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Ecology, conservation, and restoration of grazing ecosystems in the anthropocene

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and Peter Leimgruber

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Ecology, conservation, and restoration of grazing ecosystems in the anthropocene

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How Biodiversity-Friendly Is Regenerative Grazing?

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Regenerative grazing management (ReGM) seeks to mimic natural grazing dynamics to restore degraded soils and the ecological processes underpinning sustainable livestock production while enhancing biodiversity. Regenerative grazing, including holistic planned grazing and related methods, is an adaptive, rotational stocking approach in which dense livestock herds are rotated rapidly through multiple paddocks in short bouts of grazing to defoliate plants evenly and infrequently, interspersed with long recovery periods to boost regrowth. The concentrated "hoof action" of herds in ReGM is regarded vital for regenerating soils and ecosystem services. Evidence (from 58 studies) that ReGM benefits biodiversity is reviewed. Soils enriched by ReGM have increased microbial bioactivity, higher fungal:bacteria biomass, greater functional diversity, and richer microarthropods and macrofauna communities. Vegetation responds inconsistently, with increased, neutral, or decreased total plant diversity, richness of forage grasses and invasive species under ReGM: grasses tend to be favored but shrubs and forbs can be depleted by the mechanical action of hooves. Trampling also reduces numerous arthropods by altering vegetation structure, but creates favorable habitat and food for a few taxa, such as dung beetles. Similarly, grazing-induced structural changes benefit some birds (for foraging, nest sites) while heavy stocking during winter and droughts reduces food for seedeaters and songbirds. With herding and no fences, wildlife (herbivores and predators) thrives on nutritious regrowth while having access to large undisturbed areas. It is concluded that ReGM does not universally promote biodiversity but can be adapted to provide greater landscape habitat heterogeneity suitable to a wider range of biota.

Keywords: adaptive multi-paddock grazing, holistic planned grazing, livestock density, species richness, wildlife

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INTRODUCTION

Regenerative Agriculture is a broad movement that has rapidly gained prominence in the agricultural community as well as in the popular discourse and academic literature over the last 5–6 years (Massy, 2017; Lal, 2020; Giller et al., 2021). Though not formally or consistently defined (Newton et al., 2020), regenerative farming aims to provide more environmentally benign alternatives to conventional agricultural approaches to meet growing food needs while addressing critical global problems of stagnating crop yields, diminishing food quality and security, and widespread soil degradation and increased desertification (Rhodes, 2017; LaCanne and Lundgren, 2018). Restoring soil health and multifunctionality, particularly microbial activity, nutrient recycling, and carbon and water retention, is regarded as critical for developing sustainable and resilient farming systems (Sherwood and Uphoff, 2000; Schreefel et al., 2020). Sequestering atmospheric carbon into soils to mitigate climate change as well as nurturing and promoting biodiversity are also stated goals of regenerative agriculture (Gosnell et al., 2019; Newton et al., 2020). A variety of agronomic practices are considered regenerative, including mainstream and alternative agronomic practices such as minimum-till or conservation agriculture, cover- and rotational cropping, integrated crop-livestock and agroforestry systems, permaculture, organic farming, etc. (Francis et al., 1986; White, 2020). Domestic livestock can also be employed using regenerative grazing management (ReGM) to revitalize soils and grazing ecosystems (Lal, 2020).

Regenerative grazing management (hereafter abbreviated as ReGM) is an adaptive form of intensive grazing management (Teague and Kreuter, 2020; Spratt et al., 2021) in which the timing and distribution (density) of livestock grazing is carefully planned, managed, and monitored with the aim of improving rangeland productivity and overall ranching system resilience (Garnett et al., 2017; Teague and Barnes, 2017). In essence, ReGM represents a rebranding of Holistic Planned Grazing (HPG) developed by Alan Savory in southern Africa more than half-a-century ago (Savory and Parsons, 1980; Gosnell et al., 2020) and which is now applied on rangeland in many parts of the world (Teague and Kreuter, 2020). Holistic Planned Grazing, and hence ReGM, is characterized by the stocking of large herds of livestock on multiple small permanent or temporary paddocks for short periods (less than 1 day to few days) followed by long periods of recovery rest (many weeks to months) to mimic the rapid movement of concentrated ungulate herds being chased across the African landscape by predators (Savory and Butterfield, 2016). The fundamental principles of ReGM are to limit the duration of grazing to avoid regrazing of forage plants and to employ the "herd effect" to trample down dead plants, break up hard soil crusts, and incorporate dung, urine, and plant organic matter into soils to improve soil carbon, increase water infiltration and retention, and accelerate nutrient flow for grass regrowth (Savory and Butterfield, 2016; Teague and Barnes, 2017). Other grazing practices that employ a similar intensive, adaptive rotational stocking approach to regenerate rangeland or cultivated pastures include adaptive multi-paddock grazing (AMP), high-density-short-duration grazing, [ultra] high intensity grazing, mob grazing, cell grazing, time-controlled grazing, and management intensive [planned] grazing. Also common to HPG and related regenerative grazing methods is the consistent claim that they have a significantly greater potential than conventional, less intensive, grazing systems to improve rangeland and livestock condition, productivity, and biodiversity, and slow or even reverse climate change by the sequestration of large amounts of carbon into soils, even at much higher stocking rates than usually prescribed (Savory, 2013[1]; Savory and Butterfield, 2016).

Claims about the ubiquitous superiority of ReGM are controversial, divisive, and strongly contested (see Briske et al., 2013; Sherren and Kent, 2019; Gosnell et al., 2020), spurring numerous studies, reviews (Skovlin, 1987; Holechek et al., 2000; Briske et al., 2008; Nordborg, 2016; Hawkins et al., 2022) and a meta-analysis (Hawkins, 2017). These studies and syntheses have revealed varied ecosystem and agronomic responses to ReGM with little compelling empirical evidence that ReGM will improve grass and animal production and vegetation condition wherever it is applied. What has seldom been examined, however, is the assertion that the stimulation of soil and vegetation productivity by ReGM will also improve the availability and quality of resources and habitats for multifarious flora and fauna, thereby promoting multi-taxa biodiversity; only two instances of soil biodiversity responses were reported in reviews. Biodiversity (species richness and diversity indices) is included as key indicator for verifying the success of ReGM (Savory Institute, 2019) and is valued by regenerative ranchers as a fundamental driver of the ecological and economic sustainability of their farm (Stinner et al., 1997) but little information is available on the effects of intensive, infrequent grazing on different biota (Carter et al., 2014) and what synergies exist and possible trade-offs will be required to simultaneously achieve high livestock production and biodiversity conservation (Lawrence, 2019). To start filling this gap, this review examined 58 studies (see **Supplementary Data Sheet 1**—Search strategy) on the positive, negative, or neutral effects on the diversity of soil microbes, plants, invertebrates, birds, and mammals done in North America (26), Africa (17), Australia (10), South America (3), and New Zealand (2). Studies included temporal changes under ReGM, comparisons with less intensive rotational, continuous, or deferred grazing systems, or ungrazed plots or properties or nature reserves (see study details—**Supplementary Table 1**). The effects on biodiversity of dense herds of livestock penned in moveable corrals used for rehabilitating areas and as a home base for ReGM were also reviewed. Mechanism whereby different disturbances exerted by intense grazing (trampling, grazing, nutrient addition) directly or indirectly affect biodiversity are summarized followed by a brief consideration of how ReGM could be improved to better benefit biodiversity.

RESPONSE OF BIOTA TO REGENERATIVE GRAZING

The number of positive, negative, and neutral responses of various biota to ReGM is presented in **Figure 1**.

Herpetofaunal diversity was unaffected by ReGM in Africa (Fabricius et al., 2003) and Australia (Dorrough et al., 2012; Kay et al., 2017), and is not discussed further.

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[1] http://www.ted.com/talks/allan_savory_how_to_green_the_world_s_deserts_and_reverse_climate_change.htm

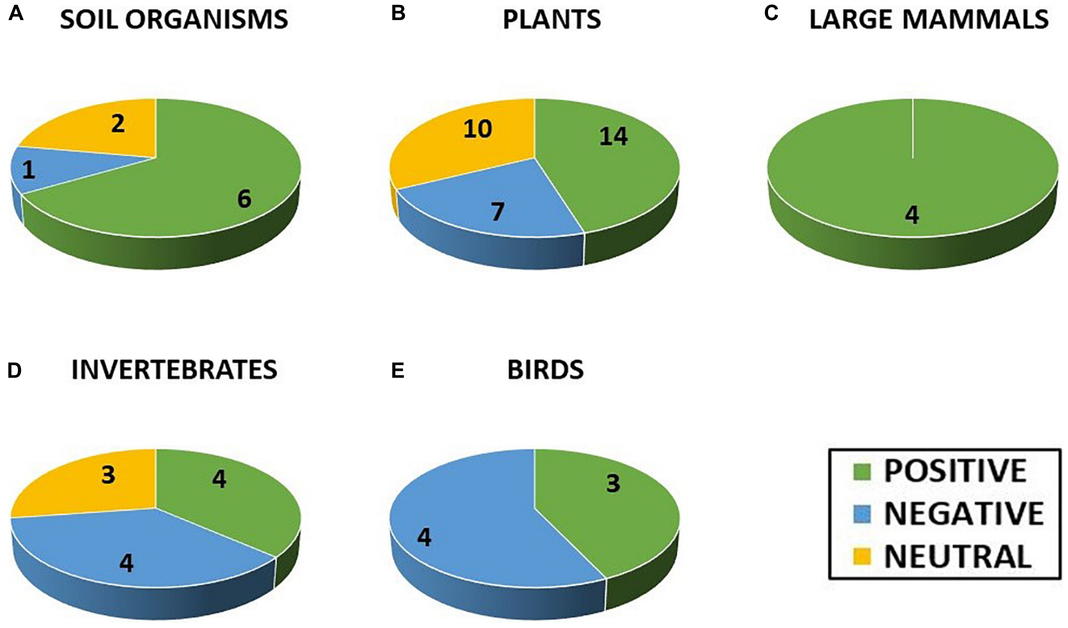

FIGURE 1 | Count of positive, negative, and neutral responses of soil organisms **(A)**, plants **(B)**, large mammals **(C)**, invertebrates **(D)**, and birds **(E)** to regenerative grazing.

Soil Organisms

Regenerative grazing generally promoted soil microbial activity. Compared to soils in ungrazed or less intensively grazed areas, soils under ReGM had larger and more active microbial biomass, especially of fungi (Beukes and Cowling, 2003; Teague et al., 2011; Girard-Cartier and Kleppel, 2017; Kleppel, 2019), and similar (Girard-Cartier and Kleppel, 2017) or higher microbe group functional diversity (Kleppel, 2019). A higher fungi : bacteria ratio would enhance the retention and availability of soil water and nutrients for microbes and plant growth (Teague et al., 2011). In contrast, Dormaar et al. (1989) recorded lower soil fungal biomass than in exclosures after more than 10 years of ReGM, in concert with poorer soil water functionality and reduced vegetation condition.

Improved soil health under ReGM had positive or neutral effects on soil micro- and macrofauna. Teutscherová et al. (2021) found that a single year of ReGM increased overall macrofaunal diversity and the abundance of earthworms, beetles, and other invertebrates such as ants, spiders, woodlice, and earwigs, which enhanced soil structure through bioturbation. In turn, improved soil structure (e.g., greater porosity) and chemistry (e.g., more organic matter) under intensive stocking benefited soil-dwelling and epigeic arthropods (Tom et al., 2006; Moulin et al., 2016) but not nematodes and protozoa (Teague et al., 2011).

Plants

The influence of ReGM on the diversity of plant species varied widely in direction and magnitude. Species richness and diversity was unaffected by ReGM in sown pastures (Scott, 2001), semi-arid grassland (Weigel et al., 1989; Hillenbrand et al., 2019; Oliva et al., 2021), semi-arid shrubland (Beukes and Cowling, 2000), and mesic (>650 mm a^{-1} MAP) grassland (Jacobo et al., 2006; Dorrough et al., 2012; Chamane et al., 2017a; Kurtz et al., 2018). Reduction in species richness under ReGM ranged from 10% (Hall et al., 2014) to over 80% (Scott-Shaw and Morris, 2015), with grasses (Allington and Vallone, 2011), forbs (Lawrence, 2019) and shrubs (McManus et al., 2018) negatively affected by intense grazing and trampling, especially during droughts (Souther et al., 2020). Regenerative grazing increased plant species (Earl et al., 2003) and life-form diversity (Barnes and Howell, 2013) over time compared to ungrazed areas (Paine and Ribic, 2002; Girard-Cartier and Kleppel, 2017) as well as to rangeland grazed continuously (Lalampaa, 2016; Odadi et al., 2017; Rantso et al., 2021; Wang et al., 2021) or rotationally at a lower intensity (Laliberté and Tylianakis, 2012).

In general, ReGM promoted the diversity and abundance of perennial, productive forage grasses (Stinner et al., 1997; Chamane et al., 2017a; Huruba et al., 2018) over perennial forbs (Loeser et al., 2007; Morris and Scott-Shaw, 2019), and exotic over native species (Ruthven, 2007), although intense stocking can be employed to target invasive weeds (Girard-Cartier and Kleppel, 2015).

Increased plant species richness under ReGM may not be agronomically or ecologically desirable if unpalatable and less productive forage grasses and non-native ruderal species are favored (e.g., Chamane et al., 2017a; Souther et al., 2020).

Invertebrates

The response of insects and arachnids to ReGM varies between taxa, season, and habitat quality (Lindsay and Cunningham, 2009; Barton et al., 2016). For example, various insect (e.g., ants, crickets, beetles, flies; grasshoppers, parasitoid hymenopterans) and arachnids were less abundant and speciose under ReGM but Hemiptera benefited from reduced vegetation cover (Fabricius et al., 2003; Debano, 2006; Lawrence et al., 2015). Fire ants invaded intensively grazed sites but did not reduce arthropod diversity (Schmid and Lundgren, 2020). Regenerative grazing increased habitat heterogeneity and food for dung beetles (Wagner et al., 2020) but destroyed spider webs and the grass structure upon which they are built; ground-dwelling arachnids were unaffected (Sebata, 2020). Invertebrates thrived where the biomass and cover of shrubs increased because of restricted grazing in riparian paddocks, resulting in higher inputs of invertebrate food into streams for trout, doubling their mass (Saunders and Fausch, 2007).

Birds

Regenerative grazing indirectly affects bird populations by modifying habitat structure and food availability. Ground-foraging birds such as quail can more successfully forage, and thus flourish, where ReGM reduces standing herbage, litter, and cover (Schulz and Guthery, 1988; Wilkins and Swank, 1992). In contrast, intense grazing reduced food reserves and cover for overwintering birds, especially during drought, decreasing their numbers and diversity (Bock and Bock, 1999). Timing is important: heavy stocking in the dormant season when food is scare reduced songbird diversity and species richness (Sliwinski et al., 2020). Applying a [shifting] range of grazing intensities across the landscape to diversify vegetation structure, including trees for birds (Dorrough et al., 2012), is key for promoting avian diversity (Davis et al., 2020) but ReGM as well as other grazing systems do not create sufficient habitat heterogeneity to suite a wide variety of birds species (Sliwinski et al., 2019).

Mammals

The abundance, diversity of mammalian herbivores is increased at nutrient hotspots created by overnight corralling (Huruba et al., 2021a,b) and on the wider rangeland managed under ReGM because of improved grass and browse quality (Lalampaa et al., 2016; Odadi et al., 2017; Crawford et al., 2019). Similarly, applying ReGM by herding (from temporary corrals) rather than by fencing, combined with a cessation of lethal predator control led to a remarkable increase over 4 years in mammalian species richness (by 24%), particularly herbivores (+33%), and the abundance and distribution range of wildlife in a semi-arid shrubland in South Africa (Schurch et al., 2021).

The only study on small mammals revealed no general effect of ReGM on rodent diversity but that some species were sensitive to intensive grazing in particular habitats (Lemos, 2014).

HOW REGM BENEFITS AND HARMS BIODIVERSITY

The three central tenets of ReGM practices regarded essential for enhanced ecosystem function and profitable livestock production—(1) the "hoof" effect on soils and vegetation, (2) even grazing for a short duration with long recovery rests, and (3) recycling and redistribution of nutrients through animal excreta (Savory and Butterfield, 2016)—can indirectly or directly favor or harm biodiversity (**Table 1**). The same type of disturbance can have contrasting effects on different taxa and even on species within taxa.

Excessive trampling, especially by cattle, generally degrades soil structure and function, although the effects are contingent on numerous site-specific factors such as soil texture and moisture, terrain, and vegetation cover (Trimble and Mendel, 1995; Bilotta et al., 2007; Byrnes et al., 2018). The contrasting reported improvements in soil health under ReGM that indirectly benefit soil biota (see Soil Organisms) could owe to the limited duration of trampling that soils experience, the breaking of impermeable hardened soil caps, and the incorporation of organic material from plants and animal excreta into the topsoil (Mwendera et al., 1997; Teague and Kreuter, 2020; Mor-Mussery et al., 2021). Trampling can also create suitable seedbeds (Huruba et al., 2018) and open the sward for ground-foraging birds (see Birds).

Plants exposed to trampling can be severely and extensively impacted; for example, fewer than 10% of forb species escaped mechanical damage to their above-ground tissues under ReGM (Chamane et al., 2017b). Tall plants, particularly soft-leaved forbs with elevated growing points are most vulnerable to trampling injury (Sun and Liddle, 1993; Morris and Scott-Shaw, 2019), which reduces their vigor and potential persistence (Morris, 2021). Grass canopies reduced or modified by trampling offer inferior habitat for arthropods, birds, and mammals that require tall swards for nesting or shelter (Fuhlendorf et al., 2006; Schieltz and Rubenstein, 2016; Oyarzabal and Guimarães, 2021)

TABLE 1 | A summary of the positive and negative effects of regenerative grazing practices on biodiversity.

	Regenerates	Degenerates
Intense trampling	• Increased organic matter and water for soil microbes and fauna. • Lower cover for ground foraging birds. • Improved seedbed for germination.	• Modified sward structure and reduced cover for breeding and shelter for arthropods and birds. • Mechanical damage to forbs. • Direct hoof impact on biological soil crusts.
Intense, infrequent grazing	• More even use of forage plants. • Long recovery periods for plants and other biota. • Minimal spatial disturbance for fauna.	• Reduced seasonal food availability for birds, especially during drought. • Reduced cover for shelter and breeding for arthropods, birds, and wildlife.
Nutrient recycling and distribution	• Increased nutrients and food for microbes, soil fauna, and plants.	• Increased soil fertility for plant dominants and non-native plant invaders.

and herbivores can also inadvertently ingest instars and adult arthropods (Van Noordwijk et al., 2012; Wang and Tang, 2019). Hooves directly impact and reduce the cover of biological soil crusts (Eldridge, 1998).

In ReGM system, the long uninterrupted periods afforded plants and animals to recover from defoliation and trampling probably contribute more to the observed neutral and positive responses of individuals and populations than the restricted periods of stocking of small paddocks or areas employed to minimize selective grazing of palatable forage plants and to prevent regrazing of grass (Ferraro and Oesterheld, 2002; Barton et al., 2016; Porensky et al., 2021). Importantly, confining livestock to a small proportion of the grazing area at any one time minimizes the spatial extent and duration of their disturbance of other animals on the property (Schurch et al., 2021).

Despite high stocking densities and grazing pressures, a uniform defoliation intensity across plant species and vegetation patches is not easily achieved using ReGM (Venter et al., 2019). Selective grazing of species and areas can favor less palatable and more grazing resistant plants, altering vegetation composition (Anderson and Briske, 1995; Augustine and McNaughton, 1998). Increased paddock subdivision does not alter grazing selectivity to the degree expected (Gammon and Twiddy, 1990) nor can it prevent the ingress of unpalatable grasses that are selectively avoided by livestock even under intense stocking (Morris and Tainton, 1996).

Controlled rotation of livestock combined with intense trampling is predicted to distribute their excreta evenly across the landscape and enrich soils with carbon and nutrients recycled from plant tissues (Savory and Butterfield, 2016). Microbial and coprophagous invertebrate populations benefit from the modest levels of carbon sequestration (see Soils) achievable under ReGM (Hawkins et al., 2022), and plants are better able to compensate for defoliation on, fertile, organic-rich soils (Maschinski and Whitham, 1989; Venter et al., 2021). Nutrients imported by penned livestock create fertility hotspots (Huruba et al., 2018) which can kickstart restoration of a species-rich, palatable grass sward (Sibanda et al., 2016) but the potential for creating loci for non-native species invasion requires investigation. Also unknown is whether increased enrichment and grass productivity under ReGM (Teague and Kreuter, 2020) could eventually dimmish plant species diversity by favoring dominant over subordinate grasses and broadleaf species (Harpole et al., 2016).

CONCLUSION AND STRATEGIC DIRECTIONS

Given the variable responses within and between taxa, it is concluded that ReGM is not universally beneficial to all biodiversity, as claimed. The assumption that any bottom-up stimulation of soil ecosystem processes and plant production by ReGM will inevitably cascade positively through the whole rangeland ecosystem to support larger and more diverse populations of all fauna and fauna is not supported. Furthermore, some direct and indirect impacts of ReGM, particularly trampling, can be pernicious and persistent for some biota. Relentless application of a uniform disturbance comprising short bouts of intense grazing and trampling across the whole property could homogenize vegetation communities and landscapes (Loeser et al., 2007; Sliwinski et al., 2020) reducing the spatial habitat heterogeneity required to sustain high biodiversity (Fuhlendorf and Engle, 2001; Benton et al., 2003). Nonetheless, the multi-paddock, controlled rotational stocking system employed in ReGM could be adapted (Teague et al., 2013) to both mitigate negative disturbances on plants and animals by applying more moderate stocking densities over most of the property (Joubert et al., 2017; Barzan et al., 2021) while at the same time creating a more heterogenous grazed landscape with habitats and living conditions suitable to a broader range of species and communities.

To engender greater landscape heterogeneity at all scales (Toombs et al., 2010), stocking density and duration and timing of grazing would need to be deliberately varied over space and time to provide a shifting mosaic of disturbance intensities that includes extremes (Sliwinski et al., 2020; Porensky et al., 2021) ranging from “overgrazed” bare patches to lightly grazed or protected paddocks especially in sensitive riparian zones (Paine and Ribic, 2002; Saunders and Fausch, 2007) and on steep slopes (Trimble and Mendel, 1995). Also important to include are other ecosystem management tools often eschewed by regenerative grazers (Savory and Butterfield, 2016), notably planned burning and long rests. Fire is essential to maintain the vegetation and of fire-dependant ecosystems such as mesic grassland and savanna (Bond, 2019; Gordijn and O’Connor, 2021), and when coupled with grazing can increase structural heterogeneity (Lituma et al., 2022) and contribute toward achieving the dual goals of biodiversity conservation and profitable cattle production (Limb et al., 2011; Bowman et al., 2016). Extended rests (of a year or longer) increase rangeland production (McDonald et al., 2019) and could create suitable habitat and grassbanks for particular bird species (Davis et al., 2020) while being restorative for animal and plant individuals and populations impacted by intense herbivory (Kirkman and Moore, 1995; Morris, 2021).

A carefully planned strategic approach would be required when adapting ReGM to better nurture and sustain diverse biological communities on ranches and in other grazing areas (Wang and Tang, 2019). The grazing strategy could consider approaches noted above that could generally promote biodiversity as well as specific management tactics targeting species and communities on the property of special conservation concern (Barry and Huntsinger, 2021).

AUTHOR CONTRIBUTIONS

The author confirms being the sole contributor of this work and has approved it for publication.

SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2021.816374/full#supplementary-material

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Identifying Ecological Security Patterns Based on Ecosystem Services Is a Significative Practice for Sustainable Development in Southwest China

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Southwest China, which is rich in biodiversity and a wide range of ecosystem services (ESs), is a strong support for local human wellbeing. This area is also one of the key components of the ecological security shelter (ESS) for national ecological security and biodiversity conservation. Due to the combination of man-made and natural factors, Southwest China has suffered serious ecological degradation that directly threatens ecological security which refers to the health status of ecosystems and ESs functions. Mapping ESs-based ecological security patterns (ESPs) is essential for designing conservation strategies that suitably combine regional environment conservation with sustainable utilization. We used the InVEST (Integrated Valuation of Ecosystem Services and Tradeoffs Tool) model to identify ecological conservation priority areas which integrated ecological sensitivity (soil erosion sensitivity, rock desertification sensitivity, landslide sensitivity, debris flow sensitivity, and freezing-thawing erosion sensitivity), ecological risk (drought risk, natural disaster risk, and socio-economic risk), and ecological conservation importance (soil conservation, water conservation, and biodiversity conservation importance). In this research, we summarized a new designing framework of ESs-based ESPs. We divided the study area into two zones and four belts including: (A) the alpine steppe and wetland zone, (B) Hengduan Mountain zone, (C) northern shelter belt (Daba-Micang Mountain), (D) central shelter belt (Wumeng-Wuling Mountain), (E) southern shelter belt (southern border of China), and (F) southwestern shelter belt (eastern Himalayas Mountain). Identifying distributions of the ESs-based ESPs has practical significance to improve local human wellbeing and to maintain sustainable development of natural-social ecosystems in Southwest China. Furthermore, ESs-based ESPs are necessary for local administrations to create rationalizing plans on balancing conservation and utilization of natural resources, so that policy-makers can put into place targeted prevention and control measures to limit the development of excessive consumption of natural resources and ecological damages, which is worth promoting.

Keywords: ecological security patterns (ESPs), ecological security shelter (ESS), ecosystem services (ESs), ecological sensitivity, ecological risk, ecological conservation importance, Hengduan Mountain, Southwest China

INTRODUCTION

Predatory exploitation and irrational utilization of natural resources have brought about serious consequences such as climate change. Combining the effects of human activities with climate change has led to complicated changes in ecosystems at the spatial or temporal multi-scale, which bring significant losses and severe impacts to human wellbeing (Zhao et al., 2018). Due to rapid economic development, urbanization, and industrialization, as well as an exponential growth in the population and consumption of energy and materials, natural ecosystems have been severely challenged for several decades in China. In the process of regional development which requires stable natural resources and eco-environmental support, population growth and economic development have led to tremendous pressure on natural ecosystems, causing degradation such as water shortages, soil erosion, carbon loss, biodiversity loss, and habitat fragmentation (Xu et al., 2019). A comprehensive understanding of the effects of ecosystem changes and corresponding security considerations is necessary for establishing regional environmental management policies (Pătru-Stupariu et al., 2020; Xiao Y. et al., 2020). With the aim to protect the fragile ecosystem, reduce natural disasters, and curb ecosystem degradation, local and central governments of China have recently launched a series of ecological policies and projects, such as the Slope Land Conversion Project (SLCP), China's Natural Forest Protection Project (NFPP) (Zinda and Zhang, 2018), Artificial Afforestation, the River Shelterbelt Project (Xiao Y. et al., 2020), and Retire Livestock and Restore Grassland (RLRG) (Wang Y.X. et al., 2018). As the main ecosystem, grassland health affects biodiversity due to the adaption of all native flora and fauna to the long-term evolutionary forces that have shaped these rangeland environments (Harris, 2010). Grassland degradation caused by livestock grazing increased in the late 1990s as several disasters occurred, including Yangtze River floods, the Yellow River running dry increasingly often, and dust-storms and sand-storms originating in western rangelands, which directly damaged ecological security (Harris, 2010). Southwest China, which is rich in biodiversity and has a wide range of ecosystem services (ESs), is a strong support for the sustainable development of the local human wellbeing (Xiao Y. et al., 2020). This area is also one of the key components of the ecological security shelter (ESS) for biodiversity hotspot conservation. A sound management of natural resources is needed if there is to be a sustainable future. Due to the combination of man-made and natural factors, Southwest China regional land cover has changed significantly and now suffers from serious ecological degradation such as severe soil erosion and the tendency to develop rocky desertification (Xiao Y. et al., 2020).

The report to the Eighteenth National Congress of China has indicated that ecological security has become a hotspot in the field of sustainable development strategies (Liu and Chang, 2015). Ecological security is a significant component of ecological civilization, which has been promoted in the overall plan of the cause of socialism, and improved its strategic position in the central government of China (Liu and Chang, 2015; Meng et al., 2021). Because of the increasing global attention being given to ecological security, the need to identify and quantify its underlying causes has sparked heated debate (Zuo et al., 2020). Ecological security, which refers to the health status of ecosystems and ESs functions, is a prerequisite for sustainability and vital for the coordination of biodiversity conservation and social development of natural and semi-natural ecosystems (Lu et al., 2018; Xu et al., 2019). Ecological security assessment (ESA) at a regional scale has emerged in an important manner to become a catalyst for positive economic development and to address the maintenance of regional sustainable development (Zhao et al., 2018). The ESA aims to identify ecosystem's stability, recognizing the ability to maintain ecological security under various scenarios of ecological risks (Zhao et al., 2018). Therefore, it needs to pay more attention to ecological security for safeguarding sustainable conservation and ecological resources utilization, infrastructure, and the ESs at different spatio-temporal scales (Hodson and Marvin, 2009). Ecological security can ensure a state of harmony between the natural ecosystem and social ecosystem, with the focus on safeguarding interactions in these components (Zhao et al., 2018).

Ecological security patterns (ESPs) are a concrete practice considering ecological security in the fields of landscape ecology, urban planning, and landscape design, which should be an implementation of ecosystem-based management (Peng et al., 2018a). The goal of the ESPs is to ensure regional ecological security and improve the dynamic balance of the relationships between natural conservation and social development. The construction of the ESPs is an important approach and basic conservation to achieve regional ecological security. The ESPs refer to the elements of landscapes, such as ecological source patches and connectivity corridors, which are critical to the security and health of ecological processes in multi-scales (Yu, 1996). The ESPs aim to provide an effective spatial approach for maintaining ecological security of natural ecosystems based on the relationship between landscape patterns and ecological processes (Peng et al., 2018a). The ESPs can not only provide basic regional conservation for essential ESs and a healthy environmental condition, but also effectively balance natural resources utilization (Zhao et al., 2018). It is an integrated approach to protecting the regional ecological shelter for sustainability (Peng et al., 2018b; Rozylowicz et al., 2019). The ESPs are able to maintain the integrity of structure, function, and processes in the natural ecosystem. They can also achieve effective control and continuous improvement of ecological environment problems. Rational optimization of the ESPs helps prevent and avoid ecological risk, reducing negative impacts such as environmental degradation (Liu and Chang, 2015). The spatial configuration of the ESPs is formed by strategic points, lines, polygons, and networks that are critical to maintaining ecological processes (Peng et al., 2018a). Mapping the ESPs is necessary for designing conservation strategies that suitably combine regional environment conservation with sustainable utilization.

The methods of selecting ecological security sources based on the ESs and evaluating resistance surfaces for the ESPs construction are well developed and fully consider land degradation and spatial heterogeneity (Peng et al., 2018a). The concept of the ESs has supported a global agenda on sustainability (La Notte et al., 2017; Jiang and Xu, 2019), and has become popular between academics and policy-makers (Raum, 2018; Jiang and Xu, 2019). The ESs can offer a promising framework to evaluate natural ecosystem management policies by making the connection between natural ecosystems and human wellbeing explicit. China has conducted systematic and comprehensive assessments of the ESs changes affected by these conservation policies across various scales, which have already been applied by policy-makers of governments at various levels and sectors (Ouyang et al., 2016). Chinese governments and scientific institutions are implementing ambitious plans across varying scales to improve our understanding and ESs management (Ouyang et al., 2016). It is a practice to design ESs-based ESPs to improve human welfare through increasing the income of local people and helping local communities to rise above poverty levels in Southwest China (Xiao Y. et al., 2020).

In this research, to design ESs-based ESPs from 1990 to 2015 in Southwest China, we documented: (1) a new framework for identifying ESs-based ESPs, (2) changes of multiple ESs, and (3) spatial distributions of the ESs-based ESPs.

MATERIALS AND METHODS

Study Site

With a total area of 22.9×10^5 km^2, the study area covers nearly 24% of the land surface of China, including Guangxi, Chongqing, Sichuan, Guizhou, Yunnan, Southeast Tibet, and Southwest Qinghai (83°53′E-112°04′E, 20°54′N-36°21′N) (**Figure 1**). The main geomorphic forms are plateau, mountain, hill and basin, and karst landforms (e.g., trough valley, peak cluster depression, and rift basin), and the hilly area accounts for more than 80% of the study area. The elevation ranges from −5 m (lower than sea level) to 7734 m. Climatic types include tropical rain forest monsoon, tropical subtropical monsoon, subtropical humid monsoon, and plateau mountain climates in Southwest China (Shi et al., 2019). The average annual temperature ranges from 0 to 24°C, and the annual precipitation is from 600 to 2300 mm, decreasing from southeast to northwest. The main types of ecosystems in the study area are forests (broadleaf forest, coniferous forest, and coniferous and broadleaf mixed forest), shrubs (broadleaf shrub, coniferous shrub, and open shrubland), and grasslands (alpine meadow and alpine steppe), accounting for 73.6% of the total area, which can provide multiple ESs such as wildlife habitats, soil and water conservation, biodiversity conservation, and climate regulation.

Data Sources

We downloaded DEM data with a 30 m × 30 m resolution from the United States Geological Survey (USGS)[1] and derived the slope and aspect from the DEM data. Ecosystem-type data (with a 30 m × 30 m resolution) were provided by Aerospace Information Research Institute, Chinese Academy of Sciences. Meteorological data were provided by the Meteorological Center of China Meteorological Administration. We obtained soil data from Chinese soil dataset[2] based on Harmonized World Soil Database version 1.1 (HWSD). Land use and cover change (LUCC) data from 1990 to 2015, settlement distributions (locations of cities, counties, and villages), roads (national highways, provincial highways, county roads, and village roads), and river data (vector) were provided by the "National Tibetan Plateau Data Center" (see text footnote 2). Seismic frequency data were downloaded from China Earthquake Networks Center.[3]

Data Analysis

Integrated Valuation of Ecosystem Services and Tradeoffs Tool Model

The InVEST model (Integrated Valuation of Ecosystem Services and Tradeoffs Tool) was cooperatively developed by Stanford University, World Wide Fund for Nature, and Nature Conservancy. It is an open-source software used to visualize and estimate goods and services from nature on a spatial scale (Wu et al., 2021). The InVEST model allows the quantification, spatial mapping, and in some cases economic valuation of the ESs, as well as the analysis of impacts and trade-offs between alternative ESs management options (Grêt-Regamey et al., 2017; Daneshi et al., 2021). This model runs in a gridded map at an average annual time step which requires relatively low data and expertise, therefore it is appropriate for assessing the impacts of land-use change on multiple ESs (Li et al., 2021). More details can be found in the InVEST user's guide (Sharp et al., 2000).

Ecological Sensitivity Analysis

We selected soil erosion sensitivity, rock desertification sensitivity, landslide sensitivity, and the sensitivity of debris flow and freezing-thawing erosion to evaluate ecological sensitivity in Southwest China. We used the universal soil loss equation (USLE model) to calculate soil erosion sensitivity based on comprehensively considering rainfall erosivity, soil texture, topographic relief, and other factors for evaluating soil erosion sensitivity related to human activities (Lin et al., 2018). Sensitivity

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[1] http://earthexplorer.usgs.gov/
[2] http://data.tpdc.ac.cn
[3] https://news.ceic.ac.cn/

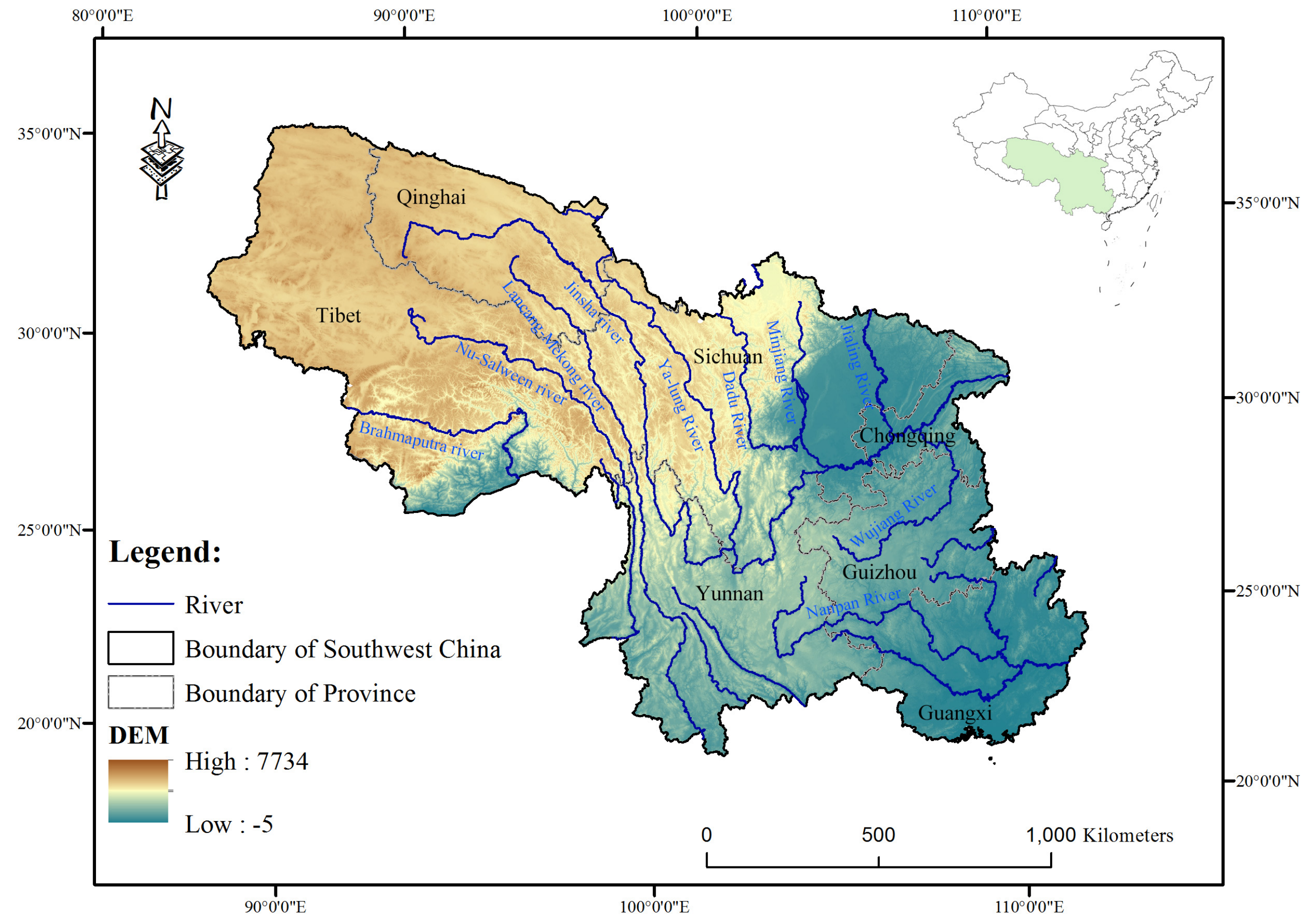

FIGURE 1 | Location of study area.

assessment of rocky desertification depended on whether the area was karst landform, with considering vegetation cover and the lithology element. According to environmental conditions and main inducing factors, we selected the distance from fault line, seismic intensity, slope, rainfall, and other factors to analyze ecological sensitivity (**Supplementary Table 1**).

We selected temperature, rainfall, topography, and vegetation types to evaluate sensitivity of freezing-thawing erosion. By superimposing sensitivity results of the five single factors above, ecological sensitivity grades of the study area were obtained. The calculation formula of ecological sensitivity is as follows:

$$S_i = \mathrm{Max}\left(C_{1i}, C_{2i}\cdots\cdots C_{mi}\right)$$

where, S_i is the ecological sensitivity level of the i-th factor, and C_{1i}, C_{2i} $\cdots\cdots$ C_{mi} are the ecological sensitivity levels of a single factor.

Ecological Risk Analysis

Based on the background characteristics of Southwest China, the risk sources were divided into nature-related risk sources and human-related risk sources. Forest, shrub, grassland and wetland, farmland, and bare land were selected as ecological risk receptors to construct the risk assessment model based on risk sources level, vulnerability, and potential loss of ecosystem (Wang H. F. et al., 2018). The risk sources level was quantitatively evaluated by relevant impact factors. Ecosystem vulnerability was determined by environmental vulnerability, landscape structure vulnerability, and potential losses of ecosystems (**Supplementary Table 2**; Wang H. F. et al., 2018). The calculation formula of ecological risk is listed below:

$$R_i = D_i \times V_u \times V_a$$

where, R_i is the ecological risk value, D_i is risk sources level, V_u is ecosystem vulnerability, and V_a is the potential loss of the ecosystem. We calculated each risk source and divided them into four grades: non-risk, low risk, moderate risk, and high risk. The comprehensive ecological risk of Southwest China was calculated using the spatial analysis toolbox of ESRI ArcGIS 10.2.2.

Assessment of Ecological Conservation Importance

We selected four ESs types which were important to maintain local ecological security, containing soil conservation, flood regulation and storage, water conservation, and biodiversity conservation in Southwest China (**Supplementary Table 3**;

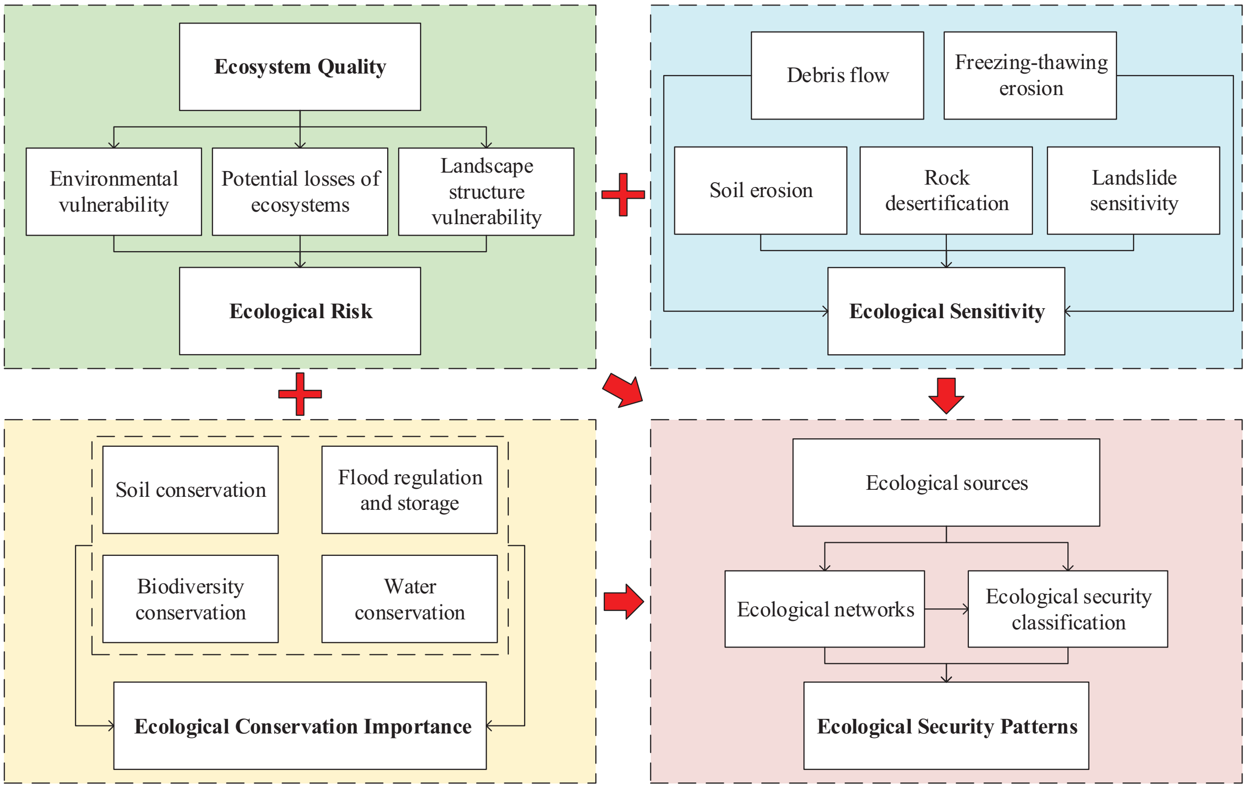

FIGURE 2 | Framework for identifying ecological security patterns based on ecosystem services.

Lin et al., 2018). Soil conservation was evaluated by calculating the amount of potential soil erosion and actual amount of soil erosion. The importance of flood regulation and storage was mainly considered through analyzing the difference of flood regulation and storage capacity in different ecosystems. We used the water balance equation to evaluate water conservation capacity of the ecosystem. We selected important species as indicators and habitat distributions of these species to assess biodiversity conservation patterns using the systematic conservation planning model. The calculation formula of the ESs and conservation importance is below:

$$\mathrm{ES_i} = \mathrm{Max}\,(\mathrm{D_{1i}},\ \mathrm{D_{2i}} \cdots\cdots \mathrm{D_{mi}})$$

where, $\mathrm{ES_i}$ is the importance level of ecological services of the i-th factor, and $\mathrm{D_{1i}}$, $\mathrm{D_{2i}} \cdots\cdots \mathrm{D_{mi}}$ are the importance of ecological services of single factors.

Framework of Identifying Ecosystem Services-Based Ecological Security Patterns

We focused on spatial distributions of the ESs-based ESPs, which could guide natural resources utilization and sustainable ecological environment development in Southwest China (Liu and Chang, 2015; Liu, 2016; Ye et al., 2018). We designed a new framework to select ecological sensitivity, ecological risk, and ecological conservation importance as basic factors to identify the ESPs of the study area (**Figure 2**).

