



RESEARCH ARTICLE

Incorporating social values and wildlife habitats for biodiversity conservation modeling in landscapes of the Great Plains

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Abstract

Context Socioecological information should be properly employed in the process of spatial analysis, planning, and management in order to respond to complex and multidirectional biodiversity issues.

Objectives We conducted this study to map socioecological hotspots, where landscapes of social significance and wildlife habitats overlap, show to what extent and how the spatial distribution of social values (SVs) of people toward their landscapes interact with wildlife habitats in socioecological hotspots, simulate the potential for habitat degradation as a result of human activities linked to SVs, identify strategic areas for landscape restoration in socioecological hotspots, where both environmental conditions and SVs support the persistence and colonization of wildlife, and detect specific areas, where SVs of people may be contradictory leading to land-use disputes.

Methods We developed a model to show the potential for habitat degradation based on the spatial distribution of SVs associated with landscapes. We restricted our study to the Upper Missouri River Basin (UMRB) and focused on habitats of five keystone mammal species to assess the validity of our model.

Results Habitat loss, habitat subdivision, habitat dispersion, and habitat shrinkage can be four

consequences of human activities for biodiversity in socioecological hotspots of the UMRB, however, the magnitude of impacts varies among landscapes and mammal species.

Conclusion Spatially explicit models to properly map SVs in relation to wildlife habitats are still associated with some uncertainties and limitations, and therefore, require further development. Change in SVs and public attitudes toward land use is essential to avoid further biodiversity loss in this region.

Keywords Socioecological hotspots · Social values · Wildlife habitats · Spatial modeling · Socioecological mapping

Introduction

Landscapes and biodiversity crisis

The Anthropocene era is associated with an accelerating rate of biodiversity loss (Dirzo et al. 2014); with an unprecedented average decline of at least 68% in wildlife populations since 1970 (WWF 2020). The widespread change in natural patterns of landscapes, among other factors (Butchart et al. 2010), has given rise to habitat degradation worldwide (Forman 1995; Pereira et al. 2010). Agriculture (Tschamtket et al. 2012), urbanization (Elmqvist et al. 2013), and

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industrial development (Ramankutty et al. 2006) have caused widespread changes in the structure of wildlife habitats (e.g. the size, shape, spatial connectivity, etc.). Historically, settler colonialism has also accelerated the process of these changes; more specifically, in North America (Ramankutty and Foley 1999; Goldewijk and Ramankutty 2004), Latin America (Meade 2016), Australia (Bradshaw 2012), and New Zealand (Ewers et al. 2006). Anthropogenic climate change is another powerful catalyst for affecting natural patterns of landscapes and consequently, wildlife habitats, leading to species extinction (Opdam and Wascher 2004; Mantyka-Pringle et al. 2015; Urban 2015; Beever et al. 2017). Up to 60% of the change in the world's land cover is attributed to direct human activities (Song et al. 2018). Cumulatively, these factors have adverse impacts on wildlife habitats, threaten the survival of a wide range of species, and alter their interactions with key components of ecosystems (e.g. soil, water, plant communities, and food sources; Turner 1989; Forman 1995).

Landscapes and social values

Landscape social values (SVs), potential conflicts and synergies among them, are believed to be a growing concern among a diverse range of stakeholders across the world (Lapointe et al. 2019; Brown et al. 2020; Włodarczyk-Marciniak et al. 2020). Methodological plurality can help science and practice to find feasible, site-specific solutions for sustainability issues in landscapes of different socioeconomic background. In this context, cross-disciplinary research on SVs is increasingly becoming an important target to advance environmental sustainability (Kenter et al. 2019). Because of the complex and evolving relationship between humans and nature over time (Riechers et al. 2020), and due to the increasing recognition of the linkages among social and ecological systems in landscapes, there is a growing interest in developing new methods through which social and ecological information can be properly integrated in the process of spatial analysis, planning, and management in order to respond to the current biodiversity and land use challenges (Alessa et al. 2008; Sherrouse et al. 2011; Ban et al. 2013; Bagstad et al. 2016; Guerrero and Wilson 2017; Karimi and Adams 2019; Okamoto et al. 2020; Zhang et al. 2020).

Mapping the SVs people assign to landscapes is of particular importance for the success of science-based conservation implementation (Bryan et al. 2011) and developing an understanding of how and why people value different aspects of ecological systems is deemed to be essential to mitigate potential conflicts among stakeholders (Ives and Kendal 2014). This can inform impact assessment of land-use plans on biodiversity and identify priorities for land-use conflict (Karimi and Hockings 2018). Despite this, standard regional-scale spatially explicit models to accurately link SVs to human activities, landscapes, and biodiversity still requires further development. Therefore, while existing methods such as Public Participation Geographic Information Systems—PPGIS (Sieber 2006), Social Values for Ecosystem Services—SolVES (Sherrouse et al. 2011), Landscape Values Mapping—LVM (Biedenweg et al. 2019), should be expanded, new models should be innovated concurrently to provide an in-depth understanding of societal dimensions of landscapes to reduce the risk of habitat degradation, increase the likelihood of habitat conservation, and identify portions of the land to target for habitat conservation, more specifically in socioecological hotspots, a term that we used in this study to define certain areas, where landscapes of social significance and wildlife habitats overlap. In the context of this study, socioecological hotspots are certain areas of landscapes that are attractive to people for multiple land uses, and simultaneously of ecological importance for landscape restoration and/or biodiversity conservation. This definition does not imply that the human-wildlife confluence does not occur in areas outside of socioecological hotspots. Urbanized landscapes, for example, are believed to be among the most dynamic areas in terms of the human-wildlife confluence (Alvey 2006; Elmqvist et al. 2013; Rastandeh 2018). In this study, however, we used field-collected SV data and then, integrated it with habitat suitability information to address our study objectives across the study region, without specific focus on the nature of landscapes (i.e. urban vs. rural; intact vs. modified, etc.).

Understanding how SVs associated with landscapes are distributed in space is a key step to inform ecosystem services analysis, land-use planning, and strategic landscape management (Sherrouse et al. 2011; Bagstad et al. 2016; Hu et al. 2019). The importance of research on human-wildlife conflict has

been articulated in the current literature (Madden 2004; Nyhus 2016; Frank et al. 2019); to date, however, less attention has been paid to the integration of SVs and biodiversity data when land-use issues are contested at the regional scale (Brown et al. 2014). Perhaps one of the main reasons for this negligence, has been the lack of accurate and detailed data, as well as applicable methods to depict social dimensions of the land. While the current literature focuses more on the rate of land-cover change to quantify habitat loss, we conducted this study to show how the spatial distribution of SVs can be employed to simulate the potential for change in the structure of wildlife habitats or shift in the spatial extent of areas suitable for species colonization/persistence; and simultaneously detect opportunities for local- and regional-scale landscape restoration and/or biodiversity conservation. In this respect, we restricted our study to the Upper Missouri River Basin (UMRB; ca. 746,000 Km²), as part of the Great Plains of the United States, mainly covered by Montana, North Dakota, South Dakota, and Wyoming, to fulfil our study objectives: (1) to map socioecological hotspots (2) to show to what extent and how the spatial distribution of SVs of people toward their landscapes interact with wildlife habitats in mapped socioecological hotspots, (3) to simulate the potential for habitat degradation as a result of human activities linked to SVs, (4) to identify strategic areas for landscape restoration in socioecological hotspots, where both environmental conditions and SVs support the persistence and colonization of wildlife, and (5) to detect specific areas, where SVs of people may be contradictory leading to land-use disputes.

Methodology

We developed a model to show the potential for habitat degradation based on the spatial distribution of SVs associated with landscapes. The central assumption was that SVs are predictive of land-use conflict (Brown et al. 2020), may trigger a broad spectrum of human activities, ranging from development to conservation, and determine how the land should be controlled and used in the future. We did not use this model to measure the risk or rate of land-cover change but to envision how the structure of wildlife habitats may be altered by SVs in socioecological hotspots of

the region through various mechanisms in ways that reduce and/or change the spatial extent of suitable areas for species colonization/persistence.

Study region

Euro-American settlement began at the second half of the nineteenth century (Lampard 1955) in the United States, including the UMRB (Fig. 1). In comparison with other parts of the United States, population density in this region is still very low (Stoy et al. 2018). There are only 23 human population centers with a population of more than 10,000 people across the region (US Census Bureau 2018). Agricultural landscapes of the region are critically important to produce human food and livestock feed (Jarchow et al. 2020). For example, respectively 30%, 13%, 11%, and 9% of wheat, soybean, cattle, and corn productions of the United States are supplied in this region (Stoy et al. 2018). Commonplace human activities including settlement development, farming, ranching, grazing, hunting and mining have substantially affected wildlife species, leading to widespread habitat degradation and biodiversity loss over the last two centuries across the region (Samson and Knopf 1994; Jarchow et al. 2020).

Data preparation

Land cover

We used the dataset North American Land Cover (spatial resolution: 30 m; Commission for Environmental Cooperation 2020) to measure the current composition of land cover classes across the UMRB.

