of livestock production in rangeland ecosystems. First, the extent of rangeland ecosystems, including man-made grazing areas, was derived from the GLC2000 land-cover and land-use map and the Integrated Model to Assess the Global Environment (IMAGE) (21, 22). IMAGE provides estimates of the extent of rangelands used for livestock grazing and man-made pastures, here together called grazed rangelands. Subsequently, we estimated a possible future extent of land cover on the basis of the projection by the International Assessment of Agricultural Knowledge, Science, and Technology for Development (IAASTD) (17), for the 2000–2050 period. In addition, we analyzed a variant of this projection, in which a high scientifically based level of productivity increase is assumed: the high levels of agricultural knowledge, science, and technology (high-AKST) variant (23). Then we derived MSA values for a gradient of grazing intensities on rangelands by conducting a systematic literature review and metaanalysis (24). These MSA values were included in the GLOBIO3 model (4), enabling the analysis of changing grazing pressure on biodiversity. We used the GLOBIO3 model to estimate current and future total MSA values, in relation to future developments according to the IAASTD baseline and the high-AKST scenario variant. In addition, we explored the sensitivity of the outcomes to the variability of MSA values.

Results

Current rangelands occur in all biomes, but primarily in the grasslands and steppe, savanna, scrubland, and tundra. Significant parts of tropical forest and temperate forest biomes also consist of, mostly man-made, rangeland (Fig. 1). In general, between 10% and 60% of the existing rangeland is used for livestock grazing (Fig. 1).

The IAASTD baseline projection indicates an increase in total grazed rangeland, i.e., used and man-made rangelands, area (Fig. 2) of just over 1 million km² (+5%) between 2000 and 2030, followed by a decrease of 0.8 million km² between 2030 and 2050, resulting in a marginal 1% net increase between 2000 and 2050. The area of natural rangelands will decline from 25 million km² to 22 million km² (–11%) from 2000 to 2050. Together, these trends reflect the hypothesis that livestock production will become less dependent on free-roaming grazing and increasingly reliant on feed produced by cropland systems.

The high-AKST scenario, with agricultural productivity increasing beyond the baseline assumptions, results in a decrease of the extent of grazed rangeland and an increase in the area of natural rangelands (Fig. 2). This effect is particularly strong in Africa, where, according to this scenario, the area of land grazed by livestock will have decreased by almost 50% by 2050, thus increasing the extent of natural rangelands (Figs. 3 and 4).

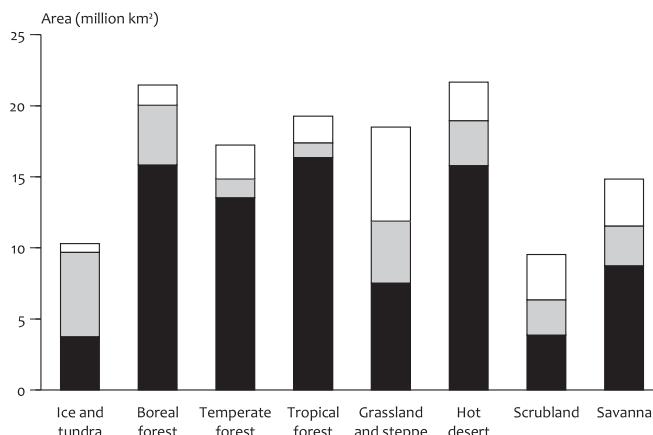


Fig. 1. Extent of used rangelands and man-made grasslands (open bars), natural rangelands (shaded bars), and other vegetation (solid bars) for biomes, derived from GLC2000 and IMAGE.