RESULTS

Changes of Ecological Sensitivity From 1990 to 2015

Regions with increasing soil erosion sensitivity covered a total area of 11.8 × 10^4 km^2, which were located northwest of the study area (mainly in the Kekexili and Changtang national nature reserve) from 1990 to 2015. Regions with decreasing soil erosion sensitivity, with a total area of 27.7 × 10^4 km^2 (12.11% of the study area), were located at Hengduan Mountain, eastern Tibet, and the Three Parallel Rivers Region (TPRR) with the Nu-Salween, Lancang-Mekong, and Jinsha Rivers (**Figure 3A**). The area with increasing rock desertification sensitivity was 33.7 × 10^4 km^2 (10.91% of Southwest China) from 1990 to 2015 and located at Wumeng-Wuling Mountain (**Figure 3B**). The area of increasing landslide sensitivity covered 42.3 × 10^4 km^2 (18.47%) which was mainly located at Hengduan Mountain during the study period (**Figure 3C**). The area of increasing debris flow sensitivity was 46.2 × 10^4 km^2 (20.16%) from 1990 to 2015 and was mainly in Hengduan Mountain and the TPRR (**Figure 3D**). The area of increasing freezing-thawing erosion sensitivity only covered 0.9% (2.01 × 10^4 km^2) of the study area, which was mainly located in Sanjiangyuan National Park

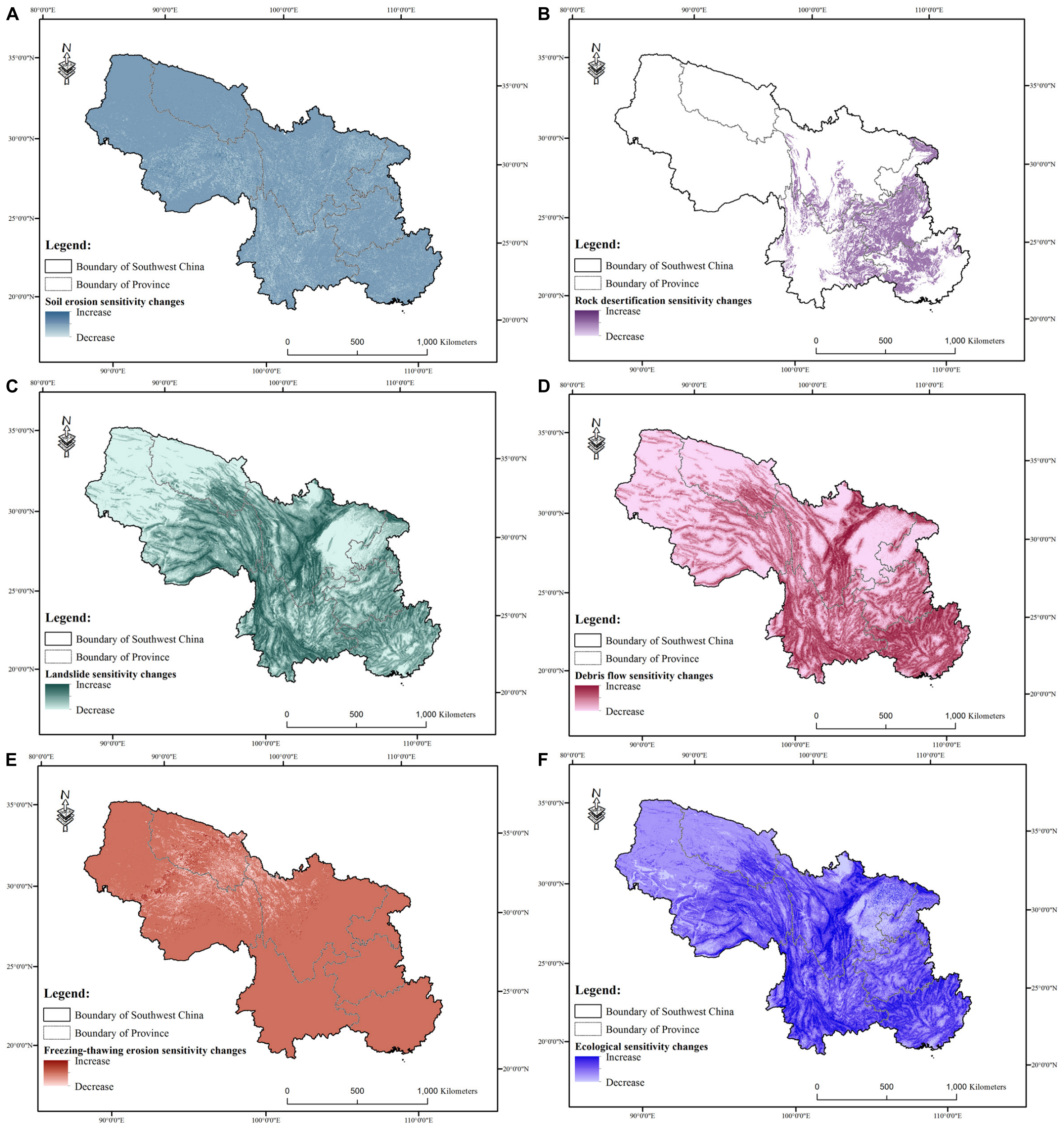

FIGURE 3 | Soil erosion sensitivity **(A)**, rock desertification sensitivity **(B)**, landslide sensitivity **(C)**, debris flow sensitivity **(D)**, freezing-thawing erosion sensitivity **(E)**, and ecological sensitivity **(F)** changes from 1990 to 2015.

during the study period (**Figure 3E**). The area of ecological sensitivity increased to 35.3% of the study area (with an area of 80.9 × 10^4 km^2) which was mainly located at Hengduan Mountain (**Figure 3F**).

Ecological Risk Changes During Study Period

The area of decreasing drought risk covered 86.0 × 10^4 km^2 (37.7% of Southwest China) and the drought risk increasing area was 6.37 × 1^4 km^2 (2.8%) which was located in eastern Tibet from 1990 to 2015 (**Figure 4A**). The deceasing area of natural disaster risk was 14.0 × 10^5 km^2 which covered 61.3% of the study area. With an area of 40.2 × 10^4 km^2, the increasing area of natural disaster risk was located at Hengduan Mountain, eastern Tibet, and the TPRR (**Figure 4B**). The area of socio-economic risk increased to 6.47 × 10^4 km^2 (2.8%) which was mainly located in metropolis and surrounding regions such as Chengdu city (capital of Sichuan province), Lhasa city (capital of Tibet Autonomous Region), Kunming city (capital of Yunnan province), and Guiyang city (capital of Guizhou province) from 1990 to 2015 (**Figure 4C**). With an area of 13.0 × 10^5 km^2, 56.9%

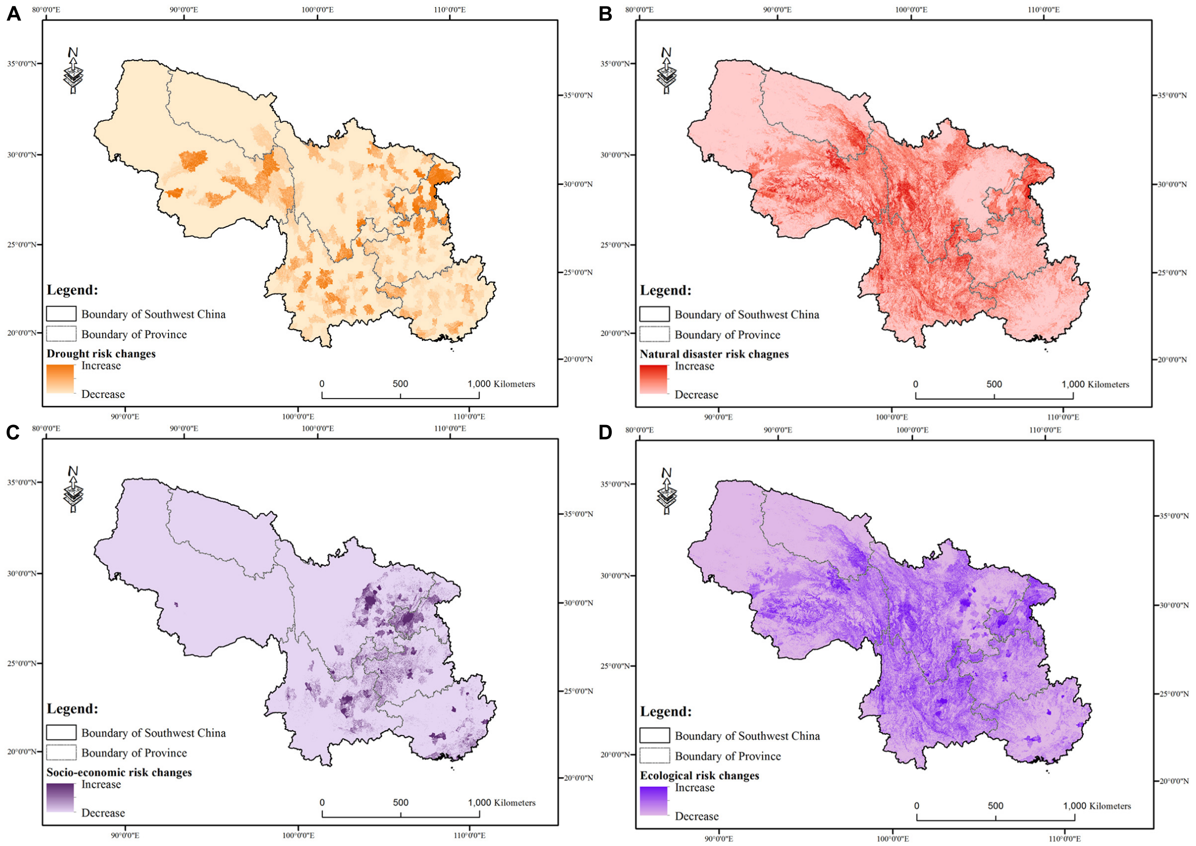

FIGURE 4 | Drought risk **(A)**, natural disaster risk **(B)**, socio-economic risk **(C)**, and ecological risk changes **(D)** from 1900 to 2015.

of the ecological risk study area decreased from 1990 to 2015 which was mainly located at Hengduan Mountain, eastern Tibet, and the TPRR (**Figure 4D**).

Ecological Conservation Importance Changes

The area of soil conservation increased to 12.1% of the study area with a total area of 27.7×10^4 km^2 which was located at eastern Tibet, Hengduan Mountain, and the TPRR from 1990 to 2015 (**Figure 5A**). With an increasing area of 51.7×10^4 km^2, 2.9% of the study area with flood regulation and storage increased which was located northwest of the study area (mainly around lakes such as Namtso Lake, Silin Co Lake, and so on) (**Figure 5B**). Covering an area of 62.9×10^4 km^2 (44.29%), the increasing area of water conservation was mainly located at Hengduan Mountain, southeastern Tibet, and the TPRR (**Figure 5C**). The area of biodiversity conservation importance only increased to 1.50×1^4 km^2 (0.7%) which was in southeastern Tibet and the TPRR region (**Figure 5D**). Biodiversity conservation importance was unchanged in the regions, covering 98.90% of the study area from 1990 to 2015. The increasing area of ecological conservation importance was 14.3×10^5 km^2 (62.52%) which was mainly located at Hengduan Mountain, southeastern Tibet, and the TPRR (**Figure 5E**).

Spatial Distributions of the Ecosystem Services-Based Ecological Security Patterns

Based on three levels of ecological sensitivity, ecological risk, and ecological conservation importance, the ESs-based ESPs of Southwest China contained of two zones and four belts for local sustainable development, A: alpine steppe and wetland zone, B: Hengduan Mountain zone, C: northern shelter belt (Daba-Micang mountain), D: central shelter belt (Wumeng-Wuling mountain), E: southern shelter belt (southern border of China), and F: southwestern shelter belt (eastern Himalayas mountain) (**Figure 6**). With a total area of 73.9×10^4 km^2, key areas of the ESs-based ESPs covered 32.2% of Southwest China (**Table 1**).

DISCUSSION

Necessity to Identify Ecosystem Services-Based Ecological Security Patterns

In the context of global climate change and anthropogenic disturbances, socio-economic development will lead to more prominent eco-environmental problems (degradation and

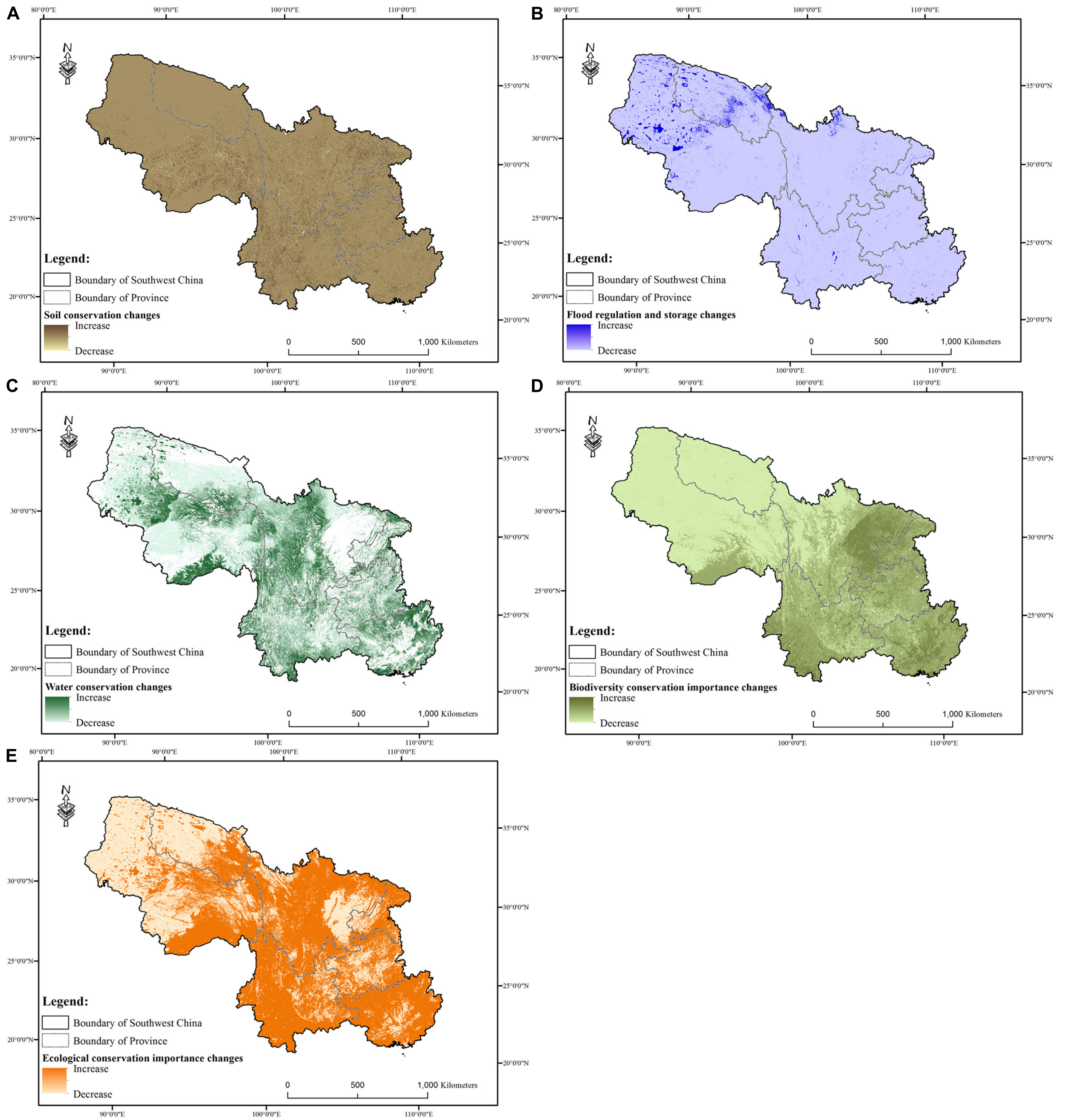

FIGURE 5 | Soil conservation **(A)**, flood regulation and storage **(B)**, water conservation **(C)**, biodiversity conservation importance **(D)**, and ecological conservation importance changes **(E)** in Southwest China during the study period.

fragmentation) (Liu, 2016; McDonald, 2018). The expansion and aggravation of these problems have led to an imbalance in the structure and function of ecosystems, which poses a threat to human safety, ecological security, and seriously hinders sustainable socio-economic development (Deng et al., 2021; Sun et al., 2021). This may also lead to the damage of ESs and reduction of ecological security level (Zhang et al., 2020). Therefore, in order to maintain ecological security it is necessary for scientists and governments to pay more attention to and recognize the great significance of ecological security in terms of both theory and practice on a global scale (Liu, 2016; Yu and Chen, 2021; Zhou D. et al., 2021). Aiming to solve problems

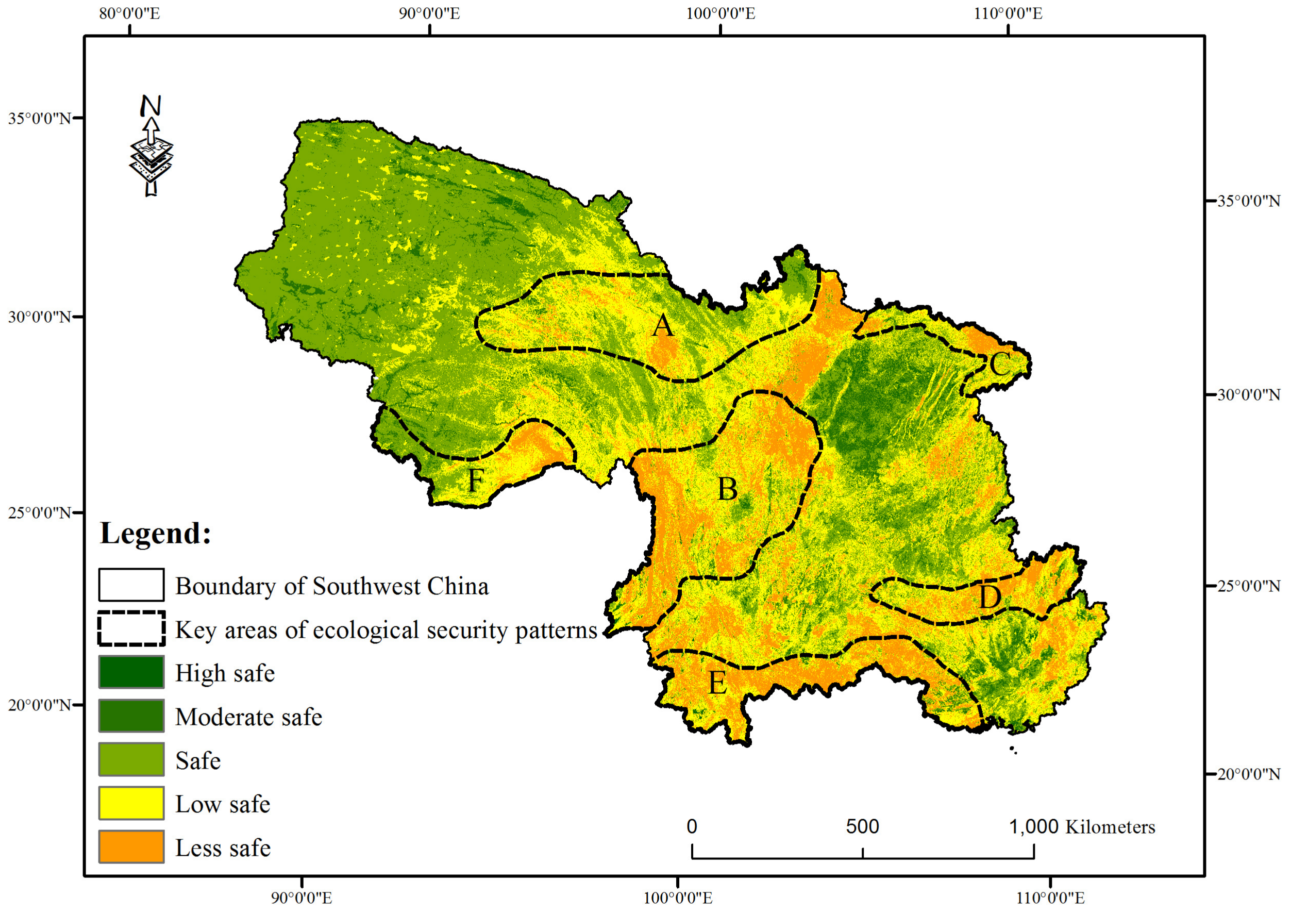

FIGURE 6 | Distributions of the ESs-based ESPs in Southwest China.

of ecological security, China governments have carried out a series of projects and plans such as ecological regionalization, ecological function zoning, ecological protection red line projects, and optimization of protected areas (Liu and Chang, 2015; Liu, 2016; He et al., 2018; Gao et al., 2020; Liu et al., 2021). Researching ESs-based ESPs is an effective path to maintain and improve the ecological security of Southwest China which plays an essential role in the ESS (Wang et al., 2020). ESS construction is a national plan to maintain ecological security function and improve ecological environment in China (Sun et al., 2012; Wang et al., 2017).

TABLE 1 | Area and percentage statistics of ecological security patterns in Southwest China.

Number	Name	Area (10^4 km^2)	Percentage of study area (%)
A	Alpine steppe and wetland zone	20.1	8.7
B	Hengduan Mountain zone	22.6	9.8
C	Northern shelter belt	4.4	1.9
D	Central shelter belt	6.8	2.9
E	Southern shelter belt	12.7	5.5
F	Southwest shelter belt	7.4	3.2
	Total	73.9	32.2

The ESs-based ESPs are regarded as an effective method for strengthening the integrity of natural and socio-economic ecosystems by combining and arranging relationships of ecological processes and the ESs (Yu, 1996; Fan et al., 2021). The ESs-based ESPs are mainly focused on ecological functions and thus ESs, and possible changes in land use patterns (He et al., 2005; Sun et al., 2021). The ESs-based ESPs, which can synthetically consider human wellbeing and ecological conservation, are of theoretical and practical significance for scientific research and government regulation. With fragile ecological conditions and serious disasters, characterized by complex topography, diverse ecosystems, and rich biodiversity, Southwest China is the key area for studying complex surface processes and ecosystem evolution, an important ESS zone of China (Liu, 2016). Designing ESs-based ESPs is an important part of strategies for regional development in China, and is becoming an important agenda for governments (Ye et al., 2018; Wu R.D. et al., 2019). The ESs-based ESPs should be used as the basic ecological line which plays an important role in controlling the disorderly development of local social economy and maintaining regional ecological security (Sun et al., 2012;

Wang et al., 2017; Peng et al., 2018a). In this study, we took into account ecological sensitivity, ecological risk, and ecological conservation importance to evaluate ecological security of Southwest China. We confirmed two zones and four belts as the main structure of ESs-based ESPs to maintain ecological security in Southwest China. Results showed that Hengduan Mountain has a high level of ecological sensitivity and ecological risk and an increasing level of ecological conservation importance. Hengduan Mountain is more likely to have eco-environmental problems under the influence of unforeseeable human activities and extreme climates (Sun et al., 2020, 2021; Xiao Y. et al., 2020). It should be of great concern to governments to deal with future climate changes and sustainable development.

Beneficial to Human Wellbeing

Natural ecosystems can provide supply, support, regulation, and cultural services to humans which are vital to human survival and development, and use capabilities of the ESs to reflect ecological security status (Pogue et al., 2020; Jiang et al., 2021; Sun et al., 2021). Human wellbeing is tied to the capacity of natural and altered ecosystems to produce a wide range of goods and services, which have always depended on the ability to respond to environmental change (Pecl et al., 2017). Recently, identifying ESs-based ESPs in biodiversity hotspots has attracted the attention of policy-makers, which can balance human wellbeing and ecosystem conservation. Effective construction and maintenance of the ESs-based ESPs can contribute to the integrity of ecosystem structure and function, biodiversity conservation, and human wellbeing improvement (Ye et al., 2018). The ESs-based ESPs can benefit ecosystems to sustain human existence and development, can also promote sustainable development, and eventually improve levels of ecological security (Liu, 2016; Ye et al., 2018; Wang et al., 2020). The ESs-based ESPs can be seen as a trade-off and synergy between ecological conservation and socio-economic development (Cochran et al., 2020; Deng et al., 2021). Designing ESs-based ESPs should be preliminarily integrated into many aspects of national and local-level government affairs, such as economic development plans, institution constructions, land-use plans, environment impact assessments, and environmental conservation policies (Wu R.D. et al., 2019). Quantifying ESs-based ESPs and revealing their spatial distributions are beneficial to stakeholders, decision-making, and improvement of human wellbeing.

Fully considering improvement of human wellbeing to identify the ESs-based ESPs is of practical importance for ecological civilization construction which is an essential means of achieving sustainable development, especially in Southwest China (Meng et al., 2021). To enhance people's livelihoods, governments of China have introduced a policy of ecological compensation named central fiscal transfer payments, which is also a regional strategy for ecological compensation (Sun et al., 2020, 2021). Ecological compensation policies should focus on rationally allocating and investing these subsidies in ecological conservation and welfare improvement to address the prevailing prioritization of human wellbeing over ecosystem conservation, especially in the ESs-based ESPs areas (two zones and four belts) (Wu X. et al., 2019; Sun et al., 2021). Specifically, the engagement of low-income sections of the population in ecological management and conservation work as forest rangers, grass guards, and wildlife watchers provides poor people with stable incomes in the ESs-based ESPs (Sun et al., 2021; Xu et al., 2021).

Significance for Practical Aspects of Sustainable Development

Although governments have made great efforts toward ecological conservation and carried out a variety of ecological plans such as the NFPP, the SLCP, and the construction of nature reserves, regional sustainable development is still not achieved (Wu X. et al., 2019). Those policies only focus on ecological functions and natural ecosystems conservation (especially habitat and biodiversity conservation) and lack consideration of human wellbeing, leading to partial policy rigidity. Hence, it is of vital importance for improving ecological policies effectiveness to balance natural ecosystem conservation and human wellbeing (Kang et al., 2021; Zhao X.M. et al., 2021). Human social systems and natural ecosystems impact the ecological security situation together and ecological conservation increasingly needs to be linked to human wellbeing improvement (Gao et al., 2021). Identifying the ESs-based ESPs is a potential solution and pathway to support ecological conservation and improve human wellbeing. We suggest that the ESs-based ESPs (especially the two zones and four belts) for sustainable development should be used as the core areas to carry out a series of projects of ecological conservation, ecological restoration, and ecological compensation based on comprehensive consideration of ecosystem conservation and human wellbeing improvement. It is beneficial to maintain the stability of ecological security and to promote the ESS. The top priorities for developing an ecological civilization in China are identifying core areas (ecological sources), strengthening ecological conservation, and improving human wellbeing (Xiao S.C. et al., 2020; Meng et al., 2021). In this regard, constructing ESs-based ESPs is a substantial step forward in achieving policy goals (Xiao S.C. et al., 2020; Dong et al., 2021). Designing ESs-based ESPs is also beneficial to construction and optimization of protected areas in China. It is a "win-win" environmental conservation scheme for sustainable development that supports both human wellbeing and ecosystem conservation, which can be used as the basic guiding principle of sustainability strategies. Policy-makers should start from the perspective of ESs-based ESPs before creating sustainable development plans to protect key ecological patches in the region first. And then, it can be rationally developed, constructed, and utilized in the remaining areas after defining the relevant conservation scope to solve the conflict between regional ecological security and socio-economic sustainable development (Kang et al., 2021).

In total, this research may provide a new way to balance ecological conservation and human wellbeing for conducting sustainable development.

CONCLUSION

In this research, the ESPs were identified by using an ESs-based designing framework in Southwest China. The results showed that the increased area of ecological sensitivity was mainly located at Hengduan Mountain, the decreased area of ecological risk was located at Hengduan Mountain, eastern Tibet, and the TPRR, and the increased area of ecological conservation importance was located at Hengduan Mountain, southeastern Tibet, and the TPRR. There were two zones and four belts that could be utilized to maintain ecological security in Southwest China. As the cornerstone to build the ESs-based ESPs, governments should pay more attention to Hengduan Mountain which was the key component to alleviate ecological sensitivity and ecological risk and to enhance ecological conservation importance in the study area. These findings provided a foundation to explore a new management pathway for maintaining ecological security and enhancing human wellbeing. Further study should concentrate on the analysis of the contribution of the ESs-based ESPs to the construction of the ESS, especially in biodiversity conservation hotspots. Furthermore, the method used in this study could also be used to quantitatively evaluate whether ESs-based ESPs were necessary to create rationalizing plans by local administrations on balancing natural resources conservation and utilization. In total, based on the ESs-based ESPs, policy-makers can make targeted prevention and control measures to limit the development of natural resources that result in excessive consumption and ecological damages, which is worth promoting.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/**Supplementary Material**, further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

XS, YX, and GL designed the research. All authors collected data in the field. YL, YS, HC, SZ, QW, and MY performed the analysis. XS drafted the manuscript. All authors contributed to the interpretation of the results and to the text.

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The Potential of Bison Restoration as an Ecological Approach to Future Tribal Food Sovereignty on the Northern Great Plains

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Future climate projections of warming, drying, and increased weather variability indicate that conventional agricultural and production practices within the Northern Great Plains (NGP) will become less sustainable, both ecologically and economically. As a result, the livelihoods of people that rely on these lands will be adversely impacted. This is especially true for Native American communities, who were relegated to reservations where the land is often vast but marginal and non-tribal operators have an outsized role in food production. In addition, NGP lands are expected to warm and dry disproportionately relative to the rest of the United States. It is therefore critical to identify models of sustainable land management that can improve ecological function and socio-economic outcomes for NGP communities, all while increasing resilience to a rapidly changing climate. Efforts led by Native American Nations to restore North American Plains bison (*Bison bison bison*) to tribal lands can bring desired socio-ecological benefits to underserved communities while improving their capacity to influence the health of their lands, their people, and their livelihoods. Ecological sustainability will depend on the restoration of bison herds and bison's ability to serve as ecosystem engineers of North America's Plains. The historically broad distribution of bison suggests they can adapt to a variety of conditions, making them resilient to a wide range of management systems and climates. Here we review bison's ecological, cultural, and economic value using four case studies from tribal communities within the NGP. We discuss the potential contributions of bison to food sovereignty, sustainable economies, and conservation of a working landscape with limited protections and significant risk of conversion. The ecological role of bison within this setting has potential due to cultural acceptance and the vast availability of suitable lands; however, it is critical to address tribal needs for funding support, enhanced community capacity, and solving complex landownership for these goals to be achieved.

Keywords: food sovereignty, Northern Great Plains, plains bison, Plains Indians, rewilding, restoration

INTRODUCTION

Climate projections for the Northern Great Plains (NGP) forewarn of warming, drying summers, erratic rainfall patterns with increased spring flooding, and increased winter snow cover (Shafer et al., 2014; Wuebbles et al., 2017; Adams et al., 2020). As changes occur, common agriculture (Ariel et al., 2021) and production practices will become less sustainable (Joyce et al., 2013; Ariel et al., 2021; Martin et al., 2021), both ecologically and economically (Whitlock et al., 2017; Boone et al., 2018; Holechek et al., 2020). In addition, the severity of adverse impacts on communities will differ depending on regional socio-economic circumstances (Lal et al., 2011; Adams et al., 2020). It is therefore critical to identify models of sustainable land management that can improve socio-economic outcomes for NGP communities and increase ecosystem resiliency to ensure future food security (Doyle et al., 2013; McNeeley, 2017).

Communities with persistent poverty are less likely to possess the resources needed to prepare for the future and, therefore, are considered more vulnerable to climate change (Lal et al., 2011). This is true of rural Native American communities, where poverty is two to three times higher than in white rural communities (Harvey, 2017). Land dispossession and forced migrations of indigenous peoples have culminated in scattered tribal governed lands having increased climate vulnerability and offering diminished economic opportunities (**Figure 1**; Farrell et al., 2021).

As of 2014, less than 50% of Native Americans from federally recognized Tribes were employed, and approximately 25% of Native American families earned incomes below the poverty line (U. S. Department of the Interior, 2014). Income disparities are particularly pronounced in NGP tribal communities, where income is 20–40% less per capita than the national average for Native Americans (Feir et al., 2018; Johns, 2020). Years of disenfranchisement have resulted in little economic development, underfunded learning institutions, and limited economic opportunities on reservations, especially in the private sector (Miller, 2018; Short et al., 2020). Often, tribal management is hindered by non-tribal regulatory frameworks that are not inclusive of tribal systems and sovereignty (Ranco et al., 2011). These issues further exacerbate the vulnerability of communities dependent on commodity-based agriculture in a region where ∼50% of available NGP lands are privately managed intact rangelands (e.g., native and planted grass, sage steppe) primarily used for conventional cattle grazing and dryland cropping (Haggerty et al., 2018a).

Despite their proximity to food production, Native Americans are twice as likely to be food insecure than white people and are 25% more likely to remain food insecure in the future (Jernigan et al., 2017). Across Montana's seven reservations, 60% of households rely on the Food Distribution Program on Indian Reservations as their primary food source (Miller, 1998). These systemic income and food insecurities suggest the value of community-based initiatives to address vulnerabilities to climate change and food sovereignty in NGP communities.

For more than 10,000 years, Native Americans hunted and lived alongside an estimated population of tens of million Plains bison (*bison bison bison*) roaming between the Rocky and Appalachian Mountains (Gilmore et al., 1999; Kornfeld et al., 2016; **Figure 2** and **Supplementary Material 1**). Bison were an integral part of life, and many origin stories tell of the connection between the people and their kin, the "buffalo" (Goble and Crow, 2009; Hubbard, 2016). With the near extinction of bison in the late 1800s, Native Americans were relegated to reservations without their primary cultural food source (**Figure 1**). In some cases, this reservation land is marginally productive, and non-tribal agricultural operators often lease substantial portions of tribal agricultural lands (**Table 1**; Anderson and Lueck, 1992; Whyte, 2013; USDA National Agricultural Statistics Service, 2019).

Over the past few decades, Tribes have worked toward the reclamation of food security and sovereignty. For Plains Indians, food sovereignty is directly tied to re-establishing bison herds within their reservations and traditional lands. While food security can be enhanced through U.S. government programs, food insecurity over the long term can inadvertently be perpetuated through these programs by preventing re-ownership of food procurement practices; combined with meager inclusion of traditional Native foods, this can disrupt tribal food sovereignty (Bye, 2009; **Box 1**). Achieving both will require developing sustainable land management strategies to conserve and enhance ecosystem resiliency and reclaim traditional foods systems (Sunderland, 2011; Berry et al., 2015).

Beginning in the 1990s, Native American Tribes organized and worked collaboratively to establish bison herds on sovereign lands (**Figure 2**). The Inter-Tribal Buffalo Council (ITBC), founded in 1991, includes members from 76 federally recognized Tribes in the U.S. ITBC acts to facilitate education and training

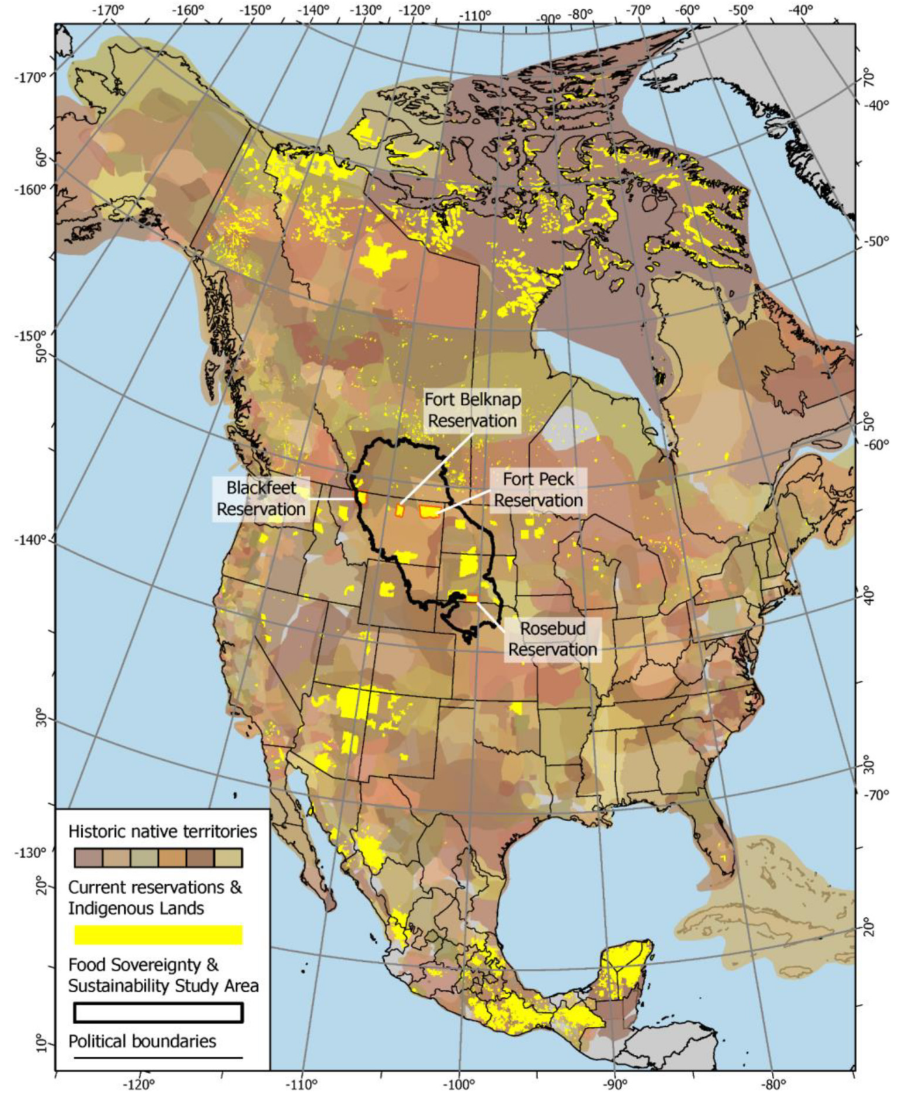

FIGURE 1 | Native territories were derived from Native Land Digital (https://native-land.ca/). Reservations and Indigenous Lands are from National Atlas of the United States (US), Indigenous communities (60–100% of population) from Mexico Indigena, and Aboriginal Lands of Canada from Geobase. Colors represent a gradient of historic native territories throughout North America, to emphasize the scale and diversity of Native American societies prior to being forced onto reservations. We note that tribal territories were fluid and underwent many shifts prior to, and during, European colonization, thus this map is only one such snapshot in time. For this reason, we omit the names of specific Tribes, instead using a gradient of tribal territories to highlight amount of land lost in comparison to where these communities currently reside.

programs, marketing strategies, transfer of surplus bison from U.S. Department of Interior to U.S. tribal lands, and technical assistance for the development of self-sustaining programs (ITBC Today). ITBC led the transfer of wild bison from Yellowstone National Park (YNP) to Native American Tribes (ITBC Today; Voggesser, 2000). In 2014, 10 Tribes and First Nations from the United States and Canada signed the "Buffalo Treaty" and committed to work together to restore bison to their historic range (Johns, 2020). Today there are 31 signatories from the United States and Canada.

Current efforts to re-establish bison herds across the United States fall on a spectrum between conservation and commercial herds. Conservation herds are established to conserve the long-term genetic health of the species and serve to engage people through cultural and educational experiences. Commercial herds serve as an alternative meat product for public consumption and economic benefits. These efforts are not mutually exclusive, as some entities manage a single herd to achieve both goals. Across North America, there are approximately 350,000 bison in private sector herds, over 30,000 in public sector (Jones et al., 2020) and not-for-profit non-governmental organization herds (NGO; i.e., American Prairie Reserve and The Nature Conservancy)

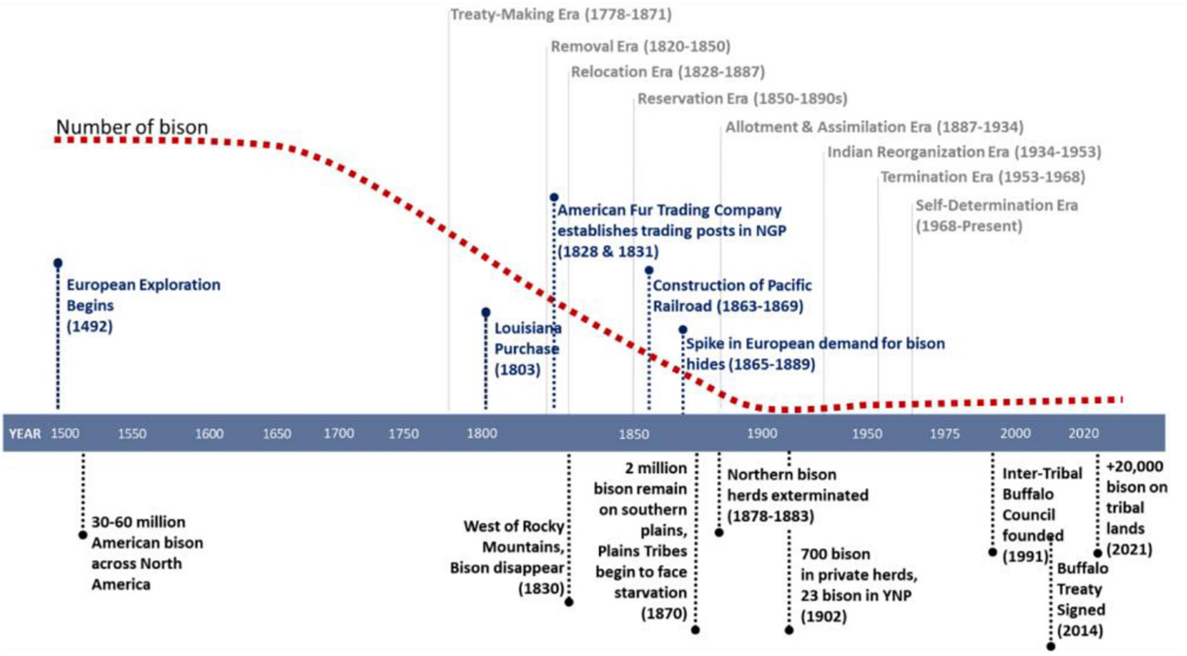

FIGURE 2 | Major events leading to decline of American bison (*Bison bison*) run in parallel with settler colonialism and the disenfranchisement of Plains people. Full details are given in **Supplementary Materials (1)**. Light gray lines differentiate between Native American eras during European expansions to the West. Dashed blue lines highlight key colonial events that contributed to decline of bison. Black dashed lines highlight key events in the near extermination of American bison (beginning with population estimate). Red dashed line illustrates the decline of bison from 30 to 60 million animals to only a few hundred in the early 1900s.

(Martin et al., 2021), and approximately 20,000 in tribal sector herds (ITBC Today InterTribal Buffalo Council, 2021).

Re-establishing bison on reservations can contribute to change in Native American communities in multiple ways: (1) spiritual, by healing the spirit of the buffalo and the people (Haggerty et al., 2018b); (2) cultural, by restoring people's connection to their heritage (McClintock, 1910) including enabling food sovereignty and security on reservations; (3) economic development (e.g., tourism, bison hunts, sale of live bison, or bison meat); (4) and ecological, by supporting ecosystem resiliency through sustainable bison grazing. Conservation herds can provide the first two benefits, but since herds are generally limited in size, they typically provide limited revenue. The third and fourth benefits involve sustainable management for both economic and ecosystem health. Commercial herds generate revenue and food, but food sovereignty and ecological benefits depend on the size and management of the herd. As Tribes work to achieve these benefits, we recognize both the economic and ecological role of each type of herds.

We argue that only when bison herds move closer to their traditional role in the NGP ecosystem can they fulfill all these roles. We refer to this process as the restoration of bison, sometimes referred to as rewilding due to existing constraints of "true" restoration (du Toit and Pettorelli, 2019; **Box 2**). It is important to recognize that these processes are bound to an existing land tenure system and jurisdictions. Thus, initiatives will be informed by the goals and diverse desires of the tribal buffalo programs and the communities they serve.

Bison were not only central to the Plains Indians' way of life, but also central to the ecosystem. Bison are considered ecological keystone species, defined as having a disproportionately large influence on their environment relative to their abundance through their coevolution with all life forms and land use behavior (Mills and Doak, 1993). For example, bison grazing promotes plant functional-group and species richness, alters patch structure across tallgrass prairie landscapes (Knapp et al., 1999; Koerner and Collins, 2013; Eby et al., 2014), and promotes higher species richness and compositional diversity in mixed-grass prairies (McMillan et al., 2019). Bison also modify their environment by moving across the landscape and creating disturbance in the form of stomping, wallowing, seed dispersal, and grazing (Harvey and Fortin, 2013); behavior that results in increased landscape arthropod, amphibian, and plant heterogeneity (Polley and Collins, 1984; Gerlanc and Kaufman, 2003; Nickell et al., 2018). Bison are migratory herbivores that can and need to move across large landscapes (Bolger et al., 2008; Plumb et al., 2009), and by altering widespread vegetation structure and composition, bison grazing subsequently impacts prairie wildlife communities (Truett et al., 2001). However, when densities are manipulated and movements are constrained, the ability of the species to have positive impacts on the landscape may be limited (Boyce et al., 2021; Kaplan et al., 2021). Modern prairie conservation relies on the keystone traits of bison to restore ecological function of grasslands; therefore, conservation measures should explore ways to allow bison to move and migrate.

TABLE 1 | Description of communities featured in case studies, with WWF Plowprint Report 2018 Area summaries for Native Nations in the Northern Great Plains (NGP) (World Wildlife Fund, 2018).

Reservation	Tribes	State	Pop.[a]	Size (km^2)		Plowprint[c] (km^2)		Intact habitat (km^2) (%)	Farm operation	
				Total area[b]	within NGP	Extent	Expansion 2009–2018		Total (km^2)[d]	Operated by Tribe, km^2 (%)
Fort Belknap	Nakoda (Assiniboine); A'aninin (Gros Ventre)	MT	3,429	2,526	2,526	248	46	2,215 (87.7)	1,799	1,668 (93)
Fort Peck	Nakoda (Assiniboine); Dakota Sioux	MT	6,800	8,564	8,564	3,667	637	4,656 (54.4)	4,524	1,367 (30)
Blackfeet	Blackfeet Nation	MT	7,000	6,317	525.6	1,227	172	4,803 (76.6)	3,663	2,026 (55)
Rosebud	Sicangu Lakota (Rosebud Sioux)	SD	21,245	3,622	3,622	226	123	3,285 (90.7)	2,499	944 (38)
All 15 NGP reservations				72,296	63,365	12,661	2,869	56,037	404,273	21,798 (54)

Farm operation (km^2) on reservations and the percentage operated by tribal members; data from 2017 USDA Census of Agriculture (USDA National Agricultural Statistics Service, 2019); data extracted by World Wildlife Fund. Market value:% market value of agricultural products sold operated by.

[a] Enrolled tribal members living on or near reservation.

[b] Total Area refers to main reservation and does not include trust lands outside of the reservation boundary.

[c] Plowed land as of 2018.

[d] Total farm km^2 includes rangelands and croplands.

BOX 1 | Definition Box 1:

1. **Food security** is the interplay between food availability, food accessibility and food utilization that varies across organizational levels: individual, household, community, national, regional, and global; we include cultural ideals such as traditional foods (Leroy et al., 2015) and the nutritional standards of food (Pinstrup-Andersen, 2009).
2. **Food sovereignty** is the right to access healthy and culturally appropriate food produced through ecologically sound and sustainable methods, and the right to define food and agriculture systems (Patel, 2009). The emphasis is on the right to produce foods and control how food is celebrated, consumed, and managed, not limited to economic and physical access to food (Bye, 2009).

BOX 2 | Definition Box 2:

1. Restoration aims to return an ecosystem to its former state, which is a challenging standard due to complex socio-ecological landscapes (Davenport, 2018). With this in mind, here we define restoration to reflect what is sometimes referred to as rewilding—the reorganization and redevelopment of species and ecosystems under new environmental conditions while sustaining ecosystem services (du Toit and Pettorelli, 2019). It is differentiated from conventional ranching practices that focus on optimizing production of provisioning ecosystem services (i.e., protein, hide and leather, hair and fiber, and bone procurement), but rather to balance emphasis on non-provisioning services (i.e., cultural, regulating, and supporting) with provisioning services (Briske, 2017). Within the context of this paper, restoration is the development of novel management practices that balance the dual roles of bison while acknowledging existing constraints. As is similarly done for conservation translocations (IUCN/SSC, 2013), we suggest conducting a feasibility assessment prior to any rewilding initiative, with additional consideration given to cultural, economic, and food sovereignty conditions, since available habitat and community objectives are likely to differ from one reservation to another.
2. Trust lands are defined as lands "in which the federal government holds legal title, but the beneficial interest remains with the individual or tribe" (U. S. Department of the Interior, 2021), and trust lands held on behalf of individuals are known as "allotments."

Furthermore, in the face of climate change, bison may be a more sustainable large grazer than cattle (Martin et al., 2021). The NGPs' mean annual temperatures are projected to increase by 2.3–2.9°C over the next few decades (Wuebbles et al., 2017). Bison respond to warming and drought by shifting diet (Craine et al., 2015; Craine, 2021) and reducing asymptotic body mass (i.e., mature body size) (Martin et al., 2018; Martin and Barboza, 2020a,b). Moreover, bison are more tolerant of extreme heat and seek shade and water (i.e., stock ponds and riparian areas) less frequently than cattle, which in turn reduces sediment load in the sensitive streams that meander through grasslands (Steuter and Hidinger, 1999; Dodds et al., 2000; Allred et al., 2013; Grudzinski et al., 2018). Bison enable stream vegetation to regenerate, enhancing the capacity of the ecosystem to support people and wildlife throughout seasonal and long-term droughts (Boyce et al., in review)[1].

