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The last continuous grasslands on Earth: Identification and conservation importance

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Abstract

Grasslands are the most threatened and least protected biome. Yet, no study has been conducted to identify the last remaining continuous grasslands on Earth. Here, we used World Wildlife Fund (WWF) and International Union for Conservation of Nature (IUCN) classifications to measure the degree of intactness remaining for the world's grassland ecoregions. This analysis revealed three findings of critical conservation importance. First, only a few large, intact grasslands remain. Second, every continent with a grassland ecoregion considered in this study contains at least one relatively intact grassland ecoregion. Third, the largest remaining continuous grasslands identified in this analysis have persisted despite last centuries anthropogenic pressures and have the best chance to withstand 21st century pressures of global change. We discuss how these regions are of critical conservation importance to global grassland conservation efforts under anthropogenically driven global change. They provide essential ecosystem services, play an important role in mitigating the effects of climate change, serve as critical repositories for grassland biodiversity, are foundational for continental migration pathways, hold unique cultural heritage, and people's livelihoods depend upon their persistence.

KEY WORDS

biome, climate change, global conservation, grasslands, International Union for Conservation of nature (IUCN), scale, World Wildlife Fund (WWF)

1 | INTRODUCTION

Grasslands are the most imperiled terrestrial ecosystem on the planet (Carbutt, 2020; Sutcliffe et al., 2005). Grasslands have experienced a far greater rate of global conversion than forests (Boakes et al., 2010), yet forestry conservation is far ahead in terms of global advocacy and action to maintain large and intact forested regions (Scullion et al., 2019; Zanotti & Knowles, 2020). Grasslands have relatively little federal or international

protection (Carbutt et al., 2017), corresponding to the least amount of safe operating space to anthropogenic pressures driving global change (Newbold et al., 2016). Grassland biodiversity is the most threatened especially endemic avian diversity which has been the most severely affected with more than 60% already lost since the 1970s in North American grasslands (Rosenberg et al., 2019). Yet, grasslands play an important role in carbon sequestration mitigating the effects of climate change (Chang et al., 2021). Consequently, the ecosystem

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services unique to grasslands, particularly those beyond agricultural production (Bengtsson et al., 2019) are threatened, especially those ecosystem services that are scale-dependent and require large regional connectivity (Zhao et al., 2020).

At global scales, organizations such as World Wildlife Fund (WWF) and The International Union for Conservation of Nature (IUCN) are leaders in biodiversity conservation. Other global bodies such as The United Nations Educational, Scientific and Cultural Organization (UNESCO) legally protect intact areas, for example, World Heritage Sites, ranging from monuments, landmarks, and natural/wilderness areas. Because grassland protection is rarely a priority (Carbutt et al., 2017), the WWF formed the Global Grassland and Savannah Initiative (GGSI) aimed at conserving both of these ecosystems given their similarities in threats (Dudley et al., 2020). In recent years, the world's temperate grasslands received focused attention with the establishment of the IUCN Temperate Grasslands Conservation Initiative (TGCI) in 2008. Furthermore, the TGCI adapted biodiversity targets as set out by the Convention on Biological Diversity (CBD) to double the at-the-time protection level (<5%) by 2020 according to CBD Aichi Target 11 (Carbutt et al., 2017). While achieving this target has certainly been met with many challenges (Zafra-Calvo et al., 2019), having large, connected, intact areas is well established in order to reduce biodiversity loss and habitat degradation and increase grassland preservation (Woodley et al., 2012).

Large and continuous ecosystems are better able to withstand global pressures of ecological change (Ponce-Campos et al., 2013). They also reduce the prevalence of infectious diseases (Keesing et al., 2010), assist in preventing pandemics (United Nations Environment Programme and International Livestock Research Institute, 2020), promote biodiversity through improved habitat (Betts et al., 2017), and allow species to move easily between landscapes compared with fragmented landscapes (Wilcove & Wikelski, 2008). Intact ecosystems are also more capable of buffering the effects of climate variability (Martin & Watson, 2016), which is exacerbated by habitat fragmentation, environmental degradation, and human intensification (Malhi et al., 2020). They are more resilient to disturbance and reduce risk of anthropogenic conversion (Folke et al., 2004) and provide the foundation for large-scale grassland strongholds under anthropogenically-driven global change. Recently, the United States Natural Resources Conservation Service of the United States of America has adopted conservation frameworks centered around defending intact grassland systems in the western United States. These frameworks are based around proactive conservation strategies by

expanding “core intact areas” which is foundational for grassland conservation this century. These efforts are likely to be more cost-effective and efficient, than reactive restorative responses (Natural Resources Conservation Service: Working Lands for Wildlife, 2021a, 2021b).

Most of our planet's terrestrial ecosystems are not intact (Plumptre et al., 2021). As a conservation community, one of our primary goals are to conserve intact systems (Mittermeier et al., 2003). Threats such as fragmentation and habitat decline in general, characterize many ecosystems today. Given the importance of intact systems for biodiversity and ecosystem services (Williams et al., 2020) in this study, we identify the last remaining large, intact grasslands in the world, and discuss their broadly significant policy-relevance to global grassland conservation.

2 | METHODS

2.1 | Study area selection and current status of global grassland conservation

We used WWF's global grassland classification system and extent of grassland ecoregions (Dinerstein et al., 2017) to align our study with existing global grassland conservation efforts. Dinerstein et al. (2017) expands upon WWF's previous classification system, Terrestrial Ecoregions of the World (Olson et al., 2001). Grassland ecoregions were further classified as desert grasslands or tropical/temperate grasslands using rainfall and temperature data from WorldClim v2 (Fick & Hijmans, 2017), consistent with previous efforts to differentiate grassland types with contrasting vegetation composition, structure, and ecological function (Woodward et al., 2004). For example, meadow steppes in the Palearctic are more analogous to North American tallgrass prairie than North American sagebrush steppe. Similarly, less productive grasslands in North America (e.g., mixed and short grass prairies) share common ecological resemblances to typical bunchgrass steppes of Eurasia. In general, desert grasslands are more arid ecosystems and contain a relatively higher shrub component than temperate/tropical grasslands (Humphrey, 1974; Paruelo et al., 1998). Temperate and tropical grasslands are more productive ecosystems located in areas of higher annual precipitation in more humid to sub-humid environments and are classified as more treeless “true prairies.” While the majority of the world's grasslands occur in temperate latitudes, which exhibit a unimodal temperature distribution, a key additional distinguishing characteristic between desert and temperate grasslands is intra-annual differences in precipitation. Desert grasslands occur in regions with a