The systematic literature review, which included 24 studies that compared species composition in grazed systems with that in natural rangelands, covered the full spectrum of rangeland ecosystems (Table S1.1). An overall degree of land-use intensity was derived from these studies by using the reported grazing intensity, e.g., based on relative stocking rates, rangeland management, visual alteration of the vegetation structure, and seasonal variation in grazing (Table S1.2). We assumed that authors report grazing intensity on the basis of their knowledge of the systems studied and that their classifications of grazing intensities implicitly account for carrying capacity. The overview of all 24 studies resulted in five different categories, including “ungrazed, abandoned rangeland” where domesticated grazers were excluded, wildlife grazers did not recover, and forests did not develop; “natural rangeland” with wildlife or livestock grazing at stocking rates close to natural; “moderately used rangelands”; “intensively used rangelands”; and “man-made grasslands” (Table 1).

We used this metaanalysis for estimating MSA values for each of the grazing intensity categories (Table S2.1). The MSA value for natural rangelands was set at 1 (Methods). The MSA values for the other categories were statistically tested against the hypothesis of having no effect. All categories showed a value sta-

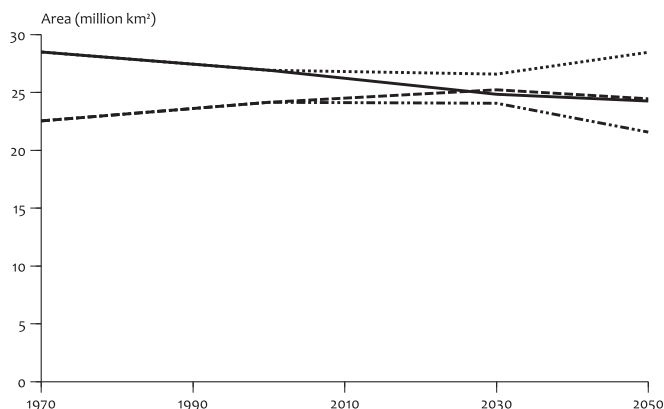


Fig. 2. Projections of future areas of natural rangelands for the IAASTD baseline scenario (solid line) and the high-AKST scenario (dotted line) and of grazed rangelands (including man-made grasslands) for the IAASTD baseline scenario (dashed lines) and the high-AKST scenario (dashed-dotted line), derived from ref. 28.

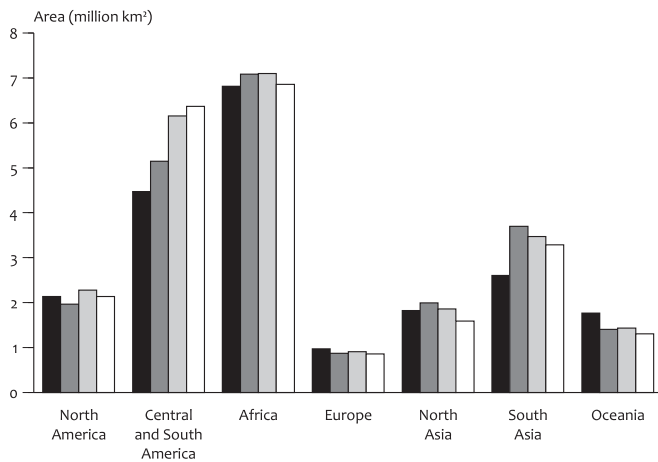


Fig. 3. Extent of grazed rangeland (including man-made grasslands) in each world region according to the baseline scenario in 1970 (solid bars), 2000 (bars with dark shading), 2030 (bars with light shading), and 2050 (open bars).

tistically significant below 1 ($P < 0.05$) (Table 1 and Table S2.1). MSA values decreased with increasing intensity, from 0.6 in moderately used rangelands to 0.3 in man-made grasslands. Ungrazed, abandoned rangelands presented an average MSA of 0.7. No significant regional differences were found for MSA values and no differences between taxa were found (Table S2.2). These values were subsequently entered in the GLOBIO3 model to calculate changes in MSA values in the projections of the future (4).