Wildlife habitats

We used the dataset Gap Analysis Project Species Habitat Maps (GAP; U.S. Geological Survey 2018) to illustrate the habitat distribution of mammal species in the UMRB. Its developers recommend the use of this dataset for national, regional or statewide biodiversity and habitat conservation planning. While it provides very useful spatial information about parts of the land that contain suitable conditions for vertebrates to occur, fine-scale features have not been considered in GAP. This dataset has been recognized as a reliable source of information for regional-scale biodiversity

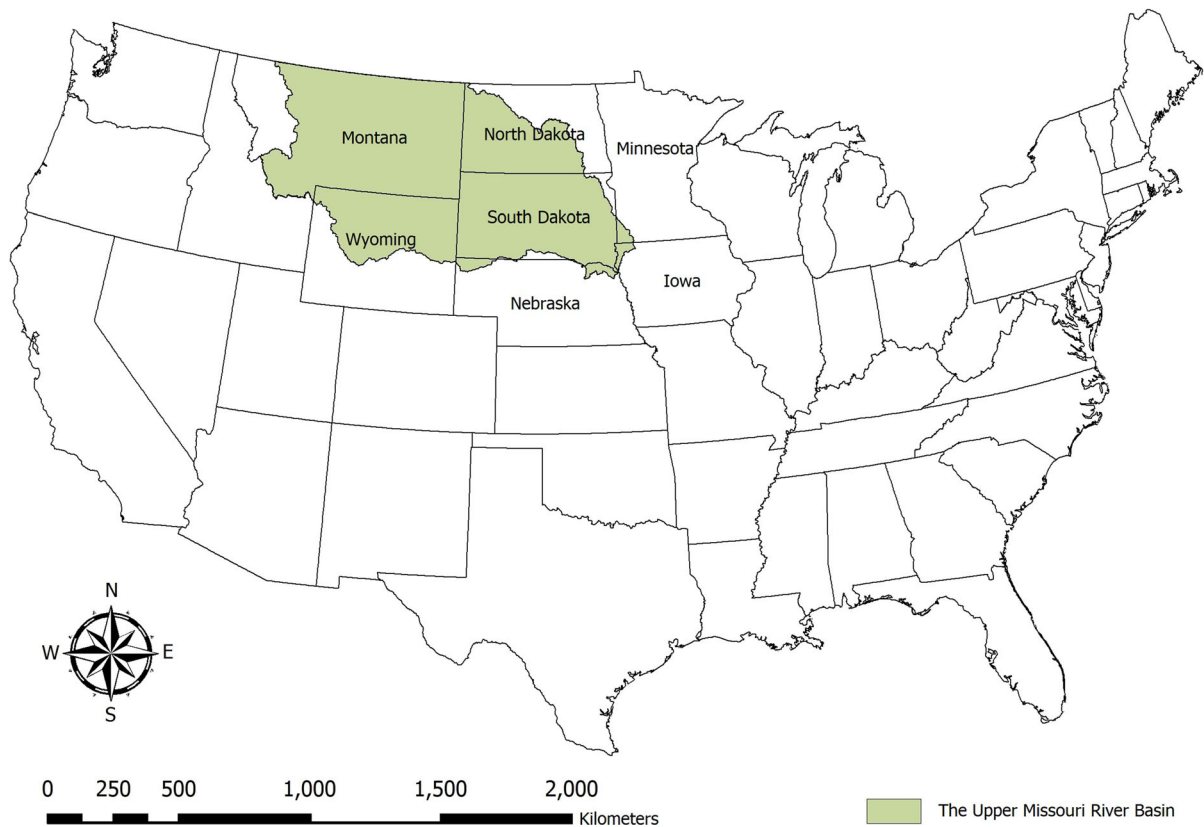


Fig. 1 The Upper Missouri River Basin

research across the United States (Gergely et al. 2019; Tarr 2019; Dietz et al. 2020). To build this dataset, species habitat suitability has been evaluated not only based on existing land cover classes, but also other determinant climatic and environmental parameters. (U.S. Geological Survey 2018). We selected five mammal species from GAP in order to validate the accuracy and capability of our model (Table 1). We considered four basic factors to sample the most relevant species for this study: (1) habitat requirements, (2) species dispersal patterns, (3) ecological mutualism relationships, and (4) cultural importance. Globally, mammal species increase habitat heterogeneity and significantly contribute to biodiversity at various spatial scales (Lacher et al. 2019). The five species we selected, in particular, can play significant roles in supporting vital ecosystem services in the region and for this reason, they are identified as keystone species in the literature. These keystone species also function as a representative set of habitat requirements for other taxa, can affect ecosystems

(Mills et al. 1993), and are of critical importance to the structure of ecosystems (Collier et al. 1997). Some, if not all, of these species can be concurrently considered as flagship and/or umbrella species (Walpole and Leader-Williams 2002; Wilkins et al. 2019), as they are well known among peoples of the UMRB, and are species of cultural importance, as well (cf. Garibaldi and Turner 2004). For each species, we extracted areas that can act as its primary habitat using GAP (U.S. Geological Survey 2018). We termed these areas as “wildlife habitats”. Although the chosen species may be present or absent in their habitats at the present time, they have suitable conditions under which species can persist and/or colonize.

Social values

During 2018 and 2019, we conducted a survey of 1009 residents from 22 cities across the UMRB. The aim was to identify where and how the land is valued by people in this region. As one part of this survey, we

Table 1 Mammals sampled for this study and their ecological roles in ecosystems of the UMRB based on (Naiman 1988; Knapp et al. 1999; Kotliar et al. 1999; Miller et al. 2000; Gökbülak 2002; Goheen and Swihart 2003; Kotliar et al. 2006; Rosas et al. 2008; Allred et al. 2011; Hoogland 2013; Nummi and Holopainen 2014; Hale and Koprowski 2018)

Common name	Scientific name	Ecological roles
American beaver	<i>Castor canadensis</i>	Water purification Erosion control Habitat provision for some species
American red squirrel	<i>Tamiasciurus hudsonicus</i>	Seed dispersal Soil fertilization
Bison	<i>Bison bison</i>	Seed dispersal Soil bioturbation Habitat provision for some species
Black-tailed prairie dog	<i>Cynomys ludovicianus</i>	Soil bioturbation Seed germination Habitat provision for some species Food provision for some predators
White-tailed prairie dog	<i>Cynomys leucurus</i>	Soil bioturbation Seed germination Habitat provision for some species Food provision for some predators

asked each participant to choose up to four SVs from a list of 11 major SVs (i.e. Aesthetics, Agriculture, Community, Conservation, Cultural, Development, Economy, Energy, Recreation, Spiritual, and Tourism; Jarchow et al. 2018; Carnes 2019) and indicate locations where his/her chosen values would like to occur on the land, within a radius of 80 km from the place of his/her residence. We defined these SVs with respect to commonplace human activities in the region, as described above (cf. Jarchow et al. 2018, 2020), and with particular attention to the results of 33 semi-structured interviews with stakeholders about SVs and landscapes of the UMRB (Carnes 2019). We built a dataset of 5046 georeferenced locations (GRLs), representing landscapes of social significance in the region. Each GRL corresponds to one specific SV and thereby, its corresponding human activities. In this study, we used an impact-sensitive classification of SVs based on previous research in the region (Jarchow et al. 2018; Stoy et al. 2018; Carnes 2019; Jarchow et al. 2020) and condensed them into five groups (Table 2). Landscapes of the UMRB are subject to change depending on the nature of these five groups of SVs. Although the impacts of these groups differ, in all cases, except for Group 5, human activities can adversely affect biodiversity through different mechanisms, including environmental (e.g. air, water, soil, noise, and light) pollutions, land-cover change, habitat fragmentation

(e.g. building and road construction), and human-induced disturbances (e.g. fires, pest, and weed dispersal; WWF 2018, 2020). Therefore, even those SVs that seem neutral to biodiversity (e.g. Group 3; Tradition), can motivate a range of human activities that lead to disturbance in wildlife habitats (e.g. the spread of pest animals, weed plant species, fires, and environmental pollutions).

We applied a radius of 5 km from the center of each GRL, termed the Radius of Human Activity (RHA; 7850 ha). We created 5046 RHAs corresponding to 5046 GRLs. We considered each RHA as a specific area within which a specific range of human activities will be dominant. Human activities often have far-reaching impacts on abiotic and biotic resources and their impacts are not limited within the locations, where people are physically present. Any change in these resources (e.g. soil degradation, water pollution, land cover conversion) can be detrimental to biodiversity (WWF 2020). According to Benítez-López et al. 2010, Barbosa et al. 2020, and Mendes et al. 2020, under normal conditions, the environmental impacts of human activities on mammals can spread up to 5 km, if not more, from the origin of impacts. We considered each GRL as an origin of the impacts of a certain SV, linked to a specific range of human activities (Table 2), on wildlife habitats and assumed its corresponding RHA as the spatial extent of its possible impacts. This method enabled us to transform

Table 2 An impact-sensitive classification of SVs applied in this study based on the nature of human activities in the UMRB (cf. Stoy et al. 2018; Carnes 2019; Jarchow et al. 2020)

Human activities	Main SVs associated with landscapes	# of GRLs
Group 1: Development	Economic investment Residential and commercial development Employment Energy extraction	1110
Group 2: Recreation	Outdoor recreation Tourism in historical or cultural sites	1289
Group 3: Tradition	Aesthetics Identity and family traditions Sacred places and religion	943
Group 4: Agriculture	Farming Ranching	1009
Group 5: Conservation	Responsibility to land	695

GRLs to measurable surfaces based on the spatial distribution of each group of SVs and to detect areas that are subject to human activities associated with five groups of SVs.

Overlay analysis

We quantified the spatial overlap between landscapes of social significance and wildlife habitats using ArcMap 10.5. We mapped the overlap between RHAs and wildlife habitats to identify socioecological hotspots, where landscapes of social significance and wildlife habitats overlap (Fig. 2). We preliminarily used four landscape metrics (McGarigal 2015) and the software program FRAGSTATS 4.2 (McGarigal et al. 2012) to quantify the structure of wildlife habitats overlapping with landscapes of social significance (Table 3). We also used these landscape metrics to characterize areas subject to various human activities, as well as the overlap between Conservation and other SVs in socioecological hotspots. The number of patches (PN) can be increased as a result of landscape fragmentation (Botequilha Leitao and Ahern 2002; McGarigal et al. 2012). An increase in PN can reduce the risk of disturbances (e.g. wildfire, flood, hurricane, disease outbreak; Botequilha Leitao et al. 2006). At the same time, landscape fragmentation limits species movement (Forman 1995; Dramstad et al. 1996; Botequilha Leitao et al. 2006). Patch size is the most important component of landscape pattern affecting biomass, nutrient storage, productivity, and species composition and diversity (McGarigal 2015). Total Area (AREA), Largest Patch (LP), and Mean Patch

Size (MPS) can quantify habitat availability in terms of patch size. These landscape metrics are species-specific and scale-dependent; therefore, their values should be interpreted with respect to the spatial ecology of species under study.