TABLE 1 The largest and most intact grasslands remaining on Earth

Selenge-Altai and surrounding steppes (Emin Valley, Tian Shan, Kazakhstan)		Nebraska Sand Hills wet Puna grassland		Central Andean steppe		Wyoming Basin steppe		Mongolian-Manchurian and Daurian grasslands		Mitchell grasslands		Maloti-Drakensberg grasslands	
Continent	Asia	North America	South America	North America	North America	North America	Asia	Australia	Australia	Africa	Africa		
Average Precip. (mm) ^a	264 ± 55	426 ± 52	699 ± 120	223 ± 47	271 ± 55	365 ± 74	900 ± 100						
Average Temp (°C) ^a (Fick & Hijmans, 2017)	2.5 ± 2.31	8.8 ± 0.3	6.1 ± 2.7	5.3 ± 1.4	−0.1 ± 1.8	24.4 ± 1.2	14.4 ± 2.8						
Area (km ²) ^{b,c}	65,134–228,370	61,212	116,873	132,577	209,637–889,459	459,495	114,782						
Regional threats	Energy development (mining) (Stubblefield et al., 2005) and oil (Werger & Van Staalduin, 2012)	Woody encroachment (Fogarty et al., 2020), energy development (wind)	Energy development (mining) (Rolando et al., 2017)	Energy development (oil and gas) (Allred et al., 2015), plant invasion (<i>Bromus tectorum</i>)	Energy development (mining and oil) (Heiner et al., 2011)	Woody encroachment (Bastin, 2008)	Energy development (mining and hydraulic fracturing), alien invasive plants (Carbutt, 2019)						
Cultural identity	Nomadic and semi-nomadic herders (Gillam et al., 2012)	Sand Hills Ranchers	Incan farmers	North American cowboy	Mongolian nomadic herders	Aboriginal farmers	Drakensberg San (Nguni and Sotho farmers)						
Unique features	A transboundary ecoregion of sparse forest within a steppe region that supports exceptional levels of biodiversity (Gillam et al., 2012)	Deepest part of one of the world's largest aquifers (Ogallala, 120–366 m)	Machu Picchu is one of the world's famous World Heritage Sites and includes the Andean grasslands.	Holds 55% of the remaining sagebrush ecosystem in western United States (Knick et al., 2003).	Contains multiple world heritage sites: Landscapes of Dauria (transboundary conservation effort); Yungang Grottoes (a cave art city); Site of Xanadu (hosts the remains of Kublai Khan's capital city).	Spans both Queensland and the Northern Territory which hosts the largest population of Aboriginal communities and lowest population of all states in Australia (0.08 people km ⁻²).	The Maloti-Drakensberg Park is a transboundary park and World Heritage Site comprised of uKhahlamba-Drakensberg Park (South Africa) and Sehlabathibe National Park (Lesotho) which was inhabited by Mammal Sites						

(Continues)

TABLE 1 (Continued)

Selenge-Altai and surrounding steppes (Emin Valley, Tian Shan, Kazakhstan)	Nebraska Sand Hills grassland	Central Andean wet Puna	Wyoming Basin steppe	Mongolian-Manchurian and Daurian grasslands	Mitchell grasslands	Maloti-Drakensberg grasslands
The Altai represents a regional unique transition zone between the forests of the Altai Mountains and Kazakh desert plains. The eastern strip of the Altai is part of the Kator-Karagay—the largest Nature Reserve in Kazakhstan and a UNESCO Biosphere Reserve	National Natural Landmark (1984)	the world (Lake Titicaca) situated in the Andean mountains across Peru and eastern Bolivia.		(Riversleigh/Naracoorte) is a World Heritage site situated in the Northern Territory part of the ecoregion.		the San people for more than four millennia. The Drakensberg mountain range is Africa's highest south of Mount Kilimanjaro.
Iconic species	Habitat for critically endangered yellow-breasted Bunting (<i>Emberiza aureola</i>), endangered steppe eagle and Saker falcon, vulnerable Great Bustard (<i>Otis tarda</i>) (Collar et al., 2017) and Eastern Imperial eagle (<i>Aquila heliaca</i>), near threatened Dalmatian pelican (Gombobaatar et al., 2012), vulnerable Chinese Mountain cat (<i>Felis</i>	Stronghold for only prairie chicken species (<i>Tympanuchus cupido</i>) not extinct, threatened or endangered	Breeding habitat for critically endangered royal cincloides (<i>Cinclodes aricomae</i>)	32% of entire near threatened greater sage grouse (<i>Centrocercus urophasianus</i>) breeding population	Once extinct wild horse (Przewalski's horse) successfully reintroduced Seasonal transboundary migration path for the Mongolian gazelle	Kangaroos and wallabies are protected in the entire Northern Territory and Eastern gray kangaroo populations have increased since the 1960s (Phelps, 2012)
		Federally endangered blowout penstemon found only found in open sand “blowouts”	The vulnerable Andean condor (<i>Vultur gryphus</i>) is the largest flying bird in South America is a native resident in Andean mountains and surrounding grasslands	(Doherty et al., 2016) Longest remaining pronghorn migration route (Tack et al., 2019)	Mongolian marmot has decreased by 75% since 1990 (Clark et al., 2006).	A few critically endangered avian species such as the night parrot (<i>Geopsittacus occidentalis</i>), curlew sandpiper (<i>Calidris ferruginea</i>) and plains wanderer (<i>Chæetops aurantius</i>) Native resident for near threatened Bearded vulture

TABLE 1 (Continued)

Selenge-Altai and surrounding steppes (Emin Valley, Tian Shan, Kazakhstan)	Nebraska Sand Hills grassland	Central Andean wet Puna	Wyoming Basin steppe	Mongolian-Manchurian and Daurian grasslands	Mitchell grasslands	Maloti-Drakensberg grasslands
<i>bieti</i>) and brood rearing habitat for the near threatened Argali (<i>Ovis ammon</i>) and Demoiselle cranes (<i>Anthropoides virgo</i>).				(<i>Pedionomus torquatus</i>) survive in this ecoregion, while two wallaby species are vulnerable (purple-necked and yellow-footed) and one endangered (bridled nailtail) (Department of Environment and Science Queensland, 2013).		(<i>Gypaetus barbatus</i>) in Southern Africa (BirdLife International)

Note: Photos sourced from Creative Commons (see Supporting Information).