The GLOBIO model suggests that *biodiversity, in terms of global average MSA*, will continue to decline, between 2000 and 2050, in rangeland ecosystems in both the baseline scenario and, to a lesser extent, in the high-AKST variant (Fig. 5). MSA loss in rangeland ecosystems is caused by a combination of pressure factors, including climate change, cropland expansion, fragmentation, infrastructural development, and livestock grazing. At the global level, the impact of livestock grazing (i.e., ignoring all other pressure factors) is expected to increase until 2030 and then decrease again, most notably in the high-AKST variant. Due to variability of the MSA estimates this difference at the global level is only marginal. In the baseline scenario, the expansion of livestock grazing causes an increase of grazing

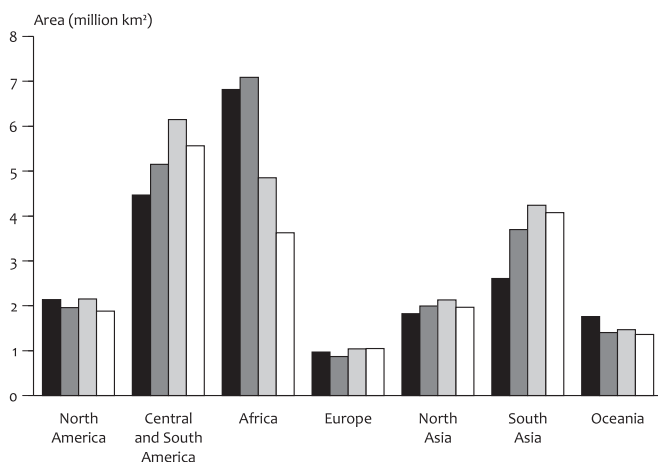


Fig. 4. Extent of grazed rangeland (including man-made grasslands) in each world region according to the high-AKST scenario in 1970 (solid bars), 2000 (bars with light shading), 2030 (bars with dark shading), and 2050 (open bars).

impacts on MSA in the Americas, whereas other regions present a slight gain in the livestock-related MSA component (Fig. 6) as a consequence of the contraction of grazed rangelands (i.e., parts of the more intensively used rangelands are converted to cropland, resulting in an average MSA increase of the remaining rangelands). The high-AKST variant suggests little or no change in the effects of livestock grazing on rangeland MSA between 2000 and 2050 for most regions, except for Africa, where MSA will be significantly higher than in the baseline scenario (Fig. 6). However, these regional trends will not stop the overall global decline in MSA, because of other factors that are expected to persist, indicated by the decreasing total MSA values shown in Fig. 5. The MSA decrease in Europe in the high-AKST variant, both compared with the baseline as well as with the 2000 situation (Fig. 6), is mainly due to the abandonment of some of the most extensively used European grassland areas, which, however, would then evolve in forest rather than rangeland. Average grazing pressure in the remaining, more intensively used, rangelands would thus be higher compared with the baseline or with the 2000 situation.

Discussion

The area of rangeland under livestock grazing has expanded in the past and, according to the IAASTD reference scenario, will continue to increase, albeit at a moderate pace, in some regions of the world, especially in Central and South America. In the rest of the world, the area of land under grazing management is expected to remain stable or even decrease. Under the same scenario livestock productivity increases, e.g., ruminant meat and milk production increases by 118% and 66%, respectively, over the same period. Increased livestock production will depend more and more on feed produced on croplands. Cropland areas, therefore, are expected to expand (14), although the bulk of the increased crop production and livestock products is assumed to come from an increase in agricultural productivity, as has been the case in the past. This result means that the environmental impacts of livestock will increasingly be associated with cropland expansion and crop production intensification. The area of natural rangelands is expected to decrease up to 2030 and subsequently remain almost stable under baseline conditions. Substantial areas could potentially be restored under conditions favoring the development and implementation of resource-efficient production technologies, as illustrated for the high-AKST variant. This variant assumes a ruminant meat and milk productivity increase of >30% relative to that in the baseline scenario. These projections reflect an accelerated replacement of pastoral livestock production by production in more resource-efficient mixed systems. Note that the model does take account of price effects, which result in higher consumption (and thus, production) levels in the high-AKST scenario than in the baseline scenario. The high-AKST scenario does not imply a complete wipeout of traditional livestock production systems. First, the trend described above does not include the areas of very extensively used seminatural grasslands, as, in both scenarios, these grasslands remain relatively untouched. Second, even when these areas are excluded, land-use intensity in Africa, in terms of output of meat or milk per hectare of managed rangeland, would still be <40% of the average of that of the EU27 countries in the year 2000. The area of arable land in the high-AKST scenario is larger than that in the year 2000, but considerably smaller than in the baseline scenario.