Landscape patterns and wildlife habitats

We simulated the impact of human activities on the current structure of wildlife habitats in the GIS environment through mapping and modeling the spatial distribution of the overlap between socially-valued human activities and wildlife habitats. We did not specifically calculate the nature and power of human impacts on wildlife habitats because human land use activities differ in terms of the potential effects that they have on the wildlife habitats they overlap. Instead, we developed and used a regional-scale spatially-explicit model to depict the spatial distribution of human activities in relation to wildlife habitats. We made three basic assumptions to run this simulation: (1) although different in terms of the nature and magnitude of impacts on wildlife habitats, human activities linked to SVs in Groups 1, 2, 3, and 4 (i.e. Development, Recreation, Tradition, and Agriculture) have the potential to increase the risk of wildlife habitat degradation in different ways; (2) human activities linked to SVs in Group 5 (i.e. Conservation) will not increase the extent of wildlife habitats, mainly because environmental requirements to provide suitable conditions for species are not necessarily met in areas that people value the land for conservation practices; however, where wildlife

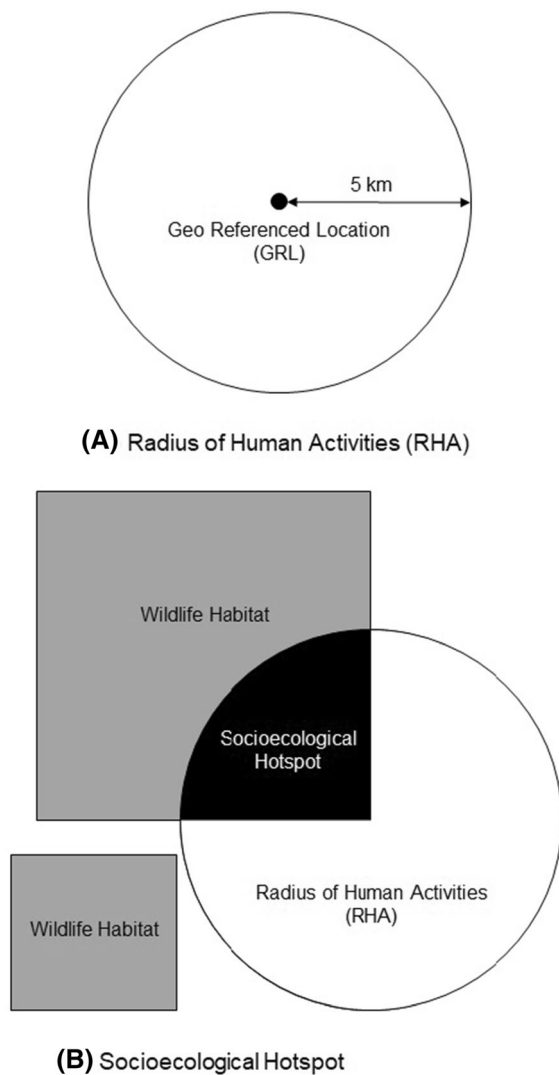


Fig. 2 The spatial concepts used in this study; **a** Radius of Human Activity (RHA) created based on a 5 km buffer from the position of each georeferenced location (GRL), representing a portion of the land subject to the impacts of human activities (i.e. landscapes of social significance); **b** a socioecological hotspot (black), where human activities and wildlife habitats overlap

habitats and RHAs linked to Conservation overlap, the chance of dedicating the land for landscape restoration and/or biodiversity conservation is high because both environmental and social factors support such practices; (3) where RHAs linked to Conservation overlap with other human activities, land-use disputes are expected.

We used six class-level landscape metrics in FRAGSTATS 4.2 (McGarigal et al. 2012) to quantify

Table 3 Landscape metrics used to quantify the structure of wildlife habitats overlapping with landscapes of social significance

Metrics	Unit	Abbreviation/range
Total area	Hectares	AREA ≥ 0
Number of patches	None	PN ≥ 0
Largest patch	Hectares	LP > 0
Mean patch size	Hectares	MPS > 0

the structure of wildlife habitats across the UMRB before and after applying the potential impact of SVs on wildlife habitats in socioecological hotspots (Table 4). To prepare accurate inputs for FRAGSTATS, we rasterized the maps generated in the process of overlay analysis using a cell size of 50 m. we applied the eight-cell-neighborhood rule to run our model in FRAGSTATS. We computed four characteristics of landscape transformation: (1) habitat loss, (2) habitat dispersion, (3) habitat subdivision, and (4) habitat shrinkage (Fig. 3). We used Class Area Proportion (CAP) to quantify the total area of wildlife habitats and habitat availability across the region; Area-weighted Mean Radius of Gyration (GYRATE_AM) to compute habitat shrinkage; Aggregation Index (AI) and Patch Cohesion Index (COHESION) to quantify habitat dispersion against habitat aggregation; and Patch Density (PD) and Effective Mesh Size (MESH) to quantify to what extent wildlife habitats may be subject to subdivision.

The chosen landscape metrics are mainly size-independent, highly recommended for in-depth landscape analysis, and central to the study of habitat loss and landscape fragmentation (Botequilha-Leitao et al. 2006; Cushman et al. 2008; Kupfer 2012; McGarigal et al. 2012). Detailed descriptions of landscape metrics and their applications to landscape quantification are provided in (McGarigal 2015).

Results

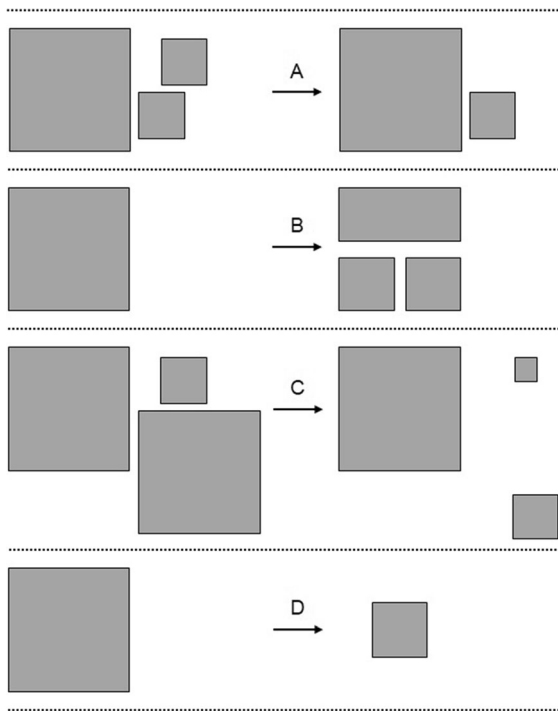
Land cover

Of 19 land cover classes defined in the dataset North American Land Cover (Commission for Environmental Cooperation 2020), 11 classes occur in the UMRB

Table 4 Landscape metrics used to quantify the potential impacts of SVs on the structure of wildlife habitats in the UMRB before and after applying the impacts of human activities on wildlife habitats

Metrics	Unit	Abbreviation/range
Class area proportion	Percent	$0 \leq CAP \leq 100$
Patch density	Number per 100 ha	$PD > 0$
Effective mesh size	Hectares	Ratio of cell size to area $\leq MESH \leq$ total area
Aggregation index	Present	$0 \leq AI \leq 100$
Patch cohesion index	None	$0 < COHESION < 100$
Area-weighted mean radius of gyration	Meters	$GYRATE_AM > 0$

Area-weighted Mean Radius of Gyration (GYRATE_AM) is equivalent to Correlation Length (CL). More information is available in McGarigal 2015

**Fig. 3** Four basic concepts used to characterize landscape transformation and habitat degradation in this study; **a** Habitat Loss; **b** Habitat Subdivision; **c** Habitat Dispersion; **d** Habitat Shrinkage. Note that these phenomena are not standalone in practice. For example, in C, Habitat Dispersion is associated with Habitat Shrinkage

(Table 5). Grassland, Cropland, Shrubland, and Needleleaf Forest are respectively the most dominant land cover classes in the region. Areas covered by the class Urban and Built-up also encompass some 2% of the land. Other strategic land cover classes, including Wetland, Water, Broadleaf Deciduous Forest, and

Table 5 Land cover classes in the UMRB measured based on the dataset North American Land Cover (Commission for Environmental Cooperation 2020)

Class	% of the UMRB
Grassland	47
Cropland	25
Shrubland	14
Needleleaf forest	8
Urban and built-up	2
Water	< 2
Wetland	< 2
Barren	< 1
Broadleaf deciduous forest	< 1
Mixed forest	< 0.5
Snow and ice	< 0.1

Mixed Forest, cover only a small fraction of the region.

Wildlife habitats

Currently, areas with suitable conditions for the black-tailed prairie dog occupy at least 15.41% ($\pm 2\%$) of the UMRB. For other mammals, the coverage is under 10% of the region (Table 6). A very small area of the region can function as primary habitat for the bison. Habitat requirements for the American beaver are met in less than 4% of the region. Habitats of this species are extremely scattered. Habitats of the American red squirrel and white-tailed prairie dog occupy 8.51% and 6.33% of the UMRB, respectively. In certain areas

Table 6 The extent of suitable areas as wildlife habitat for mammals in the UMRB

Species	% of the UMRB
American beaver	3.48
American red squirrel	8.51
Bison	0.56
Black-tailed prairie dog	15.41
White-tailed prairie dog	6.33

of the UMRB, wildlife habitats converge and overlap, and therefore, these mammals can potentially coexist.