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[1] Boyce, A., Shamon, H., and McShea, W. J. (in review). Bison restoration to shortgrass(prairie) is associated with increases in vertebrate diversity and occupancy in riparian areas. *Front. Ecol. Evol.*

Bison and North American grasslands have been evolutionarily coupled for more than 160,000 years (Woodburne, 2004), and restoration of bison will enhance the cultural, economic, and ecological sustainability of Plains Tribes and their environment. Several teams of researchers have proposed that bison are essential for the restoration of NGP (Sanderson et al., 2008; Freese et al., 2014). It is possible that the current efforts to restore bison herds to Native American lands will be the key to this future restoration, but only if these efforts provide for the needs and aspirations of Tribes. Using four case studies, we review the successes and challenges of bison restoration programs on four Native American reservations in Montana and South Dakota, United States.

We propose that bison herds currently being restored to Native American lands have the potential to provide the food sustenance, cultural reconnection, and ecological sustainability needed to meet future climate challenges. We review case studies of current reintroduction activities at four Native American reservations in the NGP to assess their progress and potential to contribute to an ecological approach to future food sovereignty in the region that can be replicated on additional Native American reservations. We discuss the viability and longevity of these programs in communities with persistent socio-economic challenges and in the context of climate change. We provide recommendations for future development of management plans with the goal of maximizing the benefits of restoring bison herds to the cultural, economic, and ecological health of the Tribes and their lands. Native Americans generally refer to bison as buffalo and both terms are used in this paper.

CASE STUDIES

The four NGP communities featured here (referred to as reservations in **Table 1** and **Figure 3**) were bison-reliant societies that are currently working to re-populate bison onto tribal lands. The programs' overarching goals are to enhance the ecological, cultural, and economic sustainability of the people and lands, draw on Indigenous science and facilitate continuity of traditional knowledge, engage Native youth in buffalo restoration efforts, and restore food sovereignty. They offer vignettes of a sustainable ecological bison restoration framework for food sovereignty on tribal lands in the NGP.

Here we compare these programs to illustrate different approaches to accomplishing these shared goals and identify challenges to expanding efforts and building long-term resiliency. While examining challenges, we considered what additional resources could be needed to support bison management in the present and in the face of changing climates across the NGP. Moreover, we illustrate common threads that may offer a successful framework for additional communities to emulate, such as operating two independent herds with one emphasizing the cultural and ecological needs of Tribe (i.e., non-provisioning ecosystem services) and one emphasizing sustainable production (i.e., provisioning ecosystem services) or all as one herd operating to integrate both of these emphases. Detailed descriptions of each bison reintroduction initiative are included in **Supplementary Material 2**. For each case study reservation, we conducted a habitat suitability assessment of tribal lands to highlight the potential for further expansion of ongoing programs. We present a bison summer Habitat Suitability Index (HSI) model based on the productivity of habitat during the summer. The model was adapted from the summer HSI model developed by Steenweg et al. (2016) for Banff National Park, Canada, and was created to estimate the extent and relative quality of remaining habitat across the historic distribution of bison in North America; details are included in **Supplementary Material 3**.

Overview

The programs examined are located across northern Montana, from the eastern foothills of Glacier National Park through the central rangelands north of the Missouri River, and in South Dakota at the northern extent of the Nebraska Sandhills (**Figure 3**). At each reservation, there is some portion of the habitat that is characteristic of the NGP, a mosaic of mixed-grass prairie and croplands, of which 54–88% is unplowed and considered intact (**Table 1**). All reservations contain a mixture of private (both tribal and non-tribal) and trust lands, used mostly for ranching of beef cattle (*Bos taurus*). Currently, tribal members manage farm operations on between 30% (Fort Peck) to 93% (Fort Belknap) of the total agricultural land available on reservations (**Table 1**). We note that in the NGP indigenous operators only capture 59% of the market value revenue (USDA National Agricultural Statistics Service, 2019).

The earliest bison herds (Fort Belknap, Blackfeet) were established in the 1970s when individual Tribes purchased bison from private ranchers. Since the 2000s, bison are now sourced from established conservation herds managed on private and public lands across the NGP within the United States and Canada (**Table 2**). Some herds established on tribal lands in this study are currently stocked with certified Bovine-brucellosis-free bison from YNP and Elk Island National Park. To assist with this effort, the Fort Peck program manages a quarantine facility to receive bison from YNP. YNP bison are authorized for transfer to Native American sovereign lands by the U.S. Department of Interior, U.S. Department of Agriculture (USDA), the Animal and Plant Health Inspection Service (APHIS), and Montana Department of Livestock (MTDOL). Once they reach the Fort Peck facility, bison must complete additional surveillance testing for one year to confirm they do not carry the disease caused by *Brucella abortus* (Turner, 2020). Each of the highlighted programs now manages between 625–900 bison, though these numbers vary annually (**Table 2**).

Both Fort Belknap and Fort Peck divide their herds into two groups: (1) a conservation herd (sometimes referred to as cultural herd) with individuals originating from YNP, and (2) a commercial herd skewed toward females and managed for non-tribal hunts or sales. The Blackfeet program has two conservation herds that are separated to maintain genetic uniqueness of their newly established herd of Plains bison derived from Elk Island National Park in Canada. The Rosebud program manages one herd with a business plan maintained for conservation and cultural purposes as well as to generate revenue and food.

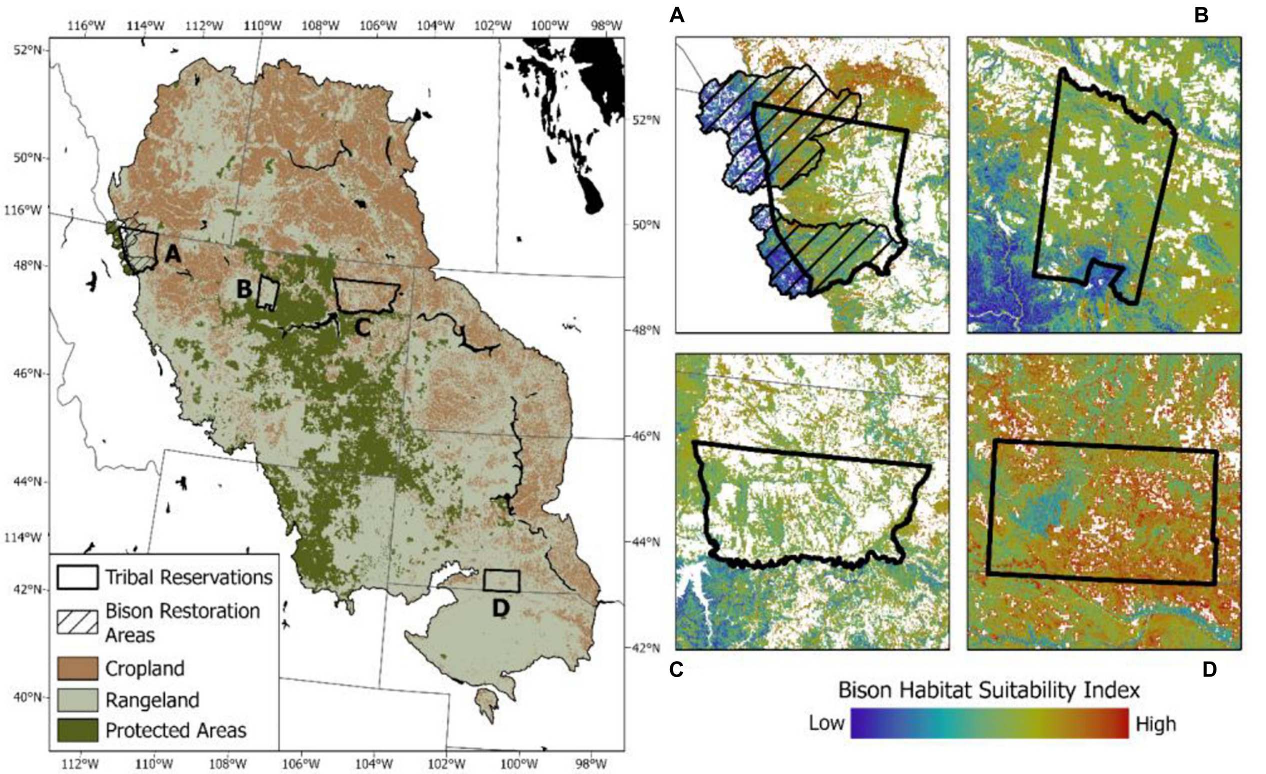

FIGURE 3 | Northern great plains study area based on Commission for Environmental Cooperation (CEC) terrestrial ecoregions—Northwestern Great Plains, Northwestern Glaciated Plains, and the Nebraska Sand Hills. Also included are the northern and southern bison reintroduction areas which extend west of Blackfeet Reservation in the northwest part of the ecoregion (hatched, **A**). Full map shows the extent of cropland (World Wildlife Fund, 2018), rangelands (World Wildlife Fund, 2018), and Protected Areas in IUCN categories I-V (Environment and Climate Change Canada [ECCC], 2020; U. S. Geological Survey [USGS] Gap Analysis Project [GAP], 2020). Individual maps show bison habitat suitability index (HSI) in the target Tribal Reservations: **(A)** Blackfeet Reservation (scale 1:2,000,000); **(B)** Fort Belknap Reservation (scale 1:1,250,000); **(C)** Fort Peck Reservation (scale 1:2,250,000); and **(D)** Rosebud Reservation (scale 1:1,250,000). HSI details in **Supplementary Materials (3)**.

Currently, each reservation has set aside between 36 and 112 km^2 for bison restoration programs, but all programs are interested in expanding pastures to further grow their herds (**Table 2**). The majority of unplowed lands within these reservations are used for cattle operations. From the HSI analysis, we estimated that between 1,828 and 4,354 km^2 of additional habitat is suitable for bison within the four tribal lands included in this study (**Table 2**).

Management Structure and Staff

Each program's management authority and support staff availability vary. Both the Fort Belknap and Fort Peck programs were originally nested under their respective Tribal Fish and Game Departments, with daily management overseen by a tribally appointed buffalo manager. This is still the structure of the Fort Peck Program, whose buffalo manager operates with part-time seasonal support from Tribal Fish and Game staff (i.e., game wardens). Fort Belknap's program became a separate tribal entity several years ago, with funds for two seasonal technicians (6-month contracts) to assist with routine maintenance and annual roundups. At present, neither program has a designated administrative secretary. Fort Belknap previously shared an administrative secretary with the Tribal Council, and Fort Peck previously had a program administrator whose salary was supported by outside partners.

The Blackfeet program is unique in that it functions as a partnership between the Buffalo Program and Iinnii Initiative (Johns, 2020), two programs that co-exist in their efforts to restore bison on the Blackfeet Reservation. The Buffalo Program is nested under the Tribal Land Department, consisting of a director, secretary, and two full-time field technicians that provide the on-the-ground management of the bison herds. The Iinnii Initiative is a separate entity consisting of a single program coordinator supported by the Wildlife Conservation Society, who coordinates collaborations with tribal organizations and neighboring sister bands in Canada. The Iinnii Initiative focuses on ecological restoration, cultural revitalization, youth engagement, and community healing, whereas the Buffalo Program is focused on direct management of herds and providing food sovereignty for the community.

The Rosebud program, or Wolakota Buffalo Range, is the most recently established of the four programs. In contrast to the previous three programs, it is overseen by the

TABLE 2 | Current status of bison herds and total suitable area for bison.

			Suitable area		Numbers^c		Management				
Program	**Year Est**	**Origin^a**	**Current area in pasture (km²)**	**HSI^b (km²)**	**Conserv**	**Produc**	**Department**	**Grazing**	**Revenue**	**Plan**	**Ecol. monitoring**
Fort Belknap	1977	YNP, WCNP, TRNP, CSP	93	1,828	100	800	Separate tribal entity	No interior fences	Hunt; Sales	No	No
Fort Peck	2001	YNP, WCNP, EINP	97	3,037	370	300	Tribal Fish and Game	Few interior fences	Hunt	Yes	No
Blackfeet	1970	CSP, EINP	36	3,669	75	550	Separate Tribal Entity	Rotational grazing	Sales	Yes	Yes
Rosebud	2020	WCNP, EINP, BNP, TRNP	112	4,354	800		REDCO	Rotational grazing	Hay	Yes	Yes

Current management of bison herds.

Data includes, the year bison herds were established (Year Est.); the origin of translocated animals; suitable area: (1) current area of bison pastures and (2) area suitable for bison on each Reservation (HIS); additional information on current management.

[a] Origin of bison, Yellowstone National Park; Wyoming, United States (YNP); Wind Cave National Park, South Dakota, United States (WCNP); Theodore Roosevelt National Park, North Dakota, United States (TRNP); Custer State Park, South Dakota, United States (CSP); Elk Island National Park, Alberta, CA (EINP); Badlands National Park, South Dakota, United States (BNP).

[b] Habitat Suitability Index: potential restoration areas estimated by extracting cells from the upper 50th percentile of habitat suitability index values and summing the area of habitat within contiguous patches ≥ 120 km².

[c] Blackfeet manages two herds but does not define them as being for different purposes. "Conservation" represents bison herd of Elk Island origin, whereas "production" herd represents large herd established in 1970s.

economic arm of the Rosebud Sioux Tribe (Rosebud Economic Development Corporation Wolakota Buffalo Range, 2021), in collaboration with Rosebud Tribal Land Enterprise, the Tribe's land corporation. The project is also being advanced by a partnership with World Wildlife Fund and with support from the U.S. Department of Interior (Rosebud Economic Development Corporation Wolakota Buffalo Range, 2021).

Management

All herds are wide-ranging and minimally handled, but management varies between having pastures with no interior fences (Fort Belknap and Fort Peck) to having pastures divided up with herds rotationally grazed (Blackfeet and Rosebud) (**Table 2**). The reasoning for subdivision varies by reservation: the Blackfeet pastures are split-up because it was not possible to lease contiguous land large enough to sustain the herd year-round, whereas for Rosebud the division of pastures is by design to help control access to pastures (similar to cattle rotation). The buffalo managers determine when to move or cull the herd based on their experience and assessment of pasture–though on three reservations there is no formal protocol for monitoring rangeland. The exception is the Rosebud program (Wolakota Buffalo Range) which contracts outside expertise through the Ranch Advisory Partners (2021) with support from World Wildlife Fund. However, all programs are also advised by regional representatives from the USDA Natural Resources Conservation Service (NRCS) concerning rangeland health and estimation of Animal Unit Months (AUMs) within the context of standards for cattle ranching (Bureau of Indian Affairs, 2021).

Every year, a portion of each bison herd is culled to maintain sustainable stocking rates. Each program differs in their method for determining which animals to cull, though all programs reported considering family and herd dynamics, with selection preference of non-breeding females and older males. In programs managing commercial herds (Fort Peck, Fort Belknap), sex ratios lean toward maintaining a high number of females (e.g., less than 1:5 males to females). Surplus bison selected for removal are either harvested for the community or sold as a hunt to both tribal and non-tribal members. Calves may also be commercially sold at live fair-bid auctions, which generate revenue from non-tribal buyers living outside the community.

Apart from semi-annual rangeland assessments by NRCS staff, ecological monitoring is currently limited to more recent research collaborations with tribal colleges. Since 2020, Blackfeet Community College students have been conducting ecological monitoring of grassland plants, soil health, and biodiversity in a portion of bison pastures in collaboration with Montana State University, with hopes of expanding the program to all pastures. Both tribal colleges at Fort Peck and Fort Belknap have also worked to incorporate research focused on bison health and plant and wildlife biodiversity within pastures, and both are actively working to increase student research opportunities related to their respective bison repopulation programs. The Rosebud program differs from the other three programs in that regular ecological monitoring was included in the initial management plan to guide both implementation and future development.

For all programs, training is informal, however, most technicians and seasonal support staff come with some prior experience in cattle ranching. The ITBC also provides training opportunities during annual meetings throughout the NGP region. Currently, most programs do not support a larger team of long-term staff, apart from experienced buffalo managers.

Economic Development

Programs offset operating costs through either live sales or meat sales following in-pasture harvesting, and two programs—Fort Belknap and Fort Peck—generate revenue from selling hunting licenses to non-tribal members. The number of bison harvested during hunts varies annually, depending on the stability of herd populations (as assessed by the buffalo manager) and availability of buyers. At Fort Belknap, the program's primary revenue comes from the sale of live surplus bison from the commercial herd, but the program also sells 10–20 non-tribal hunting licenses each year ($2,000–$7,500/each) via a license raffle. In 2018, Fort Peck began an online hunting license system that manages the sale of all non-tribal hunts under the Tribal Fish and Game Department, which significantly increased applicants and overall revenue. In addition, non-tribal hunters must also pay to enter a raffle ($20/entry, up to five entries per person) for the opportunity to hunt a bison from the commercial herd (40 total hunts), plus additional conservation and administration fees. The overall price of a hunt depends on size and age-class ($2,500–$5,000), with trophy bulls (2–3 animals per year) sold through an online auction ($5,000 minimum bid). At both programs, tribal members are provided opportunities to hunt bison through a separate raffle at a substantially reduced rate, and thus are not considered a significant source of revenue. In contrast to these two programs, the Blackfeet program does not have a hunting program. Their main source of revenue instead comes from the annual auction of calves each spring.

As the newest program, the Rosebud program is currently supported by grants and private investors, however, it has a business plan in place designed to eventually cover all operating costs through the sale of surplus bison. Once the herd reaches carrying capacity, approximately 1,500 bison, an estimated surplus of over 400 bison will need to be culled annually and could then be field harvested and sold to external markets with an estimated annual net profit of $300,000–$400,000. Bison harvested for the local community will not be sent to feedlots, instead they will be field harvested with traditional ceremonial methods. However, Rosebud is still determining how many surplus bison will be retained annually to support their local food sovereignty initiative and how many bison might be transferred to support other Native Nation bison restoration efforts.

At all programs, ecotourism activities occur occasionally depending on the availability of staff and external tourism partners, but there is no regular programming. All communities report having an interest in developing ecotourism, both for outside revenue generating activities, as well as for more community-focused programs. It should be noted that some bison pastures are important historical sites and occasionally included as points of interest for outside tour groups.

Community Engagement and Access

The benefits bison programs can provide to the community depend on a program's capacity to conduct outreach, deliver programs, and coordinate with other tribal organizations. Educational activities are generally facilitated in collaboration with an established stakeholder group, and/or the presence of dedicated staff, such as an administrative assistant or program coordinator. Both the Blackfeet and Fort Peck programs have well-established stakeholder groups that are involved in community engagement, whereas Fort Belknap is still at the early stages of development. At Blackfeet, activities are coordinated under the Iinnii Initiative through regular community engagement, celebrations, and youth programs. Unique to Blackfeet, the Iinnii Initiative coordinates activities with bison restoration programs run by neighboring sister bands in Canada. At Fort Peck, activities are coordinated by a grassroots community-led stakeholder group, known as the Pté group, that meets monthly. In contrast to these, there is currently no community-led stakeholder group at the Rosebud program. However, the program does work closely with the Sicangu Community Development Corporation (SCDC), a sister non-profit focused on restoring community-driven systems centered on Lakota values that delivers a dedicated food sovereignty initiative that is beginning to incorporate bison meat.

Programs vary in terms of how meat is distributed, and the number of opportunities for direct participation in bison harvests. Bison meat donations and distribution programs increase public access to traditional foods and contribute to cultural education programs. At Blackfeet, Fort Peck, and Fort Belknap, tribal members have access to bison meat through occasional tribal sales and through distribution programs coordinated by other tribal organizations. All programs donate a portion of culled bison (processed meat) to tribal ceremonies, cultural immersion schools, food pantries, and senior centers. Bison harvests are also donated, on a case-by-case basis, to local schools and cultural programs for experiential learning activities. These programs also offer opportunities for the community to hunt bison selected for removal from the herd. As the most recently established program, Rosebud is still in the initial stages of determining how many surplus bison will be retained annually to support the SCDC food sovereignty initiative. A pilot program is being developed that will initially allow harvest of two bison per year and provide meals for the students at the Lakota immersion school. In addition, community members will have the opportunity to buy a share of the bison produced to either harvest for consumption or relocate to personal plots elsewhere to establish additional small herds.

All programs encourage visitors to the bison pastures and work with a variety of tribal organizations to arrange educational events. The frequency of these activities depends on each program's capacity to coordinate with outside groups and the availability of funding in the case of larger community-wide events. Two examples of successful regular programing centered on revitalizing a traditional relationship with bison are (1) Blackfeet's Iinnii Days, an annual 3-day community-wide event that celebrates the bison through ceremony, educational activities, and other cultural experiential learning opportunities;

and (2) Head Start Curriculum developed by Fort Peck's Pté group, where preschoolers learn the history and cultural significance of bison in the classroom, followed by a springtime visit with their local cultural herd. All programs are also in the process of creating infrastructure to provide a gathering place for visitors, workshops, and ceremonial harvests contributing to the concept of the transition to food sovereignty.

Tribal community colleges and tribal land-grant universities play an important role in supporting each bison program's long-term goals. All communities have tribal colleges, but each varies in extent of academic offerings and level of involvement. Tribal colleges at Fort Belknap (Aaniiih Nakoda College), Blackfeet (Blackfeet Community College) and Fort Peck (Fort Peck Community College) offer associate degrees and professional certificates, apart from a new Environmental Science BS at Fort Belknap and a Nursing BS at Blackfeet. Both Fort Belknap and Blackfeet colleges recently secured grants to support the development of research and education centers, largely focused on ecological research related to bison restoration efforts. The overarching goals of these centers are to connect the community with their bison programs and to develop occupational opportunities and capacity through training the younger generation to understand and manage bison. Rosebud's tribal college (Sinte Gleska University) offers a wide range of associates degrees, and a selection of bachelors and master's degrees, but is still at the early stages of engaging with the newly founded buffalo program.

ACTIONABLE RECOMMENDATIONS

We recommend that Buffalo Programs at each reservation develop an adaptive management plan that reflects the expressed goal of retaining the wild nature of bison for both conservation and commercial herds. These plans should incorporate Indigenous science and cultural knowledge. However, more studies are needed to investigate bison grazing patterns and behavior under different management schemes and future climate scenarios, e.g., different densities, genetic origin (across NGP climate gradient), and year-round grazing vs. rotation. As part of this investigation, Tribes will need to develop monitoring protocols to ensure bison grazing is creating desired outcomes, contributing to rangeland health, and including contingency plans for extreme events, like drought, thought to become more prevalent in the region. There is also a need to conduct baseline assessments, so programs can track the cascade of ecological effects that bison restoration has on biodiversity. At present, all programs have limited capacity (e.g., trained staff, equipment) for conducting regular ecological monitoring or disease testing, apart from some intermittent collaborations with local community colleges. Communities recognize this need and share many potential questions but need additional resources and expertise to implement regular monitoring.

Within established programs, many bison pastures have reached carrying capacity. To achieve food sovereignty, bison herds will need to grow significantly larger. However, across all sectors (public, private, tribal, and NGO), the growth of bison herds is limited by the availability of land through either grazing leases or purchase for expanding pastures (Martin et al., 2021). Acquiring additional lands will rely on transition of leases from common livestock use to bison grazing which requires additional funding for leases and infrastructure, and a need to facilitate stakeholder processes in each community to address the spectrum of social tolerance for bison (Pejchar et al., 2021).

While community surveys indicate that all communities desire greater access to herds and acquisition of bison meat (Haggerty et al., 2017; McElrone, 2017; Human Ecology Learning and Problem Solving [HELPS] Lab, 2018); there is an institutional need to increase staffing to expand community engagement programming. Currently, the primary limitation reported for establishing regular programing, both for generating revenue and cultural enrichment, is the lack of staff who can assist with coordination with outside partners and make a significant long-term investment. All programs rely on a few experienced people and seek to expand to a larger team of long-term staff. Likewise, many programs do not have formal management or safety training for seasonal roundup or regulation of a hunt. Training on best practices for bison handling and sustainable ranching would be valuable to foster young managers and technicians and sustain programs.

Program expansion is largely based on the ability to produce sustainable revenue. Across all programs, most bison sales are to non-tribal members after which the bison are processed outside the community, in part due to absence of appropriately scaled meat processing facilities which results in increased costs and limits local meat distribution. A successful example is the Quapaw Nation who established a meat processing facility on the reservation as part of the community's mission to exert food sovereignty and produce meat for its citizens. At present, the demands for the facility is higher than what the business can provide to both local and outside cattle operations, which illustrates the scale of potential opportunities these facilities can provide to rangeland communities. Establishment of such facilities will create jobs on reservations and make traditional protein subsidies more affordable and accessible to community members. Apart from Rosebud, most programs do not have an updated business plan in place. Economic development plans including modern food marketing are recommended to help guide programs toward becoming self-sustaining, including support for multiple long-term staff.

DISCUSSION

Since the near extermination of bison, Native Nations have worked to repopulate bison to sovereign lands, and these initiatives are important steps toward cultural revitalization and food sovereignty for Plains Indians. The four case studies herein are vignettes of successful bison repopulation and management and provide perspectives on the challenges of restoring herds to fulfill the socio-ecological needs of local rural communities. These projects also highlight tribal lands as potential sources for restoring the NGP both in terms of an expansion of bison range and a surplus of animals for restoration projects.

This is due in part to the predominant cultural acceptance of bison, the need for establishing food sovereignty, the vast availability of suitable pasture, and the potential ability of bison to reengineer the prairie landscape. At present, Tribes have focused efforts on cultural restoration of bison in their societies while addressing food sovereignty. However, if restoration of bison to provide ecological function and services is a goal, it is critical to address tribal needs for funding, enhanced community capacity (e.g., training of staff, food distribution frameworks), solving complex landownership interactions (cross boundaries management, *sensu lato*; Pejchar et al., 2021), and developing a well-defined adaptive management plan (Briske, 2017). These needs are not unique to bison conservation within the NGP, as each of these sociological factors has been found to limit wildlife reintroduction opportunities (Berger-Tal et al., 2020) and specifically, they have limited bison re-establishment across jurisdictions in the United States (Pejchar et al., 2021).

Community-Based Restoration

Effective bottom-up, community-based conservation projects must be built around a viable conservation target, but targets vary from community to community and even within communities (Souto et al., 2014; Wilkins et al., 2019). Each tribal community and buffalo program has unique needs and objectives, through which opportunities exist to support the eco-cultural restoration of bison (Johns, 2020). Engaging communities in co-designing and planning associated with buffalo programs can build social trust and help mitigate the risk of negative public perception (Watkins et al., 2021). To that end, as demonstrated in the case studies, each Tribe has initiated community engagement activities to gain public support and rebuild a constituency for bison, based upon the perception that reconnecting the community with bison herds will provide multiple benefits (Haggerty et al., 2017; Wilkins et al., 2019).

A key benefit to restoring herds is to enable community consumption and traditional relationship with bison (Haggerty et al., 2017; McElrone, 2017; Human Ecology Learning and Problem Solving [HELPS] Lab, 2018). Restoration of bison on tribal lands can, under appropriate vision and planning, support reclamation of traditional food systems by providing a sustainable protein source to communities with some of the greatest food insecurity in the United States (Bowers et al., 2019; Feeding America, 2019). Yet, today, discounted hunting licenses remain prohibitively expensive for some community members (Speakthunder and Magnan personal observation, 2021), and donations of meat are limited to a small number of bison each year. For Native Americans, reclaiming portions of their traditional practices within a modern economic system may be an important means of developing a more sustainable and future climate adapted economic framework (Crepelle, 2019). However, Native American food and agriculture sectors, and tribal wildlife departments are disproportionately under-resourced compared to state agencies, and they have limited access to federal funds (Wagner, 2007). Yet, food sovereignty is attainable within all the case studies examined if initial capital support is provided and the food pipeline to the community is improved.

Land Tenure and Capacity Needs

Although abundant suitable land exists within the reservations, land tenure issues, including highly fractionated lands in the NGP, make it difficult for Native Nations and Native community members to utilize all these lands for their benefit (Brewer et al., 2016). This speaks to economic challenges of buffalo programs or Native Nations securing tenure on lands for bison herd establishment or expansion. Because many Tribes do not have sufficient land mass to dedicate toward large genetically diverse herds (>1,000 individuals), Tribes adapted the U.S. Department of Interior metapopulation management strategy that involves exchange and translocations among conservation herds to conserve gene diversity (Hartway et al., 2020). Within the present context, tribal bison herds cannot achieve numbers sufficient for the dual purpose of food sovereignty and restoration.

In addition to land tenure challenges, there is a need for investment in capacity. As Tribes work to grow herds, they will need to build capacity within the community to sustain the herd and the ecological integrity of the rangeland (Martin et al., 2021). In some cases, training programs are in place, but reliant on availability of a few key personnel. Integration with tribal colleges to participate in rangeland monitoring and animal management activities could be a solution to some of the personnel shortages. Regional strategies for addressing these challenges could emerge, e.g., funding and sharing expertise of tribal staff with higher level of training such as veterinarians, rangeland botanists, rangeland management specialists, ecologists, animal scientists, wildlife biologists, and natural resource managers. Programs differ in their strengths, and different communities have varying resource demands and expertise to draw from. Huge advances have been made to increase collaboration and create training opportunities through the ITBC, and efforts to further increase collaboration and regular communication between communities should be supported.

Preparing for the Future

With all the challenges in mind, Tribes—and other sectors—need to prepare for the future and adapt their management goals in accordance with climate change (Martin et al., 2021). Whyte (2013) argues that Native American collective continuance (i.e., the capacity to adapt to probable futures) will require an interdisciplinary approach that applies science, policy, and traditional knowledge to develop community-tailored adaptive management strategies. From a biophysical perspective, bison are expected to decrease mature body mass between 63 and 115 kg in response to the combined effects of projected warming (per°C mean annual temperature rise) and increasing drought (per unit of annual Palmer Drought Severity Index). This will substantially reduce the amount of meat produced per animal (Martin and Barboza, 2020a). In addition, reproductive success may decline with warming and shrinking body size (Martin and Barboza, 2020a). Lastly, the longevity of bison may decline (0.3 y/kg of body mass loss) with warming and associated shrinking body size (Martin and Barboza, 2020a). Bison will adapt to maintain themselves on the landscape, however, the increasing demand for bison meat and the changes to rangeland conditions will ultimately require allocation of more lands to bison management.

True restoration of bison on the NGP, as defined in this paper, will require additional herds, increased herd sizes, and reestablishment of migration corridors in some functional capacity (*sensu lato* "shared stewardship"; Aune and Plumb, 2019). The ecological benefit of landscape heterogeneity relies on exploiting a primary trait of bison—their desire to move. Currently, land tenure/ownership issues display a modern societal intolerance of big game movements across jurisdictions. This is true for bison as well as other species such as deer *(Odocoileus* spp.), pronghorn antelope (*Antilocapra americana*), and elk (*Cervus canadensis*), preventing formerly functioning NGP prairie ecosystems from fully reoccurring. To restore the function of migration, if not actual long-range movements, the management of bison for both production and conservation needs refinement of protocols regarding fencing and land ownership. Monitoring is essential to know whether ecological restoration is being achieved, particularly as the Tribes evolve in their management.

CONCLUSION

Native Nations hold an expanse of suitable habitat for bison, and their cultural heritage may be more conducive to bison restoration on tribal lands within the constraints of existing land tenure. Currently, the reviewed challenges outweigh the communities' capacity to fully restore bison and reconnect ecological services. However, with sustained and dedicated funding and management capacity, these initiatives can realize the outcomes desired by communities. In the near term, food sovereignty will mean an emphasis on production (i.e., provisioning ecosystem services and achieving food sovereignty). Other avenues to re-populate bison and support cultural revitalization should also be explored to complement the efforts on the reservations. For example, allowing bison onto large federal lands managed for wildlife while partnering with Native Nations in the process and decision-making may be an alternative route to restoration; this concept is loosely referred to as co-management or "shared stewardship" (*sensu lato*; Aune and Plumb, 2019).

In the future, restoration will be actualized by merging the concepts of conservation and commercial herds (with some capacity to extract surplus animals from the herd) or the growth of both herds until production meets local community food demands and conservation meets non-provisioning ecosystem service demands (e.g., carbon sequestration, water quality enhancement, facilitating increased biodiversity, and cultural connections). Both strategies rely on community support and robust expansion of staff, infrastructure, and funding. In summary, the success of restoring bison on tribal lands for the purpose of seeking ecological solutions to food sovereignty is dependent upon the acceptance and application of the pluralistic, intrinsic traits of bison being considered as both a culturally significant wildlife species and as the focus of a sustainable economic program. Acceptance of both roles may be what is needed to foster economic development and grow bison repopulation efforts, while avoiding placing a burden on the underserved communities already leading the way.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in **Supplementary Materials 2** and **3**. Further inquiries can be directed to the corresponding author/s.

AUTHOR CONTRIBUTIONS

HS, BDM, WJM, DJ, MS, and TSA formulated the idea. HS structured the manuscript through consultation with the primary and secondary authors. HS and OGC wrote the first draft. All authors contributed to revisions of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.826282/full#supplementary-material

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Less Is More: Lowering Cattle Stocking Rates Enhances Wild Herbivore Habitat Use and Cattle Foraging Efficiency

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Over a quarter of the world's land surface is grazed by cattle and other livestock, which are replacing wild herbivores and widely regarded as drivers of global biodiversity declines. The effects of livestock presence versus absence on wild herbivores are well documented. However, the environmental context-specific effects of cattle stocking rate on biodiversity and livestock production are poorly understood, precluding nuanced rangeland management recommendations. To address this, we used a long term exclosure experiment in a semi-arid savanna ecosystem in central Kenya that selectively excludes cattle (at different stocking rates), wild mesoherbivores, and megaherbivores. We investigated the individual and interactive effects of cattle stocking rate (zero/moderate/high) and megaherbivore (>1,000 kg) accessibility on habitat use (measured as dung density) by two dominant wild mesoherbivores (50–1,000 kg; zebra *Equus quagga* and eland *Taurotragus oryx*) across the "wet" and "dry" seasons. To explore potential tradeoffs or co-benefits between cattle production and wildlife conservation, we tested for individual and interactive effects of cattle stocking rate and accessibility by wild mesoherbivores and megaherbivores (collectively, large wild herbivores) on the foraging efficiency of cattle across both seasons. Eland habitat use was reduced by cattle at moderate and high stocking rates across both dry and wet seasons and regardless of megaherbivore accessibility. We observed a positive effect of megaherbivores on zebra habitat use at moderate, but not high, stocking rates. Cattle foraging efficiency (g dry matter step^{-1} min^{-1}) was lower in the high compared to moderate stocking rate treatments during the dry season, and was non-additively reduced by wild mesoherbivores and high cattle stocking rates during the wet season. These results show that high stocking rates are detrimental to wild mesoherbivore habitat use and cattle foraging efficiency, while reducing to moderate stocking rates can benefit zebra habitat use and cattle foraging efficiency. Our findings demonstrate that ecosystem management and restoration efforts across African rangelands that involve reducing cattle stocking rates may represent a win-win for wild herbivore conservation and individual performance of livestock.

Keywords: elephant, competition, facilitation, foraging efficiency, livestock-wildlife interactions, rangeland, savanna

INTRODUCTION

Over a quarter of the world's land surface is grazed by cattle and other livestock (Asner et al., 2004), which now comprise 60% of mammalian biomass globally (Bar-On et al., 2018), and underpin the livelihoods of millions of people. This livestock grazing is having large impacts on global biodiversity (Reid et al., 2014). Considering that the current network of protected areas is insufficient in size and too fragmented to ensure the future of many large herbivore species (Craigie et al., 2010), a better understanding of how wildlife can coexist with people and their livestock outside of protected areas is critical for ensuring the socio-ecological integrity of global rangelands. This is particularly true of arid and semi-arid regions of Africa (Tyrrell et al., 2017), which are home to the most diverse and threatened large mammal communities (Ceballos et al., 2015). In these regions, cattle, sheep and goats account for >90% of herbivore biomass (Hempson et al., 2017), and livestock are the primary source of food, livelihoods, and cultural value for local communities (Homewood, 2009).

A global review has indicated that livestock and wildlife interactions are generally negative (Schieltz and Rubenstein, 2016). Livestock can impact wild herbivore populations mainly via indirect exploitation competition and, to a smaller extent, direct interference competition (Loft et al., 1991; Stewart et al., 2002; Madhusudan, 2004). Exploitation competition occurs due to alteration to forage quantity and/or quality (Ranglack et al., 2015; Kimuyu et al., 2017; Keesing et al., 2018), fire regimes and vegetation structure (Kimuyu et al., 2014; Hempson et al., 2017; Odadi et al., 2017a), water availability (Connolly et al., 2021), predation risk (Ng'weno et al., 2019), and/or disease transmission (Keesing et al., 2018). However, moderate levels of grazing by livestock and wildlife can also improve pasture quality and facilitate coexistence in certain agro-ecological and climatic contexts (Brown et al., 2010; Odadi et al., 2011; McLaren et al., 2018; Young et al., 2018).

The spectrum from competitive to facilitative interactions in herbivore communities may depend on the temporal dynamics of resource availability (Veblen, 2008). In a Kenyan savanna, for instance, cattle and wild herbivores compete for forage during the dry season, but facilitation can occur during wet periods when grazing promotes the growth of higher quality grass (Odadi et al., 2011). The competition and facilitation processes can be mediated by the presence or absence of megaherbivores (>1,000 kg). There is evidence that elephants *Loxodonta africana* can dampen the negative effects of cattle on plains zebras *Equus quagga* (Kimuyu et al., 2017), by competing with cattle for forbs (Odadi et al., 2009, 2013; Coverdale et al., 2016) and facilitating zebras by altering the cover of grasses and woody vegetation (Wells et al., 2021a). Forbs can play a particularly important role in herbivore interactions because they are an important source of protein (Odadi et al., 2013).

A limitation to our current understanding of the interactions between livestock and wild herbivores is that virtually all evidence comes from simply comparing livestock to non-livestock conditions (Briske et al., 2011; Schieltz and Rubenstein, 2016). A gradient of livestock stocking rate may govern competition and facilitation with wild herbivores across seasons. The ecosystem effects along this gradient are poorly understood and, in African rangelands, may be mediated by the presence of megaherbivores. Moreover, how wildlife and season mediate the intraspecific competition among cattle at different stocking rates is also poorly understood. In this experimental study, we sought to fill this knowledge gap within the context of an African savanna rangeland in central Kenya. Specifically, we investigated: (i) the individual and interactive effects of cattle stocking rate (zero/moderate/high) and megaherbivore accessibility (presence/absence) on habitat use (measured as dung density) by the two dominant wild mesoherbivores (50–1,000 kg; zebra *Equus quagga* and eland *Taurotragus oryx*), across "wet" and "dry" seasons, and (ii) the underlying individual and interactive effects of cattle stocking rate and accessibility by wild mesoherbivores and megaherbivores (collectively, large wild herbivores) on the foraging efficiency of cattle across the wet and dry seasons. Cattle may compete more with eland (which, like cattle, are ruminants) than with zebra, which are non-ruminants. Indeed, previous work has shown that cattle at moderate stocking rates supress eland more so than zebra (Kimuyu et al., 2017). We therefore predicted that eland will be more negatively affected by increasing cattle stocking rates than zebra.

MATERIALS AND METHODS

Study Site

We conducted this study in the Kenya Long-term Exclosure Experiment (KLEE) at Mpala Research Centre (0°17′N, 36°52′E, 1,800 m.a.s.l.) in Laikipia, Kenya. Mpala Research Centre is managed for both wildlife conservation and livestock production, where cattle are the main domestic animal. Rainfall at KLEE is weakly trimodal with a pronounced dry season December-March. From 2001 to 2019, annual rainfall averaged 613 mm yr^{-1} (range: 421–1,009 mm yr^{-1}, interannual coefficient of variation: 27%). Soils are poorly drained vertisols with high clay content (>40%) known as "black cotton." Black cotton soils are widespread across Africa and with other vertisols cover >100 million hectares across the continent (Ahmad, 1996). The overstory of this savanna ecosystem is dominated by *Acacia drepanolobium* (syn. *Vachellia drepanolobium*, 97% of the canopy; Young et al., 1997), while five perennial grass species (*Brachiaria lachnantha*, *Themeda triandra*, *Pennisetum stramineum*, *P. mezianum*, and *Lintonia nutans*) comprise 85% of herbaceous understory cover at KLEE (Porensky et al., 2013). The above ground net primary productivity (ANPP) of the study site is comparable to the productivity of Serengeti grasslands with comparable rainfall (Sala et al., 2012) and somewhat higher than herbaceous ANPP estimates from an adjacent, less productive soil type (Augustine and McNaughton, 2006). Wild herbivore species at KLEE include: plains zebra, eland, oryx (*Oryx beisa)*, hartebeest (*Alcelaphus buselaphus)*, buffalo (*Syncerus caffer)*, Grant's gazelle (*Nanger granti)*, Grevy's zebra (*E. grevyi)*, common duiker (*Sylvicapra grimmia)*, steenbok (*Raphicerus campestris)*, elephant (*Loxodonta africana)*, and giraffe (*Giraffa camelopardalis)*.

Experimental Design

The KLEE plots were established in 1995 and use barriers to control access to 200 m^2 × 200 m^2 (4-ha) treatment plots by three herbivore types – wild mesoherbivores (50–1,000 kg), wild megaherbivores (>1,000 kg; elephant and giraffe), and cattle – in different combinations. KLEE consists of three replicate blocks of six herbivore treatments: (1) accessible only to cattle; (2) accessible only to wild mesoherbivores; (3) accessible only to wild mesoherbivores and megaherbivores; (4) accessible only to cattle and wild mesoherbivores; (5) accessible to cattle, wild mesoherbivores, and megaherbivores; and (6) excluding cattle, wild mesoherbivores, and megaherbivores. Here, we excluded the final treatment because it was not relevant to addressing our research questions. The treatment plots accessible to cattle are typically grazed by 100–120 mature Boran cows *Bos indicus* (sometimes with calves and/or bulls) for 2–3 days (2 hrs day^{-1}) within a 2-week period, 3–4 times per year (i.e., moderate stocking rate). The timing and number of grazing days depends on forage availability and reflects typical grazing regimes of private ranches in the region, wherein cattle graze in an area for several days before being moved to allow that area to recover.

The three treatments accessible to cattle each contain a 50 m^2 × 50 m^2 (0.25-ha) subplot (established in 2008), in which the same cattle herd is grazed for a further 30 min following the initial 2-h grazing period in the wider plot, to achieve an approximately fourfold increase in cattle stocking rate compared to the wider plot (**Supplementary Figures 1**, **2**). The five herbivore treatments plus the three high cattle stocking rate treatments make a total of eight treatments. For the five main treatments, we selected one of four 50 m^2 × 50 m^2 subplots within the central hectare of each of the fifteen 4-ha treatment plots for wildlife monitoring. In plots accessible to cattle the subplot closest to the high cattle stocking rate subplots was selected to be more comparable with the moderate cattle stocking rate plots, while subplots were randomly selected in plots excluding cattle (experimental layout illustrated in **Supplementary Figure 2**).

Because cattle only access individual plots a few times per year, responses of wildlife are unlikely to be due to direct interaction with cattle or herders. Fire has not been used as a management tool in this ecosystem for over 50 years and is rarely used by other ranches in the region. Natural-ignition fires have not occurred in decades. See Young et al. (1997) and Young et al. (2018) for further details of the experimental design.

Habitat Use by Wild and Domestic Herbivores

To assess habitat use by wild and domestic herbivores we conducted four dung surveys. Two surveys were conducted during the wet seasons of 2019 and 2020 and two during the dry seasons of 2020 and 2021. Dung surveys are a robust metric of habitat use by wild herbivores (Kimuyu et al., 2017; Wells et al., 2021a). In each survey, we counted dung along six 4 m^2 × 40 m^2 belt transects in all 24 0.25-ha subplots (three replicates of eight treatments). We crushed recorded dung to prevent recounting in subsequent surveys. We also assessed megaherbivore dung densities, because a change in megaherbivore habitat use between treatments may influence the effect of the megaherbivore-accessible treatment. Because we used dung densities as a metric of species-specific relative habitat use, we avoid issues relating to estimating population densities from dung, the decay rates of which vary across species and seasons (Nchanji and Plumptre, 2001; Rivero et al., 2004).

We modeled treatment effects on wild mesoherbivore habitat use by employing Gaussian linear mixed-effect models (LMMs) using *glmmTMB* package version 1.0.1 (Brooks et al., 2017) in R version 3.6.3 (R Core Team, 2020). To evaluate the treatment effects on wild mesoherbivore habitat use we restricted our analysis to the two most common species, zebra and eland, the combined dung of which comprised >80% of the total wild mesoherbivore dung recorded. All other wild mesoherbivore species were data limited, being recorded in fewer than two-thirds of treatments and each species accounting for <6% of total wild mesoherbivore dung. We pooled dung piles across the two temporal replicates within each season by calculating species-specific dung density per survey for each treatment plot for wet and dry seasons. This avoids issues of temporal autocorrelation associated with repeated measurements. To evaluate the individual and interactive effects of cattle stocking rate and megaherbivores on wild mesoherbivore habitat use, we coded cattle (none/moderate/high), megaherbivores (accessible/inaccessible) and the interaction between them as the fixed effect and coded block as a random effect. To evaluate the effects of cattle stocking rate on megaherbivores we coded cattle (none/moderate/high) as the fixed effect and coded block as a random effect. Due to the restricted sample size, we fit separate models for wet and dry seasons. We visually checked the normality and homoscedasticity of the residuals. We performed Tukey's *post hoc* tests for treatment comparisons using the *emmeans* package version 1.7 (Lenth et al., 2021).

Cattle Foraging Behaviour

To assess cattle foraging behaviour we followed Odadi et al. (2017a). We monitored the frequency, size, and plant species composition of bites, as well as step frequency in all 18 subplots accessible to cattle (three replicates of six treatments). For each trial we randomly selected five steers as test animals to use in all experimental plots. The order in which the treatment plots were surveyed was randomised, such that on each sampling day one randomly selected main treatment subplot and its corresponding high cattle stocking rate subplot were sampled. The animals were allowed a 7-day adjustment period prior to each trial, during which they became accustomed to being herded together and observed by researchers at close range. To evaluate seasonal variation we conducted surveys during one "wet" (May 2020) and one "dry" (February 2021) period, selecting a different group of steers for each season. The ten steers (five animals in both wet and dry periods) aged 30–40 months and averaged 311 kg (±15 *SE*).

Bite and step frequencies were recorded twice in each treatment subplot. On each sampling day, the five steers were moved to a designated experimental plot (containing one moderate and one high cattle stocking rate subplot) at 08:00–09:00 hours and removed 1–2 hours later. The steers were allowed approximately 10 minutes to settle prior to observations at the start of each day. While in the experimental plot, the steers were herded in the two subplots sequentially. To avoid biases associated with time of day, this was repeated in the same sequence such that we observed foraging behaviour in both subplots twice during the same morning. Whether the moderate or high cattle stocking rate subplot was visited first was randomly determined. While in each subplot, we observed each animal for 2-min periods, during which all bites taken and steps moved were recorded on two separate tally counters. A "bite" represents removal of a part of a plant or the whole plant, while a "step" represents the forward displacement of either front limb. Bites and steps were recorded when the focal animals were actively foraging. Focal animals were considered to be actively foraging when searching for food or eating appeared to be a primary priority. On the rare occasion that an animal being observed did not eat or move during the entire focal period, bites and steps were recorded as zero. All observations were made at a distance of less than 4 m from the focal animal, by two experienced observers. Observer identity had no detectable effect on foraging efficiency estimates in either the wet season ($Z = -0.74$, $p = 0.46$) or the dry season ($Z = 0.45$, $p = 0.65$). In total, we recorded 720 min of foraging behaviour (5 animals, each observed for two 2-min periods in 18 subplots during two seasons). For further details see Odadi et al. (2017a).

