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Authors
Zhang, Ning
Li, Ang
Yan, Yongzhi
et al.

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Ning Zhang, Ang Li, Yongzhi Yan, Amy E. Frazier, Qing Zhang & He Yin

Global grassland fragmentation is intensifying with uneven consequences for vertebrate biodiversity

Ning Zhang†[1], Ang Li†[2], Yongzhi Yan[1], Amy E. Frazier[3], Qing Zhang[1, 4]*, He Yin[5]*

1. Ministry of Education Key Laboratory of Ecology and Resource Use of the Mongolian Plateau, School of Ecology and Environment, Inner Mongolia University, Hohhot, 010021, China
2. State Key Laboratory of Forage Breeding-by-Design and Utilization, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093, China
3. Department of Geography, University of California, Santa Barbara, Santa Barbara, CA, 93106, USA
4. Collaborative Innovation Center for Grassland Ecological Security (Jointly Supported by the Ministry of Education of China and Inner Mongolia Autonomous Region), Hohhot, 010021, China
5. Department of Geography, Kent State University, 325 South Lincoln Street, Kent, OH, 44242, USA

† Ning Zhang and Ang Li contributed equally to this work and are considered co-first authors.

* Qing Zhang (qzhang82@163.com) and He Yin (hyin3@kent.edu) contributed equally to this work and are co-corresponding authors.

Abstract

Grassland fragmentation is intensifying globally, with substantial implications for biodiversity. Yet its extent, temporal dynamics and ecological effects remain unclear. Here we present a global assessment of grassland fragmentation from 1995 to 2020 and its effects on vertebrate species richness. Intact grassland area declined by 2.6% over this period, mainly owing to cropland expansion, and only about 24% of global grasslands remained structurally intact by 2020. The effects of fragmentation on species richness varied across regions and taxa. Low fragmentation increased richness in large tropical grasslands, whereas high fragmentation reduced richness in temperate grasslands, where reptiles showed the strongest and most consistent negative responses. To evaluate potential management strategies, we further compared future fragmentation under different land-use scenarios. Projections to 2045 suggest that conservation will reduce future fragmentation more effectively than restoration in 61% of ecoregions. Our findings reveal global patterns of grassland fragmentation and inform region-specific conservation strategies.

1. Introduction

Grasslands are among the most extensive and ecologically important terrestrial biomes, covering approximately 40% of the Earth's land surface[1]. They support a wide range of biodiversity and provide critical ecosystem services, including food production, water regulation, carbon storage, climate mitigation, pollination, and cultural values[2]. Despite their essential role, grasslands have historically received far less conservation attention than other ecosystems, such as forests[3]. Recent global assessments have shown that grasslands are now among the most threatened and rapidly degrading ecosystems, with fragmentation and land-use change contributing to the loss of ecological integrity and species persistence[4,5]. For example, in the United States, annual grassland-to-cropland conversion rates reached 5% between 2006 and 2011[6]. Similar processes have also been reported in other major grassland regions, such as the Río de la Plata Grasslands in South America, where at least 2.4 million hectares of grassland were lost between 2001 and 2018, representing approximately 9% of the remaining grassland area[7].

Habitat fragmentation is widely recognized as a major factor affecting biodiversity, primarily through reductions in habitat area, decreased landscape connectivity, and increased edge effects[8]. Fragmentation has often been associated with negative ecological outcomes, including population declines, elevated extinction risk, and disruption of ecological processes[9,10]. However, recent studies have demonstrated that the effects of fragmentation are heterogeneous. Depending on the spatial scale, landscape context, and species-specific ecological traits, fragmentation has been associated with negative, neutral, or even positive biodiversity outcomes[11,12]. For instance, generalist species or those adapted to edge environments may benefit from increased habitat heterogeneity[13]. In contrast, species that require large, contiguous habitats or have limited dispersal capacity are generally more vulnerable to fragmentation, primarily due to greater exposure during movements such as dispersal and foraging[14-16]. Despite theoretical advances, empirical evidence on how fragmentation affects biodiversity in grasslands remains limited, particularly at the global scale. Given their vast extent and the presence of ongoing land-use change, grasslands require large-scale assessments to understand fragmentation patterns and biodiversity outcomes.

In response to these challenges, the International Union for Conservation of Nature (IUCN) launched the Temperate Grasslands Conservation Initiative in 2008, drawing global attention to the need for grassland conservation[4]. To implement more effective conservation and restoration strategies, a precise understanding of the current state of grassland fragmentation is essential[17]. Here we quantify the global extent of grassland fragmentation, identify its potential causes, assess its effects on vertebrate species richness, and project future fragmentation under alternative land-use scenarios. We show that intact grassland area declined markedly between 1995 and 2020, that biodiversity responses to fragmentation vary across ecoregions and taxonomic groups.

2. Results

2.1 Global grassland fragmentation dynamics

We used intact grassland area as an indicator of fragmentation, with intactness defined as all pixels within a fixed-size window being classified as grassland according to the area-density method[18]. Our results showed that intact grasslands covered 2.04 million km² in 2020, accounting for 24% of the global grassland extent. However, the proportion of intact grassland varied markedly among continents, with Europe showing the lowest proportion (5.2%, 1,446 km²) and North America showing a higher proportion (30.7%, 0.45 million km²) (Fig. 1, Supplementary Tab. 4). At the national scale, relatively high proportions of intact grassland were recorded in the Falkland Islands (46.6%, 6,193 km²) and Colombia

(45%, 50,789 km²) (Supplementary Tab. 5). At the ecoregion scale, the mixed grasslands of the Nebraska Sand Hills showed the highest structural integrity, with more than 50% of grassland area remaining intact (Supplementary Tab. 6).

From 1995 to 2020, global intact grassland area declined by 2.6%, showing marked regional variation (Supplementary Tab. 4). At the national scale, 39 countries experienced declines, whereas 23 countries showed increases in intact grassland area over the same period. The most pronounced reductions were recorded in Iraq (−54.54%), Malawi (−46.84%), and Nigeria (−30.92%). By contrast, the most substantial increases were observed in Ethiopia and Kenya (Fig. 2, Supplementary Tab. 5).

A similar pattern was observed at the ecoregion scale, where 67 ecoregions showed declines and 61 exhibited increases. The largest losses occurred in the Central U.S. forest-grassland transition (United States, −61.6%), the Pontic steppe (Eastern Europe and western Central Asia, −44.9%), and the Cordillera Central páramo (northern Andes, primarily Colombia, −38.7%) (Fig. 2, Supplementary Tab. 6).

2.2 Land-use transitions associated with grassland fragmentation

We identified the predominant land-use transitions contributing to grassland fragmentation at the global scale, including cropland, forest, and sparse vegetation. At the continental scale, cropland expansion was the main transition associated with fragmentation in North America, Asia, South America, and Africa. Forest expansion was most common in Europe, and sparse vegetation expansion was dominant in Oceania (Fig. 3).