Landscapes of social significance

A large portion of the UMRB was covered by the RHAs (Table 7). This geographical extent represents landscapes of social significance that are valued for Agriculture (% of the UMRB: 5.36%), Recreation (4.12%), Conservation (3.71%), Tradition (3.38%), and Development (3.34%).

Socioecological hotspots

Landscapes of social significance overlies a large portion of wildlife habitats (ca. 3,474,870 ha; 4.65% of the UMRB). As defined, we regarded this part of the UMRB as socioecological hotspots. The values of four landscape metrics for wildlife habitats overlapping with human activities in socio-ecological hotspots are provided in Table 8. The overlap between wildlife habitats and human activities in socioecological

Table 7 Landscapes of social significance measured by RHAs for five groups of SVs in the UMRB

Core activity	RHA (ha)	Percent	% of the UMRB
Development	2,496,801	16.79	3.34
Recreation	3,075,988	20.68	4.12
Tradition	2,527,261	16.99	3.38
Agriculture	3,999,214	26.89	5.36
Conservation	2,772,032	18.65	3.71
Total*	14,871,296*	100	19.91

*This area includes overlaps between RHAs, not the total size of landscapes of social significance

hotspots ranges from 14.11 to 2.79% (Fig. 4). This chart provides quantitative information about the risk of encroachment to wildlife habitats imposed by each group of human activities in the UMRB. These results combined with information depicted in Figs. 5 and 6 suggest that wildlife habitats in socio-ecological hotspots of the UMRB can be widely influenced by multifarious human activities; however, the magnitude of impacts on species differs depending on the nature of human activities. This information should be interpreted with particular attention to the spatial ecology of wildlife species, as well as the nature of human activities. For example, as depicted in Table 8; Fig. 5, the American beaver has a high number of habitat patches overlaid by human activities (PN_{AB} : 565,243). The opposite, the values of this landscape metric for habitats of the bison and white-tailed prairie dog are very low (PN_B : 29,413, PN_{WTPD} : 52,884). Habitats of the black-tailed prairie dog are highly fragmented, specifically in areas where SVs for Agriculture are dominant (PN_{BTPD} : 215,969). In Fig. 6, the difference between the values of MPS for the white-tailed prairie dog and other species is considerable, specifically in areas where habitats of this species have overlap with human activities linked to Development and Agriculture. These findings are species-specific and have different implications for the conservation and/or restoration of these species and their habitats depending on the objectives of projects.

Landscape pattern analysis

Habitat degradation within socioecological hotspots could have far-reaching consequences for the composition and configuration of wildlife habitats, and consequently biodiversity across the UMRB (Figs. 7, 8, and 9). We found that habitat loss, habitat subdivision, habitat dispersion, and habitat shrinkage are four consequences of human activities for wildlife habitats in the UMRB; however, the magnitude and spatial extent of these impacts vary among species (Table 9).

The amount of habitat loss ranges from 17.85% in habitats of the bison to 7.89% in habitats of the white-tailed prairie dog (Table 10). We observed the highest changes in the values of CAP and PD in habitats of the bison. Habitats of the black-tailed prairie dog had the greatest degree of shrinkage ($GYRATE_{AM_{BTPD}}$: - 30.52%) and subdivision ($MESH_{BTPD}$: - 46.39%).

Table 8 The values of four landscape metrics (cf. Table 3) to quantify the structure of wildlife habitats overlaid by human activities in socio-ecological hotspots

Species—SVs	AREA (ha)	PN	LP (ha)	MPS (ha)
AB				
Development	93,770.83	94,757	3932.41	0.98
Recreation	145,330.57	123,849	7235.81	1.17
Tradition	112,737.66	94,239	2845.92	1.19
Agriculture	150,719.45	144,988	4552.11	1.03
Conservation	115,868.73	107,410	6646.93	1.07
Total	618,427.24	565,243		
ARS				
Development	183,175.54	43,237	28,803.69	4.23
Recreation	633,388.11	73,567	109,806.12	8.61
Tradition	464,537.46	61,626	57,480.45	7.54
Agriculture	188,019.65	64,922	43,521.02	2.89
Conservation	572,691.95	72,148	211,651.69	7.93
Total	2,041,812.71	315,500		
B				
Development	19,194.78	3418	3519.37	5.61
Recreation	15,012.07	2755	2860.08	5.44
Tradition	58,615.92	10,992	3053.21	5.33
Agriculture	25,131.41	2879	5407.86	8.72
Conservation	44,829.45	9369	6551.83	4.78
Total	162,783.63	29,413		
BTPD				
Development	546,251.18	154,464	27,395.32	3.53
Recreation	520,866.03	156,223	23,999.46	3.34
Tradition	480,917.05	140,680	22,940.67	3.42
Agriculture	902,352.42	215,969	81,130.52	4.17
Conservation	547,618.08	140,874	41,893.81	3.89
Total	2,998,004.76	808,210		
WTPD				
Development	157,762.21	6263	43,175.26	25.18
Recreation	180,184.71	17,510	22,188.58	10.29
Tradition	134,943.42	9973	14,716.78	13.53
Agriculture	132,137.59	5941	35,546.86	22.24
Conservation	162,257.46	13,197	50,081.57	12.29
Total	767,285.39	52,884		

Mammals have been coded as follows: American Beaver (AB), American Red Squirrel (ARS), Bison (B), Black-tailed Prairie Dog (BTPD), White-tailed Prairie Dog (WTPD)

We also observed the highest level of dispersion in habitats of the American beaver (AI_{AB} : -0.74% ; $COHESION_{AB}$: -0.73%), which can extremely limit species movement. We found that except for habitats of the white-tailed prairie dog, human activities increase habitat subdivision in all wildlife habitats. This change can restrict the movement of mammals in the UMRB while may simultaneously act as a means to protect them against natural and human-induced

disturbances. Although habitat loss was modeled to occur for the white-tailed prairie dog (CAP_{WTPD} : -7.89%), we found no further dispersion in habitats of this species ($COHESION_{WTPD}$: 0).

Conflict of interests among SVs

Parts of socioecological hotspots are potentially subject to conflict of interests among SVs. Our model

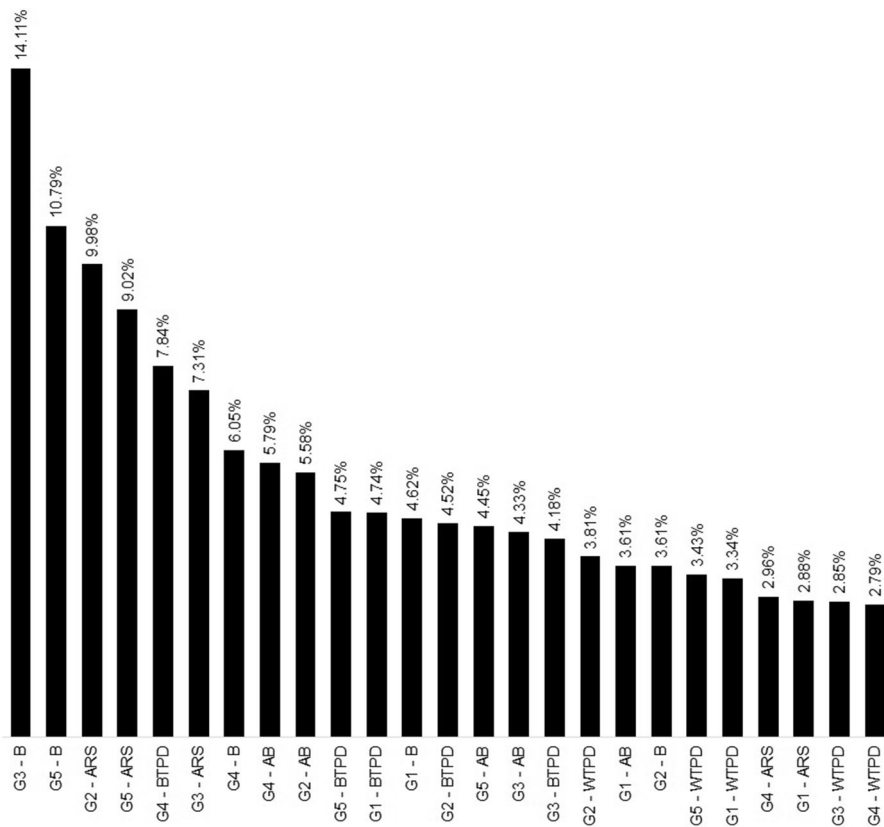


Fig. 4 The percentage of overlap between wildlife habitats and human activities in socioecological hotspots. Human activities linked to SVs have been coded as follows: Development (G1), Recreation (G2), Tradition (G3), Agriculture (G4), and

Conservation (G5). Mammals have been coded as follows: American Beaver (AB), American Red Squirrel (ARS), Bison (B), Black-tailed Prairie Dog (BTPD), and White-tailed Prairie Dog (WTPD)

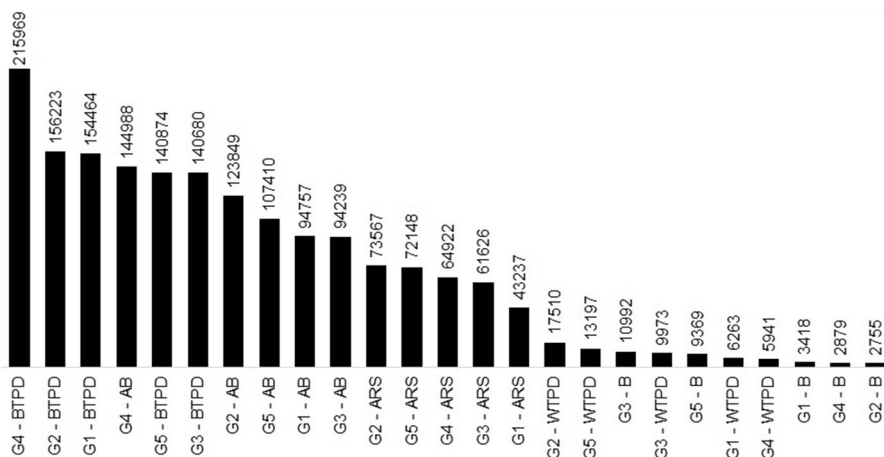


Fig. 5 The number of habitat patches overlaid by human activities in socioecological hotspots. Human activities linked to SVs have been coded as follows: Development (G1), Recreation (G2), Tradition (G3), Agriculture (G4), and Conservation (G5).