To evaluate cattle foraging efficiency, we estimated bite size in each subplot for each focal animal between the first and second rounds of bite and step counts. We followed the focal animal while it took five consecutive bites, picking a handful of plants that represented the amount consumed by the animal during each bite. We combined the plant matter collected for all five animals (totalling 25 bites) and dried it in a dessicator, weighing it every day until it reached a stabilised dry mass. In total, we recorded 50 bites (five bites from each of the 5 animals during two seasons).

We modelled treatment effects on cattle foraging behaviour by implementing Gaussian linear mixed-effects models (LMMs) using *glmmTMB* package version 1.0.1 (Brooks et al., 2017) in R version 3.6.3 (R Core Team, 2020). We calculated foraging efficiency as: $bite\ size \times bites \times time^{-1} \times steps^{-1}$. To evaluate the individual and interactive effects of cattle stocking rate and large wild herbivores on cattle foraging efficiency, we coded as fixed effects cattle (moderate/high), wild mesoherbivores (accessible/inaccessible), megaherbivores (accessible/inaccessible), the interaction between cattle and wild mesoherbivores and the interaction between cattle and megaherbivores, while coding block as a random effect. Again, we fit separate models for wet and dry seasons, due to the restricted sample size. We visually checked the normality and homoscedasticity of the residuals and tested for treatment comparisons using Tukey's *post hoc* test.

RESULTS

Cattle at High Stocking Rates Suppress Dominant Mesoherbivore Habitat Use

For both dry and wet seasons, and regardless of megaherbivore accessibility, eland habitat use was similarly reduced by cattle at both moderate (dry: −66%, $Z = -3.8$, $p < 0.001$; wet: −66%, $Z = -4.9$, $p < 0.001$) and high stocking rates (dry: −69%, $Z = -5.6$, $p < 0.001$; wet: −65%, $Z = -4.9$, $p < 0.001$; **Figure 1**).

During the dry season, high cattle stocking rates reduced zebra habitat use in megaherbivore-accessible plots, but not in megaherbivore-excluding plots (megaherbivore × cattle interaction, high: $Z = -3.2$, $p = 0.001$; see Tukey's test results in **Figure 1**). However, this effect was not observed at moderate cattle stocking rates ($p = 0.64$). There was a positive effect of megaherbivores on zebra habitat use at moderate cattle stocking rates ($Z = 5.1$, $p < 0.001$), which was negated at high stocking rates. We observed broadly similar patterns during the wet season, although not statistically significant (megaherbivore x cattle interaction, moderate: $Z = 1.6$, $p = 0.10$, high: $Z = -0.5$, $p = 0.60$).

Cattle at moderate and high stocking rates significantly reduced elephant habitat use during the dry season (moderate: −35%, $Z = -2.5$, $p = 0.01$; high: −35%, $Z = -2.5$, $p = 0.01$; but see Tukey's test results in **Figure 2**), but not during the wet season (moderate: 8%, $Z = 0.2$, $p = 0.86$; high: −42%, $Z = -1.0$, $p = 0.33$; **Figure 2**). Giraffe habitat use was unaffected by cattle stocking rate in both seasons (all p-values > 0.15).

Cattle at High Stocking Rates Reduce Cattle Foraging Efficiency, Particularly in the Dry Season

During the dry season, cattle foraging efficiency (dry g $step^{-1}\ min^{-1}$) was 66% lower under high compared to moderate cattle stocking rates ($Z = -4.5$, $p < 0.001$), except in plots accessible to megaherbivores (megaherbivore x cattle interaction, moderate: $Z = 1.9$, $p = 0.06$, high: $Z = -0.2$, $p = 0.83$; see Tukey's test results in **Figure 3**). During the wet season, however, cattle foraging efficiency was lower under high compared to moderate cattle stocking rates only in plots accessible to wild mesoherbivores but excluding megaherbivores (megaherbivore x cattle interaction, moderate: $Z = 1.4$, $p = 0.15$, high: $Z = -3.0$, $p = 0.002$; see Tukey's test results in **Figure 3**).

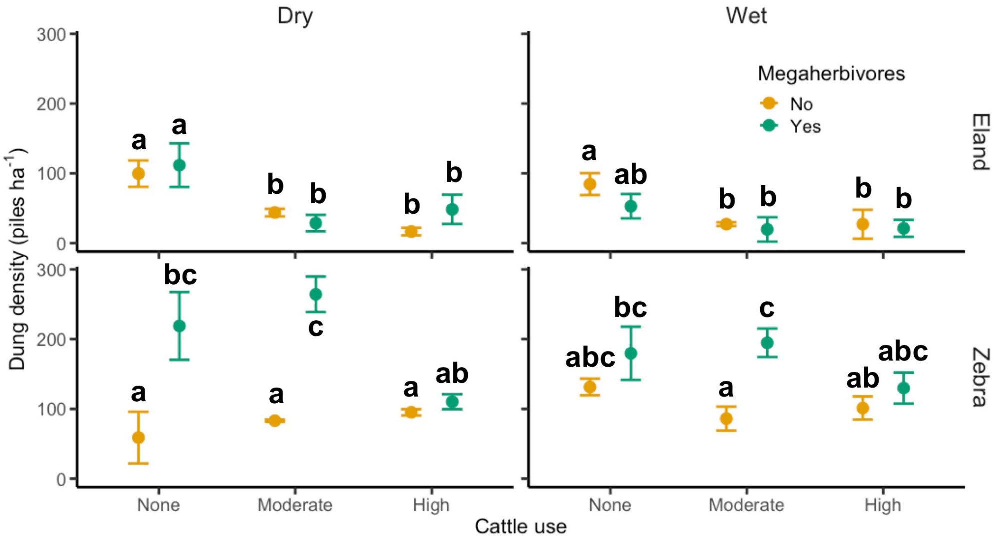

FIGURE 1 | Treatment effects on the habitat use of the two dominant wild mesoherbivore species (*M* ± 1 *SE*). Within mesoherbivore species, treatments not sharing letters are significantly different ($p < 0.05$) based on Tukey's *post hoc* tests. The three cattle stocking rates equate to: 0, ~2, and ~10 kg hr m^{-2} yr^{-1}.

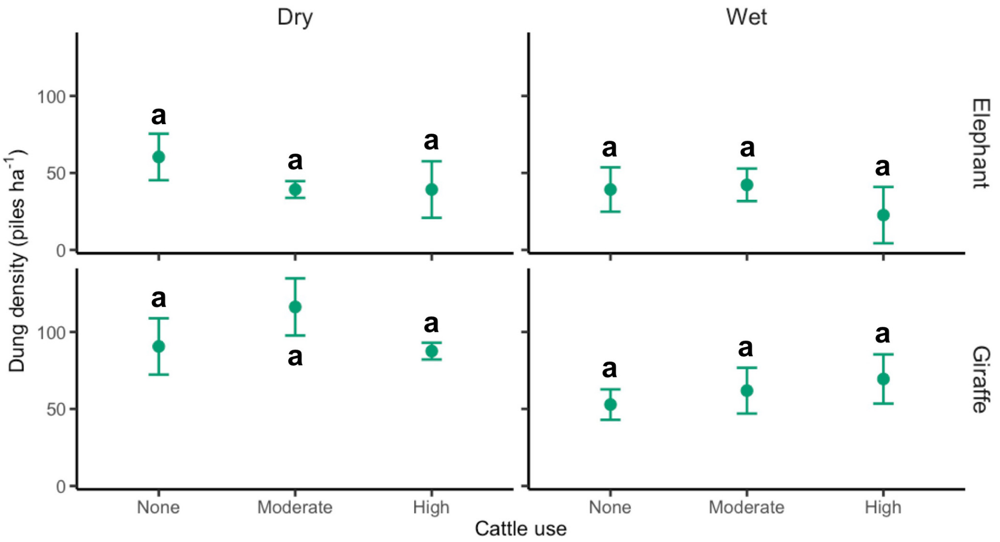

FIGURE 2 | Effects of cattle stocking rate on wild megaherbivore habitat use (*M* ± 1 *SE*). Within megaherbivore species, treatments not sharing letters are significantly different ($p < 0.05$) based on Tukey's *post hoc* tests.

DISCUSSION

The effects of cattle stocking rate on wild herbivores remains poorly understood, in part because most studies simply compare cattle presence versus absence (Briske et al., 2011; Schieltz and Rubenstein, 2016). As yet, the potential tradeoffs or co-benefits between livestock production and wildlife conservation are rarely investigated. Our results show that, overall, high cattle stocking rates were detrimental to both wild mesoherbivore habitat use and cattle foraging efficiency. We also found that megaherbivores increase zebra habitat use, but that this effect is negated at high cattle stocking rates. These findings are important to guide ecosystem management and restoration efforts across African rangelands by providing novel insights into the tradeoffs between, and potential win-wins for, cattle production and wild herbivore conservation.

Wild Mesoherbivore Habitat Use Responses to Cattle Stocking Rate

Our experimental results demonstrate that cattle at both moderate and high stocking rates suppress habitat use by eland, while zebra appeared to be more responsive to megaherbivores than to cattle. The negative effect of cattle on eland corroborates

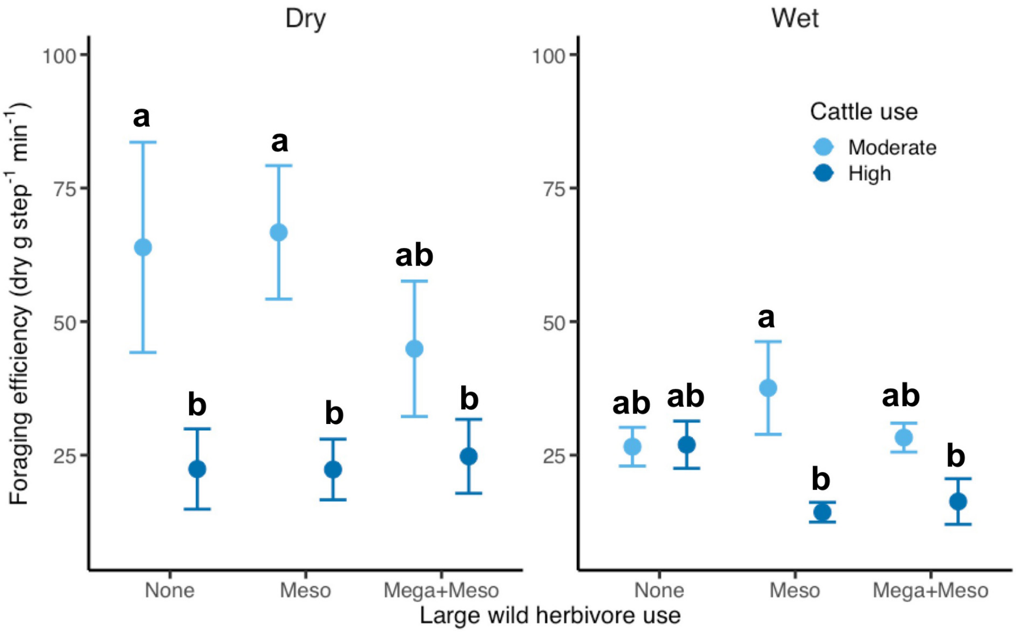

FIGURE 3 | Treatment effects on cattle foraging efficiency across seasons (*M* ± 1 *SE*). Within each season, treatments not sharing letters are significantly different ($p < 0.05$) based on Tukey's *post hoc* tests.

the largely negative effects of livestock presence versus absence on wild herbivores reported in other rangelands globally (Keesing and Young, 2014; Schieltz and Rubenstein, 2016). The strong negative response of eland to cattle stocking rates may be, in part, due to competition over forbs. Forbs are a vital source of protein for cattle (Odadi et al., 2013) and are heavily relied upon by eland (68% forbs in diet; Kartzinel and Pringle, 2020), while rarely consumed by zebra (2% forbs in diet; Kartzinel et al., 2019; Kartzinel and Pringle, 2020).

Our results confirm that zebras are facilitated by megaherbivores in this system (Kimuyu et al., 2017; Wells et al., 2021a), due to tree density reductions (Guldemond and Van Aarde, 2008) and/or facilitation of grasses (Coverdale et al., 2016). However, we show that this facilitation effect is negated at high cattle stocking rates, expressed by a sharp reduction on zebra habitat use, particularly during the dry season. This builds on previous research suggesting that megaherbivores temper the negative effects of cattle at moderate stocking rates on zebras (Young et al., 2005; Kimuyu et al., 2017). Moreover, previous studies in this system suggest that the increasing grass cover by megaherbivores that facilitates zebra, is also a result of the former reducing cattle foraging efficiency. It has been suggested that this is due to the reduction of forb cover by elephants, which translates to cattle spending more time moving in search of patches with forbs (Odadi et al., 2009, 2013). Our results suggest that zebra habitat use is reduced at high cattle stocking rates in megaherbivore-accessible plots, because the heavy grazing (mostly by cattle) overwhelms the positive effects that reduced cattle foraging efficiency (by megaherbivores and intraspecific competition with other cattle) has on grass cover.

The diversity in body sizes and feeding strategies of wild savanna herbivores precludes confident generalisations from the responses of zebra and eland to other wild mesoherbivores. However, other equids, such as Grevy's zebra *Equus grevyi*, as well as predominantly grazing bovids, such as hartebeest *Alcelaphus buselaphus* (89% grass in diet; Kartzinel and Pringle, 2020), may respond in similar ways to zebras. Likewise, the responses of eland may reflect those of species with comparable feeding strategies, such as Grant's gazelle Nanger granti and impala *Aepyceros melampus* (Kartzinel et al., 2019; Kartzinel and Pringle, 2020). Cattle grazing may also facilitate smaller-bodied short grass specialists, such as Thomson's gazelle Eudorcas thomsoni and warthog *Phacochoerus africanus* (Bhola et al., 2012; Ogutu et al., 2014; Crego et al., 2020; Wells et al., 2021a).

Our results provide further evidence that species interactions can be complex and mediated by different factors, such as season and changes in vegetation structure due to megaherbivores (Odadi et al., 2009; Kimuyu et al., 2017). Further experimental research in other grassland systems testing different stocking rates can help elucidate the nature of livestock-wildlife interactions, which livestock producers generally assume to be competitive, despite the lack of evidence (Ranglack et al., 2015; Traba et al., 2017). Such information can be important to find novel management strategies that can promote coexistence between wild and domestic species (Pozo et al., 2021).

Cattle Foraging Efficiency Responses to Cattle Stocking Rate

Increasing cattle stocking rate had a greater negative impact on cattle foraging efficiency (dry g step^{-1} min^{-1}) than did the presence of large wild herbivores, particularly in the dry season. This suggests that high cattle stocking rates (at greater numbers than large wild herbivores) increase intraspecific competition among cattle during drier periods and is a more important factor in reducing foraging efficiency than interspecific competition. The stronger influence of cattle stocking rate on cattle foraging efficiency, compared to season and large wild herbivore accessibility, highlights the importance of stocking rates in determining individual performance of domestic animals noted in other rangelands (Briske et al., 2003; Smart et al., 2010; Fang et al., 2014; Raynor et al., 2021).

Among the large wild herbivores, megaherbivores had a stronger effect on cattle foraging efficiency than mesoherbivores, possibly due to more intense competition over protein-rich forbs (Odadi et al., 2009, 2013). The effects of cattle stocking rate and megaherbivores on cattle foraging efficiency were absent or weaker during the wet season (**Figure 3**). This may be because grass and forb availability is less limited, as evidenced by differences between treatments being smaller due to grazing-induced compensatory plant growth (McNaughton et al., 1983; Charles et al., 2017; Wells et al., 2021b). However, high cattle stocking rates and wild mesoherbivores suppressed cattle foraging efficiency more than additively in the wet season (**Figure 3**). This statistically significant interaction suggests that there is a threshold number of animals (domestic and wild) foraging in a plot at which the herbivory-enhanced plant productivity is reversed and competition between herbivores intensifies. The trend toward facilitative effects of wild mesoherbivores on cattle performance at moderate stocking rates, although lacking strong statistical support (**Figure 3**), mirrors results of previous research in this system (Odadi et al., 2011). Crucially, our results show that this facilitation shifts to competition at high cattle stocking rates. The interactive effect of cattle and wild mesoherbivores was not observed in the dry season, possibly because the suppression of cattle foraging efficiency is dominated by the negative effects of cattle stocking rate and, to a lesser extent, megaherbivores.

Implications for Wildlife Conservation and Cattle Management in Rangelands

In African rangelands, pastoral societies have shared livestock foraging areas and migratory routes with wildlife for thousands of years and domestic animals remain embedded in the cultural identity and livelihoods of many pastoral communities today (Homewood, 2009; Fynn et al., 2016). Historically, wildlife co-existed in high numbers alongside pastoral communities and still do under certain conditions today (Tyrrell et al., 2017; Russell et al., 2018; Crego et al., 2020; Kiffner et al., 2020), but this relationship has deteriorated in recent decades (Reid et al., 2008; Løvschal et al., 2019). Reduced pastoralist mobility and increased livestock numbers has led to continuous grazing over the same areas, which, at high stocking rates, can result in land degradation that is detrimental to both livestock production and wildlife populations (Western et al., 2009). Our results confirm that higher stocking rates negatively affect large wild herbivores. Results also show that in the presence of megaherbivores, lowering cattle stocking rate to moderate can benefit wild mesoherbivores by alleviating interspecific competition. Moderate stocking rates were also shown to improve cattle foraging efficiency by mitigating intraspecific competition. This opens the possibility for a win-win scenario for both people and wildlife across Africa. However, herd-level cattle productivity can increase with cattle stocking rate, even while individual-level performance declines (Smart et al., 2010; Fang et al., 2014; Raynor et al., 2021). This would lead to a tradeoff between herd-level cattle productivity and wildlife conservation that requires further investigation.

Stocking rate is an important aspect of livestock grazing practices (Briske et al., 2003), but there are other factors that may influence the effects of domestic animals on native wild herbivores, such as the timing, duration, and intensity of grazing, as well as herd composition (Schieltz and Rubenstein, 2016; Odadi et al., 2017b). One of the limitations of our study was that we only investigated one rotational grazing regime at different stocking rates. Although this is representative of privately managed ranches in the areas surrounding the study site, it contrasts the largely continuous grazing in many communally managed rangelands that is linked to reduced mobility (Letai and Lind, 2013). However, our results may be representative of certain communally managed rangelands, where rotational grazing practices are becoming increasingly common (e.g., Odadi et al., 2017b). Comparisons of different grazing regimes while maintaining constant overall stocking rates would provide insights into how rangeland managers can adapt grazing practices to minimize competition with native wild herbivores (Augustine et al., 2020).

Because our study focused on cattle, it may be challenging to draw inference from our results to rangeland systems with other domestic species with differing foraging characteristics. Similar research on other domestic livestock species with different diets will be critical to complement our study, as sheep, goats, and camels are becoming more prevalent in rangelands across Africa (Ogutu et al., 2016; Løvschal et al., 2019; Volpato and King, 2019) and other continents (Bainbridge, 2007). It will also be important to investigate how observed climatic changes (Schmocker et al., 2016) will affect interactions between cattle and wild herbivores due to variations in vegetation productivity.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

HW, LS, AD, WO, DK, and TY conceived and designed the methodology. HW, JE, and MN collected the data. HW and RC analysed the data and led the writing of the manuscript. All authors contributed critically to drafts and approved publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.825689/full#supplementary-material

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Increasing Anthropogenic Disturbance Restricts Wildebeest Movement Across East African Grazing Systems

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The ability to move is essential for animals to find mates, escape predation, and meet energy and water demands. This is especially important across grazing systems where vegetation productivity can vary drastically between seasons or years. With grasslands undergoing significant changes due to climate change and anthropogenic development, there is an urgent need to determine the relative impacts of these pressures on the movement capacity of native herbivores. To measure these impacts, we fitted 36 white-bearded wildebeest (*Connochaetes taurinus*) with GPS collars across three study areas in southern Kenya (Amboseli Basin, Athi-Kaputiei Plains, and Mara) to test the relationship between movement (e.g., directional persistence, speed, home range crossing time) and gradients of vegetation productivity (i.e., NDVI) and anthropogenic disturbance. As expected, wildebeest moved the most (21.0 km day^{-1}; CI: 18.7–23.3) across areas where movement was facilitated by low human footprint and necessitated by low vegetation productivity (Amboseli Basin). However, in areas with moderate vegetation productivity (Athi-Kaputiei Plains), wildebeest moved the least (13.3 km day^{-1}; CI: 11.0–15.5). This deviation from expectations was largely explained by impediments to movement associated with a large human footprint. Notably, the movements of wildebeest in this area were also less directed than the other study populations, suggesting that anthropogenic disturbance (i.e., roads, fences, and the expansion of settlements) impacts the ability of wildebeest to move and access available resources. In areas with high vegetation productivity and moderate human footprint (Mara), we observed intermediate levels of daily movement (14.2 km day^{-1}; CI: 12.3–16.1). Wildebeest across each of the study systems used grassland habitats outside

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of protected areas extensively, highlighting the importance of unprotected landscapes for conserving mobile species. These results provide unique insights into the interactive effects of climate and anthropogenic development on the movements of a dominant herbivore in East Africa and present a cautionary tale for the development of grazing ecosystems elsewhere.

Keywords: wildebeest (*Connochaetes taurinus*), anthropogenic disturbance, NDVI, *ctmm*, ecosystem resilience, habitat loss and fragmentation

INTRODUCTION

The ability to move and exploit resources at multiple spatio-temporal scales is key to maintaining biologically viable wildlife populations (Bolger et al., 2008; Holdo et al., 2011). Rapid population growth and anthropogenic development, however, threaten species' survival by impeding access to critical resources, restricting movements to increasingly fragmented habitat patches, and threatening the sustainability of long-distance migrations (Berger, 2004; Wilcove and Wikelski, 2008; Harris et al., 2009; Kauffman et al., 2021). Widespread changes in climate further complicate these pressures, placing new demands on the plasticity of animal movement and necessitating rapid and flexible responses to shifting resources (Davidson et al., 2020).

A recent comparison of movement strategies across multiple ungulate species revealed that broad-scale variation in vegetation productivity effectively determines the movement strategy (i.e., migration, residency, nomadism) exhibited by ungulates across a range of environmental contexts (e.g., plains to tundra; Mueller et al., 2011). Likewise, in a global synthesis of tracking data from 57 mammal species, Tucker et al. (2018) found that mammals residing in areas with high levels of anthropogenic modification exhibited movements that were one-half to one-third the extent of their movements in areas with lower modification. Such contractions in movement are expected to have important implications for the maintenance of key biological processes (e.g., predator-prey interactions, nutrient cycling, disease transmission) and have been directly linked to population declines in a number of species (Boone et al., 2005; Boone, 2007; Blackburn et al., 2011; Herbener et al., 2012; Kauffman et al., 2021).

While these findings provide strong evidence that landscape and climate play central roles in governing movement dynamics and associated survival, there has been limited research into the combined effects of these factors on the movement capacity of wide-ranging species. Without this knowledge, we limit our ability to predict the impact of future changes to ecosystems that support long-distance animal movements, such as grasslands or savannas. Holdo et al. (2011) demonstrated the value of such information by modeling the predicted impacts of proposed road construction on the movement and population dynamics of the world's largest population of migratory wildebeest. Similarly, Armstrong et al. (2016) used theoretical simulations to demonstrate that developed landscapes prevented multiple species from tracking ephemeral resource fluctuations. Importantly, Boone et al. (2005) found that anthropogenic disturbance had the greatest negative impact on herbivore populations that occur in habitats with medium to high levels of vegetation productivity, because these areas support a greater abundance of species than less productive areas.

Here, we build on these theoretical insights by comparing key characteristics of movement between three populations of white-bearded wildebeest (*Connochaetes taurinus*) in southern Kenya. Central to maintaining the ecology and economy of the region (Sinclair, 2003; Hopcraft et al., 2014), wildebeest are known to be particularly sensitive to habitat fragmentation from anthropogenic disturbance (e.g., Kahurananga and Silkiluwasha, 1997), a factor which has led to precipitous declines of multiple populations of wildebeest over the past three decades (Ottichilo et al., 2001; Serneels and Lambin, 2001; Reid et al., 2008; Ogutu et al., 2011, 2013, 2014; Said et al., 2016). By relating movement characteristics (e.g., directional persistence, speed, home range crossing time) to vegetation productivity and anthropogenic disturbance, we provide new evidence into the compounding effects of climate and landscape change on an archetypal keystone species of African grasslands.

Specifically, we predicted (*P1*) that wildebeest in areas with low vegetation productivity (Amboseli Basin) would move more per day, with greater directional persistence, and an increased home range crossing time than wildebeest in areas with intermediate (Athi-Kaputiei Plains) to high (Mara) levels of productivity. This is due to the recognition that herbivore movements must increase as levels of vegetation productivity decrease to maximize forage intake and energy gain (Wilmshurst et al., 1999). In areas with high anthropogenic footprint (Athi-Kaputiei Plains), however, we predicted that the daily movements of wildebeest (*P2*) would be more restricted, leading to increased levels of tortuosity (decreased directional persistence), and reduced home range crossing times (e.g., Tucker et al., 2018).

MATERIALS AND METHODS

Study Area

Research was conducted across three study areas located principally in Kajiado and Narok counties in southern Kenya (**Figure 1**). These areas, referred to in the text as the Amboseli Basin (2°30′S, 37°15′E), Athi-Kaputiei Plains (1°30′S, 36°55′E), and Mara (1°15′S, 35°20′E), represent portions of the wildlife dispersal areas in and around Amboseli National Park, Nairobi National Park, and the Maasai Mara National Reserve, respectively. We use these names as a means of convenience to reference the geographic regions where wildebeest were initially

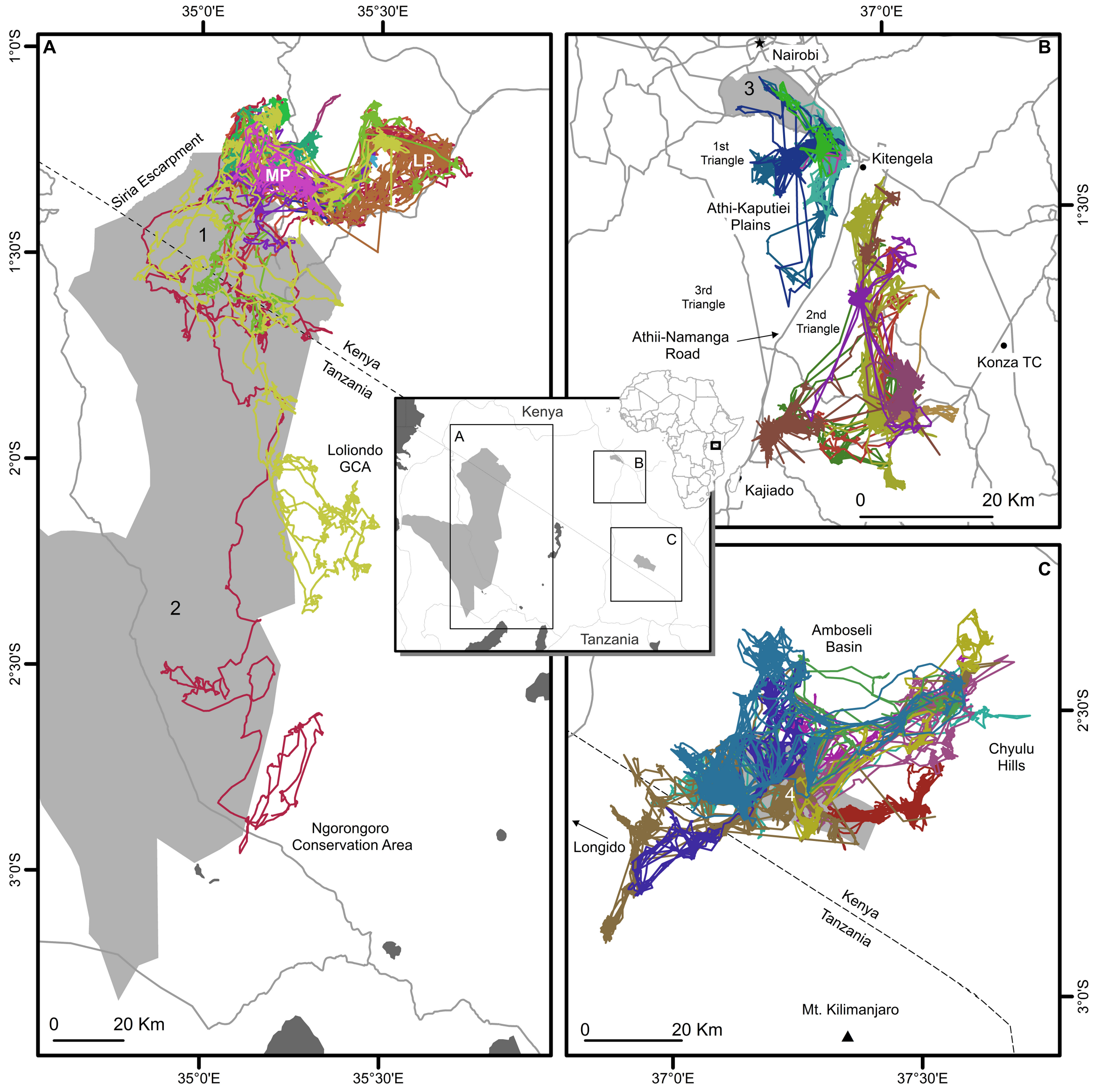

FIGURE 1 | Wildebeest movements across three study areas in Kenya. Individual wildebeest movements (colored lines) tracked from 2010–2013 and displayed across three study areas in Kenya (**A**, Mara; **B**, Athi-Kaputiei Plains; **C**, Amboseli Basin). Protected areas (1, Maasai Mara National Reserve; 2, Serengeti National Park; 3, Nairobi National Park; 4, Amboseli National Park) partially obscured. Loita Plains (LP), Mara Plains (MP), Loliondo Game Controlled Area (GCA), and Ngorongoro Conservation Area labeled in A. Major roads (gray lines) provided for reference.

collared, even though some animals we monitored moved extensively beyond the boundaries of these areas throughout the course of our study period. Thus, our description of each site includes additional habitats and portions of ecosystems that are not normally considered part of these systems, especially as it relates to the Mara.

A strong increase in rainfall along a southeast to northwest gradient is associated with increasing levels of vegetation productivity across our study systems. The Amboseli Basin is the least productive area, with rainfall averaging 568 mm yr^{-1} [range (1981–2020): 368–935 mm yr^{-1}] (Funk et al., 2015). The Athi-Kaputiei Plains experiences intermediate levels of productivity, with rainfall averaging 688 mm yr^{-1} [range (1981–2020): 425–1,061 mm yr^{-1}] (Funk et al., 2015). The Mara is the most productive area, with rainfall averaging 841 mm yr^{-1} [range (1981–2020): 640–1,197 mm yr^{-1}] (Funk et al., 2015). April is generally the wettest month of the year, with the majority of rainfall falling during two rainy seasons (short rains: November-December; long rains: March-June).

Amboseli Basin

The Amboseli Basin (6,600 km^2) is a semi-arid tropical environment located in the rain shadow of Mount Kilimanjaro. Wildebeest were observed to move from Longido in Tanzania to the Chyulu Hills in Kenya (**Figure 1**). Amboseli National Park (ANP, 392 km^2) lies at the center of this study area, providing formal protection to a small portion (6%) of the range in which wildlife disperse. The Amboseli Basin is covered primarily by open grassland, with woodlands and swamps fed from mountain run-off prevalent in the southern part of the ecosystem (Western, 1973). During the dry season, most species of wildlife and livestock are limited to areas where permanent water exists (i.e., swamps and boreholes). In wet season periods, species disperse and are more widely distributed across the ecosystem.

Over the past few decades, widespread changes have occurred across the Amboseli Basin, with average annual temperature increasing in all months of the year, but particularly in months with higher maximum temperatures (e.g., January–March) (Altmann et al., 2002). Rainfall has remained consistently low throughout the long dry season (June–October), with seasonal timing becoming more variable (Altmann et al., 2002). Traditional pastoralism is the dominant land-use. Livestock density and grazing pressure is high, a factor leading to habitat degradation and changes to the woodland-grassland mosaic (Altmann et al., 2002). Human population density, however, is low, averaging 14 people km^{-2} at the time this study was conducted (Bright et al., 2015). Rainfall is the main climatic component limiting wildebeest populations through its controlling influence on vegetation production and quality. The 2009 drought, for example, resulted in an estimated 97% mortality in wildebeest (6,800 of 7,000 individuals) (Western, 2010; Ogutu et al., 2014).

Athi-Kaputiei Plains

The Athi-Kaputiei Plains (3,425 km^2) once supported some of the highest densities of wildlife in all of East Africa (Percival, 1928; Simon, 1962). In the last half-century, however, human settlement has expanded rapidly across the region, reducing and fragmenting the remaining habitat and resulting in precipitous wildlife population declines (Ogutu et al., 2013; Said et al., 2016). Reid et al. (2008) estimated a 72% population decline in wildebeest from 1977–2004, with Ogutu et al. (2013) estimating population declines as high as 93% (a decline from 25,765 to 1,700 individuals). Recent population estimates indicate a complete extirpation of wildebeest from large portions of the ecosystem, with the total wildebeest population estimated to be as low as 509 individuals by 2014 (Said et al., 2016).

The area is sometimes referred to as the three “triangles” because of its geometric shape (**Figure 1**). The first triangle, bordered to the north by Nairobi National Park (117 km^2), is located just 10 km from the center of Kenya’s capital city, Nairobi. Human population density is greatest across this area, averaging 45 people km^{-2} at the time this study was conducted (Bright et al., 2015). Open habitat formerly existed in the 2nd and 3rd triangles (**Figure 1**), but has shrunken dramatically as the footprint of the city has expanded. Livestock keeping continues to be the dominant livelihood, outnumbering wildlife 4–1 (Reid et al., 2008). The area is extensively fenced (see Reid et al., 2008; Said et al., 2016), resulting in a 22% reduction in area accessible to wildlife and presenting severe obstructions to wildlife movement (Owen-Smith and Ogutu, 2012). A major highway, connecting Kitengela with Kajiado, and demarcating the boundary between the 1st and 2nd triangles, separates the traditional dry and wet season ranges of the species, bisecting a major migratory route. Various other infrastructure projects, including a multi-lane bypass and an elevated standard gauge railway, further restrict and/or reduce the amount of habitat available to wildebeest.

Mara

The Mara is the largest of our three study areas (19,200 km^2), extending across portions of the Serengeti-Mara ecosystem in Kenya and Tanzania. This area includes the Loita Plains, the Mara Plains, the Maasai Mara National Reserve (MMNR), the Loliondo Game Controlled Area, the Ngorongoro Conservation Area, and Serengeti National Park (SNP) (**Figure 1**). A series of conservancies lie adjacent to and north of the MMNR (1,505 km^2), comprising an additional 834 km^2 of the Mara Plains at the time this study was conducted. Seventeen conservancies now exist across the region, expanding the total area protected to 1,450 km^2. Maasai pastoralists are restricted from the MMNR, but granted limited access to the conservancies during the dry season. Livestock incursions into the MMNR, however, are common. The Mara ecosystem is bounded by the Siria Escarpment to the west, the forested Mau Uplands to the north, and the Rift Wall to the east.

Large-scale mechanized agriculture has occurred across the northern and western boundaries of the Mara ecosystem (Homewood et al., 2001; Serneels et al., 2001), resulting in sharp declines in wildebeest (Serneels and Lambin, 2001). From 1977 to 1997, the resident wildebeest population in Kenya declined by 81%, from 119,000 to 22,000 individuals (Ottichilo et al., 2001). Further declines in the resident wildebeest population have been observed over the past decade (2010–2020), coinciding with a period of rapid fence, road, and settlement expansion that occurred after our GPS tracking study concluded. These land-cover changes most significantly impacted the unprotected Loita Plains (Løvschal et al., 2017). Human population density at the time this study was conducted averaged 23 people km^{-2}, with higher densities (34 people km^{-2}) occurring in the Kenyan portion of the ecosystem where research was primarily focused (Bright et al., 2015).

Wildebeest Movement Data

We fitted 36 adult wildebeest across our three study areas (National Council for Science and Technology research permit no. NCST/RR1/12/1/MAS/39/4) with Lotek WildCell® GPS collars. Collars were fitted on animals in May 2010 across the Mara (n = 15) and in October 2010 across the Athi-Kaputiei Plains (n = 12) and the Amboseli Basin (n = 9). All individuals were selected from distinct groups. No animals were collared within national park/reserve boundaries. The mean pairwise distance between initial locations was 13 km in the Amboseli Basin, 27 km in the Athi-Kaputiei Plains, and 22 km in the Mara. All aspects of animal handling were conducted under the direction of a Kenya Wildlife Service field veterinarian and approved by the International Animal Care and Use Committee (IACUC) at Colorado State University, Fort Collins, CO, United States (Approval No. 09-214A-02).

Tracking devices were programmed to collect 16 positions per day, every hour during the day (06:00–18:00) and every

3 h at night (18:00–06:00), over a 3-year study period. We filtered the dataset, removing suspected erroneous data points using the positional accuracy information output with each data point. Only three-dimensional positions with a positional dilution of precision (PDOP) $\leq$ 10.0 and two-dimensional positions with a PDOP $\leq$ 5.0 were retained. An additional erroneous data point was removed by using tools implemented in the Continuous-Time Movement Modeling (CTMM) framework [function *outlie()* in R; Fleming et al., 2020] to identify unrealistic movements based on the speed and distance moved. Data were projected to Albers Equal Area projection, WGS84 datum. Wildebeest sex, approximate age, start/end dates of the collaring period, and fix success are summarized in **Supplementary Table 1**.

Quantifying Animal Movement

The Continuous-Time Movement Modeling (CTMM) framework (Calabrese et al., 2016) contains functions for identifying and fitting continuous-space, continuous-time stochastic movement models to animal tracking data. The framework includes variogram fitting (Fleming et al., 2014b) and non-Markovian maximum likelihood estimation (Fleming et al., 2014a) to facilitate the identification of important features inherent in the data (e.g., range residency) and optimize model fitting. Importantly, CTMM is robust to irregular sampling intervals, gaps in data collection, and complex autocorrelation structures (Calabrese et al., 2016), features common to most GPS tracking datasets. In addition, since parameter estimates and their confidence intervals derived from CTMM are based on model-based inference, animal trajectories do not need to be truncated to the same temporal interval to make comparison possible—as would be required when comparing metrics derived from straight-line displacements.

We estimated animal movement metrics, including directional persistence, home range crossing timescale, and average distance traveled per day, using CTMM following detailed instructions provided by Calabrese et al. (2016) and Noonan et al. (2019), and vignettes contained within the *ctmm* R package (Fleming and Calabrese, 2021). Analysis steps included fitting an error model to the data, investigating potential outliers, estimating the variogram, fitting movement models to the variogram structure [e.g., Brownian motion (BM), Ornstein-Uhlenbeck (OU), Ornstein-Uhlenbeck with foraging (OUF)], and performing model selection based on AICc (Akaike, 1974). For each animal, we plotted the estimated semi-variance as a function of time lag to visually inspect the autocorrelation structure (Fleming et al., 2014a) and assess if animals met the range residency assumption, indicated by the estimated semi-variance reaching an asymptote that roughly corresponds to the home-range crossing timescale (Fleming et al., 2014a; Calabrese et al., 2016).

Best fitting CTMM models were either OU or OUF (**Supplementary Table 1**). OUF models are described by three parameters [i.e., home range crossing timescale (days), velocity autocorrelation timescale (minutes), and variance (km^2)], resulting in estimates of home range, home range crossing timescale, directional persistence, and average distance traveled. For all animals fitted with OUF models, we used a simulation-based approach detailed in Noonan et al. (2019) to sample from the distribution of trajectories conditional on the data to estimate the average distance traveled per day during the duration of the tracking period [function *speed()*; Noonan et al., 2019]. Average distance traveled per day for animal movement data fitted with OU models, described by two parameters [i.e., home range crossing timescale (days) and variance (km^2)], could not be estimated.

Landscape Dynamics

To describe spatial-temporal changes in resources across each study area, we extracted MODIS (MOD13Q1) Normalized Difference Vegetation Index (NDVI) raster subsets (Carroll et al., 2004) from the minimum convex polygon (MCP) derived from wildebeest locations across each study area, buffered by 10-km, over a 10-year period (2004–2013). NDVI is known to be a reliable measure of vegetation productivity/greenness (Tucker, 1979; Goward and Prince, 1995) and has been shown to be an important predictor of movement and use for various herbivores (Pettorelli et al., 2011; Ryan et al., 2012; Stabach et al., 2017), including wildebeest (Boone et al., 2006; Hopcraft et al., 2014). Using the semi-monthly NDVI data, we calculated the temporal variability and predictability of each landscape, as described by Mueller et al. (2011). Temporal variability was calculated by summarizing the spatial average of the mean NDVI within semi-monthly periods to provide an estimate of resource phenology within years. Predictability characterizes the variation across each landscape from year to year [i.e., the repeatability (or lack thereof) of the landscape] (Mueller and Fagan, 2008). To estimate predictability, we calculated the inverse of the spatial average of the standard deviations of NDVI at each grid cell across all images within a semi-monthly period (i.e., 1 − unpredictability).

Statistical Analyses

We tested for significant differences between movement statistics by comparing results using hierarchical Bayesian fixed-effect one-way ANOVAs (McCarthy, 2007; Kéry, 2010). The variable home range crossing timescale was log transformed for analysis. We estimated marginal posterior distributions of parameters using Markov chain Monte Carlo (MCMC) methods. We fitted the model using a MCMC algorithm with 10,000 iterations and a 20% burn-in period. We assessed convergence by visually inspecting trace plots to ensure a reasonable exploration of the parameter space and confirming that the potential scale reduction factor was < 1.02 for each variable (Gelman and Rubin, 1992). We calculated the probability (*Prob*) that the mean of one group was greater than the other by sampling from each of the resulting posterior distributions (Gelman and Hill, 2007).

We fit linear regression models to investigate how average distance traveled per day differed among individuals and to what extent these distances were related to estimates of landscape productivity and human disturbance. To quantify landscape productivity at wildebeest locations, we extracted the NDVI data value at each GPS point observation, matching the spatio-temporal dynamics of the NDVI data (Crego et al., 2021) before aggregating the means for each animal. Human disturbance was similarly quantified by calculating the distance to digitized structures weighted by the estimated human population density (Bright et al., 2009). Adopted from Hopcraft et al. (2014) and referred to as "Anthropogenic Footprint," this method incorporates small-scale disturbances that would have otherwise been missed due to the coarse resolution of the human population dataset (1 km^2). Densely populated areas have the highest values, whereas areas furthest from small or sparsely populated areas have the lowest values (i.e., lowest disturbance). Further information about this data layer can be found in Stabach et al. (2016).

We created four regression models, including NDVI only, anthropogenic footprint only, additive effects (NDVI + anthropogenic footprint), and interactive effects (NDVI * anthropogenic footprint). Competing models were evaluated based on DIC (Spiegelhalter et al., 2002). NDVI and anthropogenic footprint were scaled and centered to enhance coefficient comparability. We evaluated the goodness of fit of the model to the data by calculating the Bayesian *p*-value—the proportion of times when the replicated "ideal" dataset is greater than the actual dataset (Gelman and Hill, 2007; Kéry, 2010). *P*-values close to 0.50 indicate a good model fit (i.e., no difference between the actual and replicated datasets). Model variability was displayed by randomly sampling (5,000 times) from the posterior distributions of the alpha and beta parameters. All statistical analyses were conducted in the R environment for statistical computing (R Development Core Team, 2020) using the jagsUI package (McCloskey et al., 2011), version 1.5.2.

RESULTS

Landscape Dynamics

Seasonal patterns of vegetative greenness were similar across each study area, with the Athi-Kaputiei Plains exhibiting the greatest range in landscape seasonality (i.e., difference in NDVI throughout the year) and the Amboseli Basin the least (**Figure 2A**). Across the Mara, landscape predictability was low (<0.5) for most of the year, especially from December–June (day 321–177). Landscape predictability across the Athi-Kaputiei Plains was similar to the Mara, with the short rains (February–April; day 49–81) being marginally more predictable across this region. Landscape predictability was highest across the Amboseli Basin (except in September–October; day 257–289), with the long dry season (June–November; day 177–305) being the most predictable feature across each study area (**Figure 2B**).

Animal Movements

Wildebeest across the Amboseli Basin moved more per day (21.0 km day^{-1}; CRI: 18.7–23.3) and with greater average directional persistence (36.5 min; CRI: 30.9–42.0) than wildebeest across the Athi-Kaputiei Plains [avg daily movement: 13.3 km day^{-1} (CRI: 11.0–15.5); avg directional persistence: 18.1 min (CRI: 12.8–23.3)] or Mara [avg daily movement: 14.2 km day^{-1} (12.3–16.1); avg directional persistence: 23.9 min (CRI: 19.3–28.3)] (**Figures 3A,B** and **Supplementary Table 1**). The probability that the movements (daily distance moved and directional persistence) of Amboseli Basin wildebeest were greater than those of wildebeest across the Athi-Kaputiei Plains or Mara were all > 0.99. Wildebeest across the Athi-Kaputiei Plains rarely (*Prob* = 0.05) moved with more directional persistence than wildebeest across the Mara. Similarly, the probability that wildebeest across the Athi-Kaputiei Plains (range: 8.2–17.7 km day^{-1}) moved further per day than wildebeest across the Mara (range: 8.2–20.6 km day^{-1}) was 0.26, highlighted by the overlap in the posterior distributions of this parameter (**Figures 3A,B**).

Average home range crossing timescale (log transformed) was similar between wildebeest across the Amboseli Basin (2.9 days; 95% CRI: 1.7–4.2) and Mara (2.7 days; 95% CRI: 1.7–3.7), with posterior distributions that were nearly indistinguishable. The probability that home range crossing timescale was greater for wildebeest across the Amboseli Basin in comparison to the Mara was 0.61. Wildebeest across the Athi-Kaputiei Plains had a shorter average home range crossing timescale (1.6 days; 95% CRI: 0.5–2.7) than either their Amboseli Basin or Mara counterparts. The probability that the home range crossing timescale of Amboseli Basin wildebeest was greater than that of Athi-Kaputiei Plains wildebeest was 0.94. Wildebeest across the Athi-Kaputiei Plains, however, seldom (*Prob* = 0.07) had a home range crossing timescale greater than that of Mara wildebeest (**Figure 3C**).

One wildebeest in the Amboseli Basin moved 6,197.8 km over a 728-day study period, the longest distance traversed by any animal we monitored. A second wildebeest, animal 2834, moved south from the Loita Plains to the Ngorongoro Conservation Area in Tanzania (**Figure 1**), a total net displacement of 205.4 km from its initial collaring location. Another wildebeest across the Mara, animal 2845, moved south through the MMNR and into the Loliondo Game Controlled Area before returning to within 5.9-m of its initial collaring location. Across the Athi-Kaputiei Plains, the maximum net displacement made by a wildebeest from initial collaring locations was 38.2 km, with no animal observed to cross the tarmac road (Athi-Namanga road, **Figure 1**) bisecting the seasonal habitat range of the species (**Supplementary Table 1**).