Among the countries experiencing the most severe intact grassland fragmentation (Fig. 2), land-use transitions also differed. In Iraq, for example, fragmentation is primarily associated with cropland expansion, while in Malawi, forest expansion is the dominant transition. In Niger, fragmentation is mainly associated with the expansion of sparse vegetation and cropland, while other transitions play minor roles (Supplementary Tab. 9).

Distinct patterns of land-use transitions were observed across ecoregions with the most severe intact grassland fragmentation. Cropland expansion dominates in the Central U.S. forest-grassland transition (96.34%). Forest expansion is most prevalent in the Pontic steppe. In contrast, the Cordillera de Mérida páramo shows a mix of transitions, including cropland, forest, and increases in urban and shrubland areas (Supplementary Tab. 10).

2.3 Effects of grassland fragmentation on vertebrate species richness

Given that cropland expansion is the primary driver of global grassland fragmentation, we further examined the effects of cropland-driven fragmentation on vertebrate species richness. Overall, the effects varied markedly among ecological zones and grassland area classes (Fig. 4). Based on area, grasslands were classified as small-area (< 26.38 km²), intermediate-area (26.38-36.23 km²), and large-area (> 36.23

km²) grasslands.

In mountain grasslands, most responses were weak or non-significant. Significant declines occurred mainly in intermediate-area grasslands: amphibian richness decreased by 29% under low fragmentation and by 35% under medium fragmentation, while reptile richness decreased by 43% under low fragmentation. By contrast, under low fragmentation, amphibian richness increased by 23% in large-area grasslands.

In temperate grasslands, negative effects were more consistent. Significant declines were again concentrated in intermediate-area grasslands. Amphibian richness decreased by 42% under medium fragmentation and by 40% under high fragmentation, while bird richness decreased by 42% under both levels. Reptiles showed the strongest response, with richness reductions of 44%-50% in intermediate-area grasslands and 23%-31% in small-area grasslands. Mammals exhibited no significant response.

In tropical grasslands, negative effects were mainly concentrated in intermediate-area grasslands. This pattern was most evident for reptiles, whose richness decreased by 28%-34%. In contrast, positive effects were more common in large-area grasslands. Under low fragmentation, richness increased by 57% for amphibians, 63% for birds, and 67% for mammals.

2.4 Future grassland fragmentation under different scenarios

We simulated future grassland fragmentation through 2045 under three land-use scenarios: (1) Baseline, which continues historical transition rates observed from 1995 to 2020 without any intervention; (2) Conservation, which reduces the transition rate of intact grasslands to other land-use types (e.g., cropland, urban areas) by 10%, while keeping all other transitions unchanged; and (3) Restoration, which increases the transition rate from degraded land-use types (cropland, bare land, shrubland) back to grassland by 10%, also keeping all other transitions unchanged.

The projected results indicated that by 2045, the global intact grassland area under the Baseline scenario is 2.036 million km², a 0.17% decrease from 2020. Under the Conservation and Restoration scenarios, the areas are 2.049 and 2.045 million km² respectively, representing increases of 0.45% and 0.23% from 2020. While the differences among the three scenarios are relatively small, the Conservation scenario does lead to a slightly greater improvement in grassland integrity. This occurs because the Restoration scenario increases only the transition from other land-use types to grassland, but does not reduce the transition from grassland to other land-use types, which means any gains are partly offset by the continued conversion of grasslands to other land-use types (Fig. 5, Supplementary Tab. 11).

Results at the ecoregion scale were mixed, with 61% showing greater improvements in intact grassland area under the Conservation scenario, while 15% showed greater improvements under the Restoration scenario. The Cordillera Central páramo in South America showed the largest relative increase in intact grassland area under the Restoration scenario compared with the Baseline scenario. By contrast, Willamette Valley oak savanna in the Northwestern U.S. showed a greater increase under the Conservation scenario (Fig. 5, Supplementary Tab. 12).

3. Discussion

This study presents a global-scale, systematic assessment that reveals the continuous intensification of grassland fragmentation between 1995 and 2020, addressing a long-standing gap in grassland integrity research compared to forest ecosystems[19]. More importantly, this intensification was not spatially uniform, but was particularly pronounced in some regions, indicating that global grassland fragmentation is not driven by a single process, but rather results from the combined effects of land-use change across different regional contexts.

This regional heterogeneity was especially evident in the areas with the most severe fragmentation. For example, in the Central U.S. forest-grassland transition, grassland fragmentation was primarily associated with cropland expansion. This region has long been an agricultural frontier, where extensive native grasslands have been continuously converted to cropland, a historical process that has been well documented in previous studies[20,21]. By contrast, the process observed in the Pontic steppe appears to be different. Although this region is classified as a temperate grassland ecoregion, its northern boundary adjoins the East European forest-steppe, suggesting that local land-cover change may be influenced by the expansion of adjacent woody vegetation belts[22]. In this context, the relatively high proportion of forest-related transitions is more likely to reflect localized increases in woody vegetation within steppe landscapes, rather than widespread natural forest recovery. Taken together, these findings suggest that global grassland fragmentation is a complex phenomenon shaped by multiple regional processes.

The downstream ecological risks associated with this land conversion deserve close attention. Previous studies have shown that fragmentation often shows strong spatial contagion, such that once surrounding areas are converted, the likelihood of additional fragmentation increases markedly[23]. This suggests that cropland expansion may trigger further fragmentation in adjacent grassland areas, rather than causing only isolated changes in landscape structure. In addition, edge effects created by fragmentation can further accelerate habitat loss through feedback processes, potentially pushing ecosystems more rapidly toward threshold states[24]. Therefore, the potential ecological consequences of human-driven fragmentation warrant careful attention.

While global grassland fragmentation has intensified overall, our study also identified areas where fragmentation has slowed or even reversed—offering important insights into the potential for grassland recovery. In some African drylands, grassland recovery has been promoted by active management interventions, particularly exclosures and participatory rangeland governance[25]. Evidence from Ethiopia and Kenya suggests that such measures can improve vegetation condition and enhance rangeland productivity[26,27]. Grassland recovery may also be supported by long-standing Indigenous stewardship. In northern Australia, many grassland and savanna systems have historically been managed by Aboriginal communities using traditional ecological knowledge, especially fire management practices designed to sustain vegetation productivity and ecosystem function[28]. More recently, the integration of traditional fire management with modern emissions-accounting frameworks has delivered broader benefits for biodiversity, carbon management, and local communities[29]. Together, these examples suggest that grassland recovery can emerge through both targeted management interventions and traditional ecological stewardship. However, many of these recoveries remain fragile and localized. Whether they can be scaled up to reverse long-term fragmentation trends remains an open question requiring further monitoring and research.