^aAverage precipitation and temperature taken where multiple regions are included acquired from Fick and Hijmans (2017).

^bRange in area given where multiple regions are included.

^cEcoregion area as defined by Dinerstein et al. (2017).

TABLE 2 List of all ecoregions considered in this study along with their area (km^2), % ecoregion intact in 2019 ranked from most to least intact (100 m resolution), percent of low impact area mean and standard deviation of global human footprint index where 0 refers to least influenced

Ecoregion	Type	Continent	Ecoregion area (km^2)	% intact (100 m)	% intact (500 m)	Jacobson's low impact area (%) ^a	Mean + SD global human footprint ^b	Largest patch index	Core area (km^2)
Altai steppe	Desert Grasslands	Asia	83,193.38	86.21	82.68	61.19	0.18 ± 0.13	88.73	73,817.49
Nebraska Sand Hills mixed grasslands	Temperate/ Tropical Grasslands	North America	59,123.00	80.47	85.76	1.35	0.15 ± 0.1	95.66	56,557.06
Central Andean wet puna	Temperate/ Tropical Grasslands	South America	116,873.79	74.39	77.96	35.12	0.26 ± 0.15	52.12	60,914.62
Tian Shan foothill arid steppe	Desert Grasslands	Asia	129,229.70	72.42	70.24	20.01	0.23 ± 0.15	50.45	65,196.38
Wyoming Basin shrub steppe	Desert Grasslands	North America	132,682.39	71.48	92.27	52.59	0.08 ± 0.08	99.38	131,859.76
Emin Valley steppe	Desert Grasslands	Asia	65,134.74	69.48	63.5	35.83	0.21 ± 0.18	97.47	63,486.83
Selenge-Orkhon steppe	Desert Grasslands	Asia	228,370.19	69.48	79.65	35	0.1 ± 0.05	92.84	212,018.88
Daurian steppe	Temperate/ Tropical Grasslands	Asia	209,637.31	69.11	71.63	56.89	0.11 ± 0.07	95.98	201,209.89
Cordillera de Merida paramo	Temperate/ Tropical Grasslands	South America	2797.60	67.21	6.42	75.62	0.21 ± 0.06	93.03	2602.61
Mongolian-Manchurian grassland	Temperate/ Tropical Grasslands	Asia	889,459.75	66.92	81.05	33.11	0.22 ± 0.21	93.65	832,979.06
Mitchell grasslands	Temperate/ Tropical Grasslands	Australia	459,495.91	66.26	29.22	99.45	0.01 ± 0.03	85.04	390,755.32
Kazakh upland steppe	Desert Grasslands	Asia	72,199.32	64.99	63.78	51.26	0.19 ± 0.19	68.99	49,810.31
Santa Marta paramo	Temperate/ Tropical Grasslands	South America	1238.66	62.2	16.72	98.23	0.16 ± 0.04	97.74	1210.67

TABLE 2 (Continued)

Ecoregion	Type	Continent	Ecoregion area (km^2)	% intact (100 m)	% intact (500 m)	Jacobson's low impact area (%) ^a	Mean + SD global human footprint ^b	Largest patch index	Core area (km^2)
Drakensberg grasslands	Temperate/ Tropical Grasslands	Africa	114,782.02	61.9	68.36	4.3	0.28 ± 0.15	94.5	108,469.01
Montana Valley and Foothill grasslands	Temperate/ Tropical Grasslands	North America	100,078.95	59.89	59.04	21.38	0.19 ± 0.19	42.4	42,433.47
Cordillera Central paramo	Temperate/ Tropical Grasslands	South America	12,119.70	58.94	45.68	33.36	0.27 ± 0.18	44.06	5339.94
Altai montane steppe	Desert Grasslands	Asia	142,873.81	58.85	53.94	60.46	0.09 ± 0.06	44.2	63,150.22
Northern Andean paramo	Temperate/ Tropical Grasslands	South America	29,810.50	58.5	14.19	33.3	0.25 ± 0.17	18.44	5497.06
Eastern Anatolian montane steppe	Desert Grasslands	Asia	168,381.54	57.36	62.46	7.11	0.43 ± 0.18	89.37	150,482.58
Tian Shan montane steppe and meadows	Desert Grasslands	Asia	280,611.56	56.07	47.35	53.6	0.15 ± 0.13	77.12	216,407.64
Northern Shortgrass prairie	Temperate/ Tropical Grasslands	North America	719,348.38	54.71	55.86	4.71	0.26 ± 0.2	91.66	659,354.73
Western shortgrass prairie	Temperate/ Tropical Grasslands	North America	487,149.08	53.93	65.9	9.89	0.24 ± 0.19	85.05	414,320.29
Kazakh steppe	Desert Grasslands	Asia and Europe	807,566.52	53.24	21.41	34.81	0.29 ± 0.22	91.51	739,004.12
Kopet Dag woodlands and forest steppe	Desert Grasslands	Asia	58,316.73	52.08	43.75	3.88	0.24 ± 0.14	89	51,901.89
Flint Hills tallgrass prairie	Temperate/ Tropical Grasslands	North America	27,932.26	50.55	76.59	5.74	0.25 ± 0.15	57.12	15,954.91
Yarlung Zanbo arid steppe	Desert Grasslands	Asia	59,380.73	50.51	66.03	45.48	0.19 ± 0.12	60.88	36,150.99
Highveld grasslands		Africa	241,637.79	50.01	47.59	3.42	0.34 ± 0.21	90.58	218,875.51

(Continues)

TABLE 2 (Continued)