We classified 33.7% of GPS locations (21,075 of 62,392) within the national park boundary across the Amboseli Basin. Only 3.8% of locations (3,795 of 101,265) across the Athi-Kaputiei Plains and 8.0% of locations (9,228 of 116,061) across the Mara were observed within national park/national reserve boundaries (**Figure 1**). Wildebeest across the Mara, however, used the conservancies located to the north of the Maasai Mara National Reserve extensively, increasing the percentage of locations within protected area boundaries to 73.4% (85,194 of 116,061) when included.

Our best fitting model included additive effects of NDVI and anthropogenic footprint on average daily movement (**Supplementary Table 2**), with the Bayesian *p*-value (0.495) indicating an adequate fit of the regression model to the data. Both independent variables had strong negative effects ($\beta_{\text{NDVI}} = -2.78$; CRI: −3.90 to −1.65 and $\beta_{\text{AnthFootprint}} = -2.18$; CRI: −3.33 to −1.00) on average daily movement ($a = 15.62$ km day^{-1}, CRI: 14.48–16.75 km day^{-1}). Wildebeest across the Athi-Kaputiei Plains deviated from the linear prediction in relation to NDVI but fit closely to the prediction in relation to anthropogenic footprint (**Figure 4**). All wildebeest across the

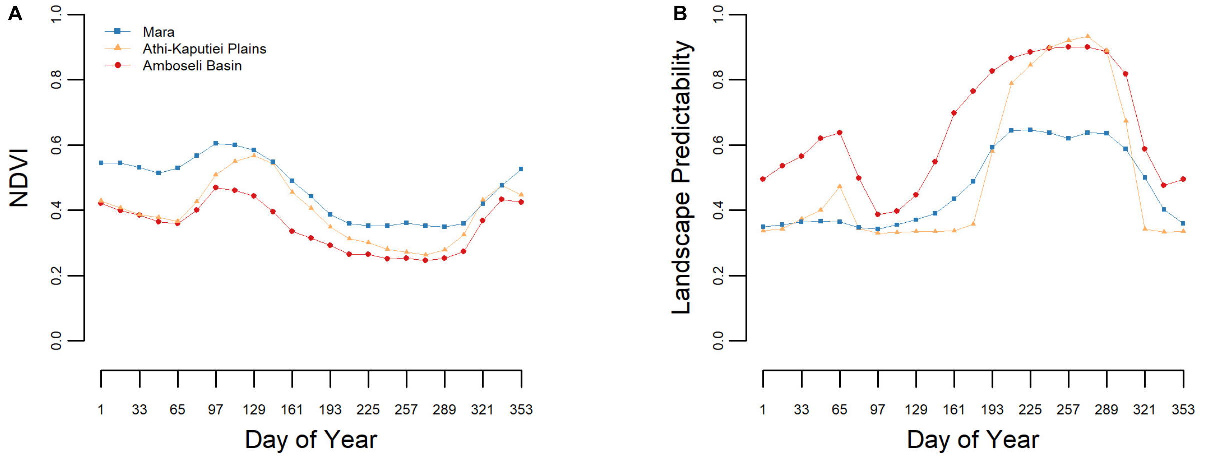

FIGURE 2 | Comparison of landscape dynamics. Landscape phenology based on 10-years (2004–2013) of MODIS NDVI data across three landscapes in southern Kenya with regard to vegetation greenness **(A)** and landscape predictability **(B)**.

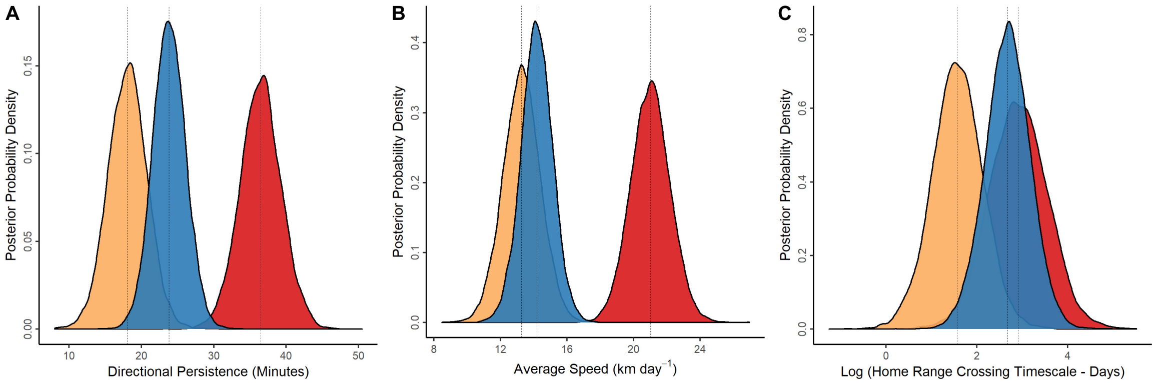

FIGURE 3 | Summary of wildebeest movement. Movement parameters estimated from continuous-space, continuous-time stochastic movement models, including directional persistence **(A)**, average speed **(B)**, and home range crossing timescale **(C)**. Posterior distributions for panels **(A–C)** shown to highlight parameter overlap. Vertical dashed lines displayed are posterior means. Amboseli Basin = red; Athi-Kaputiei Plains = orange; Mara = blue.

Amboseli Basin and Mara were located in areas with low average anthropogenic footprint (−1.3 to 0.1). Average anthropogenic footprint across the Athi-Kaputiei Plains where wildebeest were located was > 0.4.

DISCUSSION

By linking the movements of wildebeest across three study areas with contrasting dynamics of landscape productivity and anthropogenic disturbance, we found that high levels of human activity drove unexpected relationships between the movement capacity of herbivores and productivity of the landscape. For example, wildebeest movement was expected to scale positively with vegetation productivity across all sites (*P1*). However, we found movements to be most restricted at moderate levels of vegetation productivity (Athi-Kaputiei Plains). This loss of movement capacity was observed as a decrease in average daily movement, an increase in tortuosity (decreased directional persistence), and a reduced home range crossing timescale relative to sites with lower levels of anthropogenic disturbance (Amboseli Basin and Mara). Moreover, the strong explanatory power of anthropogenic disturbance relative to other variables tested (i.e., NDVI) suggests that such changes are the consequence of rapid and dramatic landscape conversion (*P2*), trends which continue across the region (Reid et al., 2008; McCloskey et al., 2011; Said et al., 2016).

Movement is intimately related to an animal's fitness, facilitating the ability to access better quality resources, encounter potential mates, and move away from an area when conditions deteriorate (Turchin, 1998; Morales et al., 2010; van Moorter et al., 2013). The importance of movement is often amplified in semi-arid and arid lands where resources are limited (Conrad, 1941; Thornton et al., 2006; Boone and Wang, 2007). While we lack data which relates movement declines with fitness consequences, our analysis complements previous work showing that habitat disturbance can have a measurable negative effect on stress hormones (e.g., fecal glucocorticoid metabolites) in

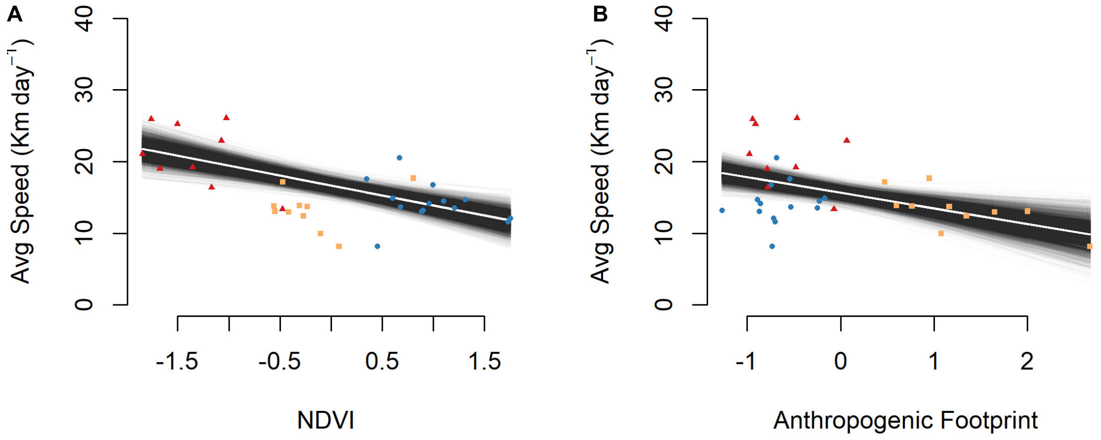

FIGURE 4 | Average daily movement (km day^{-1}) in relation to vegetation greenness (NDVI) and anthropogenic footprint. Daily movements decrease with an increase in **(A)** NDVI and **(B)** anthropogenic footprint. Independent variables have been scaled and centered. Model variability displayed by randomly sampling from the posterior distributions of the alpha and beta parameters. Amboseli Basin = red triangles; Athi-Kaputiei Plains = orange squares; Mara = blue circles.

wildebeest when vegetative conditions deteriorate (Stabach et al., 2015). Characteristics of long-term or chronic stress include a suppressed immune system, inhibition of reproductive behavior, and decreased growth (Moberg, 2000; Sapolsky, 2000; Keay et al., 2006), factors which could be detrimental to the survival of individuals or populations.

Similar to the trends observed in the Athi-Kaputiei Plains, recent work from the Mara (2017–present) suggests that severe habitat degradation (Li et al., 2020) and fence expansion (Løvschal et al., 2017; Tyrrell et al., 2022) are driving reductions in wildebeest movement and raising concerns about the persistence of this population into the future. Likewise, we expect that movement estimates from the Amboseli Basin may be conservative because this population was in a period of recovery following the devastating drought that occurred in 2009 (Western, 2010; Ogutu et al., 2014). The resulting decline in animal densities should have decreased competition for resources and reduced the distance required to access sufficient forage to meet energy demands (e.g., Merrill et al., 2021). As a result, additional research into the impacts of anthropogenic disturbance would be expected to strengthen the inference observed in this study and further align with previous research conducted on mammal movement responses across a range of terrestrial ecosystems globally (Tucker et al., 2018).

In addition to these implications for population persistence, we found it notable that collared wildebeest were located primarily outside of protected area boundaries throughout the study period. This is particularly interesting given the comparatively low levels of anthropogenic disturbance within protected area boundaries, especially across the Athi-Kaputiei Plains where park boundaries abut one of East Africa's largest cities. The observed effect could be reflective of differences in vegetation quality, predation pressure, or alternatively, a result of capture-induced bias, since we did not collar any animals within national park/reserve boundaries. Across the Athi-Kaputiei Plains, our results are at least partially biased by the Athi-Namanga road (**Figure 1**), as wildebeest did not move between the 1st and 2nd triangles during our study period. Wildebeest collared in the 2nd triangle were therefore unable to disperse to the national park. These data provide quantitative support, however, that this historic migration (see Reid et al., 2008) has completely collapsed, with concomitant effects on population abundance (Reid et al., 2008; Ogutu et al., 2013; Said et al., 2016).

Although we focused on two primary drivers of animal movement in this study (e.g., NDVI and anthropogenic footprint), we acknowledge that multiple forces shape the movement dynamics of wildebeest. Further research on water availability and livestock density may benefit from a specific focus. For example, wildebeest cannot survive without water for more than 2–3 days (Talbot and Talbot, 1963) and domestic livestock compete with wild herbivores for grazing resources (Schieltz and Rubenstein, 2016; Kimuyu et al., 2017; Crego et al., 2020; Connolly et al., 2021; Wells et al., 2022). However, data were not available at an appropriate spatio-temporal resolution to be included in this study. Moreover, Boone et al. (2006) demonstrated that NDVI is a better predictor of wildebeest movement than rainfall, suggesting that our models should sufficiently explain the variation in movement strategies we observed. We also found relatively high levels of correlation between anthropogenic footprint and the best available estimates of livestock density (Gilbert et al., 2018) for the Mara (0.57), indicating that this variable would have been removed during the first steps of model evaluation. Notably, we found little to no correlation between these metrics in the Amboseli Basin or Athi-Kaputiei Plains (0.18 and 0.04, respectively), but suspect that this was due to the mis-match between the spatial resolution of the livestock dataset (10-km at equatorial regions; Gilbert et al., 2018) and the spatial extent of each study area (6,600 and 3,425 km^2, respectively). More detailed information on livestock abundance could help to disentangle the potential confounding effects of livestock abundance with other aspects of human disturbance, but would require significant improvements in current methods for estimating livestock abundance at (relatively) small spatial scales, like those described here. Exciting new developments using high-resolution (<50 cm) satellite imagery are currently underway to map large mammals (including cattle) that could prove useful in future analyses (e.g., Duporge et al., 2020; Robinson et al., 2021).

The results of this study have important conservation implications across the region that can be applied to other systems, especially dryland systems where the ability of species to move is essential for survival (e.g., gazelle in the Mongolian steppe; Mueller et al., 2008; Dejid et al., 2019). Similarly, results from the Athi-Kaputiei Plains suggest that under scenarios of extreme climate change, the effects of anthropogenic disturbance may be compounded to a point that populations are unable to recover. Beyond the impacts to wildlife, the dramatic changes occurring to grasslands also impact the people that rely on these systems for survival. Pastoralists across the Athi-Kaputiei Plains, for example, have been voicing concerns about shrinking access to resources for decades (Galaty, 1994). Determining and conserving the dynamic extent of the ecosystem, where still possible, is thus imperative to allow for dispersal to support entire life-cycle processes and provide a means of ecosystem resilience (Allen and Singh, 2016), topics that have been highlighted by other authors (e.g., Thirgood et al., 2004; Martin et al., 2007; Bolger et al., 2008; Runge et al., 2014) and that are especially important as the duration, frequency, and intensity of drought are expected to increase (Haile et al., 2020).

DATA AVAILABILITY STATEMENT

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found below: Movebank Data Repository: https://www.datarepository.movebank.org/handle/10255/move.1095.

ETHICS STATEMENT

The animal study was reviewed and approved by International Animal Care and Use Committee at Colorado State University (Approval No. 09-214A-02).

AUTHOR CONTRIBUTIONS

RB, RR, JW, and JO conceived the project and provided project supervision and in-country coordination. RB, RR, and JW led animal captures/data collection. JS developed the analytical approach and conducted the analyses, with support from CF and RC. JS led the writing of the manuscript, with support from RB, RR, LH, RC, and PL. All authors contributed critically to the final draft and gave final approval for publication.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.846171/full#supplementary-material

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Bison Reintroduction to Mixed-Grass Prairie Is Associated With Increases in Bird Diversity and Cervid Occupancy in Riparian Areas

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In grassland ecosystems, grazing by large herbivores is a highly influential process that affects biodiversity by modifying the vegetative environment through selective consumption. Here, we test whether restoration of bison is associated with increased bird diversity and cervid occupancy in networks of riparian habitat within a temperate grassland ecosystem, mixed-grass prairie in northcentral Montana, United States. We used a long time-series of remote sensing imagery to examine changes in riparian vegetation structure in stream networks within bison and cattle pastures. We then assessed how vegetation structure influenced diversity of bird communities and detection rates of mammals in these same riparian networks. We found that percent cover of woody vegetation, and native grasses and forbs increased more rapidly over time in bison pastures, and that these changes in vegetation structure were associated with increased bird diversity and cervid occupancy. In conclusion, bison reintroduction appears to function as a passive riparian restoration strategy with positive diversity outcomes for birds and mammals.

Keywords: grassland, songbirds, buffalo, cattle, conservation, ungulates, rewilding, American Prairie

INTRODUCTION

Restoration of evolutionary grazing processes, those that replicate or mimic effects of native herbivores, is a common goal of restoration efforts in temperate grassland systems (Freese et al., 2014; Fuhlendorf et al., 2018). Grazing is a ubiquitous natural process that creates and maintains habitat for myriad grassland species (Milchunas et al., 1988; Gao and Carmel, 2020). Whereas native grazers are the preferred option for restoration, in nearly all temperate grassland systems, native grazers have been replaced with cattle (*Bos taurus*) (van Zanten et al., 2016), which are raised for milk, meat or other animal products. When managed sustainably, cattle grazing can provide the disturbance regimes and vegetation heterogeneity necessary for diverse grassland systems (Milchunas et al., 1998; Porensky et al., 2020; Boyce et al., 2021). Furthermore, sustainable cattle grazing maintains healthy soils and resilient plant communities, resulting in more intact ecosystems than row-crop agriculture, which is the primary alternative land use in many grasslands

(Krausman et al., 2009; da Silva et al., 2015). Restoration efforts in temperate grassland systems in North America have often focused on the re-introduction of the native megaherbivore; plains bison (*Bison bison bison*) (Freese et al., 2014). There is some evidence for biodiversity benefits of bison reintroduction, including increased diversity in plants (McMillan et al., 2018) and increased abundance of some grassland obligate songbirds (Boyce et al., 2021) but opportunities to evaluate its biodiversity impacts are rare (but see Allred et al., 2013; Nickell et al., 2018). Furthermore, the bison reintroduction process is both expensive (Carbyn and Watson, 2001) and controversial (Ranglack et al., 2015), so it is critical to evaluate whether these efforts are resulting in increasingly diverse and resilient ecosystems.

Most comparisons between bison and cattle have focused on differences in biodiversity or vegetation structure in upland grasslands (Greibel et al., 1998; Lueders et al., 2006; Moran, 2014; McMillan et al., 2018; Nickell et al., 2018). However, the largest behavioral differences between these species is their use of wetlands and associated woody vegetation (Kohl et al., 2013). There are several ecological and physiological differences between bison and cattle that support the hypothesis that their divergent grazing patterns and habitat preferences will differentially affect riparian systems. Cattle are known to degrade riparian areas (Kauffman and Krueger, 1984; Fleischner, 1994) due to damage or removal of riparian woody vegetation; effects that cascade into degradation of water quality and large fluctuations in stream temperatures and biogeochemistry (Larson et al., 2019). In contrast, bison are more drought and heat-tolerant, allowing them to graze farther from water, especially in hot conditions (Allred et al., 2013; Kohl et al., 2013). Compared with cattle, bison select against areas with woody vegetation and standing water, spend less time browsing, and specialize more on grasses, as opposed to forbs or woody vegetation (Peden et al., 1974; Knapp et al., 1999; Steuter and Hidinger, 1999; Allred et al., 2011; Kohl et al., 2013; Ranglack and du Toit, 2015).

The above differences predict replacing cattle with bison will have net positive impacts on quantity and complexity of riparian vegetation, but this hypothesis is largely untested. Furthermore, we predict that increases in riparian vegetation will be associated with increased diversity of bird communities (MacArthur and MacArthur, 1961; Macarthur, 1964; Cooper et al., 2020). We also predict that deer use will increase with higher shrub and tree cover after accounting for distance to the Missouri River drainage, a forested landscape that serves as a source population for cervids. Here we combine contemporary data on vegetation structure, bird community diversity and ungulate occupancy, with a long-term remotely sensed vegetation dataset to test whether bison reintroduction in a mixed-grass prairie ecosystem has resulted in higher quality riparian habitat in comparison with areas seasonally grazed by cattle.

MATERIALS AND METHODS

Study Area

We studied vegetation and animal communities associated with ephemeral streams on the northwest glaciated plains subregion of the Northern Great Plains ecosystem (Forrest et al., 2004). Our study area included parts of Blaine, Phillips and Valley counties bounded by the Milk River in the north, the Missouri River in the south and the western boundary of the Fort Belknap Indian Reservation on the west (**Figure 1**). Land ownership is a mix of private lands concentrated in the vicinity of permanent water and alluvial soils, with large blocks of public land composed of mixed-grass prairie or sage steppe. The Charles M. Russell National Wildlife Refuge is an exception, as it contains nearly 1 million acres of rugged "breaks" canyons with conifer (*Pinus ponderosa* and *Juniperus scopulorum*) savannah and includes the extensive riparian bottomlands of the Missouri River. In the uplands, conversion from native grassland to row-crop agriculture is ongoing, and conversion of riparian vegetation to hay fields for cattle forage is widespread (Gage et al., 2016).

The study area contains many waterways, from small ephemeral streams which innervate the expansive uplands, to the Missouri River, one of the largest in North America. The small seasonal or ephemeral streams are isolated strands of riparian vegetation amidst large expanses of grassland or sage steppe. Typical riparian vegetation in the region includes woody shrubs like common snowberry (*Symphoricarpos albus*), sandbar willow (*Salix exigua*), and wild rose (*Rosa* spp.). Common tree species are eastern cottonwood (*Populus deltoides*), box elder (*Acer negundo*), and peach-leaf willow (*Salix amygdaloides*). In heavily grazed areas, woody vegetation can be entirely absent, with low-growing grasses and forbs found up to the channel edge.

American Prairie is a private non-governmental organization with the mission to create the largest nature reserve in the lower 48 states[1]. American Prairie owns 423 km^2 of private land and holds the grazing leases for an additional 1,275 km^2 acres of public land as of 2021. The goal of American Prairie is to manage its lands as a fully-functioning grassland ecosystem complete with keystone grazers (bison and black-tailed prairie-dogs *Cynomys ludovicianus*) fulfilling their ecological role (Knapp et al., 1999; Freese et al., 2018). From 2005 through 2021, American Prairie has reintroduced bison to three large parcels of either private land or a mixture of private land and leased grazing allotments managed by the Bureau of Land Management (BLM; Freese et al., 2018; Boyce et al., 2021). Bison herds vary in size; approximately 150, 200, and 400 animals within 2,349, 2,963, and 10,909 ha pastures as of 2021. These herds have corresponding stocking rates of 0.77, 0.81, and 0.44 AUMs per hectare, which correspond to normal-year precipitation estimates calculated by BLM staff for public grazing allotments and by a private contractor (EMPSi Inc., Boulder, CO, United States), and conform to NRCS methodology for private parcels. Bison populations are regulated by public hunting opportunities, donations of animals to other conservation herds, and temporary chemical contraception (Freese et al., 2018). The Aaniiih and Nakoda peoples, who live at Fort Belknap Community, also maintain a large conservation herd of bison (∼900 individuals) on its 8,903 ha Snake Butte pasture. This pasture has a substantially higher stocking rate (1.21 AUMs per hectare) as those managed by American Prairie and bison were

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[1] www.americanprairie.org

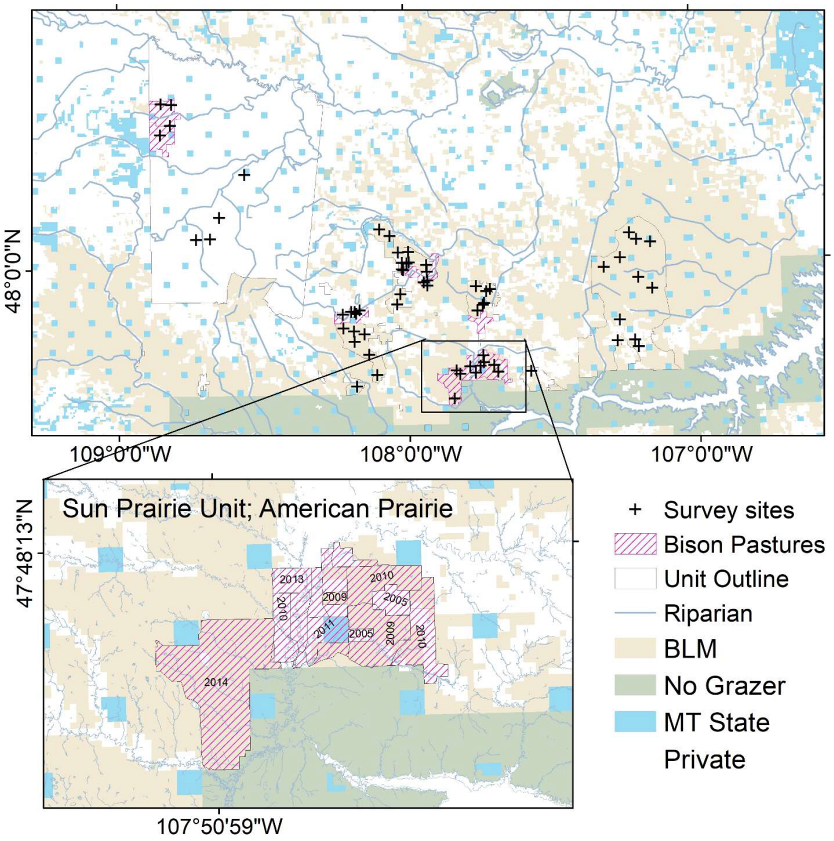

FIGURE 1 | Survey sites. Unit outlines include Fort Belknap Indian Reservation and American Prairie lands.

introduced nearly 30 years ago (Shamon et al., 2022). All bison herds are managed via continuous grazing, in which bison move freely within each grazing allotment throughout the year.

Cattle pastures within our study area were managed via deferred rotation grazing (Rhodes, 2020, BLM, personal communication). Deferred rotation refers to a management regime where allotments are divided into 3–4 pastures using barbed-wire fence, and cattle are moved sequentially through all pastures over the course of each grazing season (March–November). During winter, cattle are removed from public lands grazing allotments and sold or fed overwinter on private lands. Because private lands experience winter grazing, we separated BLM and private (Non-BLM) cattle pastures for our analysis. Cattle pastures in the region have been managed consistently using this protocol for 10+ years (Rhodes, 2020, BLM, personal communication). Cattle stocking rates on BLM lands are dictated by the same NRCS methodology used to determine bison stocking rates on both private and BLM lands. Specific stocking rates are variable over time in response to precipitation and across space in response to small differences in soil productivity. Because bison and cattle stocking rates are determined by the same methodology, we consider the effective stocking rates as similar, with the key difference that bison numbers per unit area are lower because their AUMs are distributed across a 12-month period as opposed to a shorter growing season grazing period in cattle. There are two exceptions to this principle within our study area. First, bison stocking rate on the Snake Butte pasture on the Fort Belknap Indian Reservation is substantially higher than on American Prairie bison pastures and BLM cattle pastures (Boyce et al., 2021; Shamon et al., 2022). Second, cattle stocking rates on private lands are variable depending on economic decisions by individual ranchers and details are not publicly available.

Vegetation

Current Differences in Vegetation Cover Amongst Treatments

We compared current vegetation cover proportions (2019) between treatments using a logistic regression with logit-link function; $f\left(veg\ cover\right) \sim Treatment$ (Warton and Hui, 2011). *Intercept* was set to BLM cattle, the most common form of management in the study region. We ran 8 model combinations (*2 distance categories* × *4 vegetation types*). Current vegetation cover estimates were derived from Range Analysis Platform (RAP) Vegetation Cover Dataset 2019 at 30 m resolution (Allred et al., 2021).

We assessed riparian vegetation structure across four general treatments: BLM cattle, private lands cattle, bison, and no bovine grazers. Bison pastures were then subcategorized according to the year at which bison were reintroduced to the pasture (2005, 2009, 2010, 2011, 2012, 2013, 2014), creating 10 total grazing treatments. First, we identified riparian segments using the National Hydrography Dataset (Moore et al., 2019). Next, we created two distance category buffers around streams: (1) 0 m from stream (e.g., within streambed); (2) <30 m from stream edge. Distance categories were chosen at 30 m scale which matches the resolution of the vegetation cover data used for the analysis. Distance categories highlight the gradient effects of grazing treatment on vegetation. Next, we extracted vegetation cover percentages for each pixel centroid that fell within the two distance categories of a streams using Google Earth Engine (Gorelick et al., 2017).

Long-Term Vegetation Trends

We assessed the direction and rate of change of vegetation cover using RAP Vegetation Cover Dataset 2000–2019 time-series (Allred et al., 2021). We computed a pixel-wise Mann–Kendall rank correlation and estimated Theil-Sen's slope for four vegetation types. Calculations were done using the "rkt" package (Marchetto, 2017) available from CRAN (R Core, 2018). Mann–Kendall rank correlation is a non-parametric test that is considered resilient to outliers and combined with Theil-Sen's slope has proven to be a successful predictor for time-series analysis such as vegetation and climate trends (Gocic and Trajkovic, 2013; Li et al., 2013). Mann–Kendall test provides an assessment of slope estimate uncertainty, and the slope indicates the rate of change and the direction of the trend where positive slope means increase in vegetation cover and negative slope means reduction. Overall, we calculated vegetation tends for 80 combinations of *grazing treatment (10) × distance category (2) × vegetation type (4).* Vegetation types included: (1) annual forbs and grasses; (2) perennial forbs and grasses; (3) shrubs; and (4) tree cover.

We modeled current vegetation cover and time-series slope estimates to determine differences between BLM cattle and the other nine treatments. The analysis was conducted at two distance categories, and four vegetation types separately. We only used estimates with significance level of <0.05 in this analysis. Slope estimates were used as a response variable against treatment categories using a generalized linear model framework (GLM); "stats" R base package (R Core, 2018). Intercept was set to BLM cattle grazed (most common form of management in the study region) and we ran 8 model combinations (*2 distance categories × 4 vegetation types*).

Vertebrate Surveys

Occupancy of Grazers and Browsers

We detected ungulates with camera traps (model Reconyx HyperFire 2) during two growing seasons (July–October 2018, May–September 2019). We deployed camera traps at 78 riparian sites. We placed three cameras in each survey site spaced 250–400 m apart. Cameras were set at 50 cm above ground, facing north to minimize false triggers induced by direct sun exposure. Images were sorted, identified to species, and stored in the eMammal repository (Shamon, 2021). We collected habitat data at each camera location to assess detection bias. These data included the percentage of ground cover vegetation (bare ground, grass, forb, and shrub), percentage of canopy cover, mean shrub height within 5 m in front of each camera, distance at which the camera sensor was triggered in response to an approaching human, and whether or not the camera was set on an obvious animal trail. Percent cover class and mean shrub height were estimated visually. Riparian sites were used to model cervid occupancy in relation to vegetation cover and structure, and these data were used to compare cattle and bison activity with the riparian area. We only used camera deployments which functioned for ≥7 days, which resulted in 213 deployments in the riparian area for deer species. For the bison and cattle models, we eliminated deployments from areas where no cattle were present in the pasture due to rotation to other sub-pastures or removal from the pasture entirely, resulting in 198 deployments (107 bison and 91 cattle).

To compare between bison and cattle activity at streams we used detections counts for each species. Detection counts were modeled using N-mixture models, a family of models that can estimate counts while accounting for imperfect detection (Royle, 2004; Joseph et al., 2009; Zhou and Carin, 2015). Cattle and bison densities in the tested area remained steady during the study period, therefore we do not expect bias due to population fluctuations. Model calculations were done in a two-step process where first we identified the variables that affect detection probability (binominal distribution; see detection covariates above). Detection models were ranked by Akaike information criterion (AIC) and the best fitting model was used in each N-mixture model combination (count model using Poisson distribution). We modeled both species together using "*species*" as a categorical covariate to learn about the difference in activity by streams, and bison was set as an intercept. We assumed detection probability would be the same for bison and cattle given the similarity of body size and the consistency of camera setups, therefore detection was modeled for both species together.

We estimated occupancy for three deer species (mule deer; *Odocoileus hemionus*, white-tailed deer; *Odocoileus virginianus*, and elk; *Cervus canadensis*) in riparian habitats (MacKenzie et al., 2002). We used presence-absence data instead of detection counts to avoid bias of population fluctuations between years. Model calculations were done in a two-step process where first we identified the variables that affect detection probability (binominal distribution; see detection covariates above). Detection models were ranked by AIC and the best fitting model was used in each occupancy model. Second, we modeled deer presence-absence data against proportion of vegetation cover within 100 m buffer around the camera location derived from both the RAP vegetation cover dataset and the distance from major rivers. Different combinations were tested and competing models were ranked by AIC score for each species and we considered models with <2 delta AIC as equivalent.

Bird Diversity

To characterize riparian bird communities we conducted 10-min 200 m fixed-radius point counts laid out along ephemeral or seasonal streams such that the center points of each point count were at least 500 m from the nearest neighbor point count location to avoid double-counting (Hutto et al., 1986). Each cell was visited once per field season between May 30 and July 3, in 2018 and in 2019. All birds seen or heard were recorded and estimated distance and bearing to each individual was recorded to help prevent double-counting. Point counts began at 30 min before sunrise and all counts were completed prior to 8 am to minimize variation in detectability related to time of day. Following Hutto et al. (1986), point counts were not conducted during strong wind or precipitation. We aimed to describe communities of birds associated with riparian habitats, so we removed grassland obligate species under the assumption they were detected in adjacent grassland or sage steppe. We also removed species only detected as flyovers which we could not safely assume were using habitat in the point count area (primarily raptors and waterfowl).

We used three diversity metrics to describe the bird community at each survey location: species richness (SR), Faith's phylogenetic diversity (Faith, 1992; hereafter PD), and functional richness (Mason et al., 2005; Villéger et al., 2008, hereafter FRic). Species richness is simply the number of species detected at a given site. PD describes the total phylogenetic breadth of a community, calculated as the sum of all branch lengths in a phylogenetic tree including all species in a community. Under the general assumption that ecological roles are phylogenetically conserved, PD should be a proxy for overall niche space encompassed by a given community. FRic is analogous to PD, but distance among species is not defined by their phylogenetic relatedness, but by how similar or different they are based on a variety of functional traits related to a species' ecology (Villéger et al., 2008).

To facilitate calculation of PD, we downloaded a subset of 1,000 trees from www.birdtree.org (Jetz et al., 2012) containing all riparian species detected on our counts. We produced a consensus tree and estimated all branch lengths using the "consensus.edges" function in the phytools package (Revell, 2012). To estimate FD, we compiled seven functional traits for each species from the literature. Six of seven traits were morphological measurements linked to locomotion and diet: wing chord, tail length, tarsus length, bill length, hand-wing index, and body mass (Miles and Ricklefs, 1984, 1994; Pigot et al., 2020). We also compiled information on the primary diet of each species, classified into one of six categories: invertebrates, vertebrates, seeds, fruits, plants, and omnivores. Hand-wing index, body mass, and diet data were sampled from a comprehensive dataset compiled by Sheard et al. (2020). All other morphological traits were compiled from a large dataset of passerine morphology (Ricklefs, 2017), Cornell's Birds of the World (Billerman et al., 2020) or references therein. Body mass values were log-transformed before analyses and all analyses were conducted in R v. 3.5.1 "Feather Spray" (R Core Team, 2015).

Phylogenetic diversity and species richness were calculated using the "pd" function in the package "picante" (Kembel et al., 2010). PD can only be estimated for communities of at least two species, so we assigned a PD value of 0 to communities of only one species. FRic was calculated using the "dbFD" function in the package "FD" (Laliberte and Legendre, 2010). FRic can only be estimated for communities containing at least three species, so we assigned a FRic value of zero to all communities with fewer than three species (1 site).

To describe associations between riparian vegetation and bird communities we combined data from the remotely sensed RAP platform (Allred et al., 2021) with our riparian point-count data. We fitted generalized linear models with each diversity metric (SR, PD, and FRic) as the response variable, and three of the four vegetation metrics (tree cover, shrub cover, perennial grass/forb cover) as explanatory variables. Since percentages must add to 100, the fourth category, annual grass/shrub, was excluded from the model as redundant and the parameter estimated for each included category are in comparison to annual grass/forb. Models explaining variation in raw species richness values were fit using a Poisson distribution while all other models used a Gaussian distribution.

RESULTS

Contemporary Differences in Vegetation

We found perennial grass/forb cover was significantly higher in private cattle grazed pastures and bison pastures in areas at, or closer to, the stream (category 0 m and <30 m; excluding 2014 bison pastures; **Figure 2**). In contrast, annual grass/forb cover was significantly higher at BLM cattle streams; consistent for categories 0 m and <30 m (**Figure 2**). Differences in shrub cover were variable between BLM cattle and bison pastures but were significantly lower at private cattle pastures and higher in the no-grazer area (**Figure 2**). Differences in tree cover were variable between BLM cattle and bison pastures with a tendency to be higher at bison pastures and were significantly higher at private cattle pastures and the no-grazer area (**Figure 2**).

Long-Term Vegetation Trends

We found perennial grass/forb cover trends were significantly higher in bison pastures at both distance categories and no-grazer areas for distance categories <30 m (**Figure 3**). At stream (0 m) results were variable with a tendency to be higher than BLM cattle (**Figure 4**); the opposite trend was observed for private cattle pastures. Annual grass/forb cover trends were variable with a tendency to be higher for 0 m at bison pasture and lower for <30 m at bison and no-grazer areas (**Figure 3**). Annual grass/forb cover trends were significantly higher at private cattle pastures. Differences in shrub cover trends were variable between BLM cattle and bison pastures but were significantly lower at private cattle pastures and higher in no-grazer areas (**Figure 3**). Differences in tree cover trends were variable between BLM cattle and bison pastures with tendency to be higher at bison pastures and were significantly higher at private cattle pastures and no-grazer areas (**Figure 3**).

Ungulate Occupancy

Comparison of Cattle and Bison Detection Counts

The mean and standard deviation of cattle and bison detections per 100 camera nights at riparian cameras were 106.8 ± 376.7 and 40.0 ± 107.9, respectively (number of camera deployments: n_{cattle} = 91 and n_{bison} = 107). Because cattle graze seasonally

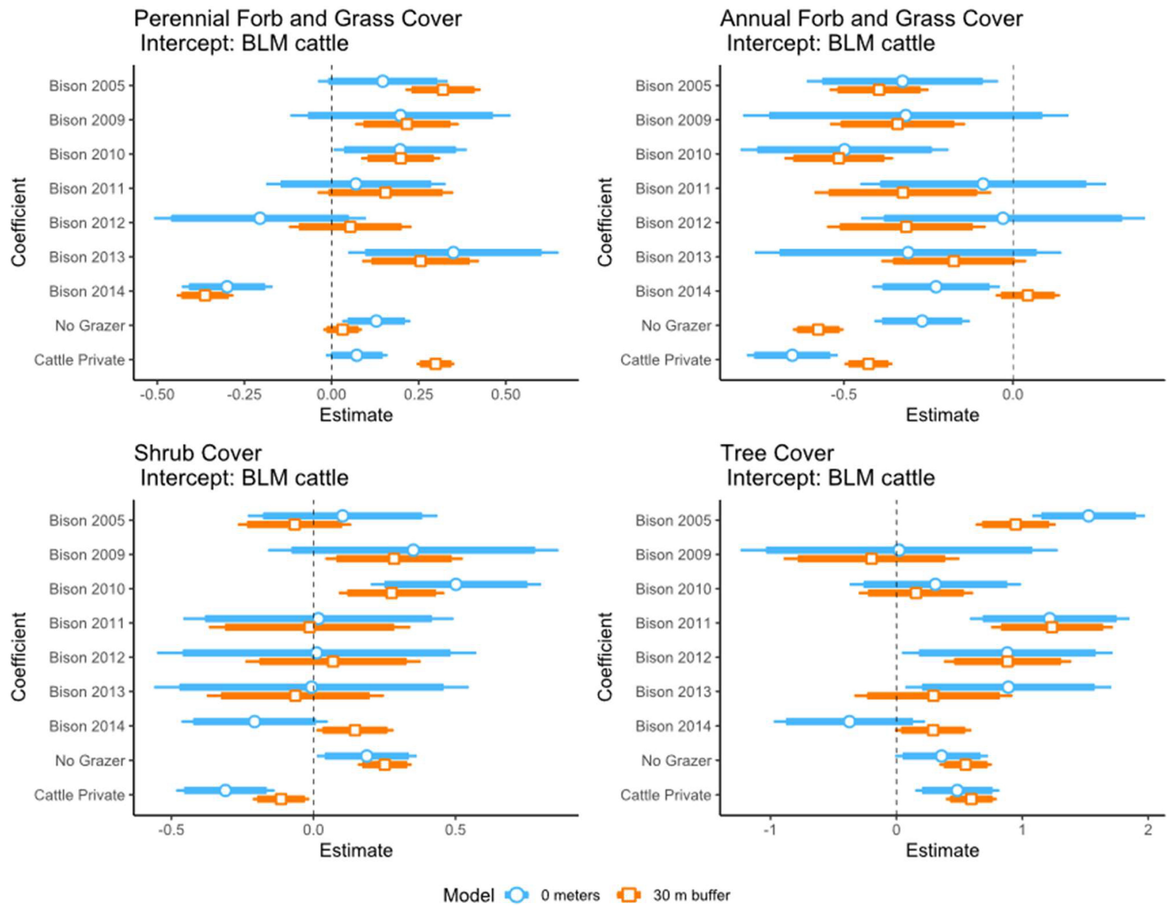

FIGURE 2 | 2019 percentage of vegetation cover in relation to grazing treatment. Intercept: BLM cattle grazed streams. Vegetation: perennial forbs and grasses, annual forbs and grasses, shrub cover, and tree cover. Treatment: BLM cattle, Bison (2005, 2009, 2010, 2011, 2012, 2013, 2014), no grazers, private lands cattle. Models were run for two distance categories: (1) 0 m from stream; (2) <30 m from stream edge.

and are rotated among multiple pastures, they were not always present during camera surveys. Accordingly, the data were subset to include only times when cattle were present, resulting in mean of 255.7 ± 553.2 cattle detections per 100 camera nights (number of camera deployments: $n = 38$). Modeling the full dataset that included times when cattle were not present at the pasture show there are no significant differences between bison and cattle overall activity in riparian areas (**Table 1**). However, modeling the dataset that only contained deployments when cattle were present in the pasture containing the camera deployment revealed that cattle are significantly more active in riparian areas than bison (coefficient = 1.4 ± 0.1 where bison category was set as the intercept; **Table 1A**).

Deer Occupancy in Relation to Riparian Vegetation Cover

Elk occupancy was primarily determined by distance to major rivers and the interaction between woody cover and distance to major rivers (**Table 1B**). Mule deer occupancy was unrelated to distance to rivers and did not show any specific relationship with vegetation cover (**Table 1B**). White-tailed deer occupancy increased with higher tree cover and higher perennial grass/forb cover (**Table 1B**).

Bird Diversity

We conducted 147 point-counts along prairie streams (**Figure 1**) and detected 59 species (mean species richness per count = 6.9; range 1–18; **Supplementary Material**). All three metrics of riparian bird community diversity (SR, PD, and FRic) increased with increasing tree cover, shrub cover, and perennial grass/forb cover in comparison with annual grass cover (**Table 2** and **Figure 4**). Across all three metrics tree cover had the largest positive effect on diversity, followed by woody shrub cover and finally perennial grass/forb (**Table 2** and **Figure 4**).

DISCUSSION

Reintroduction of bison and replacement of cattle with bison significantly impacted riparian systems in our study area. We found that streams in pastures grazed year-round by bison had a faster rate of increase of perennial grass/forb cover, as well as

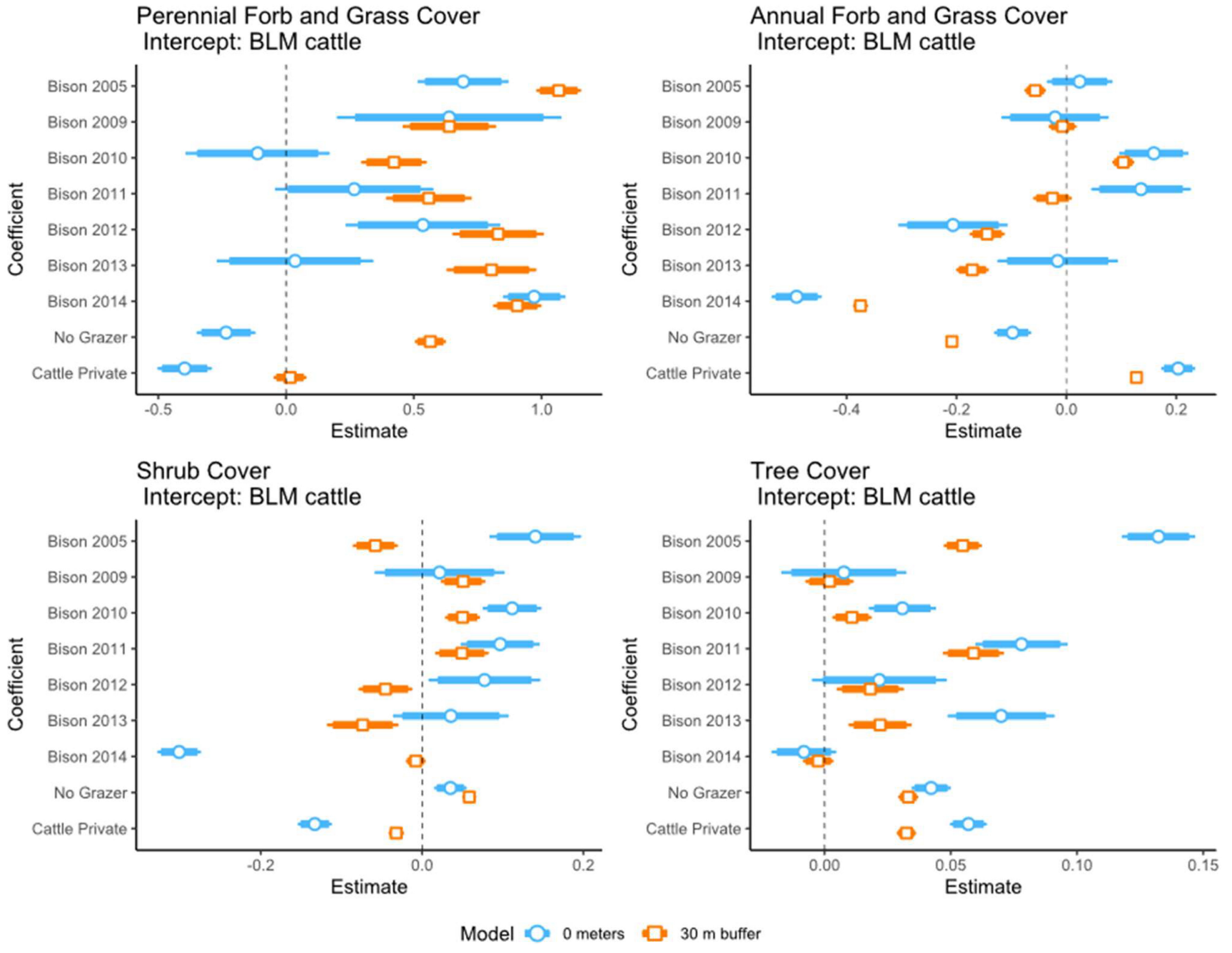

FIGURE 3 | Long-term vegetation trend estimates (slope) in relation to grazing treatment. Intercept: BLM cattle grazed streams. Vegetation: perennial forbs and grasses, annual forbs and grasses, shrub cover, and tree cover. Treatment: BLM cattle, Bison (2005, 2009, 2010, 2011, 2012, 2013, 2014), no grazers, private lands cattle. Models were run for two distance categories: (1) 0 m from stream; (2) <30 m from stream edge.

shrub and woody cover, when compared to streams in seasonally grazed cattle pastures. These trends are supported by camera trap records in streams that show cattle are detected significantly more within streams than bison and that activity is concentrated in time due to the rotation schedule. These results are consistent with previous studies showing that bison select against low-elevations and woody vegetation compared with cattle, and that bison forage farther from water (Knapp et al., 1999; Allred et al., 2011; Kohl et al., 2013; Ranglack and du Toit, 2015). We used remote sensing to document riparian area changes, but a ground-based study in the same area comparing vegetation plots within bison and cattle pastures found similar results of increased plant diversity and increased shrub cover within riparian areas of bison pastures (Yu, 2021). Furthermore, we show that streams with more trees and woody shrubs, and higher percent cover of perennial grasses and forbs relative to non-native annuals are associated with more diverse breeding bird communities and have higher rates of occupancy for two of three species of native ungulates (the exception was mule deer). The idea that greater amounts and complexity of vegetation drives increased bird diversity is hardly a new result (see Macarthur, 1964), but taken together, our results suggest that bison reintroduction, and a minimal intervention grazing management strategy, is associated with positive biodiversity outcomes in riparian habitats found within the Northern Great Plains.