Mammals have been coded as follows: American Beaver (AB), American Red Squirrel (ARS), Bison (B), Black-tailed Prairie Dog (BTPD), and White-tailed Prairie Dog (WTPD)

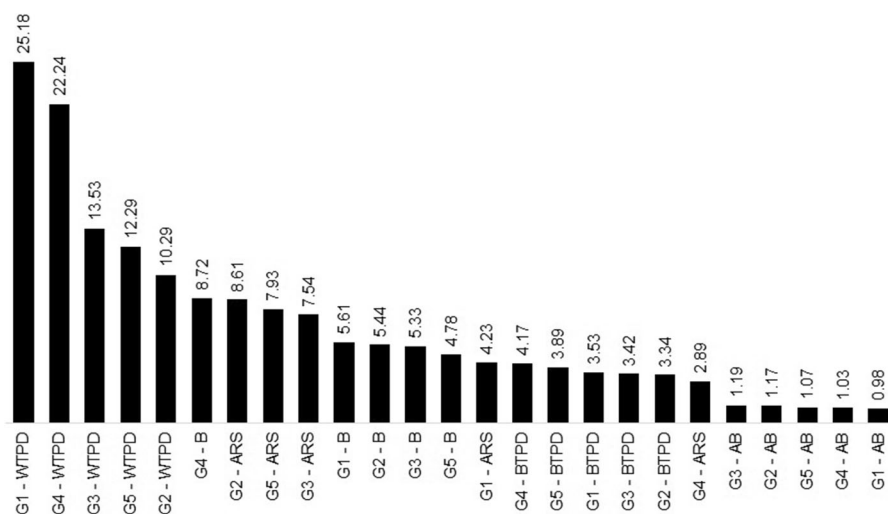


Fig. 6 The mean patch size (MPS; ha) of habitat patches overlaid by human activities in socioecological hotspots. Human activities linked to SVs have been coded as follows: Development (G1), Recreation (G2), Tradition (G3),

Agriculture (G4), and Conservation (G5). Mammals have been coded as follows: American Beaver (AB), American Red Squirrel (ARS), Bison (B), Black-tailed Prairie Dog (BTPD), and White-tailed Prairie Dog (WTPD)

revealed that in about one-third of areas identified as socioecological hotspots, SVs and their corresponding human activities are contradictory, more specifically where SVs related to Conservation and other human activities (i.e. Development, Recreation, Tradition, and Agriculture; Table 2) overlap (Fig. 8). Of the total area people value for Conservation (i.e. 3.71% of the UMRB; Table 7), 49.13% is in socioecological hotspots, meaning that about half of the land has an overlap with wildlife habitats, a potential social support for landscape restoration and/or biodiversity conservation; however, about three-fourth of this overlap (985,493 ha, 72.35%) was concurrently valued by people for other SVs (Fig. 8). These values quantify areas that are subject to conflict of interests between Conservation (G5) and other SVs (G1 to 4). In particular, the values of MPS for G1 to 4 (2.25 ha), G5 (2.63 ha), and Overlap (2.42 ha) show the potential for conflict of interests among human activities linked to SVs. This information is central to study habitat size for species, as well as the availability and abundance of habitats in landscapes of the UMRB.

Discussion

A new spatially explicit model

In this study, we developed a region-wide spatially explicit model to identify socioecological hotspots across an extensive mosaic of the Great Plains, widely influenced by different human activities. We used the model to envision the potential for habitat degradation resulting from human activities linked to SVs of people. We also provided a robust spatially explicit basis to identify the potential for conflict of interests in terms of SVs of people (i.e. Conservation and other SVs). The information that we obtained from this spatial modeling provides an insight into the spatial distribution of SVs, the extent of socioecological hotspots, potentials for habitat degradation in the future, opportunities for landscape restoration and/or biodiversity conservation, and the risk of conflict of interests among SVs in certain parts of the region. It establishes a robust platform for making inclusive decisions on land-use and resource management based on an integrated dataset of social and ecological data. For example, the results of this study indicate that while about half of the UMRB is covered by grasslands, a very small fraction of the land can function as wildlife habitat for grassland mammals (i.e. the bison, black- and white-tailed prairie dog; Table 6) and a

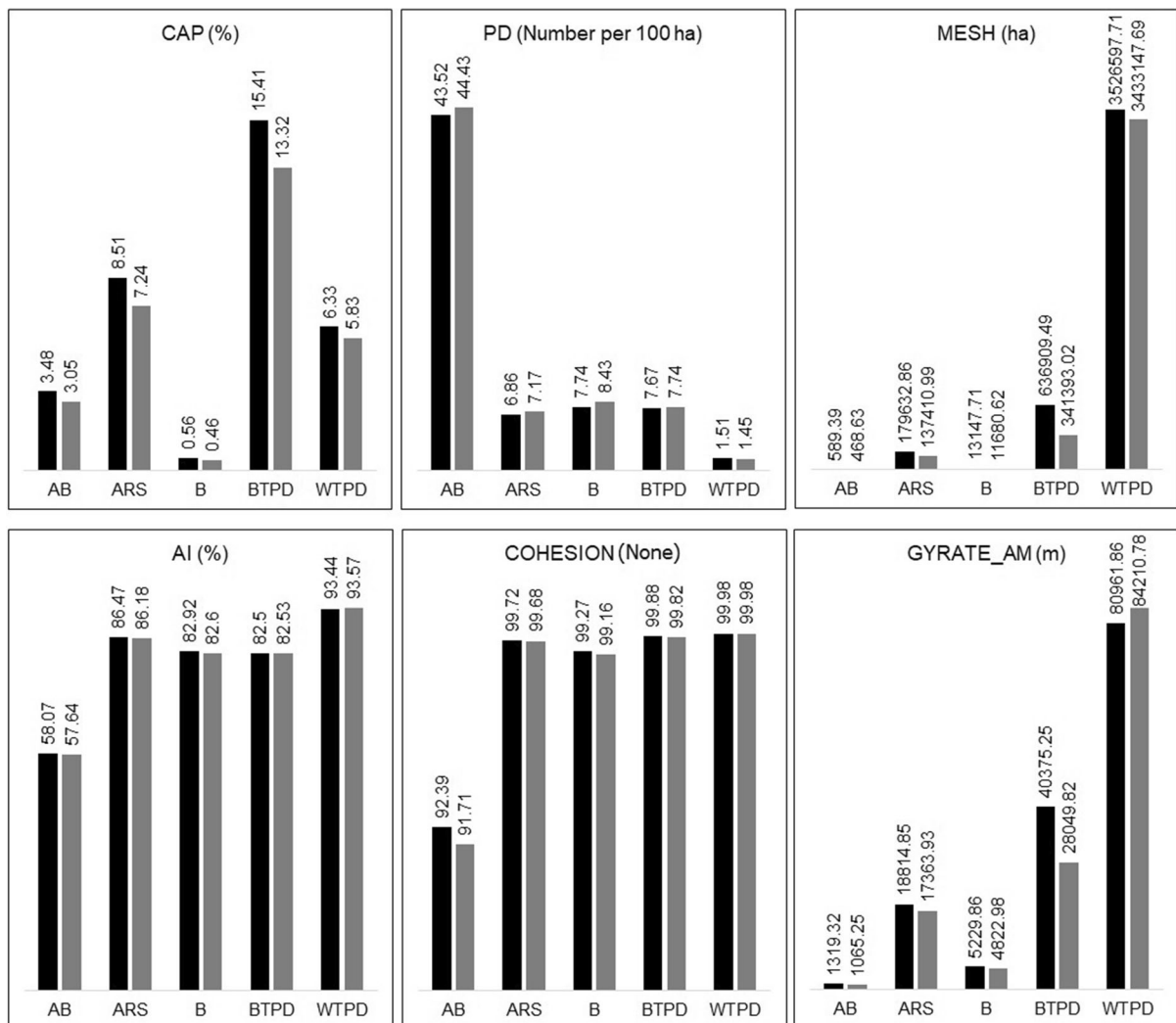


Fig. 7 The values of Class Area Proportion (CAP), Patch Density (PD), Effective Mesh Size (MESH), Aggregation Index (AI), Patch Cohesion Index (COHESION), and Area-weighted Radius of Gyration (GYRATE_AM) for habitats of American Beaver (AB), American Red Squirrel (ARS), Bison (B), Black-tailed Prairie Dog (BTPD), and White-tailed Prairie Dog

(WTPD) across the UMRB in the current (black) and simulated (grey) situations. The charts show how human activities (i.e. Development, Recreation, Tradition, and Agriculture) in socioecological hotspots can change the values of landscape metrics for wildlife habitats in the whole region

relatively large part of this fraction is subject to the impacts of human activities (Table 8). Utilizing landscape metrics in FRAGSTATS enabled us to quantify the structure of wildlife habitats before and after applying the impacts of SVs on wildlife habitats. As previously discussed by others (Forman 1995; Botequilha-Leitao and Ahern 2002; McGarigal et al. 2012), the values of landscape metrics should be interpreted based on the context and phenomenon under study. Although we provide examples of

possible interpretations here to explain how this model can contribute to a better understanding of the spatial relationship between SVs and biodiversity, we strongly believe that these interpretations remain species- and site-specific, and therefore, should not be generalized to the whole.