Ecoregion	Type	Continent	Ecoregion area (km^2)	% intact (100 m)	% intact (500 m)	Jacobson's low impact area (%) ^a	Mean + SD global human footprint ^b	Largest patch index	Core area (km^2)
Saharan flooded grasslands	Temperate/ Tropical Grasslands	Africa	178,952.04	48.64	27.48	19.28	0.2 ± 0.09	61.59	110,216.56
Snake-Columbia steppe	Desert Grasslands	North America	193,188.18	48.56	80.67	51.77	0.11 ± 0.16	93.65	180,920.73
Altai-Western Tian Shan steppe	Desert Grasslands	Asia	127,682.75	46.65	54.14	2.13	0.41 ± 0.24	39.25	50,115.48
Ordos Plateau steppe	Desert Grasslands	Asia	215,604.42	45.97	82.15	4.61	0.37 ± 0.19	84.64	182,487.58
Palouse prairie	Temperate/ Tropical Grasslands	North America	83,923.25	45.4	44.06	19.45	0.27 ± 0.19	39.05	32,772.03
Ghorat-Hazarajat alpine meadow	Temperate/ Tropical Grasslands	Asia	66,482.10	45.01	71.49	33.7	0.19 ± 0.04	60.45	40,188.43
Sayan Intermontane steppe	Desert Grasslands	Asia	34,072.18	43.76	42.14	81.4	0.12 ± 0.15	41.92	14,283.06
Great Lakes Basin desert steppe	Desert Grasslands	Asia	157,708.98	42.18	57.58	61.09	0.07 ± 0.04	62.64	98,788.91
Canterbury-Otago tussock grasslands	Temperate/ Tropical Grasslands	Oceania	53,593.89	42.07	37.21	8.74	0.21 ± 0.12	80.97	43,394.97
New Zealand South Island montane tussock grasslands	Temperate/ Tropical Grasslands	Oceania	40,006.31	39.94	18.58	59.45	0.09 ± 0.07	20.71	8285.31
Central Andean puna	Temperate/ Tropical Grasslands	South America	211,479.65	39.6	25.88	51.19	0.13 ± 0.1	43.63	92,268.57
Gobi Lakes Valley desert steppe	Desert Grasslands	Asia	139,708.31	32.13	38.21	61.02	0.06 ± 0.03	68.73	96,021.52
Great Basin shrub steppe			300,877.74	31.45	52.98	84.27	0.05 ± 0.11	79.59	239,468.59

TABLE 2 (Continued)

Ecoregion	Type	Continent	Ecoregion area (km^2)	% intact (100 m)	% intact (500 m)	Jacobson's low impact area (%) ^a	Mean + SD global human footprint ^b	Largest patch index	Core area (km^2)
Desert Grasslands	Desert Grasslands	North America	397,556.88	30.44	30.8	3.72	0.41 ± 0.2	73.64	292,760.89
Zagros Mountains forest steppe	Desert Grasslands	Asia	629,197.54	28.34	44.42	83.83	0.04 ± 0.07	17.63	110,927.53
Central Tibetan Plateau alpine steppe	Temperate/ Tropical Grasslands	North America	274,962.61	26.25	41.9	0.87	0.38 ± 0.18	34.42	94,642.13
Central-Southern US mixed grasslands	Temperate/ Tropical Grasslands	Africa	52,849.33	23.95	0.28	85.84	0.05 ± 0.09	80.5	42,543.71
Namaqualand-Richtersveld steppe	Desert Grasslands	Asia	282,369.30	22.33	58.61	58.7	0.08 ± 0.08	30.74	86,800.32
Eastern Gobi desert steppe	Desert Grasslands	Asia	64,090.22	21.71	31.51	5.14	0.41 ± 0.17	31.5	20,188.42
Azerbaijan steppe	Desert Grasslands	Asia and Europe	997,074.76	21.15	24.05	12.16	0.45 ± 0.21	32.64	325,445.20
Pontic steppe	Desert Grasslands	Asia	118,039.15	20.94	12.31	75.63	0.09 ± 0.07	20.65	24,375.08
Pamir alpine desert	Desert Grasslands	Asia	23,259.83	19.35	17.98	5.11	0.52 ± 0.18	57.71	13,423.25
Neijiang River grassland	Temperate/ Tropical Grasslands	Asia	24,934.22	18.65	14.29	2.38	0.52 ± 0.2	11.52	2872.42
Central Anatolian steppe	Desert Grasslands	South America	398,565.02	18.55	21.51	0.38	0.63 ± 0.14	53.43	212,953.29
Humid Pampas	Temperate/ Tropical Grasslands	South America	576,592.95	15.97	23.31	65.93	0.08 ± 0.08	24.06	138,728.26
Patagonian steppe	Desert Grasslands	Asia and Europe	422,383.01	14.27	70.66	35.11	0.28 ± 0.19	16.98	71,720.64
Kazakh forest steppe	Desert Grasslands	Asia	162,595.63	13.59	9.69	50.46	0.25 ± 0.19	12.66	20,584.61

(Continues)

TABLE 2 (Continued)

Ecoregion	Type	Continent	Ecoregion area (km ²)	% intact (100 m)	% intact (500 m)	Jacobson's low impact area (%) ^a	Mean + SD global human footprint ^b	Largest patch index	Core area (km ²)
Central Andean dry puna	Desert Grasslands	South America	254,932.08	12.62	4.21	60.29	0.08 ± 0.08	52.07	132,743.13
Karakoram-West Tibetan Plateau alpine steppe	Desert Grasslands	Asia	143,267.47	12.59	7.85	73.54	0.11 ± 0.08	48.31	69,212.51
Papuan Central Range sub-alpine grasslands	Temperate/ Tropical Grasslands	Asia	15,502.76	11.14	3.15	86.58	0.17 ± 0.1	24.4	3782.67
Texas blackland prairies	Temperate/ Tropical Grasslands	North America	43,381.97	11.05	44.44	0.6	0.46 ± 0.19	6.13	2659.31
Northern mixed grassland	Temperate/ Tropical Grasslands	North America	219,615.4	11.01	15.54	3.2	0.46 ± 0.18	3.78	8301.46
Amur meadow steppe	Temperate/ Tropical Grasslands	Asia	123,625.59	10.1	1.71	48.96	0.33 ± 0.27	48.56	60,032.59
California Central Valley grasslands	Temperate/ Tropical Grasslands	North America	46,490.21	8.88	7.4	2.88	0.46 ± 0.19	17.91	8326.40
Western Gulf coastal grasslands	Temperate/ Tropical Grasslands	North America	90,734.78	6.73	27.13	11.77	0.4 ± 0.24	11.1	10,071.56
Syrian xeric grasslands	Desert Grasslands	Asia	137,934.16	6.53	5.33	4.4	0.31 ± 0.17	9.71	13,393.41
Northern Tallgrass prairie	Temperate/ Tropical Grasslands	North America	82,919.54	4.44	1.5	7.5	0.48 ± 0.2	4.35	3607.00
Australian Alps montane grasslands	Temperate/ Tropical Grasslands	Australia	12,329.81	4.13	3.01	94.59	0.04 ± 0.05	46.31	5709.94
Kuh Rud and Eastern Iran montane	Desert Grasslands	Asia	126,224.75	3.76	2.91	28.19	0.18 ± 0.09	31.24	39,432.61
Central Tallgrass prairie	Temperate/ Tropical Grasslands	North America	342,466.63	3.36	2.74	2.92	0.51 ± 0.16	3.9	13,356.20