The ecological consequences of grassland fragmentation on biodiversity remain debated. This study provides insight by highlighting how fragmentation effects vary with landscape context, disturbance intensity and species traits. Our results show that species richness declines significantly under high-intensity fragmentation in temperate grasslands. This pattern is consistent with previous studies in North American grasslands, where fragmentation has also been reported to negatively affect grassland birds[30]. These studies suggest that the negative effects were mainly related to the loss of continuous habitat and stronger edge effects, which increased nest predation and brood parasitism[30].

Our results showed that, in large tropical grasslands, species richness was sometimes higher under low-intensity fragmentation, consistent with findings from a study of African savannas reporting a similar pattern[12]. The authors of that study suggested that this relationship may reflect the relatively high spatial heterogeneity and disturbance tolerance of these ecosystems, where limited fragmentation may still maintain mosaic conditions that support species coexistence[12]. Recent global work also suggests that the biodiversity effects of land-cover change are cumulative and non-linear. Low levels of fragmentation may not immediately cause biodiversity loss. However, the negative effects of habitat loss and landscape simplification become clearer as fragmentation increases[31].

Of the four taxa studied, reptiles showed the most consistent negative responses to fragmentation. This pattern is broadly consistent with previous work, which has noted that reptiles typically have relatively low dispersal ability, strong substrate or microhabitat specialization, small home ranges, and pronounced thermoregulatory constraints[32]. As a result, once continuous grasslands are divided into multiple patches, reptiles are less able to move across unsuitable matrix habitat, and local populations are more likely to be affected by patch isolation. In contrast, amphibians did not show a similarly consistent negative response, but previous studies have suggested that amphibian responses to habitat loss and fragmentation are often shaped by breeding-site availability, moist microhabitats, and local hydrological conditions[33]. Therefore, their responses to grassland structural fragmentation may be more context-dependent.

At the ecoregion scale, differences between the Conservation and Restoration scenarios appear to depend on both the current extent and recent trajectory of intact grasslands. In the Cordillera Central páramo, for example, where intact grassland area has declined by 38.7% over the past two decades, leaving only 1.8% of grasslands intact by 2020 (Supplementary Tab. 3), the Restoration scenario produced the largest relative gains, suggesting greater recovery potential in ecoregions with severely reduced and continuously declining intact grasslands. In contrast, in the Willamette Valley oak savanna, which has seen an increase of 80% over the past two decades (Supplementary Tab. 3), but where intact grassland still accounted for only 0.5% of grassland area in 2020, the Conservation scenario produced the largest relative gains, indicating that preventing further conversion may be more effective where intact grasslands remain scarce but have shown recent improvement. Overall, however, scenario differences remained modest under the conservative transition assumptions applied here, implying that larger gains in intact grassland area may require stronger or more extensive land-use interventions.

Several multinational initiatives have been launched to reduce grassland loss, including the Dauria International Protected Area between Russia and Mongolia, which has played a key role in protecting intact grasslands from further degradation. At the same time, Europe has been deploying various methods to expand grasslands, such as direct seeding, planting, and turf transplantation[23,34]. Although many well-designed methods have been developed, challenges still impede efforts to address the problems facing grasslands, such as soil erosion[35], heavy metal contamination in soil[36] , depletion of soil microbial communities [37], and reduced viability of native species[38]. Therefore, this study calls for greater attention to the development of effective and economically feasible solutions to these challenges.

4. Conclusion

This study provides a global, multi-decadal assessment of grassland fragmentation from 1995 to 2020, revealing a pervasive intensification, especially in key regions such as the Central U.S. forest-grassland transition and the Pontic steppe. These changes were primarily driven by land-use change, grassland conversion to cropland, forest, and sparse vegetation. We found that the effects of fragmentation on biodiversity were spatially heterogeneous, shaped by differences between ecoregions, fragmentation intensity, and taxonomic groups. In temperate grasslands, areas experiencing high fragmentation intensity tended to have lower species richness, a pattern most evident in birds and low-dispersal taxa such as reptiles. In contrast, in extensive tropical grasslands, species richness tended to be higher in areas with low fragmentation intensity, possibly reflecting the role of moderate habitat heterogeneity in supporting biodiversity.

Despite continued fragmentation pressures, extensive intact grasslands remain across several continents, indicating that there are still opportunity to prevent further fragmentation in these regions. Meanwhile, countries such as Ethiopia and Kenya have already demonstrated that targeted land management can effectively slow fragmentation, offering valuable lessons for future grassland conservation. We recommend prioritizing the protection of intact grasslands in regions that currently show low fragmentation (e.g., Central Asia, East Africa) to prevent irreversible degradation. For regions experiencing severe or accelerating fragmentation, targeted restoration efforts should be implemented to recover connectivity and ecological function. To support both strategies, future monitoring should integrate biodiversity records, land-use change data, and fragmentation metrics across spatial and temporal scales.

5. Methods

5.1 Study area

We delineated the spatial extent and ecological attributes of grasslands based on a two-step approach. First, we identified grassland regions using the World Wide Fund for Nature (WWF) global terrestrial ecoregion classification system[22]. Specifically, we selected ecoregions belonging to four grassland-related biome types, in which herbaceous vegetation constitutes the dominant functional group. Second, we quantified grassland dynamics within these ecoregions using the European Space Agency Climate Change Initiative (ESA CCI) land cover dataset (300 m resolution), following established practices in global land-use studies[39]. During this process, ecoregions with negligible grassland cover (i.e., grassland area approaching zero) were excluded, resulting in a final set of 166 ecoregions (Supplementary Tab. 6). At the country level, only those countries in which these selected ecoregions were present and accounted for more than 10% of the national area were retained for further analysis (Supplementary Tab. 5). In this study, grassland was treated as an operational land-cover unit representing herbaceous-dominated areas at the landscape scale. Accordingly, fragmentation was measured as the spatial continuity of grassland cover within each ecoregion. We additionally identified grasslands without restricting the analysis to ecoregion boundaries. This approach resulted in a larger estimated extent but included more small and spatially isolated patches, potentially leading to higher apparent fragmentation (Supplementary Tab. 13).

Grasslands were identified as a combination of two ESA CCI land cover types: (1) grasslands, referring to natural or semi-natural herbaceous areas with >80% herbaceous cover; and (2) shrub–grass mosaics, defined as transitional areas with >50% herbaceous cover and <50% shrub or tree cover. To ensure the reliability and long-term consistency of the ESA CCI grassland classification, we performed an independent accuracy assessment using the AREA[2] (Area Estimation and Accuracy Assessment) tool on the Google Earth Engine platform[40]. The validation followed a stratified random sampling design across continents and grassland change types, with reference data interpreted from high-resolution Sentinel-2 imagery. The results demonstrated high classification accuracy and strong temporal consistency, with overall accuracies ranging from 0.898 ± 0.048 (Asia) to 0.946 ± 0.033 (South America) and a global mean of approximately 0.91. Detailed methods and validation results are provided in Supplementary Tab. 2.