Negative impacts of cattle grazing on riparian systems are well documented, particularly intense in arid regions (Fleischner, 1994; Belsky et al., 1999), negatively impact imperiled species (Ohmart, 1994; Wilcove et al., 1998; USFWS, 2002, 2020; Dettenmaier et al., 2017), and may increase in severity with climate change (Allred et al., 2013). Cattle grazing has been shown to have negative effects on riparian breeding bird communities in Montana (Fletcher and Hutto, 2008) and across the west (Tewksbury et al., 2002). In forested systems, removal of domestic grazers may present a suitable remedy for this issue since forest succession does not rely on intense grazing by bovines as a primary source of disturbance (Hessburg et al., 2019). Because of their ecological and physiological

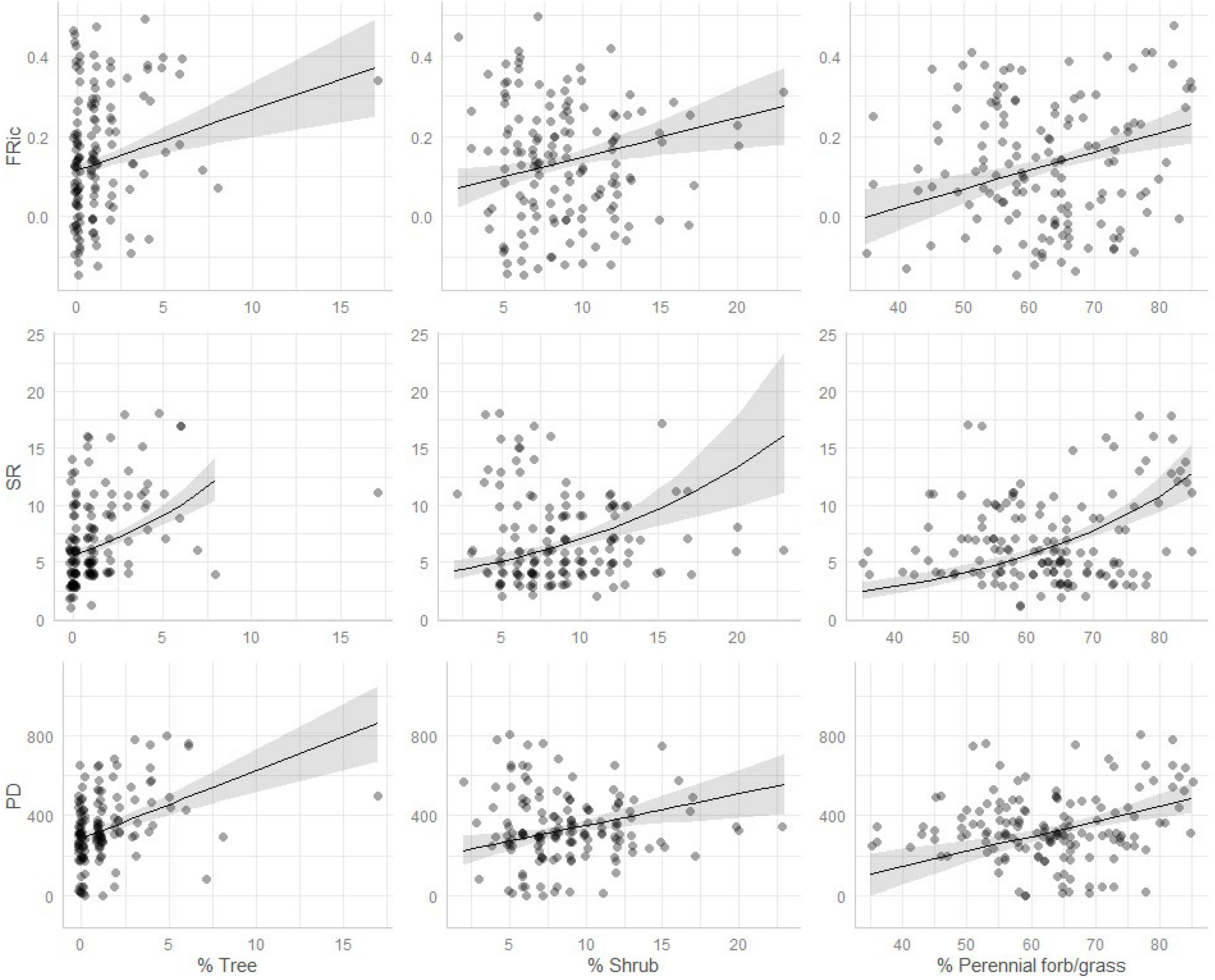

FIGURE 4 | Marginal relationships between three components of remotely sensed vegetative cover and three metrics riparian bird community diversity; functional richness (FRic), species richness (SR), and Faith's phylogenetic diversity (PD). Dots represent individual samples, lines and shading represent predicted relationships and associated 95% confidence intervals. All three vegetative components shown here are increasing in percent cover most rapidly in areas grazed by bison and areas with no grazers. Vegetation cover data are estimated from the RAP platform.

coevolution with arid grassland systems, bison are ideally suited to grassland ecosystems because they provide disturbance and thus heterogeneity in upland habitats (Gibson, 1989; McMillan et al., 2018), but have reduced impacts on riparian habitats, at least at agency standard stocking rates. Whether bison are reintroduced and managed as wild animals for ecosystem benefits, cultural benefits, or meat production, they are likely to provide ecosystem benefits if managed in a way that facilitates natural grazing patterns (Shamon et al., 2022).

Restoration in the Northern Great Plains will not only involve the introduction of large herbivores but also large carnivores. Due to their great mobility large carnivores can repopulate areas once given adequate movement corridors. Riparian systems are important movement corridors and refugia for dispersing, migrating, or resident wildlife (Machtans et al., 1996; Skagen et al., 2005). Linear features such as streams are used by both predator and prey species (Dickie et al., 2020) and forested riparian areas are key dispersal corridors for large mammals including species recolonizing grassland ecosystems in North America (Morrison et al., 2015; Gigliotti et al., 2019). Specifically, riparian corridors are used by black bears (*Ursus americanus*) for movement across grasslands in south-central United States (Gantchoff and Belant, 2017). Grizzly bears (*Ursus arctos*) use riparian areas to move through mixed use areas in British Columbia, Canada (McLellan and Hovey, 2001). Finally, mountain lions (*Felis concolor*) use riparian corridors to disperse between forest fragments (LaRue and Nielsen, 2008) and use riparian forest for dispersal through an agricultural/grassland matrix. The passive restoration of riparian corridors via bison reintroduction has the potential to increase landscape connectivity for large predators including grizzly bears and mountain lions which are actively recolonizing the

TABLE 1 | (A) Bison and cattle count model including the full dataset (all) and a subset that only includes deployments when cattle were active. **(B)** Occupancy estimation for deer species in relation to vegetation cover within a 100 m buffer around a camera and distance to major rivers.

(A)	**Detection**	**Counts model**					
	Intercept	**Intercept**	**Cattle**	**negLogLike**	**nPars**	***n***	**AIC**
Bison and cattle (all)	−3.23 ± 0.07	2.135 ± 0.07	0.127 ± 0.07	6565.58	3	179	13141.16
Bison and cattle (subset)	−3.62 ± 0.07	2.30 ± 0.08	1.43 ± 0.06	6098.20	3	128	12202.41

(B)	**Elk**	**White-tailed deer**	**Mule deer**			
Accumulative AIC models <Δ2.1	**Model 1**	**Model 1**	**Model 1**	**Model 2**	**Model 3**	**Model 4**
Intercept	−3.12 ± 0.32	−1.39 ± 0.08	−1.82 ± 0.07	−1.82 ± 0.07	−1.82 ± 0.07	−1.82 ± 0.07
Grass	0.01 ± 0.005					
Shrub		0.006 ± 0.004	−0.006 ± 0.004	−0.006 ± 0.004	−0.006 ± 0.004	−0.006 ± 0.004
Intercept	−1.55 ± 0.31	−0.54 ± 0.15	0.54 ± 0.16	0.54 ± 0.16	0.54 ± 0.15	0.54 ± 0.15
Distance to major river	−1.54 ± 0.44					
Perennial forbs and grasses		0.44 ± 0.16			−0.05 ± 0.15	
Shrub		0.19 ± 0.16		−0.01 ± 0.16		0.04 ± 0.16
Tree	0.29 ± 0.29	0.55 ± 0.19	0.23 ± 0.17	0.24 ± 0.17		
Tree × Distance to major river	0.93 ± 0.45					
negLogLike	395.43	1220.83	1479.00	1479.00	1480.00	1480.03
K	6	6	4	5	4	4
AIC	802.86	2453.66	2965.99	2967.99	2967.99	2968.06
delta	0	0	0	2.00	2.00	2.07
AICwt	0.50	0.76	0.42	0.15	0.15	0.15
cumltvWt	0.50	0.76	0.42	0.57	0.73	0.88

Northern Great Plains, and a conservation network of riparian systems would benefit the movement of multiple mammal species (Fremier et al., 2015).

In addition to movement corridors, riparian areas can serve as seasonal habitat for many species, as evidenced by our breeding bird surveys. Intact riparian and mesic areas within a grassland or sage steppe matrix are of critical importance for sage grouse brood-rearing (Aldridge and Boyce, 2007; Donnelly et al., 2016), but are subject to damage via cattle grazing (Beck and Mitchell, 2000). Sage grouse conservation is of critical importance to multiple stakeholders in the western United States (Duvall et al., 2017), but habitat manipulations for their benefit do not always improve overall biodiversity measures (Carlisle et al., 2018). To this end, grazing with bison has the potential for positive conservation outcomes for sage grouse via reduced damage to wet habitats within a grassland or sage-steppe matrix.

TABLE 2 | Models describing the relationship between raw and fitted values of avian community diversity and remotely sensed vegetation metrics from the Rangeland Analysis Platform (Allred et al., 2021).

Biodiversity metric		**Estimate**	**Std. error**	***z* value**	***p***
Species richness (SR)	(Intercept)	−0.87	0.40	−2.18	0.03
	Tree	0.10	0.01	8.37	**<2.00 e-16**
	Shrub	0.06	0.01	4.76	**1.93 e-06**
	Perennial forb/grass	0.03	0.01	7.22	**5.12 e-13**
Phylogenetic diversity (PD)	(Intercept)	−321.36	151.38	−2.12	0.036
	Tree	33.81	6.13	5.52	**1.58 e-07**
	Shrub	15.82	5.30	2.98	**<0.01**
	Perennial forb/grass	7.63	1.77	4.30	**5.59 e-05**
Functional richness (FRic)	(Intercept)	−0.26	0.10	−2.65	0.01
	Tree	0.02	0.004	3.88	**1.62 e-04**
	Shrub	0.01	0.003	2.86	**<0.01**
	Perennial forb/grass	0.01	0.001	4.11	**6.69 e-05**

All effects in model summaries are in comparison to the 4th category of land cover, annual grass/forb. Predictors significant at the P < 0.05 level are bolded.

Intact riparian systems in grasslands also buffer temperature extremes and may serve as thermal refugia during increasingly frequent and severe heat waves (Turunen et al., 2021). Increased native plant cover along stream banks increased stream stability in North Dakota grasslands (Hecker et al., 2019). Grassland streams with forested riparian buffers have increased abundance of aquatic insects (Wahl et al., 2013). A high diversity stream in a tall grass prairie system in Illinois saw some improvements (and no degradation) in stream quality following bison restoration (Vandermyde, 2017). In this way, year-round bison grazing in large pastures and with appropriate stocking rates, may facilitate increased climate resilience in grassland ecosystems.

Despite the potential ecological benefits of year-round bison grazing in comparison to seasonal cattle grazing, bison are not a singular solution to grassland conservation or restoration of the system. Bison constrained to small pastures or maintained at high stocking rates can certainly have negative effects on grassland biodiversity (Beschta et al., 2020) or individual species

(Powell, 2006). Furthermore, upland bird communities are similar between seasonally grazed cattle and year-round bison (Boyce et al., 2021), meaning that exclusion of cattle from riparian zones within a grassland matrix may result in similar overall ecosystem health compared with bison pastures. True restoration efforts of prairie riparian areas must include restoration of beaver (*Castor canadensis*) as major engineers of riparian systems (Pollock et al., 1995; Hood and Bayley, 2008).

Domestic livestock grazing has negative biodiversity effects across trophic levels (Filazzola et al., 2020), but paradoxically, grassland ecosystems require disturbance from grazers to produce the diverse vegetative niches required for maximal biodiversity (Becerra et al., 2017). Bison appear to resolve this paradox due to reduced preference for riparian habitats and vegetation, along with increased heat and drought tolerance that facilitates grazing far from water resources (Allred et al., 2013; Kohl et al., 2013). The use of bison as a restoration tool may therefore be particularly effective as northern grasslands become increasingly hot and dry, such that their role as a keystone grazer not only supports biodiversity, but also increases resilience to climate change in one the world's most imperiled ecosystems.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

AB, HS, and WM formulated the idea. AB and HS conducted the fieldwork, performed the analyses, and wrote the first draft of the manuscript. All authors contributed to revisions of the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fevo.2022.821822/full#supplementary-material

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Evaluating the Cumulative Effects of Livestock Grazing on Wildlife With an Integrated Population Model

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Livestock grazing can shape temperate grassland ecosystems, with both positive and negative effects on wildlife documented depending on a variety of grazing and site factors. Historically, research investigating the impacts of livestock grazing on wildlife has been limited by a narrow focus on simple "grazed" vs. "ungrazed" treatments or examining how grazing affects only a single vital rate in isolation. To overcome these limitations, we used a two-stage class, female-based integrated population model (IPM) to examine whether three grazing management regimes (season-long, rest-rotation, and summer rotation) differentially impacted population growth rates of sharp-tailed grouse (*Tympanachus phasianellus*) in eastern Montana and western North Dakota. We estimated 14 vital rates related to survival and fecundity and examined whether subtle cumulative effects of livestock grazing were present but not detected in prior analyses focused on single vital rates. While the management regimes did not differentially impact survival or fecundity of female grouse in our study system, we found evidence for significant cumulative impacts of grazing regime on population growth rates that were only apparent when all vital rates were evaluated concurrently. Population growth rates were higher in areas managed with season-long livestock grazing. The IPM framework encourages comprehensive investigations into the influence of covariates on critical components of species life histories and can assist in guiding management decisions in a world of limited resources. This integrated approach allowed us to more efficiently use multiple data types to provide a more complete picture of the effects of management on an important indicator species.

Keywords: grazing, grouse, integrated population model, rangeland management, rest-rotation

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INTRODUCTION

Livestock grazing is the primary anthropogenic land use (Alkemade et al., 2013) and occurs on more than 60% of the world's agricultural lands (Alexandratos and Bruinsma, 2012). Given that temperate grasslands in the United States provide habitat for more than 290 species of vertebrates, livestock grazing management has a critical influence on native wildlife communities. Domesticated grazers can alter the structure and composition of vegetation, ecosystem function, soil productivity, and therefore wildlife habitat (Adler et al., 2001; Krausman et al., 2009; Boyd et al., 2014; Kraft, 2016). Excessive grazing has been frequently cited as one of the main causes contributing to temperate grassland ecosystem changes such as decreased native plant diversity, woody encroachment, the spread of invasive species, and wildlife population declines (Smith, 1940; Kaiser et al., 1979; Brennan and Kuvlesky, 2005; Smith et al., 2018). In contrast, appropriately managed livestock grazing has also been deemed beneficial for some wildlife species (Frisina, 1991; Douglass and Frisina, 1993; Fuhlendorf and Engle, 2001; Ricketts and Sandercock, 2016; Lagendijk et al., 2019). The effects of livestock grazing management can depend on multiple factors, including the timing and intensity of stocking, species of grazer, environmental conditions, and specific site conditions (e.g., soil type, precipitation, topography) that interact at multiple scales to influence a variety of population parameters (Van Poollen and Lacey, 1979; Adler et al., 2001; Derner et al., 2009; Krausman et al., 2009; Dettenmaier et al., 2017).

Historically, evaluations of the impacts of livestock grazing on wildlife have suffered two major limitations. First, early studies were constrained to simple designs with "grazed" and "ungrazed" treatments, without regard for specific grazing parameters (Busack and Bury, 1974; Reynolds and Trost, 1980; Medin, 1989; Dettenmaier et al., 2017). To address this limitation, recent work has highlighted the effects of specific grazing factors that directly correspond to producer decisions (e.g., stocking rates, grazing systems, grazer species) on species functional groups or species of particular conservation concern, particularly grassland birds (e.g., Fuhlendorf et al., 2006; McNew et al., 2015). For example, recent evidence suggests that a patch-burn grazing regime can improve the quantity and quality of nesting sites and improve annual survival of female greater prairie-chickens (*Tympanuchus cupido*) over other grazing management regimes (McNew et al., 2015; Winder et al., 2018). These studies add another layer of understanding regarding grazing management impacts on wildlife, but they all still suffer from another significant limitation if we wish to draw inferences about how grazing management influences population dynamics.

The second significant limitation is that effects of livestock grazing management and, to our knowledge, habitat management in general, are often evaluated independently for state variables (e.g., population size), individual components of life history (e.g., vital rates, habitat use), or broader community metrics, like diversity indices or relative density (Schaub and Abadi, 2011; Robinson et al., 2014; Arnold et al., 2018). Specific evaluations of the effects of managed grazing parameters like stocking density on nest survival, for example, may provide useful information for specific management questions related to one component of fecundity (e.g., Milligan et al., 2020a), but do not yield inference regarding the broader effects on overall population dynamics and viability. A comprehensive and integrated examination of population processes can illuminate knowledge gaps and aid in the investigation of which factors affect population growth rates, while also identifying cumulative treatment effects on populations that studies of individual life history components cannot reveal.

Recent advancements in analytical approaches now allow for integrated, rather than piecemeal, evaluations of habitat management on multiple population processes and directly link observable parameters to latent population states. Integrated population models (hereafter, IPMs) within a Bayesian hierarchical framework are particularly useful for combining multiple, often dissimilar data types, and estimating parameters of interest including latent variables which are difficult to directly measure or observe in isolation (Kéry and Schaub, 2011). Generally, an integrated analysis is a joint investigation of several datasets, with inferences made based on the joint likelihood, which for independent datasets is the product of the individual dataset likelihoods. Shared parameters across multiple components of the likelihood are key elements in integrated analyses (Schaub and Abadi, 2011). Specifically, IPMs jointly analyze independent datasets relating to population size and demographic rates and the results are often more precise estimates of population parameters on which data are collected (Besbeas et al., 2002), as well as estimates of demographic components that were not directly studied (Schaub and Abadi, 2011). Not only does the estimation of derived parameters and latent variables provide a more thorough understanding of population dynamics between and within stage classes, years, and sites, but it allows for the examination of links between environmental factors and their impact on demography (Abadi et al., 2010). In this framework, the precision of estimated parameters improves (Besbeas et al., 2002; Gauthier et al., 2007; Abadi et al., 2010), allowing for a more robust evaluation of the variation among vital rates and environmental covariates. Importantly, IPMs offer the opportunity to examine variables, such as grazing management parameters, which may affect population processes subtly but chronically, effects that may not be detected by the analyses of individual demographic rates widely used in the field of ecology. The ability to detect more subtle influencing factors is a direct result of a more efficient use of all the available information about a population incorporating both survey and demographic data and should result in more appropriate interpretation of management effects on a population.

We developed an IPM to evaluate the effects of livestock grazing systems on multiple vital rates and cumulative annual population growth rates of sharp-tailed grouse (*Tympanuchus phasianellus*), an indicator species of mixed-grass prairie habitats of the northern Great Plains (Poiani et al., 2001; Roersma, 2001). Declines of prairie grouse (*Tympanuchus* spp.) have been linked to poor grazing or rangeland management but a direct investigation of grazing system on complete prairie grouse demography has not been conducted (Crawford et al., 2004; Dettenmaier et al., 2017). Our specific objectives were to: (1) estimate 14 individual population vital rates using data collected from a 3-year field study of sharp-tailed grouse in joint analysis, (2) develop an IPM that links these demographic processes to population counts based on a common survey protocol, (3) evaluate whether livestock grazing systems affected vital rates and annual population growth rates, and (4) assess the utility of an IPM approach for better identifying previously difficult to measure combined effects of grazing on a wildlife population. We were particularly interested in evaluating whether subtle, "non-significant" differences in vital rates among grazing system resulted in biologically meaningful differences in population growth rates.

MATERIALS AND METHODS

Study Area

Our study used data collected in southern Richland County in eastern Montana and McKenzie County in western North Dakota during 2016–2018 (**Figure 1**). The study area was primarily managed for cattle production and composed of Great Plains mixed-grass prairie with some areas of badlands and woody draws and ravines. Dominant native graminoids included western wheatgrass (*Pascopyrum smithii*), little bluestem (*Schizachyrium scoparium*), needle-and-thread (*Hesperostipa comata*), and blue grama (*Bouteloua gracilis*) typical of mixed and shortgrass temperate prairies in North America. Kentucky bluegrass (*Poa pratensis*) and crested wheatgrass (*Agropyron cristatum*) were common non-native graminoids. The study area included a ∼3,300-ha Upland Gamebird Enhancement Program (UGBEP) project established by the Montana Department of Fish, Wildlife, and Parks (MDFWP) in 1993 that includes four separate three-pasture Hormay rest-rotation systems (average pasture size was 292 ± 116 ha; Hormay and Evanko, 1958). Within each three-pasture rest-rotation management unit, cattle were stocked in one pasture from May–July in the first year (growing season), moved to the second pasture during August–October (post-growing season), while the third pasture was rested from grazing. The order of rotation was then changed the next year so no pasture was grazed during the same season

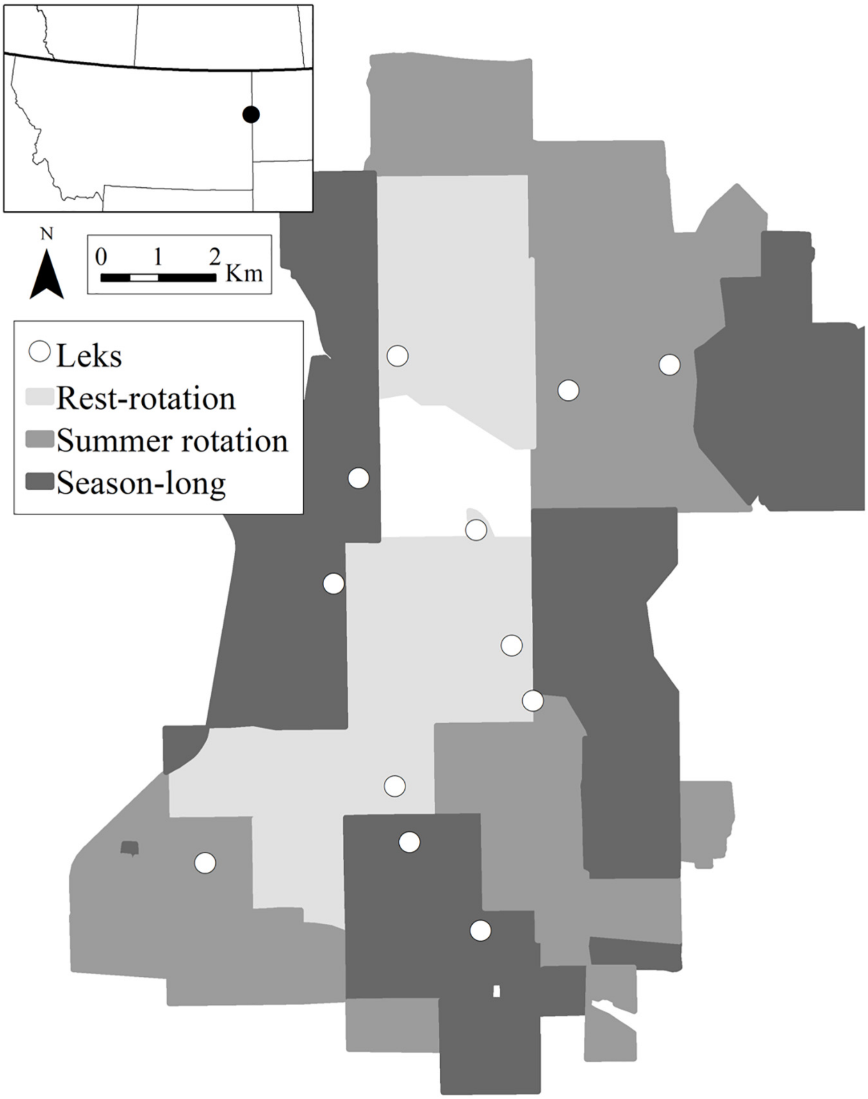

FIGURE 1 | Study area in eastern Montana and western North Dakota. Monitored leks where birds were captured are shown as white circles, with the three grazing systems shown for each pasture in gray.

in consecutive years and pastures rested in the year prior were expected to have more vegetative cover. Surrounding ranches included private land and four pastures located on United States. Forest Service National Grasslands, managed with more commonly used livestock grazing systems, including season-long (19 pastures, ∼4,800 ha, grazed: May–November) averaging 242 ± 312 ha in size and two- and three-pasture summer rotation systems (25 pastures, ∼5,200 ha). Summer rotation systems (average pasture size was 238 ± 335 ha) stocked cattle in the same pastures each year for the same 6–8 week period (approximately April–June, June–July, or August–November). Stocking rates were controlled by landowners and lessees and averaged rates were 0.93 AUM ha-1, 1.46 AUM ha-1, and 0.76 AUM ha-1 for rest-rotation, season-long, and summer rotation pastures, respectively. Topography, average vegetation productivity, soil type, and vegetation canopy greenness as measured by the Normalized Difference Vegetation Index (NDVI) in June 2018, were similar among grazing systems and are described in more detail in Milligan et al. (2020a).

Field Methods

Each year (2016–2018) during the early breeding season (March–May), we conducted repeated surveys at active leks within the study area. Observers recorded the number of males, females, and maximum number of birds sighted. Lek surveys were conducted during the capture period and each lek was surveyed a minimum of five times.

We captured grouse during March–May at 12 leks (five in rest-rotation pastures, three in summer rotation pastures and four in season-long pastures) using walk-in funnel traps. Females were fitted with necklace-style very high frequency (VHF) radio-transmitters (model A4050; Advanced Telemetry Systems, Isanti, MN, United States). Radio-marked females were located by triangulation or homing at least three times per week during the nesting period (April–July). We used portable radio receivers and handheld Yagi antennas to locate and flush nesting females so we could count eggs and record the nest location with a handheld Global Position System (GPS) unit. Nests were monitored after the expected hatch date and approached after the female was located away from the nest for at least 2 days during incubation or 1 day after the expected hatch date (Milligan et al., 2020a). We classified nest fate as successful (at least one chick produced), depredated, or abandoned, based on eggshell remains, predator sign, and/or female behavior. All animal handling was approved under Montana State University's Institutional Animal Care and Use Committee (Protocol #2016-01).

Grazing management in the study area was defined by interviewing landowners to determine the number and class of animals stocked and the timing of stocking.

Integrated Population Model

We used a Bayesian hierarchical framework to develop an IPM that combines multiple independent sources of population data including spring lek counts and a female-based stochastic population model with two stage classes (yearlings and adults). Our methodology is similar to IPMs developed previously for greater sage-grouse (Coates et al., 2018) and informed by procedures described in Kéry and Schaub (2011) and Halstead et al. (2012). We did not have sufficient sample sizes to estimate grazing effects in each year and so we estimated separate models with either fixed effects of grazing system or a random effect of year to evaluate population growth rates across grazing systems and years, respectively. Below we describe the model with grazing effects.

Population Count Data

For the 12 leks surveyed from 2016 through 2018, we compiled three repeated lek counts during a short 5-day window each year (to address the assumption of population closure). Repeated counts were entered into a single season N-mixture model to adjust for systematic downward bias in the observation data (Royle, 2004). The N-mixture model was specified as:

$$\underline{\text{State Process:}}$$

$$N_{l,y} \sim Poisson(\lambda_y)$$

$$log(\lambda_y) = \alpha_0$$

$$\underline{\text{Observation Process:}}$$

$$C_{l,}|N_{l,y} \sim Binomial(N_{l,y}\, p_{y,r})$$

$$logit(p_{y,r}) = \beta_{0,y}$$

where subscripts l, y, and r denote the specified lek, year, and repeated counts respectively. The state process models the latent unobservable number of males associated with each lek (local abundance), and the observation process models the variation among repeated counts within a year at each lek and estimates the average probability ($p_{y,r}$) of detecting a grouse. Although most birds counted on the leks are males, we assume a 1:1 sex-ratio and therefore used the male counts as a proxy for the number of females in the population, which are much more difficult to detect *via* lek surveys. The assumption of an equal sex ratio was supported by the sample of captured adult birds (211 females and 220 males).

Survival

We modeled annual survival for each stage class of female grouse monitored *via* radio-telemetry, survival of first and second nests, and survival of chicks from hatch until 35 days of age as continuous processes observed at discrete intervals. For each discrete monthly interval, adult birds were classified as dead, alive, or censored. We constructed histories of nests and chicks using days as time intervals (Halstead et al., 2012). Using a constant hazard model, we assumed the probability of mortality was equal across the length of the study and assumed that risk of mortality was independent among individuals, with the exception of chicks within broods. Left censoring occurred prior to individuals entering the study (time of capture for adult grouse, initiation of laying for nests, and hatch date for chicks) allowing for staggered entry common to radio-telemetry and reproductive ecology studies. Right censoring occurred after mortality, loss of radio, and for birds still alive at the end of the study period (after year 2018), meaning that all individuals had a recorded mortality event or were eventually right censored. The survival function for the constant hazard model was estimated as:

$$S_{ijy} = e^{-CHiy}, \text{ where } CH_{ijy} = \sum_{j=1}^{T} UH_{1:j,iy} \text{and}$$

$$UH_{ijy} = exp(g_0 + b_{age,ij}{}^{*} x_{age,ij} + b_{grz}{}^{*}_{1} x_{grz1} + b_{grz}{}^{*}_{2} x_{grz2})$$

Subscript i references individual grouse, nests, or chicks and subscripts j and y reference units of time and survival year respectively. T is the last time interval in the monitoring period. Symbol g_0 is the mean baseline hazard and models for adult survival, first and second nest survival, and chick survival included random effects for individual female age ($b_{age,ij}$) where the indicator was equal to one for adults (i.e., $x_{age} = 1$ for adults) to account for individual variation. Parameters b_{grz1} and b_{grz2} are the magnitude of the expected change in the ln(hazard ratio) depending on grazing management system, where season-long is the reference category and indicator variables specify rest-rotation ($x_{grz1} = 1$) and summer rotation ($x_{grz2} = 1$) systems. Hazard ratios measure an effect on an outcome of interest over time, in this case the effect of grazing system on grouse survival and is interpreted as the relative likelihood a particular group will experience the event of interest compared to the reference group. For example, a hazard ratio of 0.5 would mean that a female grouse in that grazing system is half as likely to experience mortality at a particular point in time compared to a grouse in the reference grazing system, season-long. A hazard ratio equal to one implies no difference in treatment from the reference group, and therefore, if the 95% credible interval includes one, there is no evidence of a difference in probability of survival between the treatment group and the reference group.

To classify grazing system for models of adult and chick survival, we simply used the system with the most locations during the time period of interest. For first and second nests, we used the grazing system in which each nest was located to specify the grazing management system. We used uninformative priors for all parameters.

Fecundity

Fecundity was defined by several sub-models, each of which specifically estimated important reproductive vital rates for sharp-tailed grouse. Parameters estimated by individual stochastic sub-models included nest propensity (*np;* first nest = *np1* and second nest = *np2*), nest survival (*ns*; described above), clutch size (*cl*), egg hatchability (*h*), chick survival (*cs*; described above), and juvenile survival (*js*). We did not monitor juvenile grouse after they gained independence at 35 days of age. One of the advantages of IPMs is the estimation of vital rates for which no data were collected (Kéry and Schaub, 2011). Information on juvenile survival rates specifically for sharp-tailed grouse is lacking. Therefore, we used an informative prior [beta(100, 150)] in our sub-model of juvenile survival (*js*) based on published rates in the literature for prairie-chickens (Pitman et al., 2006; McNew et al., 2012) for survival of juvenile birds from independence at 35 days of age to recruitment the following spring (March 1). We also used an informative prior for first nest propensity for each stage class, using more conservative values than rates reported in the literature [beta(97, 5) for adults and beta(90,12) for yearlings] due to concerns about the potential for missing first nests that failed early during the laying period (Taylor et al., 2012; Mathews et al., 2018). We assumed nest propensity was constant among years. Thus, fecundity was estimated as:

$$F_{ga} = ((np1^{*}_{a} cl1^{*}_{a} ns1^{*}_{ga} h^{*}_{a} cs^{*}_{ga} js) +$$

$$((1 - ns1_{ga})^{*} np2^{*}_{ga} cl2^{*}_{a} ns2^{*}_{ga} h^{*}_{a} cs_{ga} * js))/2.$$

Subscripts reference grazing system (g) and stage class (a). We divided the value of F by two because our model is female-based and we assumed an equal sex ratio.

Second nest propensity (np) was modeled as:

$$y_{np2,y} \sim Binomial(p_{np2,y}, n_{np2,y})$$

$$logit(p_{np2,y}) = b^{*}_{age,y} x_{age,y} + b_{grz}{}^{*}_{1} x_{grz1} + b_{grz}{}^{*}_{2} x_{grz2}$$

where $y_{np2,y}$ represents the number of renests, $n_{np2,y}$ is the number of unsuccessful first nests in each year (y) and logit($p_{np2,y}$) is a function of female stage class ($b_{age,y}$) and parameters with indicators for grazing system (b_{grz1} and b_{grz2}).

The expected mean clutch size (μ_{cl}) at clutch c in year y is a linear function of the change in the expected count of magnitude $\beta_{age,}$ nesting female stage class. Clutch sizes of first and second nests were modeled as being drawn from a Poisson distribution and estimated as:

$$y_{cl,y} \sim Poisson(\mu_{cl,cy})$$

$$log(\mu_{cl,cy}) = \beta^{*}_{age} x_{age,cy}$$

Egg hatchability (h) was compiled from nests that were successful (one or more eggs hatched) and estimated as arising from a binomial distribution following the same equation for second nest propensity, where the initial clutch size represented the number of trials with a binary outcome (hatch or not hatch) and the number of hatched eggs represented the number of successes. We included the same random effect for female stage class.

Chick survival (cs) was modeled as described above based on flush counts of chicks at approximately 35 days post-hatch arising from a binomial distribution (logit-link function). The initial brood size represented the number of trials and chicks that survived to day 35 were the successes. The estimated model included random effects for female stage class (b_{age}) as well as parameters with indicators for grazing system (as described above; b_{grz1} and b_{grz2}). We assumed a constant hazard function and the model followed the form used for adult and nest survival and was estimated as:

$$y_{cs,y} \sim Binomial(p_{cs,y}, n_{cs,y})$$

$$logit(p_{cs,y,35}) = b_{age,y}{}^{*}x_{age,y} + b_{grz1}^{*}x_{grz1} + b_{grz2}^{*}x_{grz2}$$

Joint Likelihood

After defining the sub-models, we specified the joint likelihood which is the product of the component likelihoods of the population count data (from the *N*-mixture model), stage class survival data, and fecundity data. In concert, the subcomponents of the IPM were used to derive posterior distributions for grouse vital rates and enabled us to estimate the total female population across the study area in each year. The mean expected number of recruits into the yearling stage class (μ_{1yi}) was estimated as:

$$\mu_{1yl} = N_{(1,y-1,l)}{}^{*}F_{(1,y-1)}^{*}S_{8(1,\,y-1)} +$$

$$N_{(2,y-1,\,l)}^{*}F_{(2,y-1)}^{*}S_{8(2,\,y-1)},$$

where subscripts *a, y,* and *l* correspond to stage class (*a* = 1 for yearlings and 2 for adults), year, and lek site respectively. N_a represents the initial number of each stage class in each year at each lek site *l*. Symbols F and S_8 represent fecundity and eight-month survival derived from individual sub-models described above. The number of yearling recruits (N_{1yl}) is:

$$N_{1yl} \sim Poisson(\mu_{1yl})$$

We represent the number of yearlings surviving into adulthood ($N_{new(2yl)}$) as being drawn from a Binomial distribution given the annual survival of yearlings from the previous year and the number yearlings from that lek the year before.

$$N_{new(2yl)} \sim Binomial(S_{12(1,\,y-1)}, N_{(1,\,y-1,\,l)})$$

Similarly, the number of surviving adults from the prior year ($N_{old(2yl)}$) is estimated as being drawn from a Binomial distribution with a mean of the annual adult survival from the year before and the number of adults from the lek the prior year, represented as:

$$N_{old(2yl)} \sim Binomial(S_{12(2,\,y-1)}, N_{(2,\,y-1,\,l)})$$

Given the information in the constructed Lefkovitch matrix and abundance estimates for both stage classes, we estimated abundance at each lek in each year, where total adults (N_{2yl}) is the sum of new adults ($N_{new(2yl)}$) and returning adults ($N_{old(2yl)}$) and total abundance (N_{tot}) is the sum of total adults (N_{2yl}) and yearlings (N_{1yl}):

$$N_{(2yl)} = N_{new(2yl)} + N_{old(2yl)}$$

$$N_{tot} = N_{2yl} + N_{1yl}$$

Population totals across the study area are estimated by summing lek site totals for all leks in each year. From the derived abundance estimates, we calculated the finite rate of population change (Caswell, 2001; Gotelli and Ellison, 2004) by dividing total abundance in year y + 1 by the total abundance in the previous year y. Thus,

$$\lambda_y = \frac{N_{y+1}}{N_y}$$

where subscript y represents year. Posterior distributions of estimated parameters were summarized by mean and 95% credible intervals (CrI).

We used the packages rjags (Plummer, 2018) in Program R (version 3.6.2; R Core Team, 2018) with Markov chain Monte Carlo methods to obtain posterior samples of the parameters of interest, running three independent chains of 50,000 iterations, thinned by a factor of five, after a burn-in of 100,000. Mixing was sufficient and convergence was achieved as confirmed by examining trace plots and R-hat values (< 1.01; Gelman and Rubin, 1992) after estimation.

Sensitivity Analysis

To evaluate the relative contributions of individual demographic rates to population dynamics, we calculated the posterior distributions of correlation coefficients between annual population growth rates and each of the demographic rates. The strength of the correlation reflects the strength of the contribution of one demographic rate with the temporal variation in population growth rates (Kéry and Schaub, 2011; Schaub et al., 2012). We described the posterior distributions using the median because they were skewed and we calculated the probability that the correlation coefficients were positive.

RESULTS

During the study period, we located 188 grouse nests laid by 128 individual females, of which 147 were first nests and 41 renesting attempts. We evaluated chick survival for 93 broods (2016; n = 25, 2017; n = 36, 2018; n = 32). To estimate adult survival, we used data from 153 female sharp-tailed grouse, some of which were monitored in multiple years resulting in 172 bird years (2016; n = 55, 2017; n = 64, 2018; n = 61). Of the total bird years, 66 primarily used rest-rotation, 46 primarily used season-long, and 60 used summer rotation.

Estimated vital rates (**Table 1** and **Figure 2**) from the IPM generally agreed with those estimated from previous independent analyses (Milligan et al., 2020a,b). For example, first nest survival was 0.47 ± 0.09, 0.39 ± 0.09, and 0.40 ± 0.09 for season-long, summer rotation, and rest-rotation pastures, which corresponded with previous independent estimates (season-long: 0.48 ± 0.07; summer rotation: 0.38 ± 0.06; rest-rotation: 0.32 ± 0.06;

TABLE 1 | Estimated vital rates (with 95% credible intervals) for each stage class (yearling and adult) of sharp-tailed grouse in eastern Montana using a female-based integrated population model.

Variable	Yearling	Adult
First nest propensity	0.88 (0.81–0.94)	0.95 (0.90–0.98)
Second nest propensity	0.74 (0.50–0.91)	0.71 (0.48–0.88)
First clutch size	11.88 (11.23–12.55)	12.22 (11.59–12.86)
Second clutch size	9.75 (8.52–11.07)	8.89 (7.80–10.04)
First nest survival	0.51 (0.33–0.68)	0.44 (0.27–0.60)
Second nest survival	0.64 (0.29–0.90)	0.67 (0.38–0.90)
Hatchability	0.92 (0.90–0.94)	0.91 (0.89–0.93)
Chick survival	0.23 (0.19–0.27)	0.20 (0.16–0.24)
Juvenile survival	0.40 (0.34–0.46)	
Adult survival	0.43 (0.30–0.56)	0.60 (0.05–0.69)

Milligan et al., 2020a). Credible intervals of all fecundity parameters and overall recruitment within each stage class overlapped across the three grazing systems (**Figures 2A–E**), although chick survival trended higher in summer rotation pastures.

Credible intervals for adult survival within each stage class overlapped for all three grazing systems, but adult survival trended higher in season-long pastures, particularly compared to summer rotation pastures (**Figure 2F**). Annual survival estimates were within the range previously reported for sharp-tailed grouse (Robel et al., 1972; Connelly et al., 1998) and averaged 0.41 ± 0.14 across stage classes and grazing systems (range: 0.21–0.60). Previously reported annual survival rates and standard errors for the same population were 0.50 ± 0.05 in 2016, 0.28 ± 0.04 in 2017, and 0.46 ± 0.05 in 2018 (Milligan et al., 2020b).

Estimated population growth rates (λ) were 0.75 ± 0.08 for season-long, 0.48 ± 0.09 for summer rotation, and 0.58 ± 0.09 for rest-rotation pastures (**Figure 3A**). This translated to a significant difference in growth rates between season-long and summer rotation with 95% credible intervals that did not overlap zero (**Figure 3B**). Differences were also potentially biologically meaningful, with season-long grazing representing a 57 and 30% increase in population growth rates over summer rotation and rest-rotation, respectively. Collectively, estimated rates of population growth indicated a declining population from 2016 to 2017 (λ = 0.68, 95% CrI: 0.53–0.81), but the largest decrease was between 2017 and 2018 (λ = 0.59, 95% CrI: 0.44–0.74) which corresponded to significant drought.

Adult survival (0.67, 95% CrI: 0.29–0.88) and yearling survival (0.45, 95% CrI: -0.10–0.78) had the highest correlation coefficients with population growth rates, with 0.99 and 0.95 probabilities, respectively, that they were greater than zero, suggesting that there was a positive association with population growth. The relative contributions of first nest survival (0.11, 95% CrI: -0.42–0.61), second nest survival (0.07, 95% CrI: -0.47–0.57), and chick survival (0.11, 95% CrI: -0.43–0.59) were much lower but were still predicted to be positively associated with population growth (first nest survival: 0.66, second nest survival: 0.60, chick survival: 0.66).

DISCUSSION

We evaluated the cumulative effects of livestock grazing management on sharp-tailed grouse with an IPM, which allowed us to overcome the two most significant limitations of previous research investigating the effects of grazing management on wildlife. Namely, we moved beyond the simplicity of "grazed" vs. "ungrazed" treatments and the limited inference of focal examinations of a single vital rate. The IPM allowed us to take a holistic approach and examine grazing management's cumulative influence on multiple vital rates within the same hierarchical model, providing more power to detect subtle impacts of the grazing treatments on sharp-tailed grouse population dynamics (Kéry and Schaub, 2011; Schaub and Abadi, 2011). Although previous independent analyses suggested no difference in multiple vital rates between three grazing systems, our combined approach suggested that there were cumulative differences in overall population growth rates. Population growth rates were significantly higher in areas managed with season-long livestock grazing than in areas managed with within-season rotational grazing.

Viewed collectively, grazing management did influence the population dynamics and growth rates of our study population, with potentially biologically meaningful differences among all three systems, despite the fact that vital rates for both fecundity and survival were not significantly different across the three grazing regimes and this result was consistent across female stage classes (yearling and adult). While we did not evaluate the effect of grazing management on all estimated vital rates, we would not expect some vital rates, such as egg hatchability, to be affected by management factors and we included management effects on all key survival and reproduction rates (e.g., nest survival) that have been shown to influence grouse population dynamics (Hagen et al., 2009; McNew et al., 2012). The lack of an effect on individual vital rates contrasts with previous research that found effects of another grazing system, patch-burn grazing, on multiple vital rates of greater prairie-chickens (McNew et al., 2015; Winder et al., 2018). However, unlike patch-burn grazing, grazing regimes in our study area did not have a meaningful impact on vegetation and pasture-level heterogeneity (Milligan et al., 2020a), which could explain why we only detected subtle cumulative impacts on population growth when all vital rates were examined concurrently.