TABLE 2 (Continued)

Ecoregion	Type	Continent	Ecoregion area (km^2)	% intact (100 m)	% intact (500 m)	Jacobson's low impact area (%) ^a	Mean + SD global human footprint ^b	Largest patch index	Core area (km^2)
Sulaiman Range alpine meadows	Desert Grasslands	Asia	23,849.78	2.52	5.82	3.63	0.26 ± 0.09	29.92	7135.85
East European forest steppe	Temperate/ Tropical Grasslands	Asia and Europe	730,145.99	1.91	2.35	19.57	0.46 ± 0.2	1.06	7739.55
Ethiopian montane grasslands	Temperate/ Tropical Grasslands	Africa	221,146.94	0.89	15.37	1.54	0.52 ± 0.16	9.24	20,433.98

Note: Largest patch index ranges from 0 to 100 where 100 represents an intact grassland patch at the scale of the ecoregion. Core area is the proportion of the ecoregion area that is characterized as part of the largest patch index in km^2 .

^aValues obtained from Jacobson et al. (2019).

^bValues obtained from the Wildlife Conservation Society (2005).

bimodal precipitation distribution, whereas temperate grasslands occur in regions with a unimodal precipitation pattern (Humphrey, 1974; Prentice et al., 1992). Based on these criteria, 70 grassland ecoregions were included in this study (see Table 2 for a full list of ecoregions).

This analysis focused on broader-scale and historically contiguous grassland regions, so multiple other grassland systems embedded within various ecosystem types were not analyzed in this article (e.g., grassland mosaics within woodland/forest, flooded grasslands, and certain meadows such as those found in the Taiga and tropical and sub-tropical zones of the world). Savanna ecoregions, which are characterized by the co-existence of grasses and trees, were also not the focus of this article. However, similar anthropogenic threats are facing these other grassy ecosystems and they hold considerable conservation importance (Osborne et al., 2018).

2.2 | Data analysis

2.2.1 | Data collection

For each ecoregion, we considered only grassland pixels classified (discrete classification) by the European Space Agency's (ESA) Copernicus program (Copernicus Global Land Cover Layers: CGLS-LC100 collection 3) for 2019 at 100 m resolution. This was the most recent data available at the time analyses were conducted. These landcover maps were derived from the PROBA-V 100 m time-series set, a database of high-quality land cover training sites and several ancillary datasets, reaching an overall accuracy of 74%. For herbaceous vegetation the producer accuracy was 61.7% and the user accuracy 66.2% (Buchhorn et al., 2020). In addition, we utilized the Moderate Resolution Imaging Spectroradiometer (MODIS) land cover product MCD12Q1 v6 (Sulla-Menashe & Friedl, 2018) for the years 2001 and 2019 at 500 m resolution to validate findings obtained from the ESA dataset by (a) conducting the same analysis (for 2019) to assess data sensitivity based on resolution and (b) to obtain a temporal indication of grassland intactness over time (2001 vs. 2019; Figure S2, Table S1).

2.2.2 | Calculating grassland intactness

Grassland intactness was defined by the area of grassland pixels (discretely classified) that meet the first order queen contiguity (henceforth, “queens” rule) criteria (Anselin, 1995). This identifies a focal grassland pixel surrounded by eight other first-order-neighboring grassland pixels within each ecoregion. Accounting for the entire