To assess the robustness of fragmentation derived from the ESA CCI dataset, we performed a supplementary analysis using the recently published Global Pasture Watch 30 m annual grassland dataset (2000–2022)[41,42] . Although limited to binary grassland/non-grassland classification, the dataset provides higher spatial resolution and serves as an independent reference for trend validation. Despite differences in spatial resolution and classification schemes, both datasets consistently revealed an increasing global trend in grassland fragmentation. Although regional patterns occasionally diverged—showing directionally inconsistent trends at the ecoregion level—this overall agreement supports the robustness of our ESA CCI–based findings (Supplementary Tab. 3).

We chose to use the 300 m ESA CCI land cover product as our primary dataset for three main reasons. First, despite the availability of higher-resolution (30 m) datasets, the 300 m product offers a longer temporal coverage, enabling a more comprehensive analysis of multi-decadal trends. Second, it provides consistent annual global land cover maps, which allow for more nuanced detection of fragmentation dynamics. Third, the ESA CCI product has been widely validated and is recognized for its reliability in large-scale ecological assessments[39].

5.2 The assessment of global grassland fragmentation

Based on the Landscape Continuum Theory proposed by McIntyre and Hobbs (1999), the transformation of ecosystem landscapes does not occur abruptly from an intact to a fragmented state, but rather follows a continuous gradient driven by both the degree of habitat loss and the intensity of matrix modification[43]. This theory emphasizes the process-based and functional nature of ecological fragmentation, moving beyond traditional binary classifications of fragmented versus non-fragmented, and focusing instead on the dynamic trajectory of structural change. To quantitatively apply this framework in spatial analysis, this study adopts the Area Density (AD) metric[18] , which measures the proportion of same-type habitat pixels within a fixed-size neighborhood to evaluate local-scale landscape connectivity. AD values are classified into seven categories: intact (AD = 1.0), interior (0.9–1.0), dominant (0.6–0.9), transitional (0.4–0.6), patchy (0.1–0.4), rare (0–0.1), and none (AD = 0). These thresholds are ecologically meaningful: AD = 1.0 indicates undisturbed core habitats with minimal edge effects; AD < 0.1 represents highly isolated patches where critical ecological processes such as dispersal, reproduction, or predation are unlikely to be sustained; and AD = 0 indicates total habitat loss. Intermediate thresholds such as 0.6 and 0.4 are commonly regarded as tipping points at which landscape connectivity collapses and ecological processes become severely constrained[18]. This classification system aligns with the continuous nature of ecological degradation and is particularly applicable to ecosystems such as grasslands, where fragmentation boundaries are diffuse and disturbance gradients are gradual. By linking structural metrics with functional ecological thresholds, the method enables a more refined identification of fragmentation intensity and facilitates process-based landscape diagnosis.

To determine the appropriate neighborhood size for fragmentation analysis, we performed a semivariogram-based spatial autocorrelation analysis. The semivariogram characterizes the decline in spatial similarity with increasing distance and was used to identify the scale at which spatial dependence becomes negligible. The results indicated that spatial autocorrelation stabilized at the 7×7 pixel scale, suggesting it as the optimal window size for detecting ecologically relevant fragmentation patterns (Supplementary Tab. 7). This finding is consistent with the standard window size adopted by Riitters

(2000)[44].

5.3 Land-use transitions associated with intact grassland fragmentation

Intact grassland fragmentation typically occurs when surrounding grassland is converted to other land-use types[45]. To characterize the spatial context of fragmentation, we analysed land-cover transitions around pixels where intact grassland was lost between 1995 and 2020. Accordingly, we identified all pixels that transitioned from intact to non-intact status between 1995-2020. For each pixel that transitioned from intact to non-intact grassland, we defined a central 7 × 7 window and analysed the 120 surrounding pixels outside this window. This neighborhood configuration captures the immediate spatial context of fragmentation while avoiding contamination from the focal area itself [44,45]. The most frequently occurring land-cover type was recorded as the dominant transition type for that fragmentation event. Land-cover transitions were grouped into eight categories—agriculture, forest, wetland, urban, bare land, shrubland, sparse vegetation, and water bodies—based on a standardized classification system.

To characterize regional variation, we performed spatial overlay and summary analyses at the levels of continents, countries, and WWF-defined terrestrial ecoregions, quantifying the proportion of intact grassland fragmentation events associated with each transition type.

5.4 Assessing the effects of grassland fragmentation under agricultural expansion

To quantify the consequences of grassland fragmentation on vertebrate biodiversity, we used the proportional loss of intact grassland as a proxy for fragmentation intensity. The analysis focused on fragmentation specifically associated with transitions to agricultural land between 1995 and 2020. Spatial analysis was conducted using a global grid system with 50×50 km cells (~2,500 km^2), covering all grassland ecoregions. This resolution balances spatial heterogeneity with the ecological scale of species distribution data[46]. A standardized four-step data screening protocol was applied: (1) Geometric integrity – grid cells with less than 90% valid land coverage (due to projection artifacts or border effects) were excluded; (2) Historical baseline – cells lacking intact grassland in 1995 were removed to ensure measurable fragmentation; (3) Dominant land cover – only cells where natural or semi-natural grassland was the primary cover type were retained; (4) Data completeness – cells with missing species richness or covariate values were excluded.

Species occurrence data for birds, mammals, amphibians, and reptiles were obtained from the IUCN global species range database. Presence–absence matrices were generated for each taxonomic group, and species richness per grid cell was calculated and log-transformed to reduce skew and sampling bias.

Fragmentation attributable to cropland expansion (hereafter, *Cropland_fragmentation*) was calculated as the proportion of intact grassland pixels within each grid cell that transitioned to a non-intact state and were previously identified (see Section 5.3) as associated with agricultural land conversion. To classify fragmentation intensity, we first assigned grid cells with zero values to the no-fragmentation category. The remaining non-zero values were then divided into three classes—low, medium, and high—using quantile thresholds based on their empirical distribution.

Generalized additive models (GAMs; *mgcv* package in R) were used to evaluate the effects of grassland fragmentation on vertebrate species richness across global grasslands. The response variable was log-transformed species richness, and the primary predictor was fragmentation intensity (*Cropland_fragmentation*), as defined above. Additional predictors included remaining grassland area (*GA*), biome classification (*Biome*), and vertebrate class (*Class*). To account for potential ecological heterogeneity, the full model incorporated all main effects and selected two-way interaction terms. The model formula was:

$$\textit{Species richness} \sim \textit{Cropland\_fragmentation} + \textit{Class} + \textit{Biome} + \textit{GA} + \textit{Cropland\_fragmentation: Class} + \textit{Cropland\_fragmentation: GA} + \textit{Cropland\_fragmentation: Biome} + \textit{Class: GA} + \textit{Class: Biome}$$

5.5 Prediction of the global intact grassland status in 2045 under different scenarios

We employed the Patch-generating Land Use Simulation (PLUS) model to predict future land use dynamics, with a focus on evaluating how global grassland distribution patterns and fragmentation may evolve by 2045 under different scenarios. The PLUS model incorporates an adaptive inertia competition mechanism and employs the random forest algorithm to calculate land conversion potential with higher accuracy[47]. To achieve this, we analysed land-use changes between 1995 and 2020 and examined their relationships with key drivers, including annual mean land surface temperature, precipitation, elevation, population density and nighttime light. Based on this analysis, we derived land-use transition rules. Using these rules, we predicted future land-use scenarios and estimated how grassland areas might evolve under different conditions.