We observed that landscape metrics accurately quantified habitat loss, subdivision, dispersion, and shrinkage for habitats of five keystone species. As such, the model functioned as a tool to evaluate how

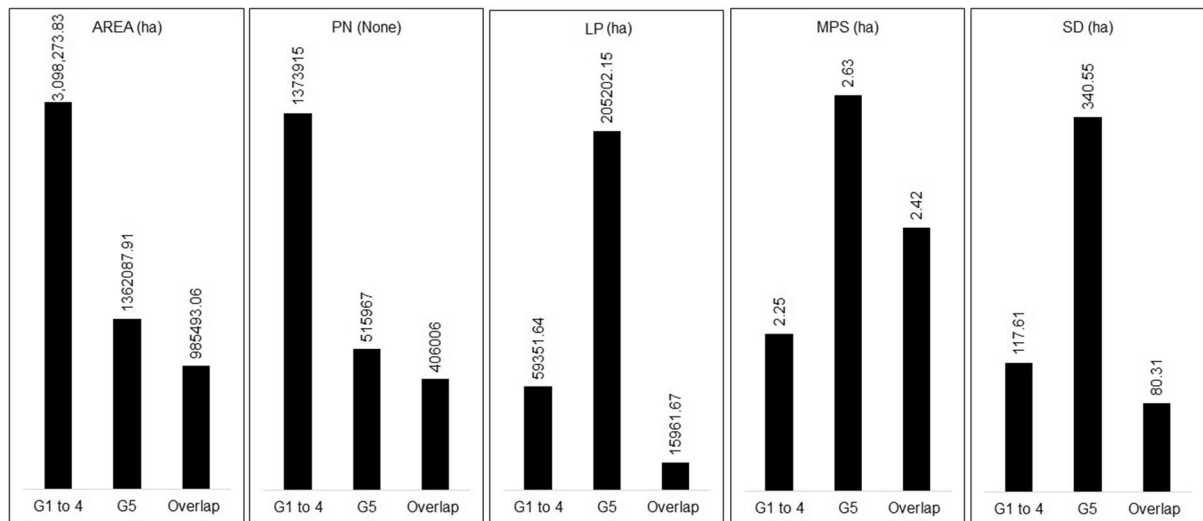


Fig. 8 The values of Total Area (AREA), Patch Number (PN), Largest Patch (LP), Mean Patch Size (MPS) and Standard Deviation (SD) for areas subject to Development (G1), Recreation (G2), Tradition (G3), Agriculture (G4), and Conservation (G5) in socioecological hotspots. The overlap between

areas people value for Development, Recreation, Tradition, and Agriculture (G1 to 4) and parts of the land that are valued for Conservation (G5) is characterized by AREA, PN, LP, MPS, and SD

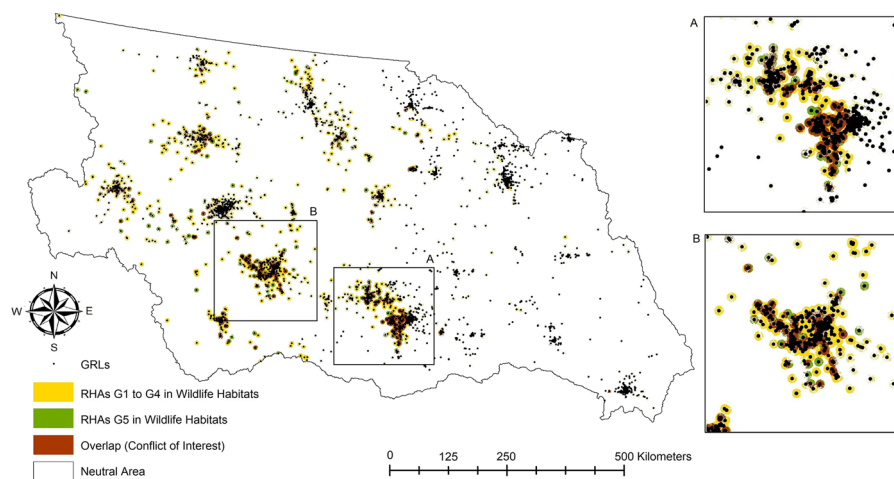


Fig. 9 The spatial distribution of overlaps between human activities (Radius of Human Activities; RHAs) and wildlife habitats in socioecological hotspots. Areas overlaid by human activities related to Development, Recreation, Tradition, and Agriculture (yellow) may negatively affect the structure of wildlife habitats. Areas overlaid by human activities related to Conservation (green) may have the social support for landscape restoration in wildlife habitats. Where human activities related to Development, Recreation, Tradition, and Agriculture overlap

with human activities related to Conservation (red), the potential for conflict of interests for land-use is higher. Neutral Areas (white) are expanses of the land that are not considered as socioecological hotspots. There is no overlap between human activities and wildlife habitats in this area. Georeferenced locations (GRLs; black) represent areas where people value the land based on a range of human activities classified in Table 2. Note that in each RHA, not the whole area overlaps with expanses of wildlife habitats (cf. Fig. 10)

SVs may influence biodiversity. Human perceptions of good governance and social impacts are among strong predictors of increasing public support for the longevity of conservation practices (Bennett et al.

2019), human perceptions about the impacts of conservation on the livelihood can determine how local communities decide on land-uses (Bennett and Dearden 2014), and education and community co-

Table 9 The difference between the values of landscape metrics Class Area Proportion (CAP), Patch Density (PD), Effective Mesh Size (MESH), Aggregation Index (AI), Patch

Cohesion Index (COHESION), and Area-weighted Radius of Gyration (GYRATE_AM)) before and after applying the impacts of human activities linked to SVs on wildlife habitats

Species	Difference between the current and simulated landscapes; Increase (+), Decrease (–)					
	CAP	PD	MESH	AI	COHESION	GYRATE_AM
AB	– 0.43	+ 0.91	– 120.76	– 0.43	– 0.68	– 254.07
ARS	– 1.27	+ 0.31	– 42,221.87	– 0.29	– 0.04	– 1450.92
B	– 0.10	+ 0.69	– 1467.09	– 0.32	– 0.11	– 406.88
BTPD	– 2.09	+ 0.07	– 295,516.47	+ 0.03	– 0.06	– 12,325.4
WTPD	– 0.50	– 0.06	– 93,450.02	+ 0.13	0	+ 3248.92

Mammals have been coded as follows: American Beaver (AB), American Red Squirrel (ARS), Bison (B), Black-tailed Prairie Dog (BTPD), White-tailed Prairie Dog (WTPD)

Table 10 The percentage of change in the values of landscape metrics after applying the impacts of human activities linked to SVs on wildlife habitats

Species	% of change; Increase (+), Decrease (–)					
	CAP	PD	MESH	AI	COHESION	GYRATE_AM
AB	– 12.35	+ 2.09	– 20.48	– 0.74	– 0.73	– 19.25
ARS	– 14.92	+ 4.51	– 23.51	– 0.33	– 0.04	– 7.71
B	– 17.85	+ 8.91	– 11.16	– 0.38	– 0.11	– 7.78
BTPD	– 13.56	+ 0.91	– 46.39	+ 0.04	– 0.06	– 30.52
WTPD	– 7.89	– 3.97	– 2.65	+ 0.14	0	+ 4.01

Mammals have been coded as follows: American Beaver (AB), American Red Squirrel (ARS), Bison (B), Black-tailed Prairie Dog (BTPD), and White-tailed Prairie Dog (WTPD)

management have been suggested to mitigate land-use disputes in areas of conservation importance (Liu et al. 2010). In this respect, our model and its outputs have the power to inform land-use policy and resource management at the local scale, as well. Fig. 10, for example, illustrates how spatial information obtained in this study can be used to inform stakeholders about the risk of habitat loss resulting from Development. Such derivatives can be extrapolated from the outputs depending on the scale and nature of the issue under consideration.

Mammal diversity in ecosystems can be used as an indicator to determine the impacts of humans on biodiversity (Morrison et al. 2007). Between 1900 and 2015, more than 170 mammal species have lost $\geq 30\%$ of their geographic ranges and more than 40% of species have experienced $> 80\%$ range shrinkage, worldwide (Ceballos et al. 2017). Urbanization and agriculture are among the main drivers of biodiversity

loss worldwide (WWF 2020). Although the UMRB is not considered as an urbanized region (Stoy et al. 2018), land conversion, mainly from grassland and wetland ecosystems to cropland (Wright and Wimberly 2013; Wimberly et al. 2018), has been an underlying ecological issue in the region since the 1850s, and there is new evidence to show the rate of urban growth in parts of the region is increasing, as well (US Census Bureau 2018). Therefore, the impacts of Development and Agriculture on mammals are higher compared to Recreation and Tradition in the UMRB. In this study, however, we assumed that human activities linked to Recreation and Tradition would have profound impacts on wildlife habitats, even if these impacts can be indirect and/or slower. Outdoor recreation is associated with a wide range of environmental issues (Mieczkowski 1995; Holden 2016). For example, even if land-cover change is properly controlled, noise pollutions force mammals