The IPM we constructed can also be used to investigate more aspects of grazing management, such as stocking rates, and evaluate their influence on population dynamics to inform management decisions. Unfortunately, differences in average stocking rates among grazing systems prevent us from making causal inferences regarding the mechanisms of improved population growth rates in areas managed with season-long grazing. Previous studies suggest that stocking rate can be of greater importance than grazing system in terms of the cascading effects on wildlife habitat and therefore wildlife populations (Briske et al., 2008, 2011). Stocking rates in our study were below levels recommended as moderate by the U.S. Department of Agriculture Natural Resources Conservation Service under normal precipitation, so further investigation with

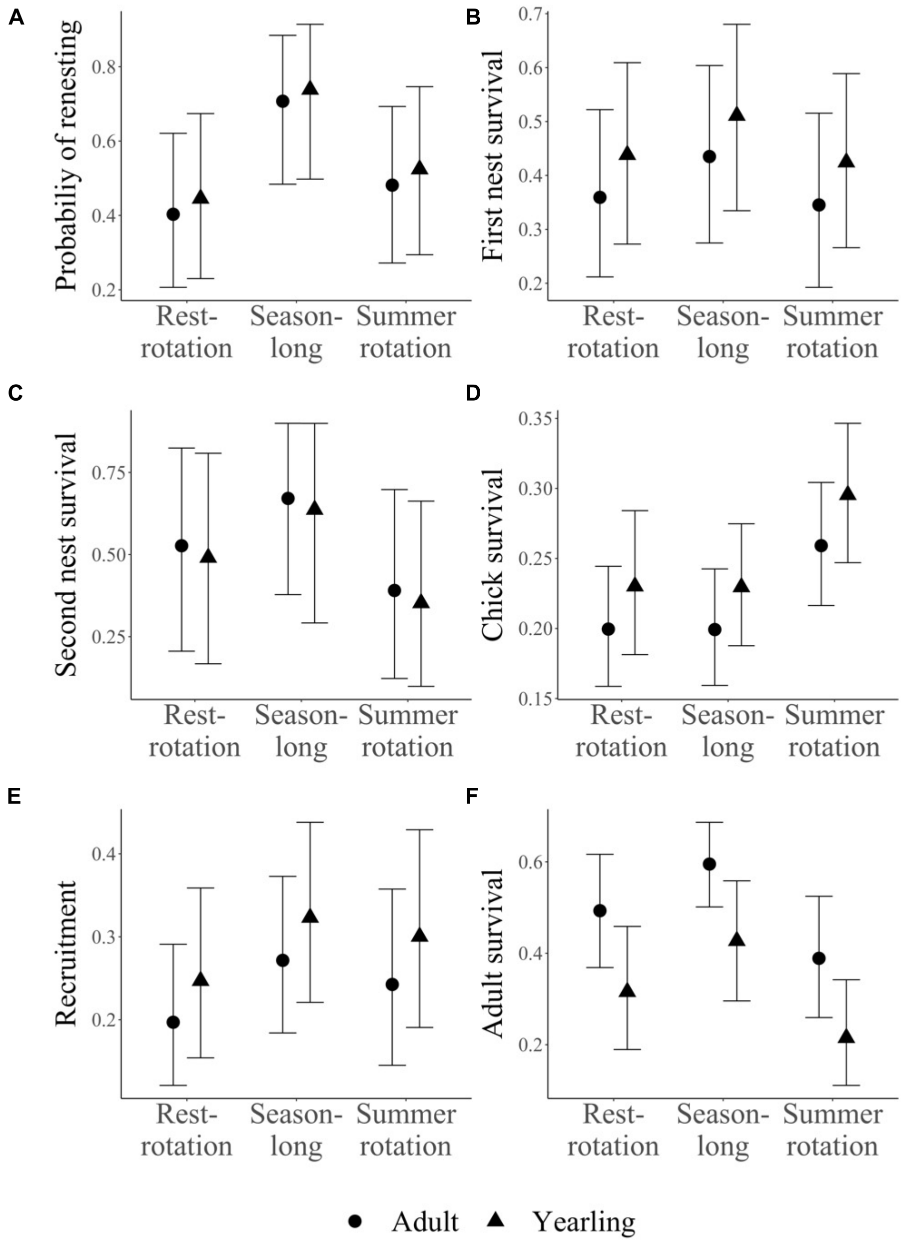

FIGURE 2 | Estimated vital rates (± 95% credible intervals) for each grazing system and stage class (yearling and adult) using a female-based integrated population model for sharp-tailed grouse in western Montana. Four vital rates (**A–D**; renesting propensity, first and second nest survival, chick survival) that varied by grazing system and additional parameters which were either assumed to be constant across grazing system (clutch size, egg hatchability) or for which we did not have data to estimate grazing effects (first nest propensity, juvenile survival) were combined to estimate recruitment **(E)**. Recruitment **(E)** and adult survival **(F)** were then used to calculate population growth rates for each grazing system.

more varied stocking rates over variable levels of precipitation would be beneficial in understanding the effects of livestock management on wildlife populations. Testing the effects of other grazing management components on demography would further enhance our knowledge about the importance of livestock in shaping grassland ecosystems and would help to determine whether other components of grazing management have meaningful direct or cumulative effects on survival and fecundity (Dettenmaier et al., 2017). In addition, a spatially explicit approach could further evaluate fine-scale effects of both management and environmental variables on population dynamics (Chandler and Clark, 2014). We only categorized females based on the grazing system in which they were located most often, but it is possible that using multiple systems may be an important strategy or that only a small amount of a particular resource is required to support survival or

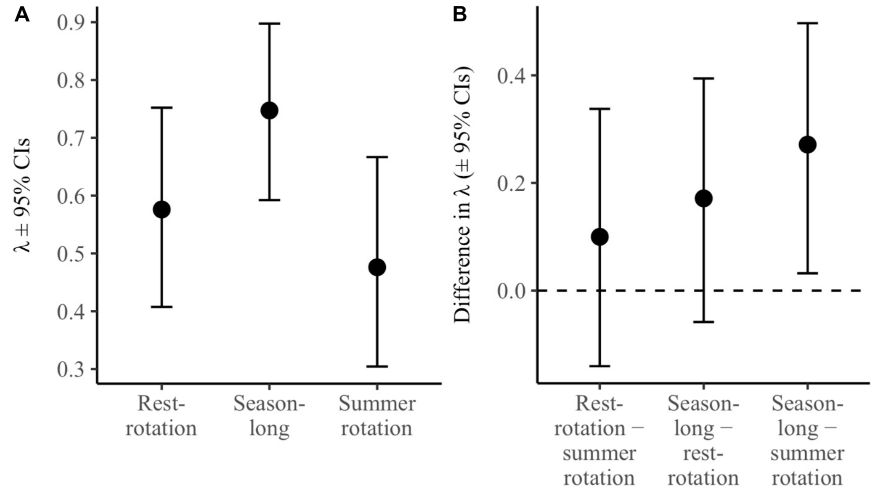

FIGURE 3 | Estimated population growth rates (**A**; λ ± 95% credible intervals) for each grazing system using a female-based integrated population model for sharp-tailed grouse in western Montana. Panel **B** depicts the relative difference between estimated growth rates (± 95% credible intervals) between each pair of grazing systems, with credible intervals that do not overlap zero suggesting a significant difference between the two grazing systems.

reproduction, which would be better captured with a spatially explicit approach.

While some studies have found population growth rates in prairie grouse are more sensitive to changes in nest or chick survival (Hagen et al., 2009; Gillette, 2014), our sensitivity analysis indicated that adult survival was primarily responsible for changes in population dynamics. This concurs with a study of greater prairie-chickens that found that adult and juvenile survival were more important than reproduction for declining populations (McNew et al., 2012). Our estimates of nest survival were also within the range previously reported for sharp-tailed grouse (McNew et al., 2017), suggesting less room for improvement, whereas estimates of adult survival during the non-breeding season were severely depressed during the drought in 2017–2018 (Milligan et al., 2020b). Overall, our estimates of population growth rates depict a declining population, which was substantiated by field observations. The most significant declines occurred between 2017 and 2018, which coincided with a severe drought, suggesting that precipitation may have a large impact on population trends, as seen in other grouse species (Blomberg et al., 2012; Coates et al., 2018). While our estimates suggest significant population declines, grouse populations are cyclical and our study almost certainly did not capture an entire cycle, suggesting caution should be exercised when extrapolating our estimates to longer time periods.

Integrated population models provide a path for researchers and managers to squeeze the most information out of the data they collect (Kéry and Schaub, 2011; Schaub and Abadi, 2011). Due to their hierarchical nature and the borrowing strength provided by IPMs, even limited data sets can yield valuable information and robust results. When faced with a lack of empirical information ("data poor" parameters), whether due to species life history or the realities of research and management funding, IPMs can be used to great effect to shed light on critical life history components for wildlife (Abadi et al., 2010). A powerful strength of IPMs is allowing researchers to evaluate the effects of management or environmental variables across multiple vital rates within a single framework to allow more subtle, cumulative effects to be detected if present (Kéry and Schaub, 2011; Schaub and Abadi, 2011). The importance of cumulative or sub-lethal effects on organisms was initially noticed in the field of biological toxicology (e.g., Duquesne et al., 2004) but has been increasingly noted in other disciplines within the field of ecology as affecting survival, fecundity, space use, physiology, and behavior (Strauss, 1991; Nellemann et al., 2000; Sheppard et al., 2009; Williams et al., 2016; Heim et al., 2017; Messinger et al., 2019). Incidental cumulative impacts related to human activity or deliberate management actions have the potential to be significant and can sometimes explain the difference between observed and predicted population demographics. IPMs are useful for highlighting these differences, as shown by our results suggesting that cumulative effects of grazing regimes were only detected when all vital rates were evaluated concurrently, even though there were no significant impacts on individual vital rates. An integrated approach to modeling facilitates analysis of complex ecological data sets, uses all available information, and enables us to tease apart drivers of observed population dynamics we may otherwise have difficulty explaining (Arnold et al., 2018). The field of ecology and natural resource management would benefit greatly from adopting a more integrated approach whenever possible.

DATA AVAILABILITY STATEMENT

Publicly available datasets were analyzed in this study. This data can be found here: https://www.wildlifehabitatecologylab.com/data.html.

ETHICS STATEMENT

The animal study was reviewed and approved by the Montana State University IACUC.

AUTHOR CONTRIBUTIONS

MM collected data, conducted analysis, and wrote manuscript. LM designed the study, secured funding and permits, conducted analyses, and wrote manuscript. All authors contributed to the article and approved the submitted version.

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Effect of Grazing Treatments on Phenotypic and Reproductive Plasticity of *Kobresia humilis* in Alpine Meadows of the Qinghai-Tibet Plateau

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Plant phenotypic and reproductive plasticity is strongly influenced by long-term grazing activities. It is important to understand the life history of dominant plant species, such as *Kobresia humilis* of alpine meadow, for the stability and sustainable grazing administration meadow on the Qinghai-Tibetan Plateau (QTP). We compared the effects of different grazing treatments (grazing yak, Y; grazing Tibetan sheep, S; and grazing Tibetan sheep and yak, S+Y) on the reproductive and phenotypic plasticity of *K. humilis* in an alpine meadows on the northeastern margin of the Qilian Mountains in China. The results showed that different grazing treatments had significantly effects on the *K. humilis* phenotype and reproductive plasticity. The Y treatment significantly reduced the plant height, crown width and *K. humilis* biomass, but increased the density, which was 1.27 and 1.53 times higher than that in the S+Y and S treatments, respectively. Further, the S+Y treatment significantly increased the crown width, biomass, and future life expectancy of *K. humilis*. Whereas the S treatment increased the height of *K. humilis* significantly, which was 1.57 and 1.10 times higher than that in the Y and S+Y treatments, respectively. Both Y and S treatments significantly increased the sexual reproduction efficacy of *K. humilis* but reduced the storage efficacy. The storage efficacy at S+Y treatment was highest among these treatments. Further, grazing treatments did not change the resource allocation strategy of *K. humilis*, while the sexual reproductive efficacy was significantly higher than the vegetative reproduction efficacy. The storage efficacy was significantly higher than the growth efficacy among the different grazing treatments. The increase of Cyperaceae indicates the degradation of Cyperaceae—Poaceae meadows. This study showed that grazing Tibetan sheep is a more sustainable grazing method in cold season pastures of alpine meadows on the QTP.

Keywords: alpine meadow, grazing treatments, sexual reproduction, vegetative reproduction, phenotypic plasticity

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1 INTRODUCTION

The Qinghai-Tibet Plateau (QTP) lies between 26° and 39° N and 73°–104° E, most of which are located in southwestern in China. It is not only an important ecological barrier, but also a vital pastoral area. Grazing has existed for thousands of years as the main interference in the alpine meadows on QTP (Huang et al., 2016). In recent years, the alpine meadows have been degraded to varying degrees due to overgrazing (Dai et al., 2021; Wang et al., 2021; Zhang et al., 2021). In response to grazing pressures and environmental factors, phenotypic and reproductive plasticity allows plants to regulate their life history strategies (Sommer, 2020). Previous studies have shown that asexual reproduction facilitates the expansion of populations and the full utilization of environmental resources due to a faster reproduction rate (Pereira and Coimbra, 2019). Sexual reproduction increases the genetic diversity of the plant community and increases the adaptability of the offspring to changing environmental conditions (Dembicz et al., 2018; Wilson Sayres, 2018). Comparing the differential effects of different grazing livestock combinations on the reproduction of dominant forages can provide the basis for grassland grazing management.

The role of grazing in vegetation community succession has been widely studied. Many studies have concluded that grazing affects the vegetation community composition by influencing plant regeneration rate, photosynthetic rate, biomass, and plant diversity, and is an important factor in the community succession (Li X. et al., 2018; Sigcha et al., 2018; Török et al., 2018; Schmitz and Isselstein, 2020; Rysiak et al., 2021). However, few studies have explored vegetation community changes from the perspective of the reproductive strategies of dominant species. Peng Z. et al. (2020) suggested that grazing and rainfall showed a bidirectional regulation of reproductive characteristics of *K. humilis*. Sexual reproductive index, plant height, and the number of single leaves decreased with decreasing rainfall and increasing trampling intensity (Peng Z. et al., 2020). Xiao et al. (2018) found that trampling by yaks and Tibetan sheep during grazing was the main cause of grass differentiation, and the high hoof pressure of yaks was more detrimental to grass growth (Xiao et al., 2018). Pan et al. (2021) showed that under grazing conditions, the trampling period had the greatest effect on morphological traits of *K. humilis*, followed by livestock species. Understanding the reproductive strategies of dominant species in alpine meadows can help determine the relationship between livestock population and the ecology of the region. This is also important for understanding the ecological adaptations of plant populations to different livestock grazing.

Kobresia humilis is an important dominant species in alpine meadow. By studying the reproductive and phenotypic plasticity of *K. humilis*, we determined the impact of grazing treatments on *K. humilis* populations and Cyperaceae—Poaceae meadow. The specific objectives of this study were to 1) investigate the ways in which grazing treatments affect the vegetative reproduction and asexual reproduction of *K. humilis*; and 2) select grazing practices that are more suitable for the sustainable use of alpine meadows on the QTP. We hypothesized that: 1) grazing treatments significantly affected the reproductive strategy of *K. humilis* through the regulation of phenotypic plasticity; and 2) grazing yaks increased sexual reproduction by reducing the storage efficacy of *K. humilis.*

2 MATERIALS AND METHODS

2.1 Study Site

The experimental site was located near the Tianzhu Alpine Grassland Ecosystem Experiment Station on the northeastern edge of the QTP in Zhuxixulong Township, Tianzhu Tibetan Autonomous County, Wuwei City, northwestern Gansu Province, China (**Figure 1**) (Li W. et al., 2018). The experimental site at an altitude of about 2960 m. Its geographical coordinates are 102°40′-102°47′ E longitude and 36°31′-37°55′ N latitude. The climate of the region is characterized by cold and wet conditions, intense sunshine, and large diurnal temperature differences. The summer monsoon brings higher temperatures and precipitation. The average annual temperature ranges between −0.3°C and 0°C. Meanwhile, the cumulative annual temperatures greater than 0°C and 10°C are 1581°C and 1026°C, respectively. The annual precipitation was 416 mm, concentrated in the growing season. The annual evaporation was 1590 mm, four times as much as the precipitation. These data were obtained in 2021. The soils of the study area belong to the alpine Chernozem according to the soil classification proposed by Spaargaren and Deckers (1998). According to the classification of soil types in China, the soil in this region is alpine meadow soil (Bai et al., 2022).

2.2 Experimental Design

In this study, we selected three connected grasslands of the same type to ensure consistency in soil and vegetation before the grazing treatments were conducted while also conducting spot experiments with grazing treatments. The three pastures were divided into three grazing treatments, namely, grazing yaks (Y), Tibetan sheep and yaks (S+Y), and Tibetan sheep (S). These are cold season pastures, and the grazing time is from October to May of the next year. The grasslands were extensively distributed, and each experimental plot was enclosed by a 1.5 m-high wire fence. In the three plots, a total of 12 squares of 1 m × 1 m were set up. Please refer to **Figure 1** for the location of the sample plot.

No non-grazing treatments were used in this study. There are substantial financial costs and logistical difficulties associated with managing Tibetan sheep and yak grazing in repeated grasslands. Therefore, in this study, the experiment was designed using a pseudo-replicate sampling method developed for practicality, meaning samples from the same treatments were sampled in the same meadow. However, the sampling areas in each meadow were sufficiently large, with Y, S+Y, and S measuring 11.33, 10.00, and 18.67 ha, respectively. According to Oksanen (2001), the experimental design used here is statistically sound, thus, the results are reliable. According to a survey of local households conducted during sampling, grazing was continually done for 39 years, i.e., from 1983 to 2021. Grazing rates were not significantly different for each grazing plot (**Table 1**). Additionally, **Figure 2** shows the biomass of the grassland functional group in 2021. The soil nutrients are showed in **Table 2**. The density of rodents is very low and has no negative impact on the grassland on the meadow.

Different capital letters indicate significant differences in grassland functional group biomass among the treatments ($p < 0.05$).

2.3 Sample Collection and Measurement Analysis

2.3.1 Sample Collection

K. humilis samples were collected in September 2021, according to the method described by Ren (1998). From a

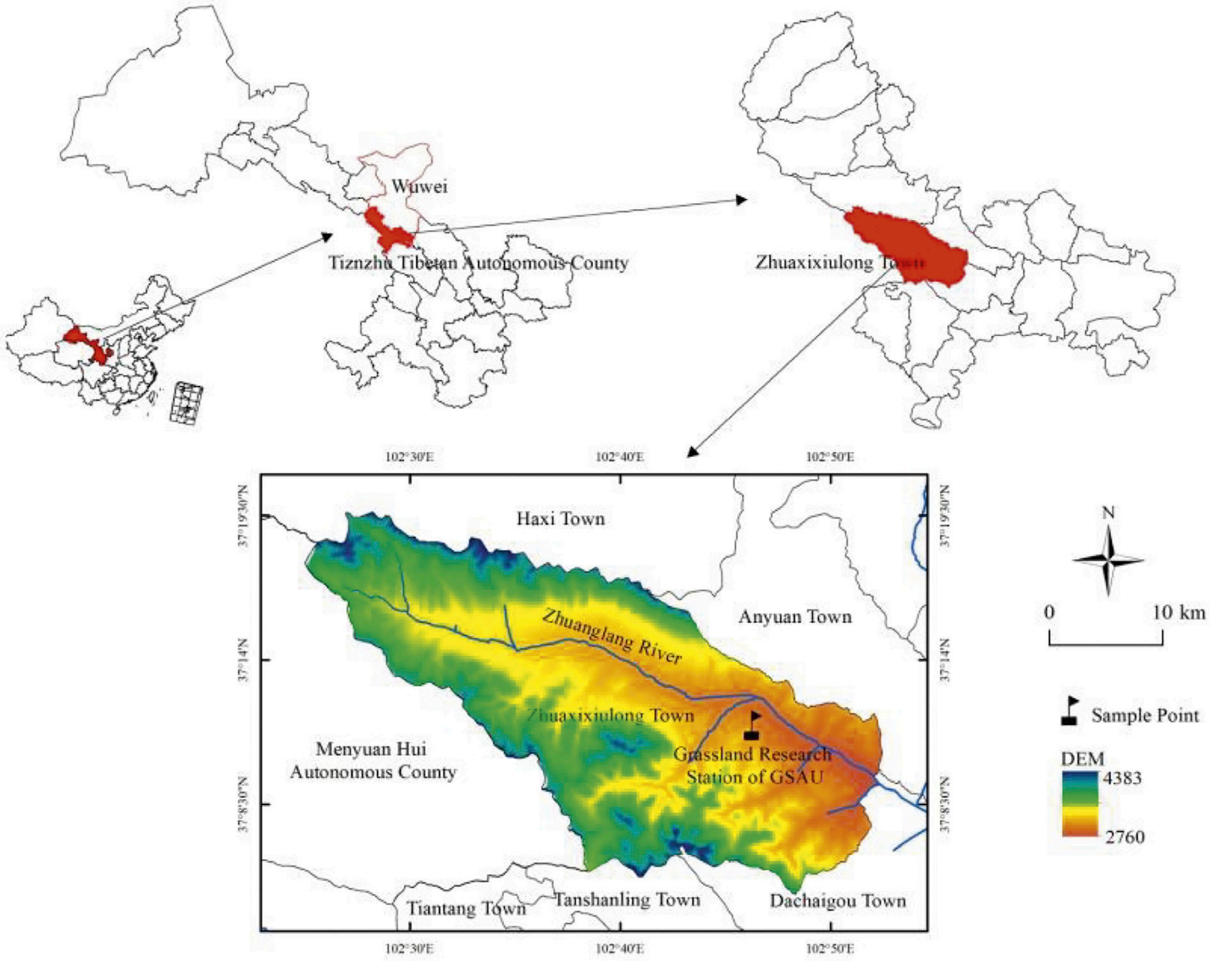

FIGURE 1 | Schematic diagram of the experimental site. *Administrative division data were obtained from the Resource and Environment Data Center of the Chinese Academy of Sciences (http://www.resdc.cn), and digital elevation model data, with a spatial resolution of 30 m, were obtained from the Geospatial Data Cloud (http://www.gscloud.cn/).

TABLE 1 | Grazing rate of each treatment (sheep unit month·ha^{-1}).

Years	S	S_Y	Y
2011–2021	82.50 (0.54)Aa	82.96 (1.89)Aa	84.26 (2.26)Aa
2001–2010	82.48 (1.54)Aa	83.29 (2.45)Aa	83.67 (1.12)Aa
1983–2000	82.84 (1.45)Aa	84.04 (3.04)Aa	84.42 (3.17)Aa

total of 15 samples, 30 representative plants were selected randomly; thus, 150 plants were sampled from each plot, and 450 plants in total were sampled from the three sample plots. The spikes of *K. humilis* were individually cut, stored in a paper bag, complete plants were subsequently dug up, clean the soil from the roots, then transported to the laboratory in paper bags. The samples were placed in an electro-thermostatic blast oven (Hengzi, GZX-GF101-3-BS- II, Shanghai, China) and were later subjected to 105°C for 0.5 h to acquire dead samples. Subsequently, the samples were dried at 65°C until constant

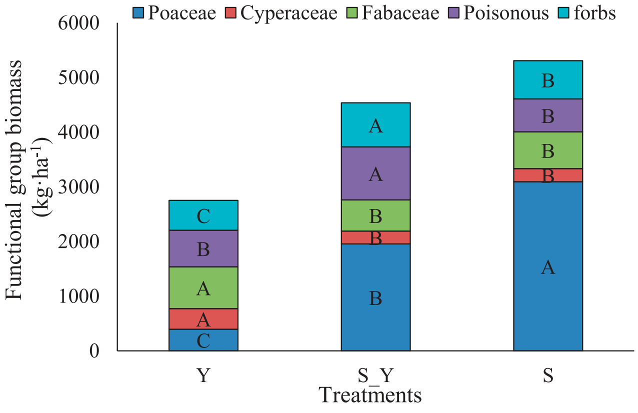

FIGURE 2 | Biomass of alpine meadow functional group according to grazing methods in 2021.

TABLE 2 | Effects of different grazing patterns on soil nutrition in 2021.

	S	S+Y	Y
TN (g/kg)	6.53 (0.30) A	6.03 (0.36) A	5.20 (0.49) B
TP (g/kg)	0.90 (0.01) A	0.86 (0.02) B	0.71 (0.04) C
TK (g/kg)	16.46 (0.29) A	16.88 (0.43) A	16.63 (0.60) A
SOC (g/kg)	149.37 (8.84) A	135.17 (9.84) B	113.27 (9.16) C
AN (mg/kg)	406.08 (9.40) A	382.08 (13.16) B	379.20 (11.27) B
AP (mg/kg)	20.98 (1.50) A	19.42 (1.22) A	15.93 (0.88) B
C:N	13.29 (0.88) A	13.06 (1.41) A	12.77 (1.72) A
N:P	7.19 (0.34) A	6.96 (0.45) A	7.31 (1.02) A
C:P	95.39 (5.57) A	90.29 (5.74) A	92.21 (11.16) A

The data in the table are expressed as mean (standard deviation). Capital letters indicate significant differences among the grazing treatments (p < 0.05).

weight was attained and then measured for indices in the next step.

2.3.2 Measurement Indexes and Related Calculations

Plant height: Height from the ground to the plant top.

Crown width: Crown diameter of the plant.

Plant density: Number of *K. humilis* plants per m^2.

Reproductive branches density: Number of branches with spikes per m^2.

Reproductive branch height: Height of branches with spikes.

Nutrient branch density: Number of branches without spikes per m^2.

Spike length: Length from the base to the tip of the spike.

Number of seeds: Number of seeds on each spike.

Seed size: Length, width, and height of the seeds measured using Vernier calipers.

Effective spike ratio: Proportion of spikes with ≥5 seeds (Yan and Hou, 2018).

The biomass, sexual reproduction efficacy, vegetative reproduction potency, storage efficacy, growth potency, seed yield, and effective spike number ratio were calculated for each trait. The calculation methods are showed in **Table 3**.

2.4 Data Analysis

Before the data analysis, we performed the normal distribution equal variance test on the relevant data and found that the assumptions were satisfied. One-way analysis of variance was used to analyze significant differences between the different grazing treatments. All data were presented as mean ± standard deviation. SAS was used for all statistical analysis (100 SAS Campus Drive Cary, NC 27513-2414, United States) and Microsoft Excel 2012 (Microsoft Corp., Redmond, WA, United States) was used for graphical representations. The levels of significance were set at $p < 0.05$.

3 RESULTS

3.1 Effect of Grazing Treatments on Phenotypic Plasticity of *K. humilis*

The **Figures 3A–C** shows the effects of grazing treatments on plant height, crown width, and the density of *K. humilis*, respectively. The Y treatment significantly reduced the plant height ($p < 0.05$) by 29.93% and 36.20% compared to the S+Y and S treatments, respectively. The maximum height recorded was 14.2 cm in the S treatment, which was significantly higher than that in the other treatments ($p < 0.05$). The *K. humilis* crown width was significantly higher in the S+Y treatment (8.8 cm) than that in the Y treatment (5.9 cm) and S treatment (6.3 cm; $p < 0.05$; **Figure 3B**). Further, the *K. humilis* density significantly differed between treatments ($p < 0.05$), with the highest density in the Y treatment (24.6 individuals/m^2) and the lowest density observed in the S treatment (15.84 individuals/m^2; **Figure 3C**).

Figure 4 illustrates the distribution of *K. humilis* resources among traits due to the grazing treatments. Treatments significantly affected the biomass of *K. humilis*, with the following trend: S+Y > Y > S ($p < 0.05$). The biomass of the reproductive branches was significantly higher in the S+Y treatment than in the other treatments ($p < 0.05$), and significantly higher in the Y treatment than in the S treatment ($p < 0.05$). Seed biomass was the highest in the S+Y treatment and

TABLE 3 | Definition of different plant indicators and their calculation formulas.

Calculation index	Definition	Unit	Calculation formula
Reproductive structure	Biomass of breeding traits	g	Reproductive branch biomass (g) + Seed biomass (g)
Nutrition structure	Biomass of nutrient traits	g	Nutrient branch biomass (g)
Storage structure	Biomass of storage traits	g	Root biomass (g) + Rootstock biomass (g)
Growth structure	Biomass of growth traits	g	Biomass of reproductive structure (g) + Biomass of nutrient structure (g)
Sexual reproductive efficacy	Percentage of resource allocation for reproduction functions	(%)	[(Reproductive branch biomass (g) + Seed biomass (g)]/[Total biomass (g)] × 100
Vegetative reproductive efficacy	Percentage of resource allocation for nutrient growth	(%)	[(Nutrient branch biomass (g)/Total biomass (g)] × 100
Storage efficacy	Percentage of resource allocation for storage functions	(%)	[(Root biomass (g) + Rootstock biomass (g)]/[Total biomass (g)] × 100
Growth efficacy	Percentage of resource allocation for growth functions	(%)	[(Reproductive structure biomass (g) + Nutrient structure biomass (g)]/[Total biomass (g)] × 100
Seed yield	Mass of seeds per unit area	($kg \cdot ha^{-1}$)	Reproductive branch density (per m^2) × Number of seeds per spike × The 1000-grain weight (g) × Effective spike number ratio (%)
Effective spike number ratio	Proportion of spikes with ≥5 seeds	(%)	(Effective number of spikes/total number of spikes) × 100

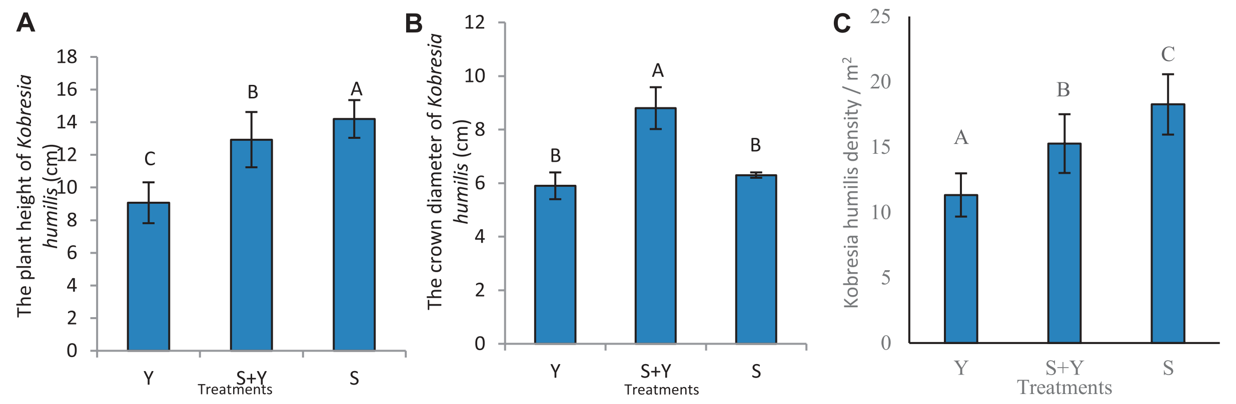

FIGURE 3 | Effect of grazing methods on the phenotypic plasticity of *K. humilis* with the **(A)** response of plant height, **(B)** canopy width, and **(C)** density per m^2. Different capital letters in the figure indicate significant differences between grazing methods ($p < 0.05$).

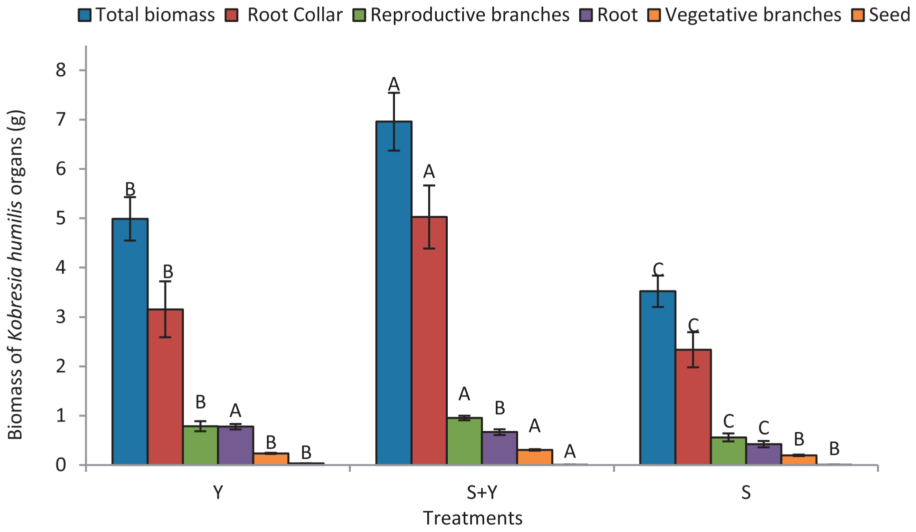

FIGURE 4 | Effect of grazing methods on material partitioning patterns of *K. humilis*. Capital letters indicate significant differences in the biomass of each trait under grazing methods ($p < 0.05$).

was not significantly different between the Y and S treatments ($p > 0.05$), with values ranging from 0.0032 g (Y treatment) to 0.0039 g (S treatment).

3.2 Effects of Grazing Treatments on the Reproductive Plasticity of *K. humilis*

3.2.1 Effect of Grazing Treatments on the Sexual Reproductive Characteristics of *K. humilis*

The grazing treatments caused significant differences ($p < 0.05$) in the reproductive branch density of *K. humilis*, with a maximum (248.33 per m^2) and minimum (67.5 per m^2) values occurring in the S+Y and S treatments, while it was 195.83 per m^2 in the Y treatment (**Figure 5A**). The plants in the S treatment shows a spike length of 1.52 cm (**Figure 5C**), which was significantly higher than that observed in the S+Y and Y treatments ($p < 0.05$). Compared to the different treatments, the Y treatment significantly increased the effective spike ratio (**Figure 5D**), which was significantly higher than that of the other treatments ($p < 0.05$); the ratio in the S treatment was slightly lower, while the effective spike ratio in the S+Y treatment was significantly lower than that of the other treatments ($p < 0.05$).

The Y treatment significantly increased the length and width of *K. humilis* seeds ($p < 0.05$), whereas the S treatment significantly increased the seed thickness ($p < 0.05$) (**Figure 6A**). **Figure 6B** shows that the S+Y treatment significantly reduced the 1000-grain weight of *K. humilis.* The seed number per spike was significantly higher in the S+Y treatment than in the other treatments ($p < 0.05$) (**Figure 6C**). Further, the S treatment significantly reduced the seed yield of *K. humilis* compared to the Y and S+Y treatments ($p < 0.05$), while there was no significant difference between the Y and S+Y treatments ($p > 0.05$) (**Figure 6D**).

3.2.2 Effect of Grazing Treatments on the Vegetative Reproduction Characteristics of *K. humilis*

Figure 7 depicts the effects of grazing treatments on the vegetative reproduction characteristics of *K. humilis*. The S+Y treatment significantly increased the nutrient branch density ($p < 0.05$), which was 3.33 and 1.42 times higher than that in the Y and S treatments, respectively. The Y treatment had the lowest nutrient branch density, which was significantly lower than that in the other treatments ($p < 0.05$) (**Figure 7A**). **Figure 7B** shows that the number of tillers per plant was the highest (12.07) in the Y treatment, which was significantly higher than in the other treatments ($p < 0.05$), while that in the S+Y treatment (6.07) was significantly higher than in the S treatment (4.8) ($p < 0.05$). The number of leaves per tiller in the S+Y treatment was significantly higher than the other treatments ($p < 0.05$), while there was no significant difference between the number of leaves per tiller in the Y and S treatments ($p > 0.05$) (**Figure 7C**). Moreover, the relationship between the different treatments was as follows: S+Y > Y > S.

3.3 Biomass and Reproduction Efficacy of Each Functional Structure

3.3.1 Reproductive Structure Biomass and Reproductive Efficacy

Grazing treatments significantly changed the biomass of sexual reproductive structures, with the following trend: S+Y > Y > S; additionally, the difference between the vegetative biomass among the treatments was significant ($p < 0.05$) (**Figure 8A**). The maximum biomass of vegetative reproductive structures occurred in the S+Y treatment, which was significantly higher than in the Y and S treatments ($p < 0.05$); however, the differences

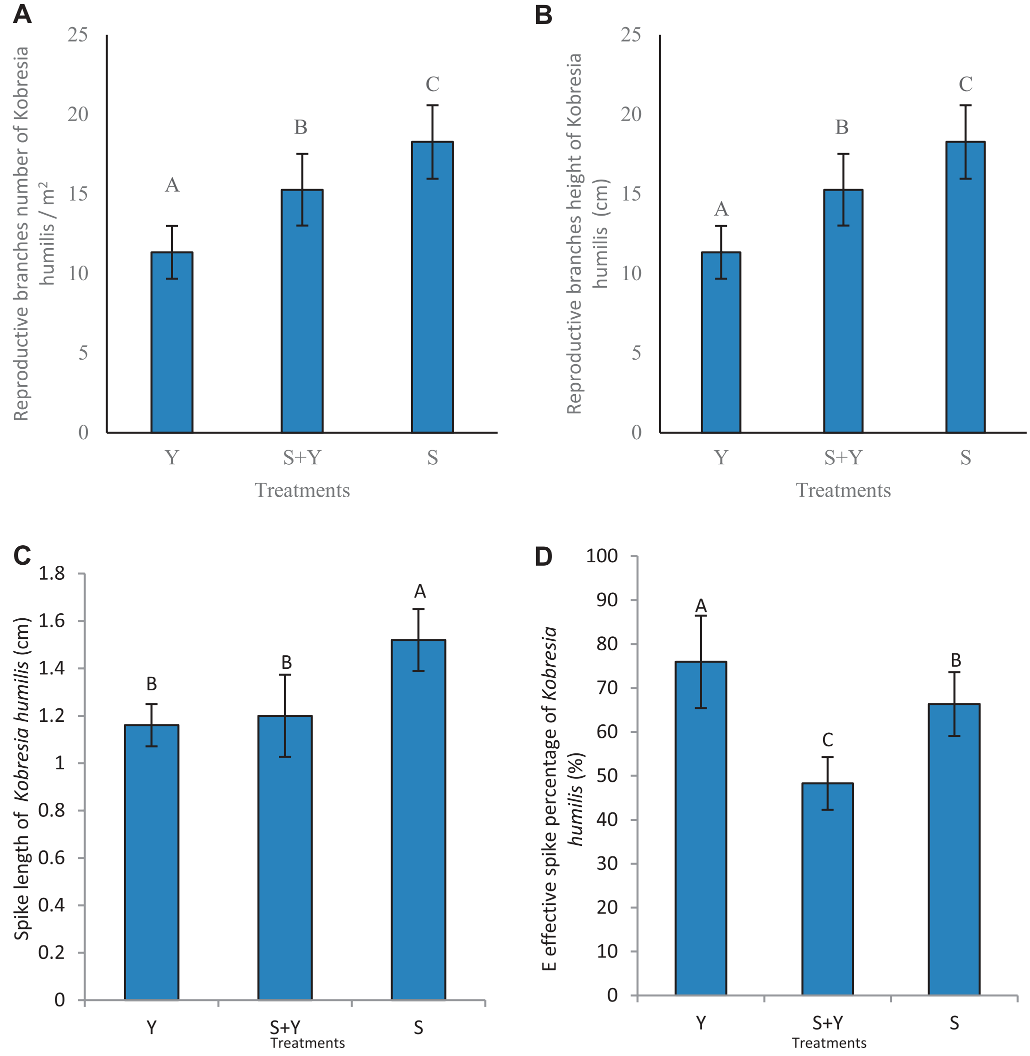

FIGURE 5 | Effects of grazing methods on different sexual reproduction characteristics of *K. humilis*: **(A)** reproductive branch density, **(B)** reproductive branch height, **(C)** spike length, and **(D)** effective spike number ratio. Capital letters indicate significant differences between grazing methods ($p < 0.05$).

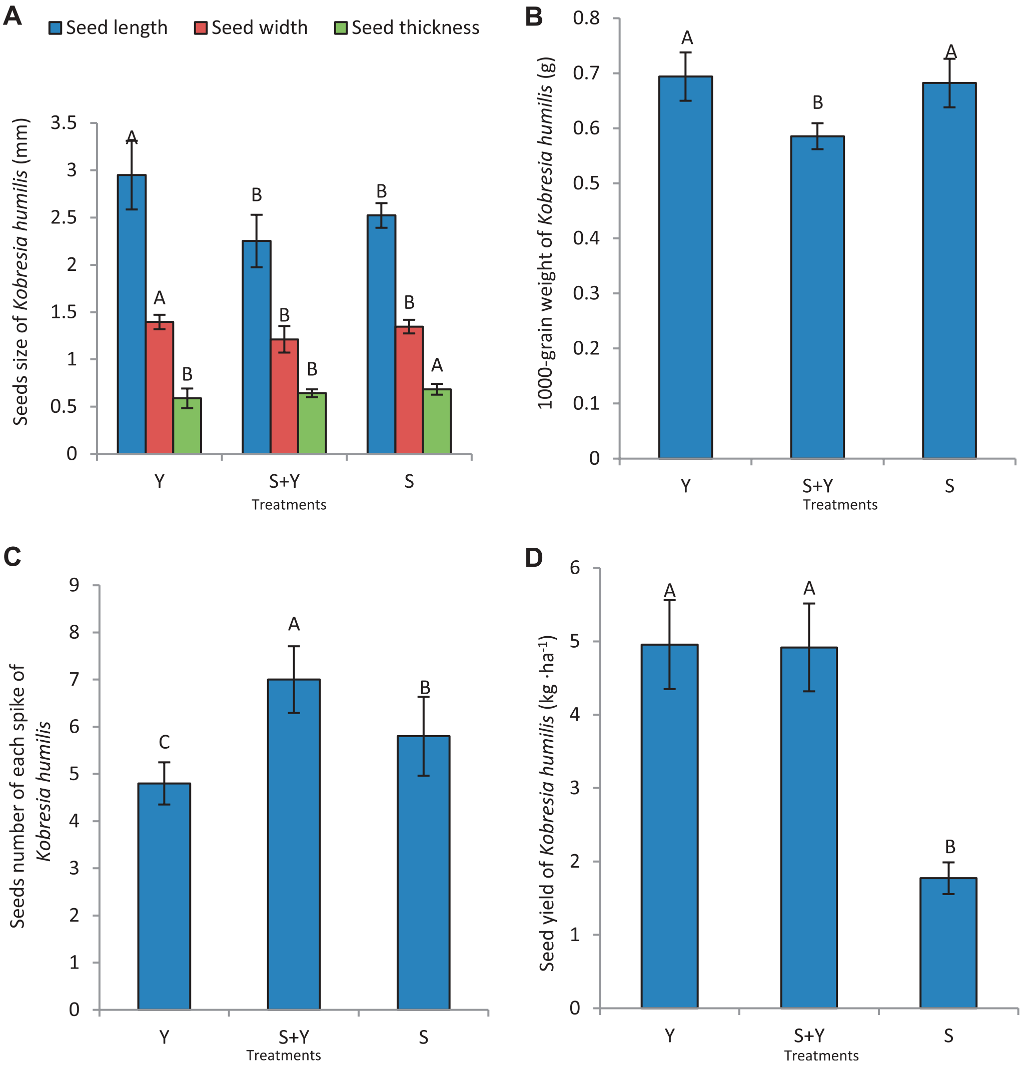

FIGURE 6 | Effects of grazing methods on seed indicators of *K. humilis*: **(A)** seed size, **(B)** 1000-seed weight, **(C)** seed number per spike, and **(D)** seed yield. Capital letters indicate significant differences between grazing methods (p < 0.05).

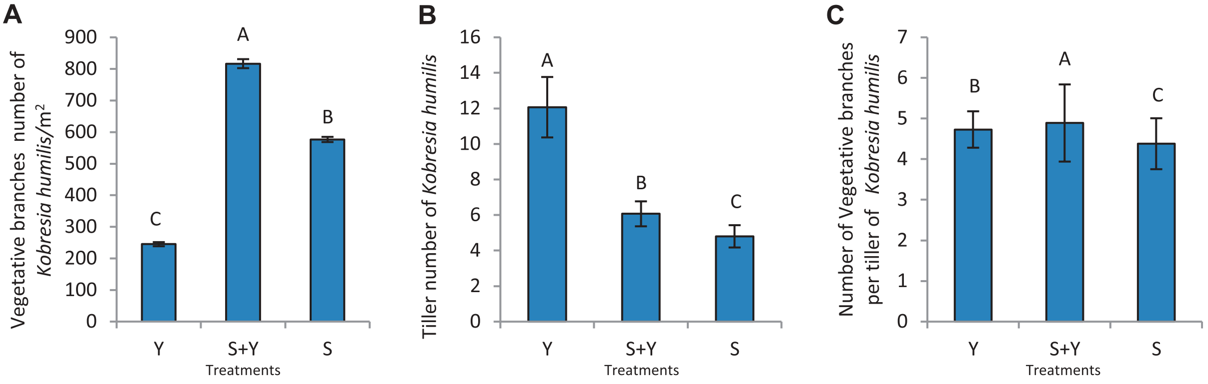

FIGURE 7 | Effects of grazing methods on vegetative reproduction of *K. humilis* in terms of **(A)** nutrient branch density, **(B)** number of tillers per plant, and **(C)** number of nutrient branches per tiller. Capital letters indicate significant differences (p < 0.05) among grazing methods.

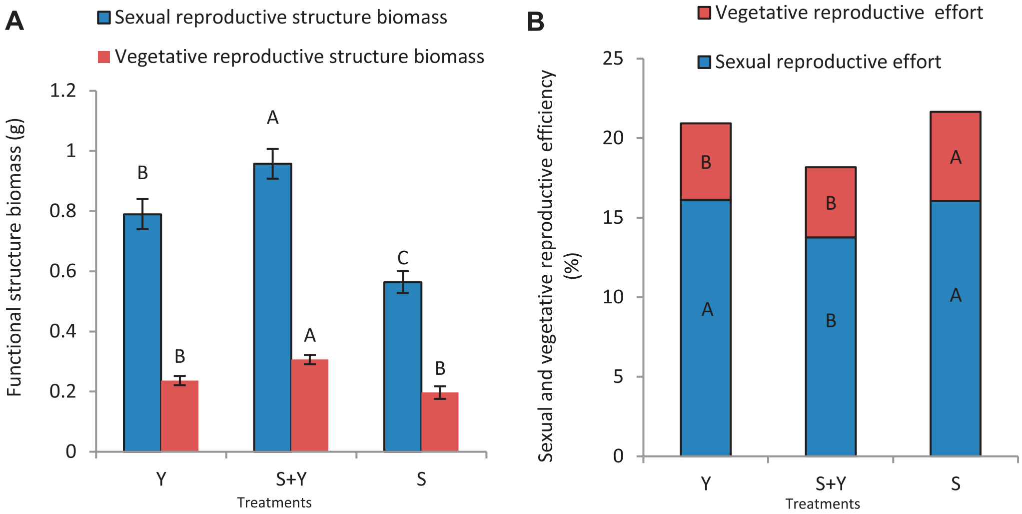

FIGURE 8 | Trade-off between grazing methods on sexual and vegetative reproduction of *K. humilis* in terms of **(A)** reproductive structure biomass and Nutrition structure biomass and **(B)** reproductive structure effectiveness and nutritional structure effectiveness. Capital letters indicate significant differences ($p < 0.05$) among grazing methods.

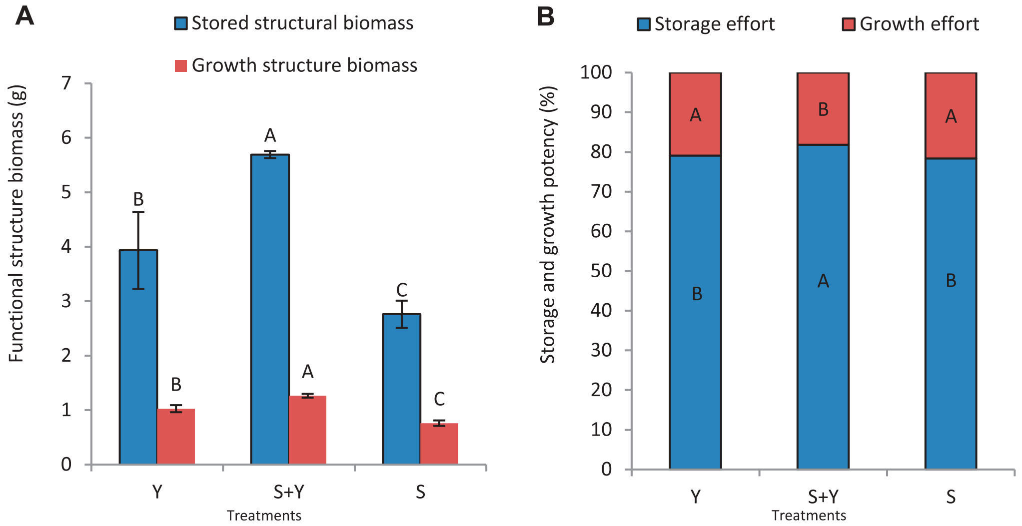

FIGURE 9 | Trade-off between grazing methods on the storage and growth of *K. humilis* in terms of **(A)** storage structure and growth structure biomass, and **(B)** storage structure and growth structure effectiveness. Capital letters indicate significant differences among grazing methods ($p < 0.05$).

between the S and Y treatments were not significant ($p > 0.05$). **Figure 8B** illustrates the difference between the sexual and vegetative reproduction efficacy. The difference in the sexual reproduction efficacy between the S and Y treatments was not significant ($p > 0.05$); moreover, the reproduction efficacy in the S+Y treatment (13.76%) was significantly lower than that in other treatments ($p < 0.05$). Further, the vegetative reproduction between the Y and S+Y treatments was not significant ($p > 0.05$), and both were significantly lower than the S treatment ($p < 0.05$).

The S+Y treatment significantly increased the allocation of resources to the storage structure ($p < 0.05$), and the biomass of the storage structure in the Y treatment was significantly higher than that in the S treatment ($p < 0.05$) (**Figure 9A**). Further, the pattern of change in the growth structure was the same as that of the storage structure, with the following trend: S+Y > Y > S, and a significant difference was observed between the treatments ($p < 0.05$). **Figure 9B** shows that the S+Y treatment significantly increased the allocation of resources in the storage structure ($p < 0.05$), and the storage efficacy did not differ significantly between the S and Y treatments ($p > 0.05$). Additionally, no significant difference was observed in growth effectiveness between the S and Y treatments ($p > 0.05$).