The overall balance of the opposing effects of the high-AKST variant on rangelands in different regions demonstrates the complexity of the processes involved and the importance of following an integrated approach.

It must be appreciated, though, that also in regions where the model results suggest clear environmental benefits of high-AKST

Table 1. Average MSA values for different grazing intensities, resulting from the metaanalysis

	Short description	MSA	SE
Natural rangelands	Rangeland ecosystems determined by climatic and geographical circumstances and grazed by wildlife or domestic animals at rates similar to those of free-roaming wildlife	1.0	—
Moderately used rangelands	Rangelands with higher stocking rates: grazing has different seasonal patterns or vegetation structure is different compared with natural rangelands	0.6	0.04
Intensively used rangelands	Rangelands with very high stocking rates: grazing has different seasonal patterns and vegetation structure is different compared with natural rangelands	0.5	0.06
Man-made grasslands	Rangeland with high degree of human management, including converted forests	0.3	0.08
Ungrazed abandoned rangelands	Original grasslands no longer in use, lacking wildlife grazing and no forests developed	0.7	0.07

developments, such developments also have some inherent risks and challenges that need to be addressed:

Although yield increases such as those assumed for the high-AKST scenario are biophysically and technically possible (25, 26), their realization is a major challenge, especially in regions where they could be most beneficial, such as in sub-Saharan Africa, but where progress is hindered by a combination of socioeconomic and institutional constraints that need to be tackled concurrently (10, 27, 28).

Although yield increases are a precondition for preserving land for nature without compromising food security, these increases are not automatically achieved (29).

Restoration of nature in abandoned areas by natural succession may lead to land degradation if no specific interventions are set in place (30).

Although increased yields, overall, result in improved food security, some groups of farmers and farm workers are likely to become negatively affected. Traditional pastoral culture and the rich knowledge that pastoral people have about ways to adapt to climate change, for example, are in danger of being lost.

Intensification based on high AKST is not a matter of doing more of the same on a smaller area of land. It must be an eco-efficient intensification, i.e., covering the interrelationships and trade-offs among production, conservation, economic, and social values (31–33).

Although in-depth discussion of these challenges is beyond the scope of this paper, it should be clear that policies targeting the

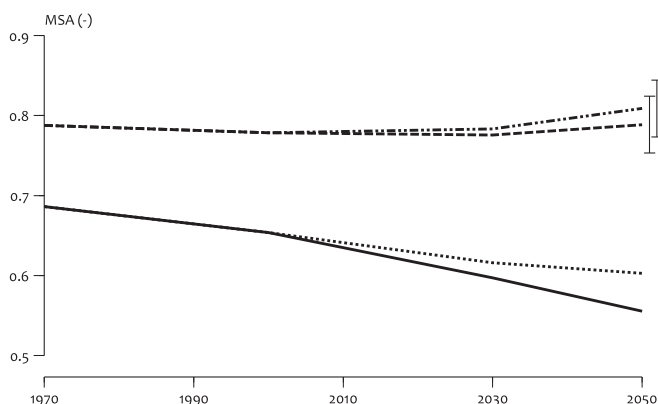


Fig. 5. Global average MSA estimates, considering all environmental factors for the baseline scenario (solid line) and the high-AKST scenario (dotted line) and the effect on MSA of livestock grazing only, for the baseline (dashed lines) and the high-AKST scenario (dashed-dotted line). The error bars indicate $2 \times$ SD derived from the variability of MSA values.

development and implementation of high-yielding agricultural practices are an important component, but are not sufficient for tackling rangeland biodiversity loss. The reverse is also true. Policies aimed at the preservation of rangeland biodiversity are deemed to fail if they do not concurrently address the challenge of meeting future food demands.