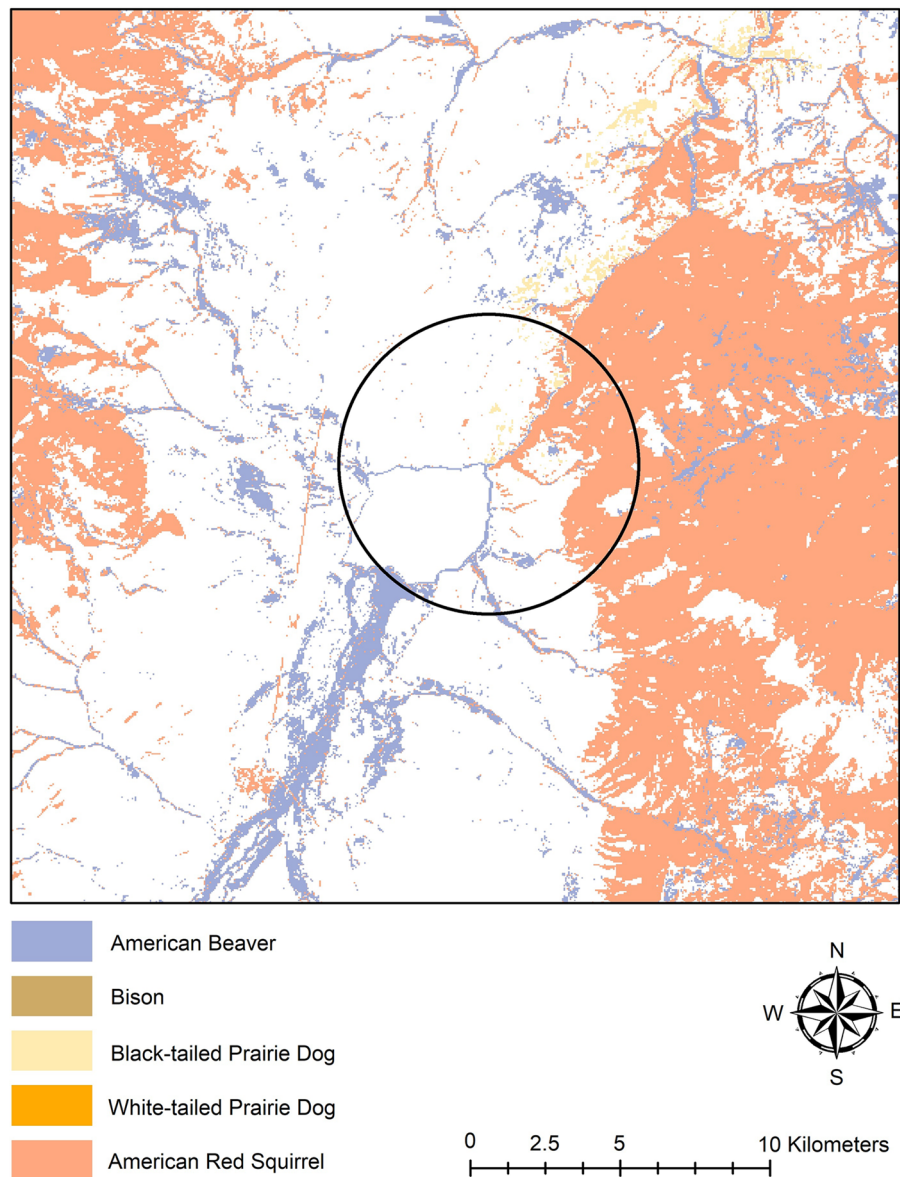


Fig. 10 A local-level example of mapping SVs for envisioning the potential for habitat degradation as a result of human activities. The wildlife habitat data was retrieved from GAP (U.S. Geological Survey 2018). This map depicts a RHA related to Development overlapping with wildlife habitats. Landscape

to leave their habitats (Slabbekoorn et al. 2018) and light pollutions have widespread impacts on many of them (Gaston et al. 2013). Human infrastructures to support recreational activities also increase the risk of landscape fragmentation, weed and pest dispersal (Pickering and Mount 2010) and fires (Barros et al. 2015). Human activities associated with Tradition also

metrics used in this study to quantify the impacts of Development on structure of wildlife habitats show the risk of further habitat degradation in certain areas of the UMRB (cf. Fig. 7 and Fig. 8)

adversely affect wildlife habitats through the spread of invasive species (Naylor et al. 2001; Radosevich et al. 2007), landscape fragmentation (Jordan 1993; Aldrich et al. 2006; Sorice et al. 2012), and the extraction of natural resources (Hessburg and Agee 2003). A meta-analysis of 76 studies of 62 mammal species world-wide showed a strong effect of different human

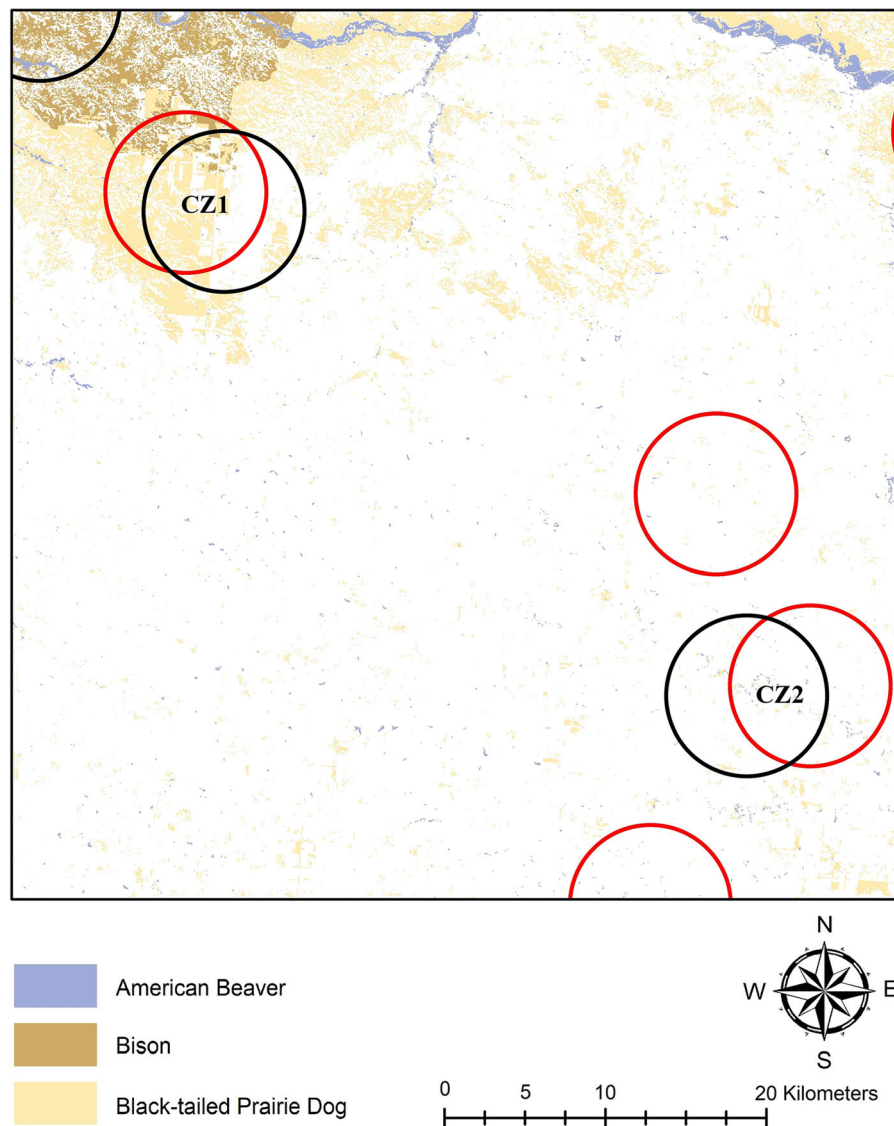


Fig. 11 A local-scale example of conflict of interests between human activities, where two RHAs linked to two different SVs overlap: Development (red) vs. Conservation (black). The wildlife habitat data was retrieved from GAP (U.S. Geological Survey 2018). There exist two conflict zones (CZ1 and CZ2) on

this map. The overlap in CZ1 has a higher impact on wildlife habitats whereas in CZ2, the level of threat to biodiversity is considerably lower because the amount of wildlife habitat in CZ2 is small

activities, including hiking, walking, and hunting, on daily patterns of wildlife activity (Gaynor et al. 2018). These activities are linked to Recreation and Tradition in the region (cf. Arthun and Holechek 1982; Flores 1991; Isenberg 2020).

Implications for biodiversity conservation

Habitat degradation

We observed 25 interactions between human activities and wildlife habitats in socioecological hotspots of the UMRB (Fig. 4). More interactions are also possible when two or more than two RHAs overlap. Irrespective of these overlaps between human activities and

wildlife habitats, there is also a high chance of overlap between two or more RHAs. As an example, Fig. 11 shows the capacity of our model to detect the potential for conflict of interests among human activities at the local scale, where RHAs of different human activities overlap. Such applications of the model are sensitive to the spatial ecology of species of interest, land-use legacies, human population density, and study scales (cf. Pacione 2009).

One important action to take in the face of these issues is to increase the multifunctionality of landscapes, perhaps because landscape multifunctionality could have disproportionate benefits on biodiversity conservation (Schulte et al. 2017). Multifunctional landscapes can mitigate the impacts of human activities on biodiversity through strategic placement of conservation practices within agricultural landscapes (Meurk and Swaffield 2000; Jarchow et al. 2015). In the UMRB, about one-fourth of the land is covered by croplands (Table 5). In addition to agricultural lands, the concept of multifunctional landscapes has been extended to describe how the land can be shared between people and wildlife in urbanized landscapes (Rosenzweig 2003).