We projected the state of global grassland fragmentation in 2045 under three land-use transition scenarios. (1) Baseline scenario: Continuation of historical grassland-to-other-land transition rates observed from 1995 to 2020, with no additional interventions. (2) Conservation scenario: A 10% reduction in the transition rate from intact grasslands to other land-use types (e.g., cropland, urban areas), while keeping all other transitions unchanged, simulating stricter protection efforts to slow grassland loss. (3) Restoration scenario: A 10% increase in the transition rate from degraded lands (cropland, bare land, shrubland) back to grassland, with all other transitions unchanged, simulating ecological restoration efforts to enhance grassland recovery. The ±10% adjustment reflects standard practice in land-use scenario modeling, with 10–20% shifts commonly used to simulate moderate interventions [48].

Data availability

The annual mean land surface temperature, digital elevation model and nighttime light data are distributed through NASA Earthdata, including products available from the Land Processes Distributed Active Archive Center (https://www.earthdata.nasa.gov/centers/lp-daac). Global precipitation data can be accessed through the NOAA Physical Sciences Laboratory (https://psl.noaa.gov/data/gridded/). The global population density data used in this study were obtained from the LandScan platform developed by Oak Ridge National Laboratory and are publicly available from the data provider(https://landscan.ornl.gov/). The terrestrial ecoregion map used to define ecological regions is available from the RESOLVE Ecoregions 2017 / WWF terrestrial ecoregions dataset (https://ecoregions.appspot.com/). Expert-derived polygons of amphibians, mammals and reptiles are available from the IUCN Red List spatial data portal (https://www.iucnredlist.org/resources/spatial-data-download). Bird distribution polygons can be requested from BirdLife International through the DataZone portal (https://datazone.birdlife.org/contact-us/request-our-data). The 300-m land-cover dataset used in the main analysis is the European Space Agency Climate Change Initiative Land Cover product (https://www.esa-landcover-cci.org/?q=node/164). The supplementary robustness analysis used the Global

Pasture Watch annual 30-m global grassland dataset (2000-2022) (https://zenodo.org/records/13890401). Underlying data for the main manuscript figures are included in source data files deposited in Figshare. Processed data supporting the findings of this study, including data for grassland fragmentation mapping, land-cover transition analysis and biodiversity impact assessment, are available at https://doi.org/10.6084/m9.figshare.28236503.

Code availability

The R scripts used to reproduce the main analyses presented in this study, including grassland fragmentation mapping, land-cover transition analysis and biodiversity impact assessment, are available at https://doi.org/10.6084/m9.figshare.28236503

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Competing interests

The authors declare no competing interests.

Author contributions

Ning Zhang, He Yin and Qing Zhang conceived the study. Ning Zhang and Ang Li assembled and analysed the data. Ning Zhang, He Yin, Qing Zhang and Ang Li wrote the first version of the manuscript. Yongzhi Yan and Amy E. Frazier contributed to the interpretation of the results and manuscript revision. All authors reviewed and edited the manuscript.

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Figure captions

Fig. 1: Global patterns of grassland fragmentation in 2020 measured using area density (AD).

a The inset bar chart shows the proportion of grassland area in each fragmentation category across six continents. **b–g** Spatial patterns of grassland fragmentation in North America, Europe, Asia, South America, Africa and Oceania. Each pixel was classified into one of seven fragmentation categories based on its AD value: intact (AD = 1.0), interior (0.9–1.0), dominant (0.6–0.9), transitional (0.4–0.6), patchy (0.1–0.4), rare (0–0.1) and none (AD = 0). Continent abbreviations are as follows: NA, North America; EUR, Europe; AS, Asia; SA, South America; AF, Africa; OA, Oceania.

Fig. 2: Relative changes in intact grassland area from 1995 to 2020 at national and ecoregion scales.

a Percentage change in intact grassland area in 2020 relative to 1995 for each country. **b** Percentage change in intact grassland area in 2020 relative to 1995 for each ecoregion. Yellow to red colours indicate increasing intact grassland area, whereas blue colours indicate declining intact grassland area.

Fig. 3: Land-use and land-cover changes associated with grassland fragmentation at global and

continental scales.

Bars represent the percentage of fragmentation attributed to each of the eight LULC change types: agriculture, forest, wetland, urban, bare land, shrubland, sparse vegetation, and water bodies.

Fig. 4: Effects of grassland fragmentation associated with cropland expansion on vertebrate species richness, across different grassland area classes and biomes.

Point colour indicates fragmentation intensity, classified into four levels based on the tertile distribution of intact grassland area loss (IGA_loss): No (IGA_loss = 0), Low (< 0.09), Medium (0.09–0.15), and High (≥ 0.15). Thresholds correspond to the 33rd and 66th percentiles of non-zero IGA_loss values. Point shape represents grassland area class: Small (≤ 26.38 km^2), Intermediate (26.38–36.23 km^2), and Large (≥ 36.23 km^2), also based on tertile grouping. Relative effects are expressed as percentage changes in species richness compared to the no-fragmentation baseline (IGA_loss = 0). Positive values indicate higher species richness relative to non-fragmented conditions, whereas negative values indicate lower species richness under fragmentation. Error bars indicate 95% confidence intervals; effects were considered statistically significant when the 95% confidence interval did not overlap zero. Biome abbreviations: Montane = Montane Grasslands & Shrublands; Temperate = Temperate Grasslands, Savannas & Shrublands; Tropical = Tropical & Subtropical Grasslands, Savannas & Shrublands.

Fig. 5: Scenario-dependent changes in projected future intact grassland area for the year 2045.

a Dominant scenario for increasing intact grassland area in each ecoregion, showing whether the Conservation scenario or the Restoration scenario results in a larger gain, or whether the two scenarios have comparable changes. In a, yellow indicates that the Restoration scenario produces a larger increase, green indicates that the Conservation scenario produces a larger increase, and blue indicates that the two scenarios produce comparable changes. **b–h** Percentage change in intact grassland area in 2045 under two scenarios relative to the Baseline scenario for the globe and six continents. In b–h, green bars indicate the Conservation scenario, and yellow bars indicate the Restoration scenario.

Editorial summary:

Global grassland fragmentation has left only ~24% of grasslands intact by 2020, with contrasting biodiversity effects and conservation outperforming restoration in 61% of ecoregions, based on global fragmentation mapping, vertebrate richness analyses, and land-use scenario projections.