Nature in rangeland ecosystems differs considerably between world regions. In northern and central Europe most grasslands used for grazing are man made, developed from former forests. These ancient systems are considered seminatural grasslands and valued as one of the most species-rich ecosystems in this region (12, 34). Large areas of seminatural rangelands either have been converted into croplands during the past century or have been abandoned. Conservation and restoration of seminatural grasslands is one of the main objectives of current biodiversity policies throughout Europe. In many world regions, forests are being converted into either cropland or man-made grasslands, especially in Latin America, where livestock grazing is a primary cause of deforestation (e.g., refs. 11 and 35). In many other regions, livestock grazing has developed on natural rangeland, such as grass-dominated systems or open woodlands (6). These grazed rangelands range from traditional pastoral systems to farm settlements and fenced-in grasslands.

We show that shifts in livestock production would have a major impact on biodiversity change in rangeland ecosystems. Grazing intensity is difficult to measure directly as it depends on the relative stocking rate of livestock, the carrying capacity of the ecosystem, and additional management of the land. We derived a grazing intensity gradient from studies that were selected for metaanalysis. Many authors provide only a qualitative description, as they focus on comparison between sites (Table S1.2 and literature cited therein). The lack of quantitative indicators for grazing intensities makes the assessment of the impact of grazing difficult.

The results of our study partly depend on the accuracy of MSA estimates derived from the metaanalysis. Due to the limitation of data availability, the estimated MSA values are not region specific and bear considerable uncertainty. The sensitivity analysis shows that the results are robust enough to draw the following general conclusions.

The projected changes in biodiversity, in terms of MSA, show a continual decreasing trend over the coming 40 y, in both scenarios, whereas the impact of grazing is expected to be reduced (Fig. 5). This result is mainly because the reduced impact by grazing is offset by increasing impacts by factors such as climate change, nitrogen deposition, and infrastructural development. The effect of livestock grazing is expected to decrease, especially in the high-AKST variant. In Africa, where the area of used rangelands decreases considerably under high AKST, natural rangelands can be restored, and MSA values show substantial improvement compared with the baseline scenario (Fig. 6). In Latin America, where the conversion of nature to man-made grasslands is avoided in the high-AKST variant, no further de-

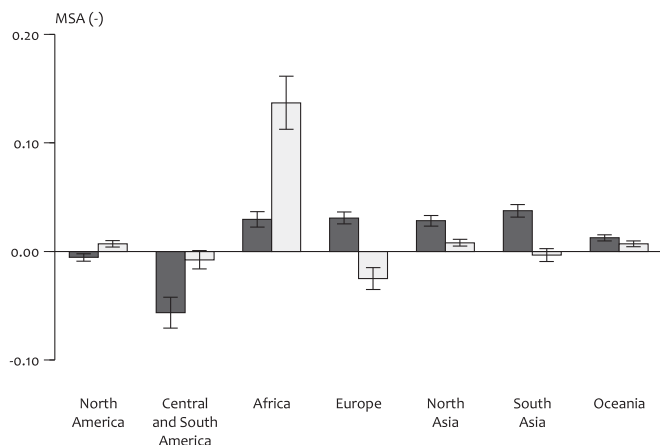


Fig. 6. Changes in the effects of grazing pressure on rangeland MSA from 2000 to 2050, according to the baseline scenario (bars with dark shading) and the high-AKST variant (bars with light shading). Error bars indicate ± 1 SD, derived from variability in MSA values.

cline of MSA values is expected. The situation will remain approximately stable in North America and North Asia and may have contradictory effects in Europe, where high-AKST values decrease compared with the baseline (Fig. 6).

This result suggests that policies that foster high agricultural growth in croplands and a shift toward higher livestock productivity in mixed crop livestock systems release the pressure on biodiversity in rangeland ecosystems in regions where productivity is still low. By these policies the conversion of rangelands into cropland can also be slowed down. In particular, the African rangelands will be positively affected. In regions where technology is advanced and productivity is already high no positive effect of increased productivity on biodiversity can be expected.