The changes that we detected in the values of landscape metrics suggest that human activities linked to SVs can lead to landscape transformation through habitat loss, subdivision, dispersion, and shrinkage; however, the magnitude of changes was not the same for all mammal species. For example, habitats of the bison could be heavily encroached by human activities (Tables 8, 10; Fig. 4). Habitats of the American beaver and black-tailed prairie dog were also subject to the risk of habitat loss and a high level of exposure to human activities. If the land is used in the future based on SVs, the structure of patches of vegetation suitable for the persistence and colonization of these three mammals is expected to be adversely affected across socioecological hotspots (cf. Tables 2, 8, 9, 10; Fig. 7).

We observed that the American beaver is extremely sensitive to human activities, perhaps because this species is completely confined to water bodies and riparian zones (Collen and Gibson 2000). In the process of landscape simulation, the change in the value of GYRATE_AM for habitats of this species indicated that its habitats may be severely influenced by human activities. Habitats of the American red squirrel is less likely to be influenced by SVs linked to

Recreation or Tradition. In addition, a very small portion of the land, which can provide habitat for this species, overlaps with areas valued for Development and Agriculture (Fig. 4). Except for PD, the values of other landscape metrics that we used to compute its habitats declined after applying the impacts of SVs (Fig. 7). The American red squirrel can contribute to the natural regeneration of forest ecosystems of the UMRB (i.e. Needleleaf; Broadleaf Deciduous; Mixed; Table 5; Goheen and Swihart 2003). Thus, habitat degradation can have adverse consequences for both this species and forest ecosystems of the region in the long run.

Conservation and restoration

To rewild (Foreman 2004; Manning 2011) the Great Plains of the United States, landscape restoration is essential. Habitat requirements of keystone species should be considered as an integral part of this process. Bison positively impact the diversity of arthropods (Nickell et al. 2018) and plant communities, including forbs and graminoids of tallgrass prairie landscapes (Rosas et al. 2008). In areas covered by the class Grassland (47% of the UMRB; Table 5), colonies of black- and white-tailed prairie dogs can increase vegetation heterogeneity (Gervin et al. 2019) and support biodiversity through the provision of habitat and food source for a wide range of invertebrates, amphibians, reptiles, birds, and mammals (Hoogland 2013). These mammals also contribute to soil bioturbation (Table 1). The presence of the American beaver is positively correlated with a higher level of plant and bird species richness (Cooke and Zack 2008; Law et al. 2017); enhances water quality (Demmer and Beschta 2008); and leads to greater diversity in wetlands (Law et al. 2019), forests (Nummi and Kuuluvaine 2013) and streams (Gibson and Olden 2014). The importance of this species is so high that some researchers call for restoring its habitats in urban landscapes (Bailey et al. 2019).

In this study, approximately 2.7 million ha of the land that people valued for Conservation have an overlap with wildlife habitats (Table 7); however, a large portion of this overlap is also valued for other human activities (Fig. 8). The remaining areas have the capacity to serve as strategic zones for landscape restoration and/or biodiversity conservation, mainly because they contain suitable environmental

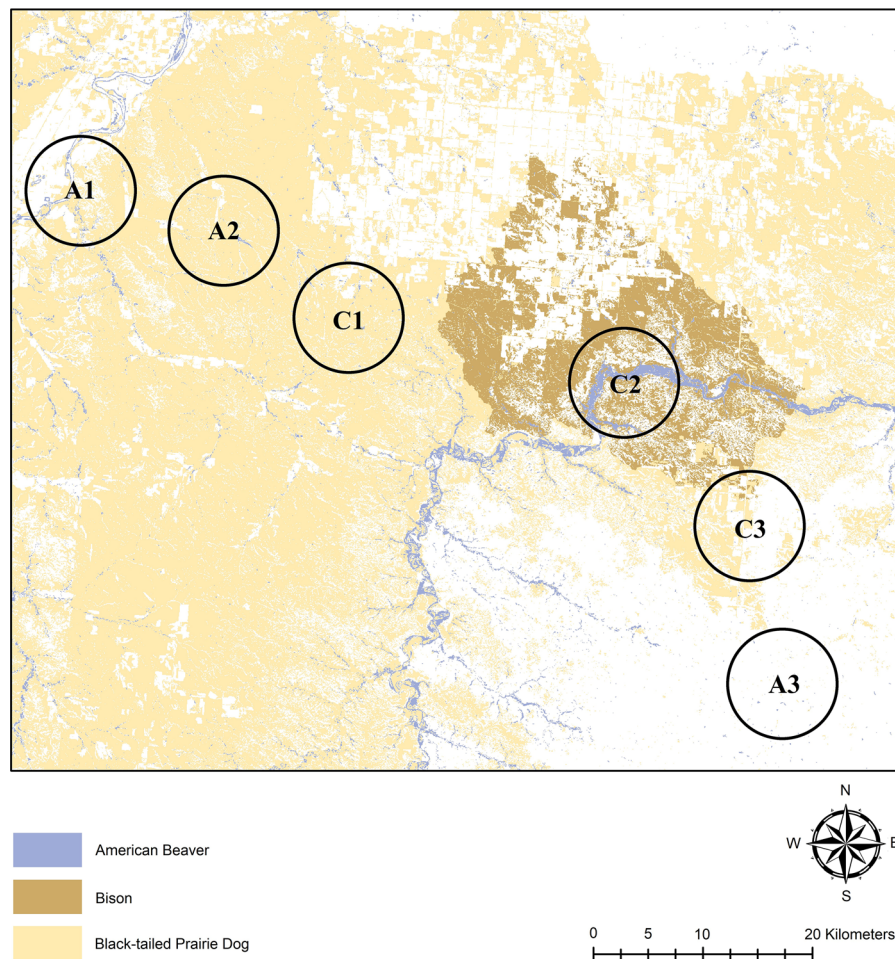


Fig. 12 Six RHAs mapped to show the impacts of Agriculture (A) and Conservation (C) on wildlife habitats. The wildlife habitat data was retrieved from GAP (U.S. Geological Survey 2018). According to this map, two RHAs related to Agriculture

overlie expanses of biodiversity significance, where the land simultaneously has the capacity to function as habitat for keystone species (i.e. A1 and A2). The location of the third RHA (i.e. A3), however, is less harmful to biodiversity

conditions for species persistence and colonization, and at the same time, also have the social support needed to implement conservation and restoration practices. Previous research shows that public support can enhance the odds of success in landscape restoration and/or biodiversity conservation practices (Norton 2016; Sullivan and Molles 2016; Butler and Schultz 2019) and change in public attitudes toward environmental and land-use issues is essential to build a proper platform for biodiversity conservation through landscape restoration (Novacek 2008; Manfredo 2017). Our model developed an in-depth understanding of the spatial distribution of social support for landscape restoration and/or biodiversity conservation in socioecological hotspots of the UMRB. Fig. 12, for

example, shows six RHAs linked to Agriculture and Conservation in a mosaic of the UMRB. In this mosaic, areas valued for Conservation can provide opportunities for restoration and/or biodiversity conservation. Areas that wildlife species coexist should take precedence for conservation/restoration. In this part of the UMRB, priority must be given to C2, C3, and C1, respectively.

Limitations

We put forward four important limitations associated with this study that should be considered in future research.

First, our model and its outputs were sensitive to the spatial scale of land cover data (cell size: 30 m), the thresholds defined in FRAGSTATS (e.g. RHA: 5 km, cell size: 50 m), as well as the spatial ecology of chosen species derived from the literature. The nature and magnitude of impacts imposed by human activities on the structure of wildlife habitats are not the same. In addition, not all species respond to these impacts in the same way. Particular attention should be placed on these issues to avoid the misinterpretation of results. Where the spatial scale and/or species of interest are different, these issues should be cautiously considered. Second, given the scale of study region, the model should be checked at different scales to avoid the misinterpretation of data. For example, after applying the impacts of human activities on wildlife habitats, the values of *GYRATE_AM* and *AI* increased in habitats of the white-tailed prairie dog. However, based on a local-scale monitoring of the current spatial distribution of suitable habitats for this species, we found that in the process of landscape simulation, some dispersed and isolated habitat patches were eliminated in a way that the values of these landscape metrics increased. Third, the accuracy of interpretations at the local scale depends, to a large extent, on the spatial and ecological knowledge of stakeholders who may have different, if not conflicting, interests and priorities. Fourth, the methods that we used to map SVs determined the spatial distribution of locations that people value for specific human activities. We sampled 22 human population centers across four states of Montana, North Dakota, South Dakota, and Wyoming to provide the most accurate picture of the locations that people value their landscapes for particular human activities. Despite this, we still assume that the location of sampled human population centers, as well as the place of residence could partly influence the spatial distribution of SVs.

Conclusion

In this study, we developed and used a spatially explicit model to provide an integrated picture of possible interactions between landscapes of social significance and wildlife habitats in a large mosaic of the Great Plains of the United States. If used as predictors of land-use disputes, our model showed SVs

of people toward their landscapes have the potential to act as drivers of landscape transformation through habitat loss, habitat subdivision, habitat dispersion, and habitat shrinkage; however, the magnitude of impacts varied among human activities and species across landscapes of the UMRB. The results of this study raised concerns about the future of biodiversity in the UMRB and concurrently depicted opportunities for landscape restoration and/or biodiversity conservation, where social support and environmental conditions are well aligned. As discussed, the model that we used to map SVs in relation to wildlife habitats was associated with some uncertainties and limitations, and therefore, further research is required for its development. Concurrently, change in SVs and public attitudes toward land use is essential to avoid further biodiversity loss in this region.

In light of this study, we define three questions for future research: (1) how can the capacity of this spatially explicit model be improved to address more complex issues related to the coexistence of human and wildlife in socioecological hotspots?; (2) how can this model be used as a catalyst to inform a wide spectrum of stakeholders and make a multi-scale change, from community to region, in SVs and attitudes toward land-use issues?; (3) how can the model be used by other researchers in other parts of the world to evaluate its capacity and relevance to the current socioecological challenges?

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