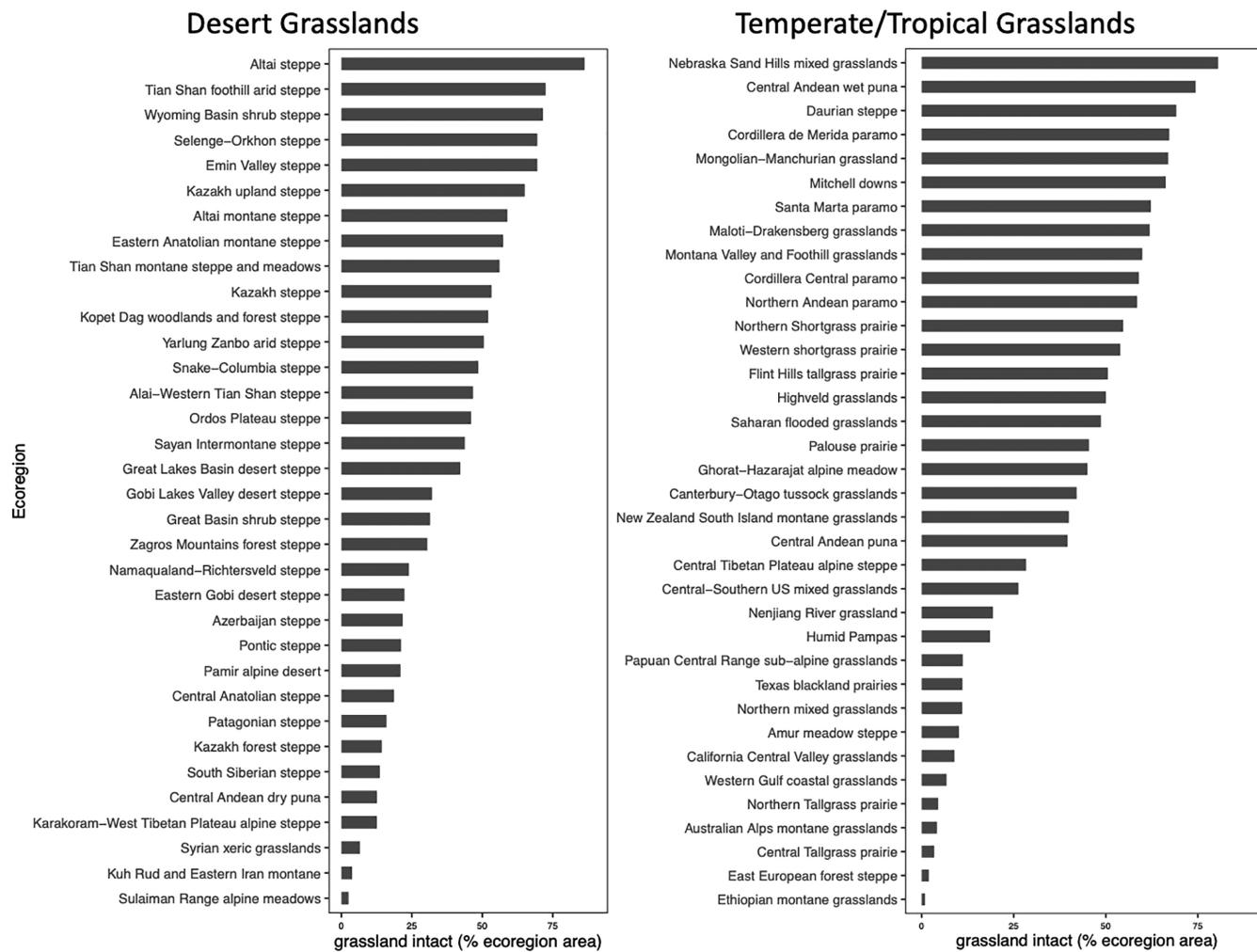


FIGURE 1 Grasslands intact (% ecoregion area) ranked globally in descending order for desert grasslands and temperate/tropical grasslands

ecoregion, grassland intactness was calculated by quantifying the area (percent) of the ecoregion that met the queens rule criteria and discards any grassland pixels that do not meet this requirement, for example, boundary cells, fragmented cells. The only boundary cells included are ones that are connected to a focal cell, where all other cells are connected to the focal cell as well. This analysis does not account for grassland quality; all grassland pixels are included under this criterion, irrespective of land use, which is beyond the scope of this study.

To supplement our measure of ecoregion intactness, the largest patch index was calculated to quantify core area within each grassland. The largest patch index is the area of the largest grassland patch (i.e., connected grassland pixels) divided by the total landscape area (in this case, a grassland ecoregion). The largest patch index can have values ranging from 0 to 100 inclusive, where 100 represents a landscape comprised of a single

patch of the specified class type (i.e., a single patch of grassland in an ecoregion; Jaeger, 2000). Using this index, the exact area (km^2) that makes up the largest grassland patch can be calculated because the size of each ecoregion area was obtained from Dinerstein et al. (2017). We also extracted the percent of low impact area (obtained from Jacobson et al., 2019) and the mean and standard deviation of global human footprint index (obtained from Wildlife Conservation Society (WCS), 2005) where 0 refers to least influenced for each ecoregion in our study.

All landcover data was extracted using Google Earth Engine (Gorelick et al., 2017). All analyses were conducted in program R v3.6.1 (R Development Core Team, 2017) using the landscapemetrics (Hesselbarth et al., 2019) and terra (Hijmans et al., 2021) packages. Rainfall and temperature data for each region were extracted to characterize the regions annual climate patterns (Fick & Hijmans, 2017).

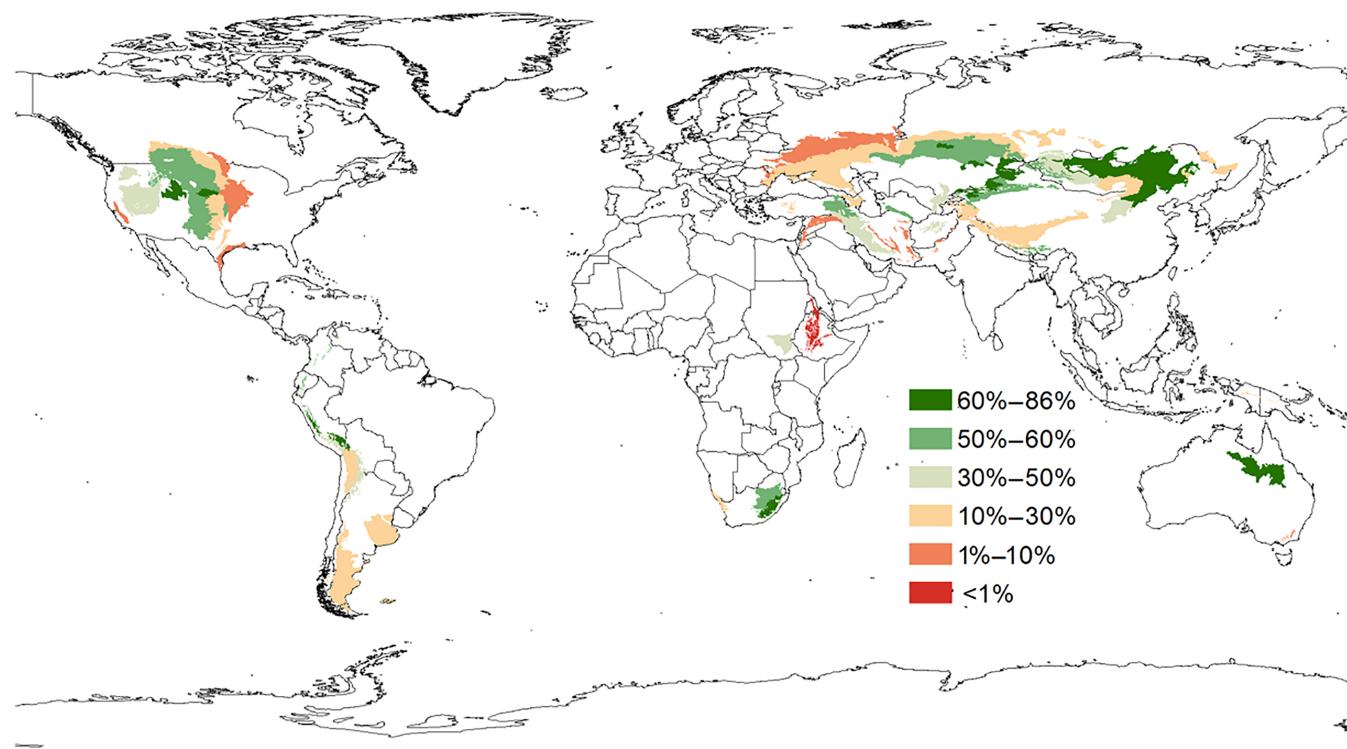


FIGURE 2 The last remaining intact grasslands (>60% area intact) occur in the temperate regions of the northern hemisphere shown within a close network of relatively intact (35%–60%) grassland systems. Data acquired from ESA Sentinel-2 at 100 m resolution

3 | RESULTS

Using a simple rule of landscape intactness, only seven grassland regions remain relatively intact at large scales (Table 1). In fact, more grasslands are nearly entirely converted than are relatively intact. Twenty-one of the world's grassland ecoregions are less than 20% intact, whereas only 14 are at least 60% intact (Figure 1). Most of the intact grasslands also contained the largest grassland patch index and was, in general, accompanied by a low Global Human Footprint (according to the WCS, 2005; Figure S2), but not necessarily representative of Low Impact area (Jacobson et al., 2019). Results comparing intactness to these other indices are summarized in Table 2 for each ecoregion.