Despite the positive effects of increased productivity on biodiversity, other drivers, such as climate change, infrastructural development, and conversion to croplands, continue to affect rangeland biodiversity. An integrated approach including policies for multiple drivers may avoid the result that positive effects of policies targeted at one driver are offset by negative effects of another driver.

Methods

The relation between grazing intensity and biodiversity was quantified using data from peer-reviewed literature selected through a systematic literature search. The effect of grazing is described in terms of relative mean species abundance (MSA) of originally occurring species, which compares the species composition of livestock grazing systems with adjacent natural systems, for example wildlife reserves (4).

Studies were collected in two batches. The first batch contained literature entirely based on a former review for the GLOBIO3 model (4), yielding 15 papers on grazing intensity. The second batch was compiled from a search using the keyword sequence *species AND [grassland OR rangeland] AND graz* AND [intact OR natural OR primary OR virgin OR mature OR pristine] AND [*diversity OR richness OR abundance*]* of the SCOPUS database. This search yielded 300 papers. We selected papers from 10 journals with >10 papers that met the search criteria and rejected those that were obviously not of interest according to title and abstract. From the 49 remaining papers only those were selected that met the following criteria: Does the paper contain data on species abundance? Could one of the land-use categories studied be considered natural or close to natural? Does the paper describe the effect of grazing? This procedure yielded an additional 9 papers containing sufficient data to calculate MSA values. Together with the 15 papers from the other batch, this procedure resulted in 24 papers, from which datasets were derived and MSA values calculated (Table S1.1). Grazing intensity was extracted from the paper by scoring four indicators: reported intensity by author, sometimes with corresponding stocking rate, ungrazed

or abandoned (0) natural grazing (1), moderate grazing intensity (2), high grazing intensity (3); visual alteration of the vegetation structure, not or slightly altered (0), significantly altered in height or species composition, including exotics (1); rangeland management, no management (0), presence of management such as soil disturbance, clearance of vegetation and application of fertilizers, planting or sowing grass or feed crops (1); and seasonal variation, only seasonal grazing corresponding to natural grazing pattern (0), continuous grazing regardless of the season (1). The four indicators were combined into four grazing intensity classes, using the following rules: If the reported intensity of rangeland management equals 0, and the description is clear on the absence of wildlife grazing, e.g., by fenced enclosures, then the land is regarded as “ungrazed”, abandoned rangeland (36, 37); if the reported intensity equals 1, then the intensity class is that of man-made grasslands (38, 39); if the sum of the reported intensity, visual alteration of the vegetation structure, and seasonal variation equals 1, then grazing is regarded as “natural” (40–42); if this sum is 2 or 3, then the land is considered moderately used grazing land (43, 44); and if the sum is 4 or 5, then the intensity class is intensive (44, 45).

Each dataset consisted of samples from locations with different grazing intensities, containing observations from different points or subsamples. The observations were summarized to a mean or sum of individuals found for each species. For each study k , each species i , and each grazing intensity e the abundance is denoted as n_{ike} with variance $V(n_{ike})$. The idea behind MSA is to describe the relative difference between the original ecosystem and the disturbed state of the same ecosystem. So only the species found in samples from the natural rangeland were included.

Ratios of the abundance of single species found in disturbed and undisturbed ecosystems are the basis on which to calculate MSA. Disturbances of ecosystems often lead to the decline of many species and simultaneous increases in others. Both decreases and increases signal disturbance. To avoid averaging out the relative changes of declining species by the increasing species, we capped the ratios at 1, so surpluses of individuals from the disturbed ecosystem would be ignored. The ratio r_{ike} is calculated by dividing n_{ike} , the abundance of a species in a disturbed ecosystem by the abundance found in the original ecosystem, n_{iko} if $n_{ike} < n_{iko}$; otherwise $r_{ike} = 1$. For each study the ratios r_{ike} are summarized by taking the overall mean R_{ke} . The MSA_e for each grazing intensity e is calculated from all R_{ke} derived from the individual studies,

$$MSA_e = R_e = \frac{\sum_k (R_{ke} / V_{ke})}{\sum_k 1 / V_{ke}}$$

where V_{ke} is the pooled variance of the ratios of species abundances for each study and copies for differences between studies. For more detail see *SI Methods, section 1*.