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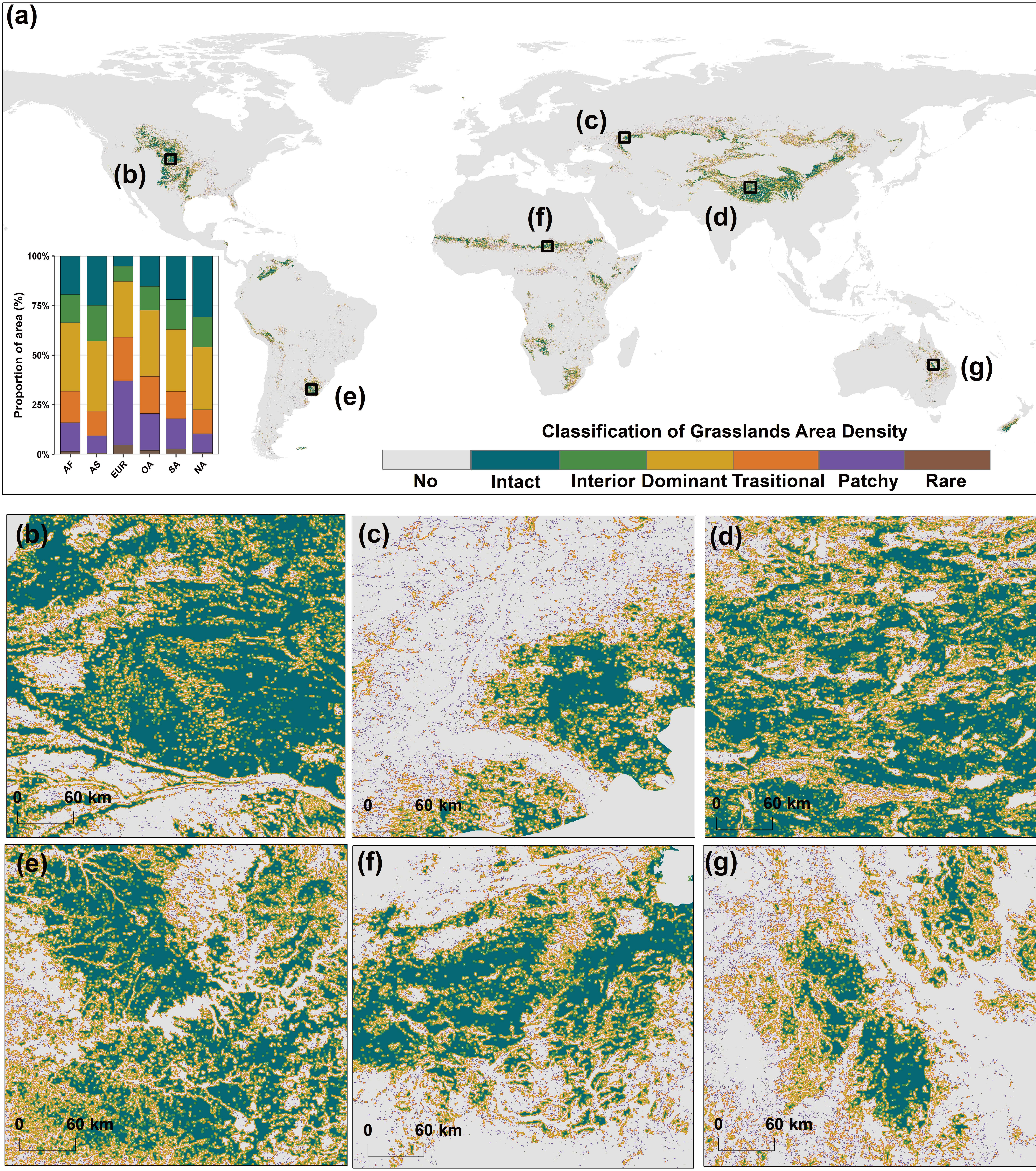
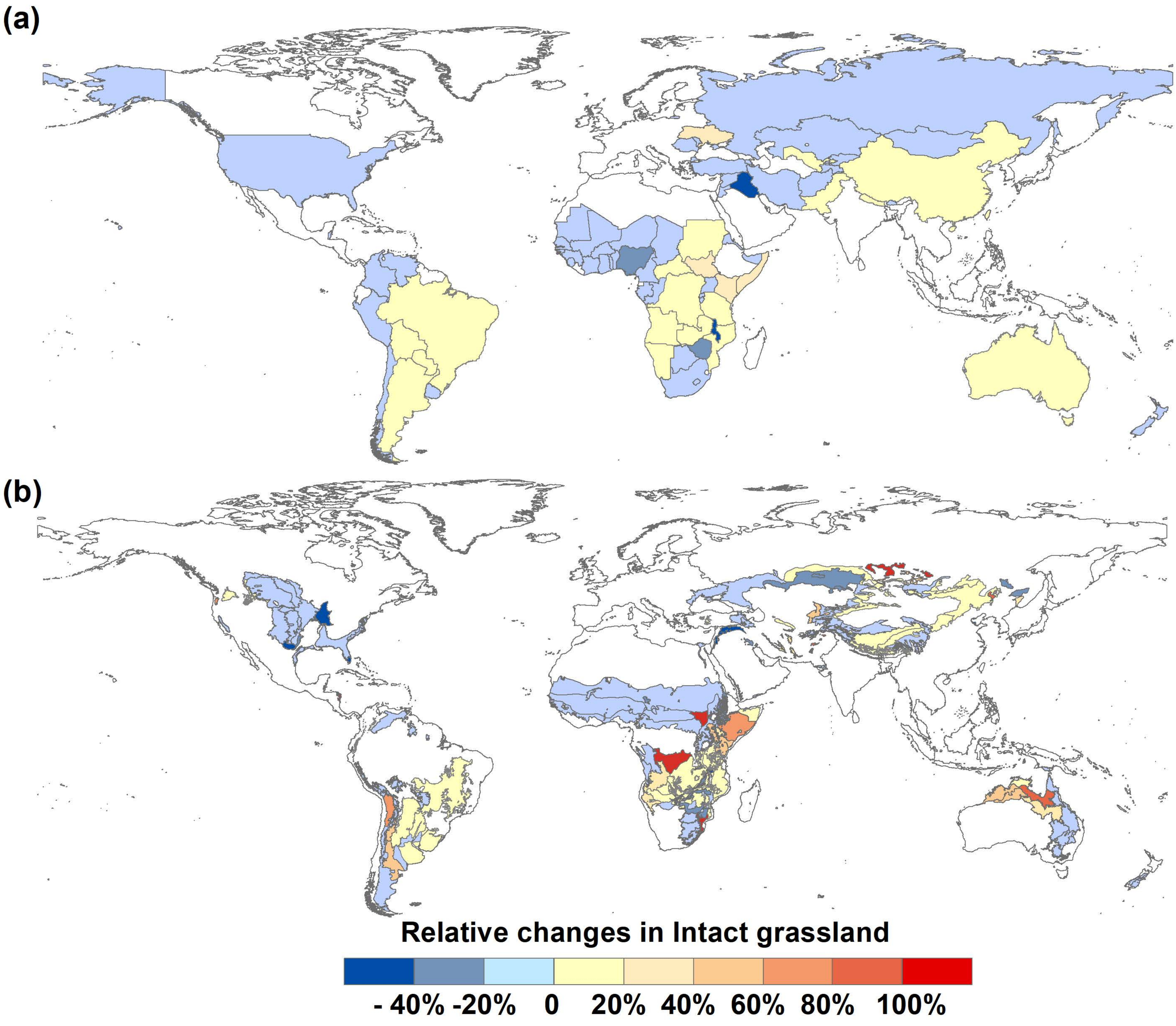