At least one of the top seven most intact grassland regions occurs on every continent with a grassland ecoregion considered in this study (Table 1). These include the Selenge-Altai and surrounding steppes and the Mongolian-Manchurian and Daurian grasslands in Asia, the Wyoming Basin steppe and the Nebraska Sand Hills in North America, the Central Andean Wet Puna in South America, the Mitchell Downs grassland in Australia and the Maloti-Drakensberg grassland in Africa. Of the top seven intact regions, all are adjacent to, or nested within, other relatively intact grassland

ecoregions (35%–60%; Figure 2) and provide a buffer against regions that have undergone large-scale conversion. Only the Nebraska Sand Hills is also adjacent to some of the least intact grassland ecoregions on the planet (<30%, Figure 2).

Comparing the intactness of grassland ecoregions between ESA to MODIS revealed strong agreement (Table 2 and compare Figure 2 with Figure S1 for spatial reference). Only one ecoregion identified as >60% intact with ESA was less intact with MODIS (Mitchell Downs grassland; 66% ESA vs. 29% MODIS). However, multiple other ecoregions were >60% intact with MODIS. These included the Ordos Plateau, Snake-Columbia, Eastern Anatolian montane, and Yarlung Zanbo (Tsangpo) arid steppes and the Flint Hills prairie, Ghota-Hazarajat alpine meadow, and Western shortgrass prairie grasslands. In general, these ecoregions were also fairly intact with ESA, but only just below the most intact grassland regions.

One advantage of MODIS is the longer time series of the data and opportunity to assess changes in intactness for the world's grassland ecoregions. MODIS indicates that most regional grasslands are in a state of decline since 2000 (47 of 70; Figure S3). Only three ecoregions showed a >5% increase in intactness area (Figure S3). These were the Eastern Gobi Desert steppe (48% in 2000

vs. 58% in 2019), Ghorat-Hazarajat alpine meadow (63% in 2000 vs. 71% in 2019), and the Gobi Lakes Valley steppe (32% in 2000 vs. 38% in 2019).

4 | DISCUSSION

4.1 | Preserving the last grassland ecoregions on Earth in the Anthropocene

Few intact grassland regions remain on Earth and their rarity challenges the global grassland conservation community to mobilize conservation efforts and prepare for global change pressures. The likelihood of grassland loss increases as adjacent habitat is converted (Boakes et al., 2010). Urbanization, industrialization coupled with commercial agriculture and afforestation are primarily responsible for global grassland loss this past century (MacDougall et al., 2013). Only a few large grassland regions have withstood these global pressures or for various reasons have not been targeted for development/land conversion. For example, some areas could be too remote and inaccessible (for now). These intact regions are highly biodiverse areas that preserve rich traditional knowledge and cultural heritage (Table 1). Yet, there is no globally unified grassland conservation effort that has managed to identify these unique ecosystems and prioritize their conservation importance as anthropogenic pressures mount in the 21st century. This is, in part, because programs such as the IUCN TGCI were constrained by funding resources because grasslands are generally not viewed as attractive as other systems, for example, forests (Carbutt et al., 2011, 2017).

The last remaining intact grasslands possess some of the most unique and iconic wildlife on the planet (*Iconic Species*, Table 1). In North America, the Wyoming Basin hosts some of the last remaining great mammal migrations (Joly et al., 2019). The largest populations of greater sage-grouse and pronghorn—the fastest land mammal in North America, are found in the Wyoming Basin. The Nebraska Sand Hills provides habitat for the only prairie chicken not extinct or listed as endangered or threatened (Svedarsky et al., 2000), and serves as key stopover locations for mass-migration of avian species along North America's Central Flyway spanning Mexico to Canada (Johnsgard, 2012). In South America, the Central Andean wet puna along with the dry puna, is part of the most widely distributed ecosystem in the tropical Andes (Herzog et al., 2017). It maintains a high degree of endemism for open habitat species such as the Slender-billed and dark-winged miner and the Mountain caracara (Gibbons et al., 2016). In southern Africa, the Maloti-Drakensberg grasslands provide key breeding habitat for

several grassland-obligate avian species, for example, the vulnerable yellow-breasted pipit while the high cliffs in the Drakensberg mountain range is home to the largest southern core population of the locally endangered Bearded vulture (*Gypaetus barbatus meridionalis*) in the southern Africa (Hugo & Altwegg, 2017; Krüger et al., 2006). In the Asian grasslands, the Selenge-Altai and the Daurian-Mongolian-Manchurian regions all form portions of the Central Asian flyway from Russia to India (Palm et al., 2015). The Selenge-Altai region is also an important breeding ground for the vulnerable Great bustard, the critically endangered Yellow-breasted bunting and the vulnerable Chinese Mountain cat and a number of endangered raptors (e.g., Steppe eagle, Saker falcon, and Eastern Imperial eagle). The successfully reintroduced wild Przewalski's horse roams the vast Daurian-Manchurian-Mongolian grasslands (Slotta-Bachmayr et al., 2004), and these grasslands are valued for continental-scale migrations, for example, Mongolian gazelle can have ranges up to 32,000 km² annually (Olson et al., 2010).