A random-effects metaanalysis was done, using the R 2.12.0 software, to derive a pooled effect size for the different grazing intensities. Linear mixed-effect models were estimated for MSA to check for differences between regions and taxa.

Rangeland Extent and Intensity. The extent of rangeland ecosystems is difficult to estimate, as it depends on the definition of rangelands and the resolution of measurements. Global estimates depend on remotely sensed data and as the technology rapidly evolves, measurements of land cover type also change. We estimated rangeland extent from the Global Land Cover database of 2000 (GLC2000) (21). The GLC2000 categories of rangeland ecosystems are “shrub cover, closed–open, evergreen”; “shrub cover, closed–open, deciduous”; “herbaceous cover, closed–open”; “sparse herbaceous or sparse shrub cover”; and “regularly flooded shrub and/or herbaceous cover”. Extent of rangelands used for livestock grazing was estimated using livestock density maps from the Food and Agriculture Organization (Rome) and assumptions on the area needed (46). In IMAGE, two intensity categories are considered: pastoralism and mixed grazing systems (25). These two categories are assumed to correspond with the moderate grazing intensity and high grazing intensity from this study.

Scenarios. The *baseline scenario* in our study is the reference case of the IAASTD (33). This baseline scenario was developed using several linked models, including, *inter alia*, the IMPACT agriculture-economy model (23) and the IMAGE model (22). IMPACT is a partial equilibrium model, which accounts for food demand, food production, resource availability, trade, and commodity prices. These results were then used as input in IMAGE (version 2.4) to compute the areas of land needed in various sectors and a number of other environmental parameters (22). The reference scenario depicts the world developing over the next decades in a business-as-usual mode, with-

out anticipating deliberate policy interventions. For population, the scenario is based on the United Nations medium projection, leading to a total population of ~9.2 billion by 2050, an almost 50% increase since 2000. Global economic growth is assumed to be close to 3% annually, over the 2000–2050 period, resulting in a doubling of GDP by 2050. Together, these drivers lead to an increasing food crop demand (an increase of ~80% between 2000 and 2050). Diets are projected to become more meat intensive, especially in low-income countries. Globally, meat demand increases by 115% between 2000 and 2050, with annual growth rates of ~1.7% (early in the scenario period) to 1.4% (between 2025 and 2050). About 70% of crop production growth is projected to come from yield increases, implying an expansion of cropland from 1.5 billion hectares, today, to >1.6 billion hectares, by 2050. The increase in meat consumption is expected to lead to a significant increase in the number of animals. At the same time, however, there is a gradual shift from extensive to more intensive forms of animal husbandry. This shift implies that some net expansion of grazed rangelands and man-made grasslands still occurs, but it levels off soon after 2025.

The high-AKST variant assumes accelerated investment in the development and adoption of agricultural knowledge, science, and technology, leading to a worldwide extra 40% increase in crop yields (14) and an extra 20% increase in livestock productivity, between 2005 and 2050, compared with in the baseline scenario. For livestock production it has been calculated that this result would lead to an extra dependence on feed from crops.

Biodiversity estimates at global and regional levels are estimated using the IMAGE 2.4 model combined with the GLOBIO3 model (4). Both models are briefly described in *SI Methods, section 2*. The impact of the variability of MSA values, derived from the metaanalysis, on the scenario outcomes was explored by varying the parameter setting in a Monte Carlo analysis. The variability of MSA values is due to, e.g., regional differences, taxonomical differences, and differences in study design. SDs for global and regional MSA estimates were derived from this sensitivity analysis. We compared the outcomes per region between baseline and the high-AKST scenario with Student's *t* test, using unequal variances.

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