(a)
(b)
(c)
(d)
(e)
(f)
(g)
100%
75%
50%
25%
0%
Proportion of area (%)
AF
AS
EUR
OA
SA
NA
Classification of Grasslands Area Density
No
Intact
Interior
Dominant
Trasitional
Patchy
Rare
0
60 km


(a)
(b)
Relative changes in Intact grassland
- 40%
-20%
0
20%
40%
60%
80%
100%

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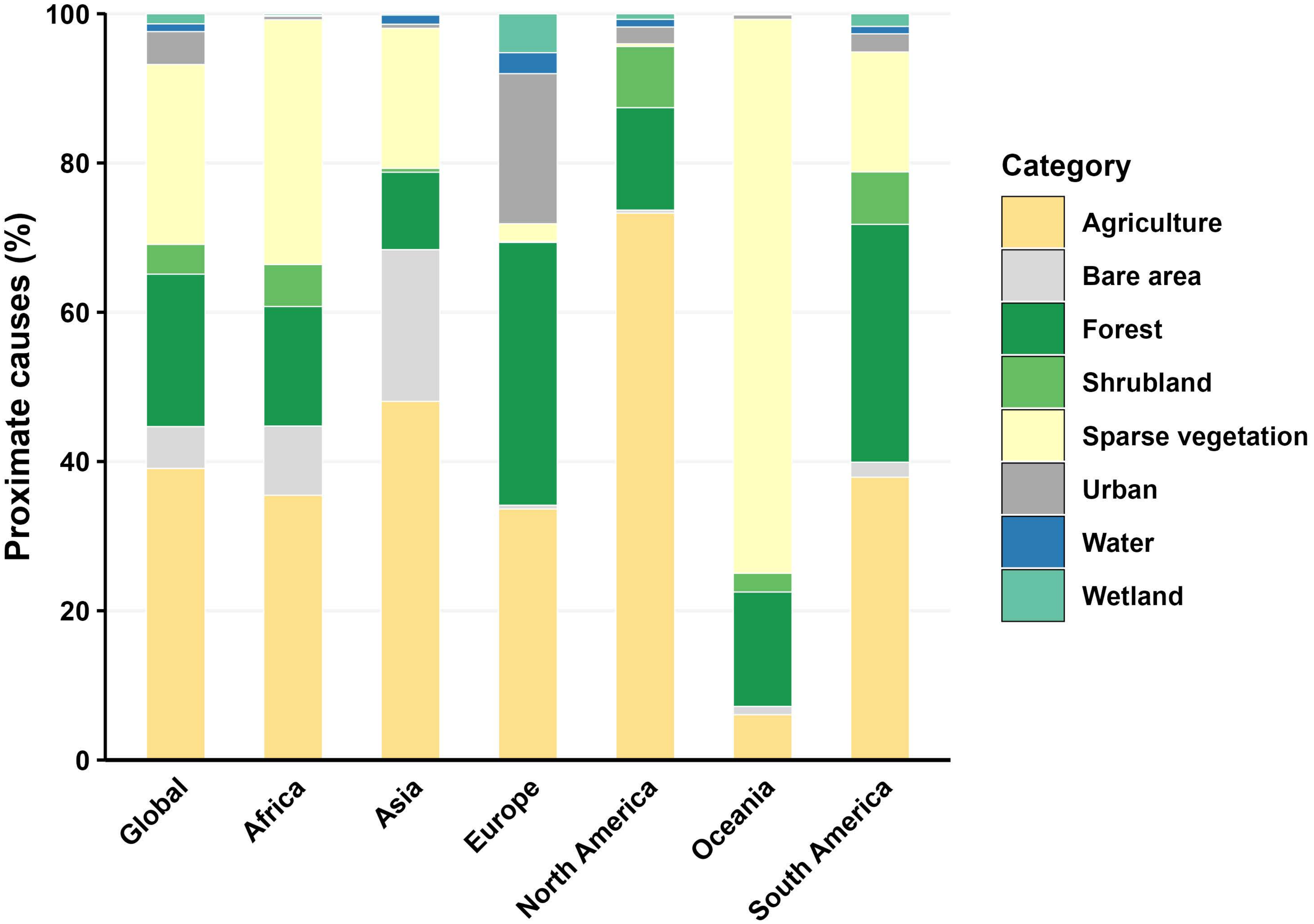
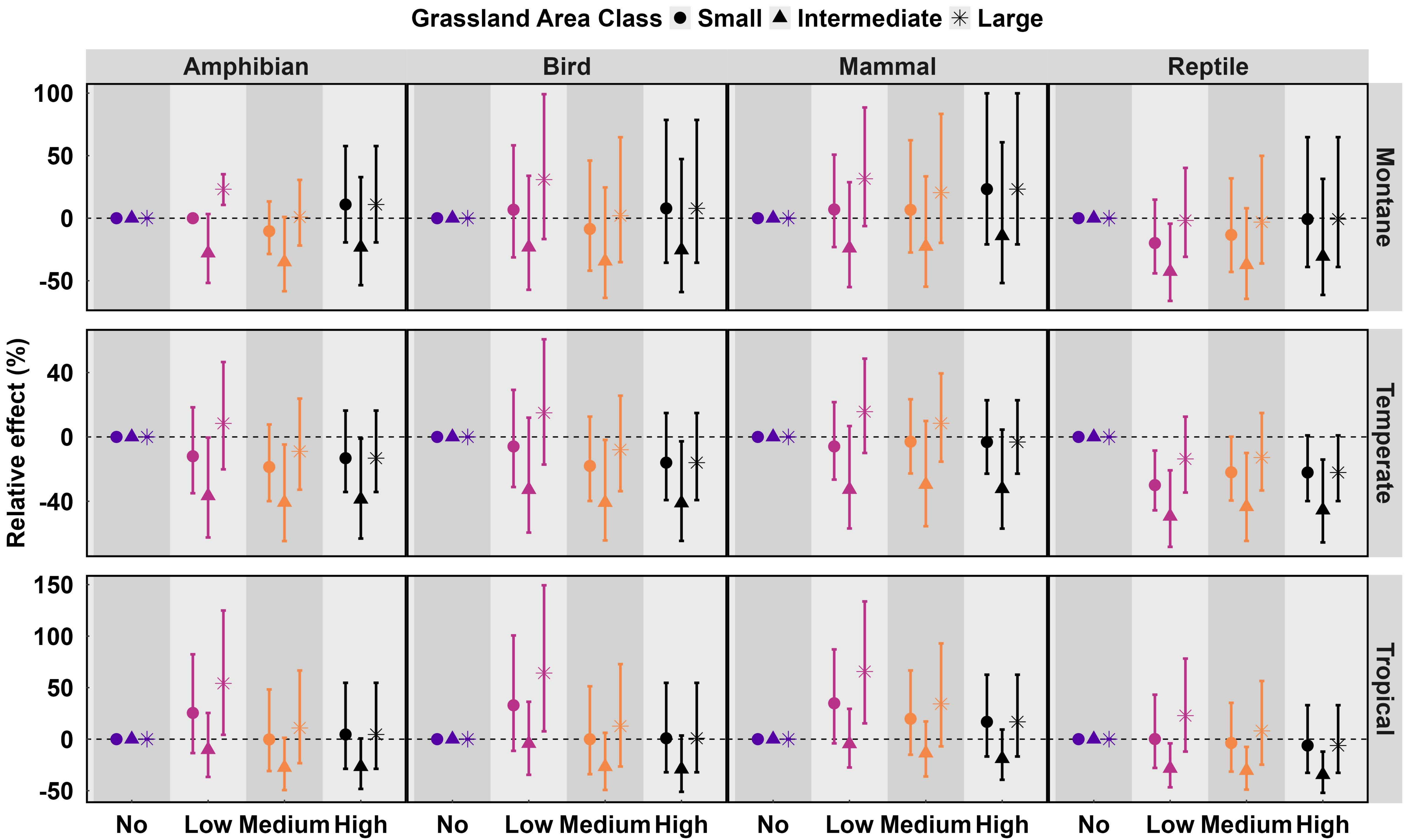
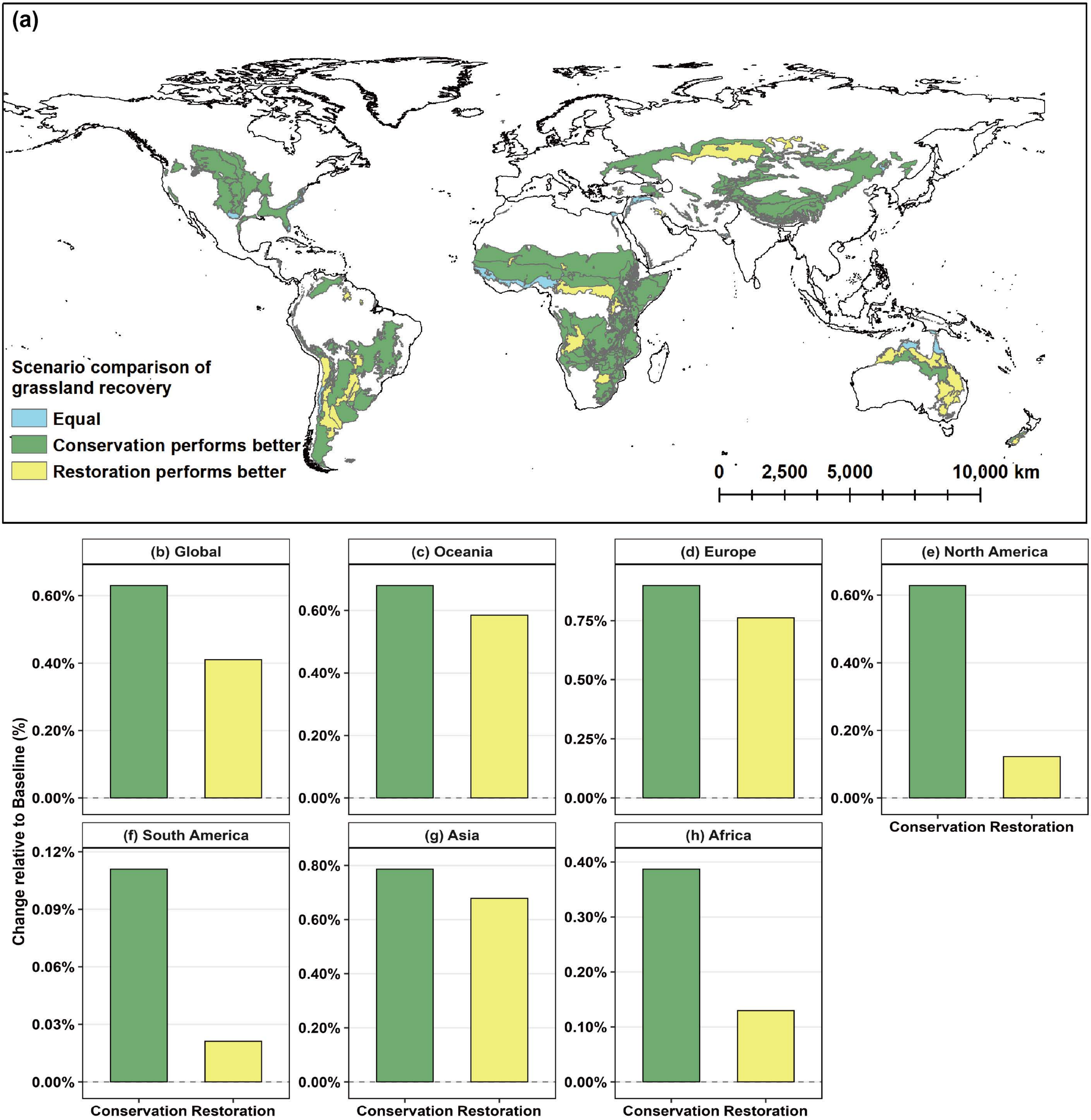



Grassland Area Class
Small
Intermediate
Large
Amphibian
Bird
Mammal
Reptile
Montane
Temperate
Tropical
Relative effect (%)
100
50
0
-50
40
0
-40
150
100
50
0
-50
No
Low
Medium
High


(a)
Scenario comparison of grassland recovery
Equal
Conservation performs better
Restoration performs better
0
2,500
5,000
10,000 km
(b) Global
(c) Oceania
(d) Europe
(e) North America
(f) South America
(g) Asia
(h) Africa
Change relative to Baseline (%)
0.00%
0.20%
0.40%
0.60%
0.25%
0.50%
0.75%
0.03%
0.06%
0.09%
0.12%
0.80%
0.10%
0.30%
Conservation
Restoration