Protected areas are considered vital for biodiversity persistence in an era of global change, but strategies for large-scale conservation differ among continents for the world's most intact grasslands (Laurance et al., 2012). For example, the Maloti-Drakensberg grasslands are only about 6% protected (Carbutt et al., 2011). Despite this low level of protection, the Maloti-Drakensberg grasslands are the largest and most protected of all temperate grasslands in southern Africa (Carbutt et al., 2011) owing to the Maloti-Drakensberg Park World Heritage Site (Carbutt & Martindale, 2014). In Mongolia, a national mandate has achieved two-thirds of its aim to place 30% of the country's land under national-level protection by 2030 as part of the *Mongolian Sustainable Development Vision 2030*. Furthermore, a transboundary agreement between Mongolia and Russia was established in 1994 comprising of four protected areas to create the *Dauria International Protected Area* (DIPA). In the wet puna—the high elevation deep soil grasslands of South America—several national parks and reserves are found within the greater region, yet the area remains one of the most overgrazed regions in South America (Rolando et al., 2017). While in North America, the Wyoming Basin has one of the largest contributions of public lands in a “checker-board” style of public and private lands ownership (56% public; Carr et al., 2015). Only the Sand Hills of Nebraska, the most intact temperate grassland region in the world, does not contain some form of a large-scale grassland conservation strategy.

Efforts to conserve large intact regions go beyond nature conservation; they also better conserve the cultural heritage unique to regional grasslands. Knowledge

on pastoralism has been passed down over generations and forms the basis of each region's economy (Davies & Hatfield, 2007) and cultural identity (Table 1). For example, nomadic communities are part of a 1000+ year sustainable pastoral system in the Selenge-Altai and Daurian-Mongolian-Manchurian regions. This type of traditional ecological knowledge is at risk of being lost (Gomez-Bagethun et al., 2013), given global trends of grassland loss. In Australia, the passing on of "biocultural knowledge" to younger generations is seen as one of the major drivers of indigenous land management in the Northern Territory region of Australia (Hill et al., 2013). In the Andes of South America, current agricultural practices are a combination of traditional Incan (>5000 year old practices such as irrigation systems and agricultural tools) and modern techniques which are passed along through community learning (Koohafkan & Altieri, 2011). Preserving traditional ecological knowledge is a hallmark principle for enhancing resilience to global change (Sühs et al., 2020), and programs such as *Agenda 2063: The Africa We Want* recognize the importance of preserving cultural heritage early on (Maciejewski & Drimie, 2019).

The case to conserve the world's last remaining regional grasslands requires greater societal appreciation of their unique value as a major global biome (Carbutt et al., 2017; Curtin & Western, 2008). Even with a simple measure, few grasslands show high levels of intactness globally. Our study contributes to a large body of knowledge highlighting the degree to which temperate grassland ecosystems have been adversely affected by anthropogenic impacts (Hoekstra et al., 2005; Jacobson et al., 2019; Kennedy et al., 2019; Riggio et al., 2020). Establishing and growing cores areas in these regions would provide further resilience toward global threats. Ecoregions characterized by high levels of intactness were also characterized by large core areas, which is crucial to further global grassland conservation efforts (Woodley et al., 2012).

There are multiple grassland regions in the world that are relatively intact and have high human footprints. If we only consider a protectionist approach to global grassland conservation, that is, only targeting areas with low human impact areas, then we are ignoring many of the world's most intact grasslands regions. Finding that there are multiple regions where grasslands are relatively intact, but have higher human footprints, suggests that there is hope for grassland conservation in the Anthropocene. These grassland regions could hold the clues on how grassland conservation can coexist with modern human activities and impacts and can serve as a test for other biome types struggling with similar issues. We note that many of these regions that are intact with

high human impacts are often viewed as primitive management systems, with a low-tech approach that relies instead on a strong cultural association where ecosystems and food production systems are tightly coupled to the land and to the ecosystem (Table 1). For example, the Nebraska Sand Hills in North America, the most intact temperate grassland in the world, is listed as a low proportion of low human impact according to Jacobson et al. (2019), but has a long history coexisting with herbivores such as bison in the past, and cattle today. While the change in dominant herbivore certainly comes with ecological consequences (Allred et al., 2011), this area remains intact with a low degree of fragmentation. Some local landowners in the Nebraska Sand Hills are part of conservation groups (e.g., Sand Hills Taskforce, Buell et al., 2013) that actively work on conserving native prairies by engaging in projects such as stream restoration for water access and Eastern red cedar (*Juniperus virginiana*) removal programs—the biggest threat to the Sand Hills this century. Our study suggests that intact grassland regions with high human footprints should also be prioritized for conservation. Global partners pioneering efforts such as "International Year of Rangelands and Pastoralists" and "Protecting and restoring endangered grassland and savannah ecosystems" recognize that the complexities surrounding grassland conservation in the Anthropocene requires integration of grasslands and production systems (Bengtsson et al., 2019; Carbutt, 2020). If we assume all regions with cattle as "highly impacted by humans," we will ignore some of the most intact grasslands remaining today.

5 | CONCLUSIONS

Globally, grasslands are one of the most under-valued vegetation types (Buisson et al., 2018), so it is no surprise that only a few intact grassland systems are left. Anthropogenic pressures on global grasslands are mounting this century (Lark, 2020; Stephens et al., 2008). Not only is global climate change a pressing concern for grassland conservation, but also there has been a history of conservation programs and general scientific guidance that incentivizes their conversion. Some of the last remaining large grasslands are being prioritized for energy development (Allred et al., 2015), agricultural conversion (Lark et al., 2020), and novel introductions of trees (e.g., the Bonn Challenge [Verdone & Seidl, 2017]). Trees have no place in native grasslands as restoration agents nor as a means to better sequester carbon (Bond et al., 2019; Veldman et al., 2015, 2019); productive grasslands are adequately effective at sequestering atmospheric carbon (Conant, 2010). These are major threats to the grassland

biome, but the reality for global grassland conservation is clear. Already, few global grasslands remain intact, and these regions will follow the same trend observed elsewhere if global grassland conservation efforts fail to deal with biome-scale threats. We have identified some of the last remaining large, intact regional grassland landscapes, and they hold some of the greatest promise to withstand the pressures tied to human-driven global change and preserve the legacy of grasslands as one of the great biomes on Earth.

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CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

AUTHOR CONTRIBUTIONS

Rheinhardt Scholtz and Dirac Twidwell conceived, designed, and wrote the article.

DATA AVAILABILITY STATEMENT

All data can used in this study can be freely obtained online via NASA (MODIS) and Copernicus (Sentinel-2) respective websites.

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