4 DISCUSSION

4.1 Morphological Changes of *K. humilis* in Response to Individual and Population Scales Under Grazing Treatments

K. humilis is one of the dominant species in the alpine meadows of the QTP (Dai et al., 2021). Studying its morphological changes in response to grazing treatments is important for the sustainable utilization and maintenance of species diversity in the QTP alpine meadows (Guo et al., 2017; Zhang Q. et al., 2019). Our results showed that *K. humilis* developed adaptive strategies in response to different grazing disturbances, with significant differences observed in monocot biomass and material partitioning patterns among the different grazing treatments. The plants improved their adaptation to grazing by adjusting resource allocation to occupy a favorable ecological niche in a continuously disturbed environment (Kruk et al., 2021). In our study, the S+Y treatment resulted in the highest biomass per plant, while the Y treatment showed the lowest biomass per plant. This may be due to several reasons. First, cold season pasture grazing by yaks and Tibetan sheep not only reduced the biomass of *K. humilis*, but also significantly reduced the height of pasture. As one of the early re-greening forage resources, the lower plant height provided sufficient sunlight for the re-greening of *K. humilis* in the S treatment. High photosynthetic efficiency increased the material accumulation of *K. humilis*, which in turn increased the biomass of the individual plants. Li et al. (2021) showed that the physical mechanisms of compensatory growth usually include increased photosynthetic efficiency, release of apical dominance, and redistribution of resources (carbohydrates, water, and nutrients). Thus, the S+Y treatment produced compensatory growth in *K. humilis*, which could have also increased the biomass. The earlier re-greening also provides an advantage for *K. humilis* to utilize ecological niches (Zhang L. et al., 2019). This relatively reduced the competitive pressure of *K. humilis* with other species under S+Y treatment (Wang et al., 2014). Further, higher soil bulk density and lower nutrient content in the Y treatment than that in the S+Y treatment (**Table 2**) may also lead to the dwarfing of *K. humilis*. In addition, interspecific competition could also change the phenotypic plasticity. In the S treatment, Pinaceae were the dominant functional group, and interspecific competition due to niche occupancy put great pressure on the growth of *K. humilis* (Peng F. et al., 2020). To compete for water, light, and nutrients, *K. humilis* increased its plant height. The root collar is the organ of *K. humilis* to store nutrients, which plays an important role in completing its life. The biomass of all traits in this experiment indicates that the grazing treatments only promoted the redistribution of material in *K. humilis* but did not reverse the distribution pattern of material in each trait.

Bradshaw (2006) noted that changes in plant morphology are one of the driving forces of community succession (Kalske and Kessler, 2020), and are a mechanism to increase plant adaptation under high levels of disturbance. This is a result of long-time interaction between plants and domestic animals (Li et al., 2021). In this experiment, we found that although the Y treatment of *K. humilis* was small, the density per unit area was high at the population scale. The adaptive strategies adopted by plants in response to grazing are divided into two main types: avoidance and tolerance (Kennedy and Barbour, 1992). Our results suggest that plant adaptation to grazing can be understood using both theories together. From the growth hindrance theory, plant dwarfism in the Y treatment is strongly related to hoof pressure of grazing animals. The average hoof pressure of yak and Tibetan sheep is 6.89 kg/cm^2 and 3.13 kg/cm^2, respectively, and the ratio of average hoof pressure between yak and Tibetan sheep is 2.2:1; additionally, the average trampling intensity of yak is 7.3 times higher than that of Tibetan sheep (Yang H. et al., 2019). The high intensity of trampling increased the compactness of the surface soil, which limits the growth of *K. humilis* and is detrimental to the storage of nutrients within the plant, resulting in dwarfism. In addition, the reduced plant height may also be a grazing avoidance mechanism developed by *K. humilis* in response to long term foraging. Although grazing yaks in cold season pasture feed on withered vegetation from forage grass to survive, the loss of yak manure and greater trampling intensity also lead to soil nutrient deficiencies and soil structural damage (**Table 2**), reduce the number and diversity of beneficial microorganisms in the soil (Wang et al., 2022), which have a profound impact on the soil over time (Yang C. et al., 2019). These conditions have altered *K. humilis* morphology, forcing *K. humilis* to adopt a tolerance strategy, choosing to reduce plant height to accommodate reduced soil quality and greater trampling intensity (Zhang et al., 2020). Secondly, the plant height in the Y treatment is relatively high, and dwarf plants are less likely to be foraged by yaks. Reducing the plant height as an avoidance strategy preserves the ability of *K. humilis* to grow and reproduce and helps *K. humilis* to maintain its position in the sedge-grass community. Apparently, grazing yaks induced defenses in *K. humilis* at the population scale. To counteract the negative effects of plant dwarfism in interspecific competition and species survival, *K. humilis* used its limited resources to increase the number of individuals and thus occupy more ecological niches, with the aim of increasing the survival rate of the population. Previous studies have shown that yak trampling is more likely to stimulate *K. humilis* buds and tillers than Tibetan sheep (Pan et al., 2021). Changes in morphology may also be due to environmental constraints, including interspecific competition, abiotic limitations to growth and periodic biomass destruction (Buisson et al., 2019). In the S+Y treatment, *K. humilis* was taller but less dense, which was caused by the competition with the dominant species, Poaceae, due to environmental conditions. Grime and Pierce (2012) and Voile et al. (2012) showed that *K. humilis* limits intraspecific trait variation and allocates more nutrients to morph establishment to maintain the existing ecological niche width when environmental conditions are harsh.

4.2 Effects of Grazing Treatments on Reproductive and Life History Responses of *K. humilis*

Trade-offs are a central concept in life history theory (Wolf et al., 2007) wherein grazing intensifies environmental stress in plants, making it difficult for optimal allocation of resources (Hanushek, 1992; Prendergast, 2002). The results of this study showed that the grazing treatments significantly affected the trade-off strategy between sexual and asexual reproduction of *K. humilis*. Moreover, grazing disturbance in the Y treatment promoted sexual reproduction of *K. humilis* and reduced the input of vegetative reproduction. Notably, plants in the Y treatment did not use resources to increase the number of reproductive branches and density, but to improve sexual reproduction inputs by increasing the proportion of effective spikes and increasing the seed size and yield. The results of the Y treatment indicated that *K. humilis* extended its population to more open spaces by increasing its investment in seeds to avoid resource limitation caused by grazing yaks. As a Cyperaceous forage plant, *K. humilis* uses internal tillers to expand outward to increase its crown width. Thus, its crown width was significantly and positively correlated with *K. humilis* longevity (Dai et al., 2019).

Wilson and MacArthur (1967) divided the life history strategies of organisms into r-selection (miniaturization of adults, large individual numbers, small body size and high reproductive allocation) and k-selection (slow individual development, small numbers and large individuals). Grime (1979) proposed the concept of c-selection, means that plants to maximize their competitiveness under the condition of low environmental severity and low interference intensity. In our study, the significantly small crown width in the Y treatment suggested that this treatment facilitated the inclination of *K. humilis* to r-selection in its life history strategy, that is, high reproductive energy allocation and short epoch cycle. This life history strategy allows *K. humilis* to better adapt to the fluctuating living conditions induced by grazing yaks in the alpine meadows, and shaded and humid environmental conditions, thereby maximizing the population growth rate (Junk and Piedade, 1997). Compared to the other treatments, the *K. humilis* in S treatment devoted more resources to increasing reproductive branch height, spike length and seed weight, and had the lowest density of the three grazing treatments. This was possibly due to the dominance of Poaceae grass in the S treatment. *K. humilis* employs c-selection that maximizes individual competitiveness in response to the strong interspecific competition posed by Poaceae Salahuddin et al. (2018). Although the reproductive branch density, seed number, and seed yield in the S+Y treatment were significantly higher than those in the other treatments, sexual reproduction efficacy was significantly lower than that in the other treatments. This may be due to environmental changes that induced *K. humilis* to select minimal reproductive allocation and to store resources for a longer lifetime (k-selection). Further, the number of tillers in the Y treatment was significantly higher than in the other treatments, which was likely due to the coupling effect of high trampling intensity and foraging by yaks. Pan et al. (2021) showed that grazing yaks fragmented plants and activated their shoots to promote vegetative reproduction. In contrast, the number of tillers as shoot banks of *K. humilis* increased significantly.

Moreover, heavy foraging of *K. humilis* by yaks suppressed the plant height, thereby increasing the number of tillers. Both nutrient branch density and number were significantly lower in the Y treatment than in the S+Y treatment. This indicates that although yak grazing activated the *K. humilis* shoot pool and improved the grazing tolerance of *K. humilis* (Wang et al., 2017), it did not stimulate further development of shoots into nutrient branches. Many studies have shown that increase investment in sexual reproduction decreases investment in vegetative reproduction, suggesting that there is a significant trade-off between sexual and vegetative reproduction (Wang et al., 2018; Liu, 2020; Endo et al., 2021). Our results support this suggestion. Yuan et al. (2020) showed that simulated grazing of large herbivores favored asexual reproduction of *Hordeum brevisubulatum* to the detriment of sexual reproduction. This was a result of different simulated grazing intensities at the jointing stage, which increased tiller emergence yield and improved the compensatory growth capacity of tillers. Such findings are contrary to our conclusion that reported sexual reproduction efficacy was significantly higher than vegetative reproduction efficacy in all treatments. The development of shoots into nutritional branches may be related to photosynthetic rate, growth hormone levels, and animal saliva (Zhang et al., 2009). The adaptive strategies of plants to grazing can be reflected not only in the number of resources allocated, but also in the time of resource allocation (Liu et al., 2019; Keep et al., 2021). For perennial plants, a complex trade-off between current reproduction and future growth exists (Quesnel et al., 2018). The reproductive behavior of the perennial plants depends on the potential relationship between the number of resources currently available for growth and the number of resources stored for future reproduction (Friedman, 2020). The rootstocks and roots, act as nutrient storage organs for *K. humilis* and play crucial roles in the life history strategies and material distribution trade-offs (Song et al., 2020). In our study, storage efficacy was significantly higher than growth efficacy in all treatments, suggesting that future growth investment was more important for *K. humilis* in the trade-off between the present and the future. Some studies suggest that high storage may be an important factor in maintaining an inter-annual perennial regime in response to changes in abiotic factors, such as moisture and temperature, (Warschefsky et al., 2016; Freund Saxhaug et al., 2020). If future life expectancy is low, the energy allocated to current reproduction is high; conversely, if future life expectancy is high, the investment in reproduction is correspondingly reduced (Lundgren and Des Marais, 2020). The results of our study suggested that the growth effectiveness in the Y and S treatments was significantly higher than that in the S+Y treatment, while the storage efficacy was significantly lower than that in the S+Y treatment. Among the current future choices, the Y and S treatments reduced the future life expectancy of *K. humilis*, by favoring utilization of limited resources to promote current growth. The Y treatment reduced the crown width, increased the seed size and quality, and sacrificed current individual life length to compete for the utilization of ecological niches and maintenance of genetic diversity. In contrast, *K. humilis* in the S treatment devoted more resources to maintaining individual height and increasing competition for light resources with the Poaceae forage grass.

Compared with other treatments, S treatment increased *K. humilis* height, but significantly decreased the density of *K. humilis*. Cyperaceae—Poaceae meadows is the main vegetation type for alpine meadow. It was showed that the dominance of Cyperaceae in the community tends to increase in a mildly degraded alpine meadows (Han et al., 2019; Bourles et al., 2020), and thus is considered as a sign of decreasing grassland productivity. We found that the increase of yaks during grazing improved the purpose and sexual reproduction efficiency of *K. humilis* in the vegetation community, resulting in the degradation of alpine meadow. In contrast, Poaceae grasses are conducive to grazing due to their high biomass, good palatability, and benefit to sustainable development of alpine grasslands. Considering the morphological traits and reproductive characteristics of *K. humilis* in alpine meadows by grazing treatments, mono-grazing Tibetan sheep is more beneficial to grassland health and grazing utilization in alpine meadows.

This study was limited as only adaptive changes of *K. humilis* morphology and reproduction were explored. In future studies, the comprehensive effects of plant and soil should also be considered to provide a scientific basis for sustainable grazing utilization of alpine meadows.

5 CONCLUSION

In general, grazing treatments significantly altered the morphological characteristics and reproductive strategies of *K. humilis*. Grazing yaks alone increased the density and sexual reproductive efficacy of *K. humilis*, and mixed grazing by yaks and Tibetan sheep increased the canopy and biomass of *K. humilis*. In addition, sexual reproductive efficacy was significantly higher than nutritional reproductive efficacy and storage efficacy was significantly higher than growth efficacy in all treatments. This indicates that the main reproductive mode of *K. humilis* in this area is sexual reproduction and as a perennial forage grass, *K. humilis* stores most of its material to increase its future life expectancy. The Y treatment reduced sexual and nutritional reproduction, which favored the development of meadows to graminoid-grass type meadows. Gramineae meadows are more suitable for grazing utilization of alpine meadows due to their better palatability and biomass. Therefore, considering the health and sustainable utilization of alpine meadows, grazing Tibetan sheep in cool season pastures is a suitable grazing method.

DATA AVAILABILITY STATEMENT

The original contributions presented in the study are included in the article/supplementary materials, further inquiries can be directed to the corresponding author.

AUTHOR CONTRIBUTIONS

LW collected samples, analyzed data and wrote the manuscript. YJ did a part of sample work. CX selected the sampling location. XY designed the experiment and modified the manuscript.

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Global meta-analysis: Sparse tree cover increases grass biomass in dry pastures

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Agricultural and ecological droughts, extreme heat and aridity have high impacts on livestock and pasture systems worldwide. Finding ways to adapt production systems and increase biomass under these new conditions is urgently needed. The availability of tree shade in these pastures could potentially ameliorate the impacts of warm weather. Yet, the effects of tree cover on the productivity of livestock rangelands are hotly debated. We performed a global meta-analysis to evaluate the effects of tree cover on grass biomass during contrasting seasons within the same system and along environmental gradients in tropical and temperate productive systems. We also assessed the levels of canopy density at which tree cover effects are observable. We observed that trees facilitate grass biomass during dry seasons, especially in the tropics and dry regions. These positive effects are more likely to occur at intermediate levels of evapotranspiration and irradiance. Our findings suggest that integrating trees in pastures might increase resilience of current livestock production systems to drier and warmer conditions.

KEYWORDS

facilitation, livestock, rangeland, silvo pastoral system, tree-grass interaction, tropics, temperate, tree shade

Introduction

Livestock rangelands expand through tropical and temperate regions covering approximately 25% of our planet (Steinfeld et al., 2006). They differ in structure and composition from practically treeless pastures to landscapes with scattered trees or woody plant patches within a matrix of grasses. How trees and grasses interact has fascinated rangers, ecologists, and conservationists alike because the outcome determines the resources available to livestock and wild species (Scholes & Archer, 1997; Treydte et al., 2007; Harvey et al., 2011; Costa et al., 2016) and therefore food security (Vira et al., 2015), ecosystem services (Millennium Ecosystem Assessment, 2005) and nature conservation (Harvey et al., 2008). Tree-grass interactions have enormous implications for the management of rangelands under climate change and the conservation of biodiversity. Agricultural and ecological droughts, extreme heat and aridity have high impacts on livestock and pasture systems (IPCC, 2021). Increasing tree cover in rangelands could contribute to ameliorate the impacts of higher temperatures, and erratic rains as climate change progresses (Murgueitio et al., 2011; Altieri et al., 2015;

Solorio et al., 2017). This climate change adaptation strategy in productive systems could also have positive effects on biodiversity conservation. By increasing tree cover, wild species movement across landscapes is facilitated, fostering genetic diversity and migration that may contribute to maintaining ecological networks. However, the management of multifunctional landscapes aiming to promote win-win solutions that combine sustainable production with nature conservation and climate change mitigation remains challenging (Bustamante et al., 2014; Mbow et al., 2014).

Early work on tree-grass interactions emphasized competitive effects and promoted a view on production systems where grasses would benefit from treeless landscapes (Walter & Burnett, 1971; Walker & Noy-Meir, 1982; Walker & Salt, 2012). Young trees and grasses usually compete for water and soil resources, but as trees become taller and reach deeper soil layers, competition for soil resources becomes less relevant for trees and light competition more relevant for grasses (Bazzaz, 1979; Smith & Huston, 1990). This emphasis on negative interactions was softened in the nineties by the appreciation of positive effects of trees on grass productivity under abiotic stress conditions, such as droughts and heatwaves or poor soil fertility (Belsky, 1994; Holmgren et al., 1997; Scholes & Archer, 1997; Valladares et al., 2016).

There is a vast literature on the effects of trees on grasses in natural ecosystems such as savannas (Blaser et al., 2013; Dohn et al., 2013) and woodlands (Jackson & Ash, 1998; Barbier et al., 2008). Yet, the debate on the overall effects of trees on grasses in productive systems persists. Different studies have reported contrasting results about the levels of tree canopy density and the environmental conditions under which trees may have positive, negative or neutral effects (Treydte et al., 2007; Moustakas et al., 2013; Bernardi et al., 2016; Ansley et al., 2019). The most recent syntheses of the published literature have found tree facilitation on grasses to be stronger under N_2-fixing trees and in dry environments (Rivest et al., 2013; Mazía et al., 2016). We build upon these last studies to systematically evaluate whether tree cover increases grass biomass 1) during contrasting seasons, 2) along expanded environmental gradients in tropical and temperate pastures, and 3) at different levels of canopy density. We report, for the first time, the contrasting seasonal effects of trees on productive systems around the globe and show that trees have stronger positive effects on grass yields under intermediate levels of abiotic stress. These findings contribute to promote win-win solutions in current livestock production systems with focus on climate change mitigation, food security, and sustainability.

Methods

Paper selection

We searched for studies that evaluated grass performance (i.e., dry matter) under two contrasting seasons and two or more levels of tree cover. Searches were conducted in Web of Science (1945–2020) using the following keywords: “shade” OR “light” OR “irradiance” OR “shelter” OR “tree*” OR “canop*” OR “crown” OR “Sun*” OR “arbol” OR “cobertura arborea” OR “luz” OR “irradiaci?n” OR “protecci?n” OR “sombra” OR “dosel arbo*”; “drought” OR “water” OR “precipitation” OR “wet” OR “humid” OR “dissecat*” OR “arid*” OR “irrigat*” OR “dry” OR “rain*” OR “microclimat*” OR “temperat*” OR “sequia” OR “desecaci?n” OR “agua” OR “precipitaci?n” OR “humed*” OR “irrigaci?n” OR “seco” OR “microclima” OR “temperature”; “grass” OR “forage” OR “fodder” OR “grass” OR “pasture” OR “animal producti*” OR “producti*” OR “herbs” OR “herbace*” OR “forraje” OR “pasto” OR “hierba” OR “pastizal*” OR “leche” OR “carne” OR “pastura”; “pasture” OR “S?lvo-pastor*” OR “Agro-s?lvo-pastor*” OR “Agros?lvopastor*” OR “livestock” OR “wood* pasture*” OR “wood* grassland” OR “wood* rangeland” OR “ranching land” OR “pastureland” OR “ganado” OR “ganader*” OR “vaca” OR “cattle” OR “s?lvopastor*.” We chose dry matter as it was the most commonly used indicator of forage biomass. We registered the levels of tree cover and expressed it in a percentage scale of irradiance where 100% would represent the irradiance that reaches and open microsite (i.e., 0% of tree cover). This relative scale is adequate to compare the response of species that naturally occur under different ranges of light availability (Holmgren et al., 2012). We decided not to include studies that reported grass performance at only one season or one level of tree cover because we wanted to explicitly assess season-tree cover interactions. We screened publications for studies that included grass responses within the same calendar year or continuous year, specific location or coordinates where the study was carried out, and period in time when the measures were taken. We only considered studies conducted in the field and with natural tree shade.

The search from 5,135 papers yielded 174 studies from 33 suitable publications. When publications involved several grass species or irradiance levels, each species and each irradiance level was treated as a separate study. We decided to include several studies from the same paper because, although it tends to reduce the overall heterogeneity in effect sizes, excluding multiple results from a paper can underestimate effect sizes (Gurevitch & Hedges, 1999; Karst et al., 2008).

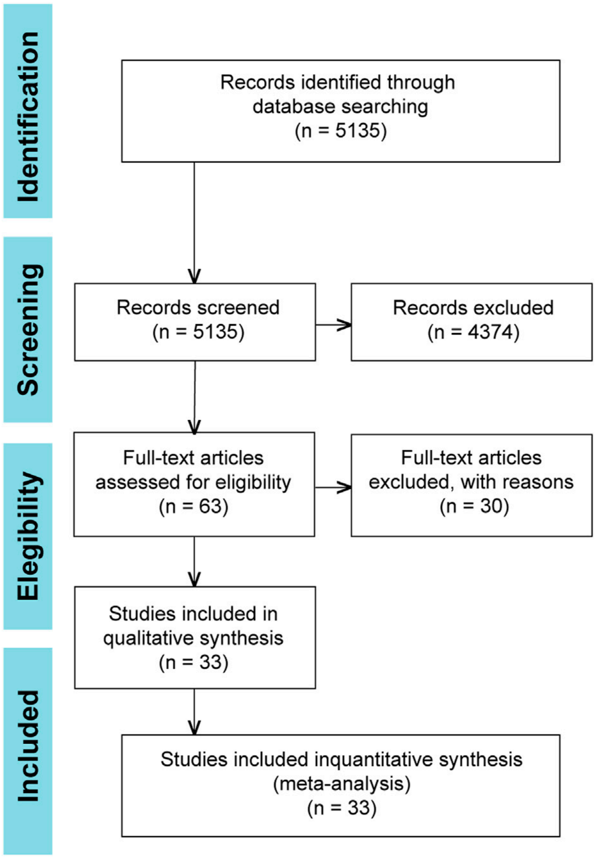

FIGURE 1
Flow diagram for the selection of manuscripts.

Data collection

Mean values of grass dry matter were collected from text and tables in the main publication and/or supplementary information. We used WebPlotDigitizer (Rohatgi, 2020) to extract mean and standard error values from figures when raw data was not provided. If not provided, standard deviations were back calculated from standard errors and sample sizes ($SD = SE \times \sqrt{n}$). When there were multiple studies within the same publication, we calculated several means (i.e., one per study), pairing the different levels of tree cover with the one with the lowest tree cover (highest irradiance). Some publications reported multiple responses under the same levels of tree cover within the same season, thus we averaged those responses to one value per tree cover level and season.

For each record in our dataset, we converted the grass dry matter mean to kg/ha/d and classified the grass species as C_3 or C_4. We registered the location, country and biome where the study took place. We obtained evapotranspiration (mm/day), monthly precipitation (mm) and maximum daily temperature (°C) based on the period of time of the records and coordinates, and distinguished between dry and wet seasons. Environmental data was obtained using the R package climatrends (de Sousa et al., 2020). The literature search workflow is presented in Figure 1.

Effect size calculations

Following identification, means (X), standard deviations (SDs), and sample sizes (n) were extracted from the published studies. If not reported, these statistics were derived from other metrics. We conducted a meta-analysis to assess the effects of tree cover and season on grass biomass following (Koricheva et al., 2013). For each study, we calculated the effect size using the natural log of the response ratio [ln (RR)] and its associated variance (ν_{lnRR}). The estimate of ln (RR) and for each study is based on X, SDs, and replicate numbers for control and treatments (Hedges et al., 1999). Positive ln (RR) values indicate facilitative effects and negative values indicate net competitive effects of tree cover on grass biomass.

We used the escalc and rma. mv functions in the metafor package in R 4.0.3 (R Core Team, 2020) to calculate the ln (RR) and to perform the statistical analysis. To address the question of how tree cover influences the response of grasses under contrasting seasons, we performed several multivariate meta-analysis models with random effects. We first analyzed whether the effect of tree cover differs between seasons and C3/C4 species across the different biomes. We used the ln (RR) for tree cover as the response variable, and the Seasons, biome and C3/C4 species as predictors (with interactions: Seasons *C3/C4). We assessed the effects of tree cover along environmental gradients of evapotranspiration, monthly precipitation, maximum, daily temperature and irradiance. We grouped biomes into two major regions: Temperate (i.e., Temperate, Mediterranean and Desert biomes) and Tropical (i.e., Tropical and subtropical biomes). Mediterranean and desert biomes were grouped in the Temperate region based on their mean annual precipitation and mean annual temperature. We fitted meta-regression models with evapotranspiration, major region and C3/C4 species as predictors (with interactions Evapotranspiration*C3/C4 and major region* C3/C4). Both linear and quadratic regressions were fit and the best model chosen using the Akaike Information Criterion corrected for small sample sizes (AIC_c, Supplementary Table S1). The same models were fitted replacing evapotranspiration for maximum daily temperature and monthly precipitation separately. Lastly, we analyzed the type of response of the effect of tree cover to irradiance and tree type (i.e., functional group) with Irradiance, Tree type, Seasons and C3/C4 species as predictors (with interactions Irradiance* Seasons, Irradiance * Tree type and C3/4* Seasons). In all the models we included the Study nested within the Paper as random factors.

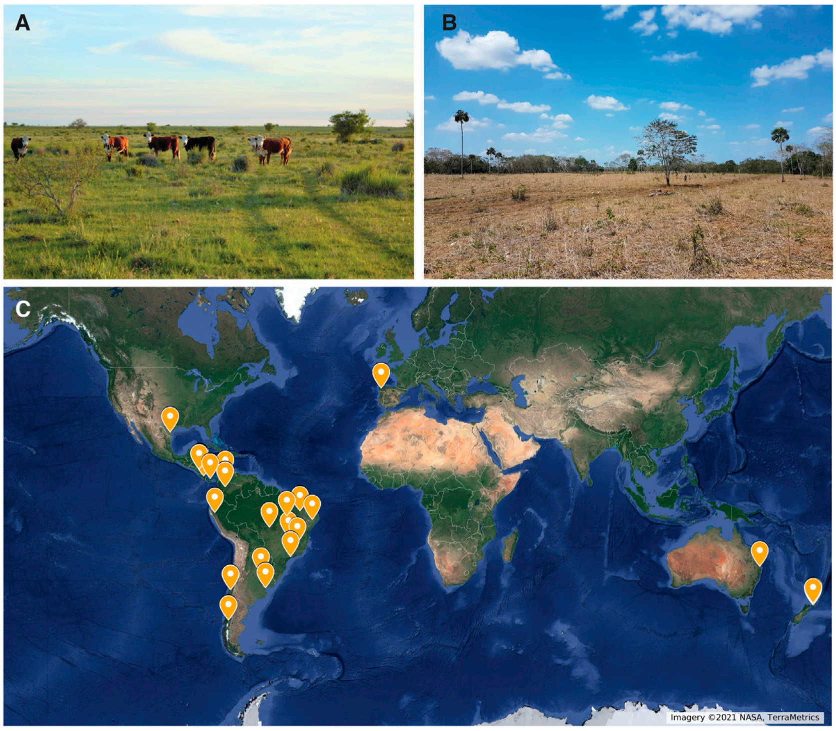

FIGURE 2
(A) Temperate pastures in Durazno, Uruguay during the dry season. **(B)** Dry tropical pastures in Yucatan, Mexico during the dry season. **(C)** Worldwide locations of studies. Studies from the same site are represented by a single dot.

Results

Tree cover effects vary between seasons and biomes

We identified 174 studies that assessed grass biomass under contrasting seasons and levels of tree cover across seven biomes following PRISMA guidelines (Moher et al., 2009, Supplementary Figure S1). About 61% were conducted in the tropics and 39% in temperate regions (Figure 2).

The effect of tree cover on grass biomass varied between biomes, seasons and C3/C4 grass species (p < 0.0001, Figure 3; Supplementary Figure S2; Supplementary Table S2). We found the largest tree facilitative effects in the Desert and Xeric shrublands, especially during the dry season. In tropical and subtropical biomes, we found mostly tree facilitative effects on C4 grasses during the dry season. Also in the Mediterranean, tree facilitative effects, for the dominant C3 grasses, were higher during the dry season than during the wet season. In contrast, in temperate regions the effects varied per biome; in temperate grasslands, savannas and shrublands, tree facilitative effects on C4 grass species occurred only during the wet season; while in broadleaf forests we found neutral effects on C3 grasses during both seasons and higher facilitative effects on C4 grass species during the dry season.

Tree cover effects depend on rainfall, temperature and irradiance

The positive effects of trees on grass biomass for C3 and C4 grasses peak at intermediate levels of daily evapotranspiration (4 and 5 mm for C3 and C4 grasses, respectively) and become negative at both ends of the evapotranspiration gradient (Figure 4A). We grouped the biomes in two major regions: tropical and temperate, and did not find differences between them.

When analyzing the contribution of rainfall and temperature separately, we found contrasting patterns on the role of trees on grass biomass along these climatic gradients. The effects of trees on both C3 and C4 grasses became increasingly negative as seasonal rainfall increases (p < 0.005, Figure 4B), especially for C3 species (p < 0.0001), in both tropical and temperate regions. While we found only negative effects on C3 grass species along the whole gradient of precipitation, we observed neutral to slightly positive effects on C4 grasses when monthly precipitation drops below ~50 mm.

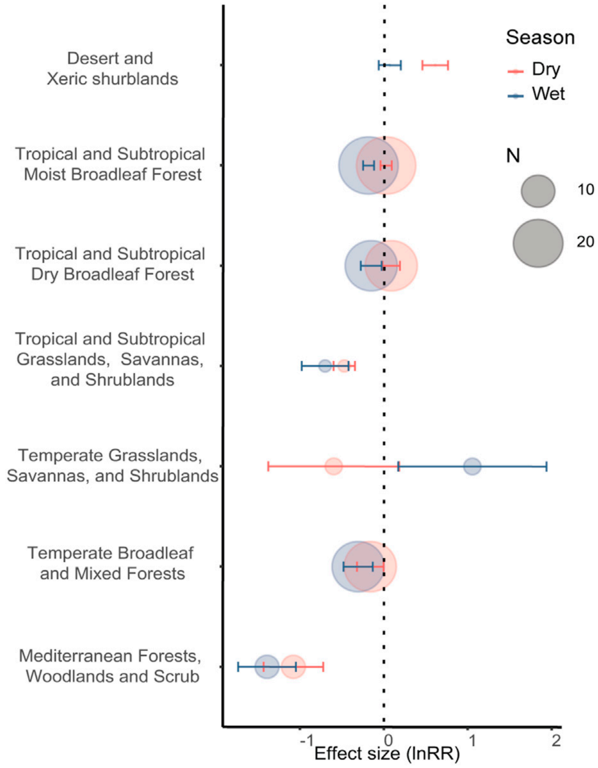

FIGURE 3
Tree effects on grass biomass in the dry and wet seasons across biomes. Facilitative effects are stronger in Desert and Xeric biomes and Tropical and subtropical biomes where C4 grasses occur, especially during the dry season. Tree effects vary in the temperate biomes: facilitation occurs in grasslands where C4 grasses dominate; in temperate forests mostly neutral to negative effects are observed. Dotted lines indicate zero effect sizes. 174 studies were identified of which 61% were conducted in the tropics and 39% in temperate regions. Point size indicates the sample size.

The nonlinear patterns of how trees and grasses interact are mostly explained by temperature. In the tropics, the effects of trees on C4 grass biomass are mostly neutral at intermediate maximum daily temperatures (~35°C) and become negative at both colder and hotter ends of the temperature gradient (Figure 4C). Also in temperate regions, trees have neutral effects on C3 grasses at intermediate temperature (~27°C) that become negative at both ends of the gradient of maximum daily temperature. In temperate regions, trees have positive effects on C4 grasses as conditions become warmer than ~32°C (Figure 4D).

Tree cover density determines the levels of irradiance received by grasses. Overall, we found that the positive effect of trees on grass biomass peaks at roughly 60%–80% of irradiance and becomes negative at lower or higher irradiance levels (Supplementary Figure S2). This facilitative effect tends to be higher under N_2 fixing trees than under Non-N_2 fixing trees although it is not significantly different ($p = 0.5$). The response of grasses to the irradiance levels are strongly dependent on the rainfall season and the grass type. C4 grasses respond negatively to lower irradiance levels especially during the rainy season. In contrast, C3 grasses are facilitated by intermediate levels of irradiance both in the dry and wet seasons (Figure 5).

Discussion

Here we report for the first time the contrasting seasonal effects of trees on productive systems around the globe. Our meta-analysis shows that the effects of trees on grass biomass have been studied more often in tropical and subtropical pastures than in temperate pastures. Overall, our results indicate that positive effects of trees on grasses: 1) are higher during seasonal droughts, especially on C4 grasses in tropical pastures and 2) peak at intermediate levels of evapotranspiration, temperature and irradiance, and at low levels of precipitation. These findings show that water, temperature and light, are key resources for grass growth and their interactions can shape the nature of tree-grass interactions in a wide range of productive ecosystems.

Facilitation is higher during seasonal droughts in the tropics

This meta-analysis shows that trees increase grass biomass in pastures during seasonal droughts and that these effects are stronger in tropical pastures where C4 grasses dominate, than in temperate pastures where C3 grasses are more common. The higher tree facilitative effects during droughts on C4 grasses can result from a combination of mechanisms that ameliorate abiotic stress. Although C4 grasses have been widely promoted across tropical productive systems (Edwards et al., 2010) for being highly tolerant to water stress and high temperatures (Chaves et al., 2003), they still benefit strongly from the shade of trees. During seasonal droughts in the dry tropics, when temperature and evapotranspiration increase sharply, the canopy of trees ameliorates environmental stress by reducing temperature and mediating irradiance levels even for highly tolerant C4 grasses.

In temperate regions, we found mostly, but not exclusively, neutral to negative effects of tree cover on grass biomass. C3 grasses occur more often in temperate regions and have a higher tolerance and photosynthetic capacity in colder temperatures (Saborsky & Mitsui, 1982; Gardner et al., 2017). Interestingly, the only positive effect of trees we found in temperate regions was described for open temperate savanna, specifically on C4 grasses during the wet

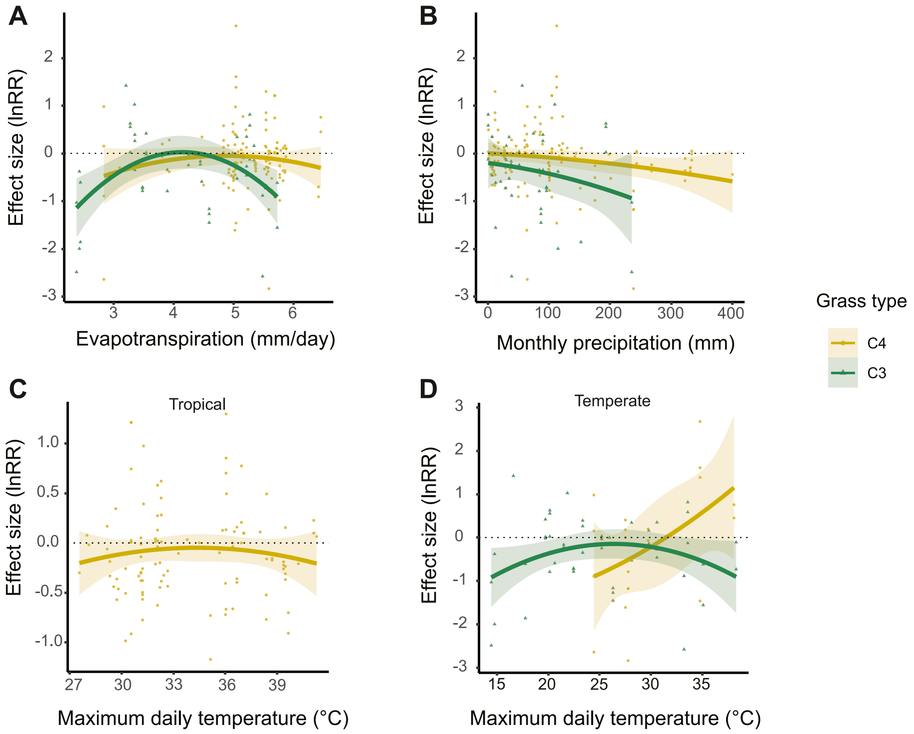

FIGURE 4
Tree effects on C3 and C4 grass biomass along gradients of **(A)** evapotranspiration, **(B)** monthly precipitation and maximum daily temperature in tropical **(C)** and temperate regions **(D)**. Dotted lines indicate zero effect sizes.

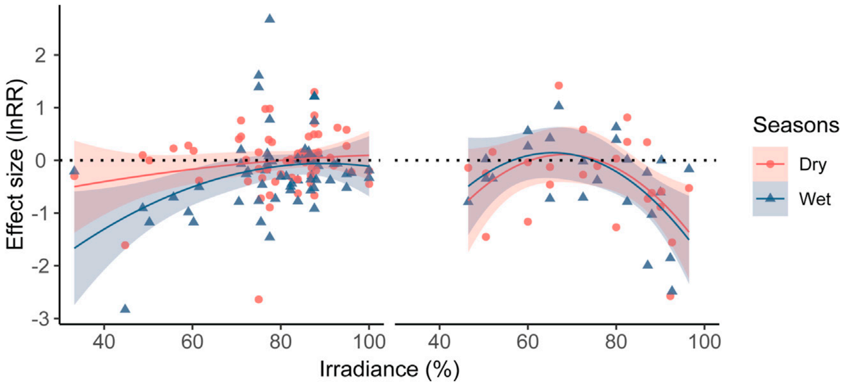

FIGURE 5
Tree effects on C3 and C4 grass biomass along the irradiance gradient in the dry and wet seasons. Dotted lines indicate zero effect sizes.

season. This is very contrasting to the facilitative effects for C4 grasses in the tropical pastures which occur mostly in the dry season. Temperate savannas are open biomes with high levels of irradiance which in combination with high water availability are less stressful for grasses. However, the wet season often corresponds with the coldest period of the year. In such open biomes, trees might ameliorate temperature in an opposite direction than in the tropics. While in the tropics abiotic amelioration implies a reduction in high temperature levels, in the temperate pastures, amelioration may be related to an increase in temperature under the tree canopy (Zellweger et al., 2019), creating a warmer microclimate that would benefit C4 grasses during wet and cold seasons.

Facilitation tends to peak at intermediate abiotic stress

We found a shift from neutral effects to negative effects of trees on grasses as monthly precipitation increases. Previous meta-analyses on the effect of trees on grass biomass in natural savannas also found stronger facilitation at drier places (Moustakas et al., 2013) or with decreasing annual precipitation (Dohn et al., 2013).

Our meta-analysis also revealed non-linear patterns of tree facilitative effects on grasses. These effects peak at intermediate levels of evapotranspiration, temperature and irradiance and can be lost at very low or high levels. Tree cover plays a key role in the interplay between positive and negative effects. In plant communities, the shade of neighboring plants is expected to increasingly ameliorate drought stress as conditions become drier (Bertness & Callaway, 1994), although these facilitative effects may be lost under extremely stressful conditions (Holmgren & Scheffer, 2010; Soliveres et al., 2015; Zhang et al., 2018). These non-linear effects of shade and drought have been found in meta-analyses of plant performance in field and experimental conditions (Holmgren et al., 2012) as well as in agroforests (Blaser et al., 2018). We now found comparable results for productive livestock pastures.

Although there was a tendency for N_2-fixing trees to have slightly higher facilitative effects than Non-N_2-fixing trees on grass biomass, we did not find significant differences between these two tree functional groups. N_2-fixing trees have been reported previously to increase pasture yields as drought pressure increases abiotic stress on livestock grazing systems (Rivest et al., 2013). Palm trees are highly abundant in tropical livestock pastures where farmers preserve them for their multipurpose value (Martínez-Ballesté et al., 2008; Macía et al., 2011), however, their effect on grasses is still poorly known compared to other groups of trees that have been studied more in detail. We found only one publication where the effects of palm trees on livestock pastures have been reported (Esquivel, 2007). Field experiments and long-term observational studies are needed to understand the effects of palm trees on grasses and determine whether they can contribute to increasing resilience to drought in livestock pastures.

We compared studies from seven different biomes that varied in time, period of the year of sampling, duration, and research methodology. Despite this variation, we identified higher facilitative effects of trees on grasses during seasonal droughts, especially in the tropical biomes where C4 grasses dominate and to a lesser degree in the temperate pastures. We showed that these effects are not only strongly related to the available levels of precipitation but also to temperature and irradiance. Understanding the effect of trees is crucial for managing and transforming current livestock production systems into multifunctional landscapes with increased resilience to seasonal droughts around the globe. We encourage the integration of trees with intermediate canopy density (i.e. ~20%–40%) in drier and warmer pastures, especially in the tropics where trees have positive and neutral effects on grass biomass. Positive and neutral effects of trees on grass biomass imply that trees can be used in productive pastures to ameliorate abiotic weather conditions favoring, or at least not compromising grass yields, while also contributing to other ecosystem services such as biodiversity conservation, carbon sequestration, habitat provision, construction materials, etc.

Challenges ahead

Our understanding of how trees influence the functioning of productive pasture systems is still fragmented. The existing literature has focused on identifying the effects of different types of trees according to their functional traits such as N_2-fixation or deciduousness (Rivest et al., 2013; Mazía et al., 2016) but we lack holistic assessments of the direct and indirect effects of tree diversity on livestock productivity. One major challenge is to widely assess how tree diversity affects both grass and animal production and how these effects can be translated into economic benefits for farmers while considering multiple ecosystem services at meaningful temporal scales.

Most of the studies we identified were carried out in the neotropics, especially in Latin America, which may reflect different cultural traditions in either how farmers perceive the separation between productive versus natural landscapes or how scientists study them in different regions around the world. We encourage researchers to bridge across scientific disciplines to expand the knowledge of tree-grass interactions in agroecosystems and multifunctional landscapes across environmental gradients and cultures. Merging the existing traditional knowledge from farmers with the ecological theory developed in natural and productive systems could facilitate generating effective strategies for sustainable productive systems that can contribute to biodiversity conservation and be better adapted to changing climate conditions.

Data availability statement

The raw data supporting the conclusion of this article can be found in the repository https://10.5281/zenodo.6824373 (Hernández-Salmerón and Holmgren 2022).

Author contributions

IH-S and MH conceived the ideas, designed the study, analysed and interpreted the results, and wrote the manuscript. IH-S screened all potential papers, extracted the data and prepared the figures.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.949185/full#supplementary-material

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Effects of vegetation patchiness on ecosystem carbon and nitrogen storage in the alpine grassland of the Qilian Mountains

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Vegetation patchiness is common in degraded grasslands. Vegetation patchiness enhances the spatial variability of grassland soil organic carbon and total nitrogen. Stripped vegetation patches have a great impact on ecosystem carbon (C) and nitrogen (N) storage. Using field surveys, we examined the effects of patches on the ecosystem carbon and nitrogen storage of four typical alpine grass species patches (viz: *Leymus secalinus, Koeleria pers, Stipa aliena, and Leontopodium nanum*). The results indicated that ecosystem C, N, and respiration were significantly higher in intact vegetation patches than in stripped vegetation patches. Also, stripped vegetation patches recorded higher quantities of soil gravel content than the intact patches. In *Leymus secalinus* and *Koeleria pers* species patches, soil approximately contributed about 62% and vegetation about 38% to ecosystem carbon and nitrogen storage, whereas in *Stipa aliena* and *Leontopodium nanum* species patches, close to 80% of ecosystem carbon and nitrogen were found in the soil while close to 20% were stored in the vegetation. Soil total phosphorus (TP), total potassium (TK), available phosphorus (AP), soil microbial biomass carbon (MBC), and soil microbial biomass nitrogen (MBN) were higher in intact vegetation patches than in the stripped vegetation patches. Ecosystem carbon and nitrogen were observed to have a significant correlation with soil gravel content and vegetation productivity. Stripped vegetation patches resulted in decreased plant biomass input and an increased rate of soil erosion. We conclude that grassland patchiness resulted in the decline of ecosystem carbon and nitrogen storage due to a reduction in vegetation input and an increase in soil erosion. Grasslands are likely to have a higher possibility of serving as a C sink if the input of organic matter exceeds its output via sustainable management practices.

KEYWORDS

alpine grassland, stripped vegetation patches, ecosystem C and N, ecosystem respiration, intact patch, vegetation input

Introduction

Grasslands are a key part of the global ecosystem that account for a significant portion of Earth's area and have a major function in influencing climate change by serving as a C sink (Li et al., 2013; Qin et al., 2015). They also have a substantial role in food security by serving as feed for beef and dairy livestock (O'Mara, 2012; Gang et al., 2014). Grassland ecosystems are experiencing increasingly unsustainable land use and climate change which could have catastrophic shifts in their structure and the services they provide (Scheffer et al., 2009; Dakos et al., 2019). Throughout the world, grasslands are said to store carbon in the soil at an estimated rate of 0.5 Pg C per year and this is about one-quarter of the possible soil C sequestration globally (Wu et al., 2014a). The accumulation of carbon is dependent on vegetation productivity, and nitrogen is one of the key nutrients that enhance a plant's photosynthetic ability (Freschet et al., 2018). Therefore, C sequestration is usually closely linked to soil nitrogen. Hence, studies on soil organic carbon (SOC) and soil N storage are vital for the determination of their possibility for sequestration or emission (Qi et al., 2021). A little change in carbon storage could have a significant effect on CO_2 in the atmosphere, and hence, the global C cycle and balance. The enhancement of carbon storage is a vital factor in ensuring grassland ecosystems' sustainability (Wang et al., 2014). All the same, grasslands are considered one of the most altered biomes on Earth (Pineiro et al., 2006). Grasslands are likely to have a higher possibility of serving as a high C sink if the input of organic matter exceeds its output via sustainable management practices; however, many grasslands have low carbon inputs and tend to be poorly managed and degraded (Shrestha and Stahl, 2008).

The Alpine grassland is one of the most vital grassland types and accounts for more than 66% of the grasslands on the Qinghai–Tibetan Plateau (QTP) (Miehe et al., 2019). Over the decades, these grasslands have experienced widespread degradation, leading to a decrease in water retention ability, biodiversity, carbon sequestration, grassland productivity, soil nutrients, and value for recreation (Bao et al., 2019; Li et al. ,2013; Lü et al., 2016; Qin et al., 2014; Zhang et al., 2016). However, high-altitude terrestrial ecosystems are regarded as major constituents of the global cycles of carbon and nitrogen (Lozano-García et al., 2016; Zhang et al., 2018). The top soils of these ecosystems have substantial amounts of SOC, soil nitrogen (TN), root carbon, and nitrogen (Jia et al., 2017). These ecosystems, to a high degree, are fragile and susceptible to external effects such as overgrazing, burrowing activities of mammals, and soil erosion which often lead to patchiness (Gao et al., 2009; Qin et al., 2014). As a result of these disturbances, intact vegetation would be isolated into archipelagos of small fragments and regenerating bald patches embedded in matrixes (Akiyama and Kawamura, 2007). This patchiness results in a reduction in ecosystem carbon and nitrogen storage (Nie et al., 2013; Haddad et al., 2015) and increased spatial variability of the distribution of carbon and nitrogen (Yan et al., 2016).

Patchiness can indicate the state and functionality of ecosystems (Heras et al., 2011); patches with different sizes and types indicate major differences in biomass, soil moisture, and properties (Chen et al., 2017; Qin et al., 2019). Therefore, obtaining an insight into the effects of patchiness on ecosystem N and C storage is a vital step in disclosing the process and mechanisms of the degradation of grasslands (Lin et al., 2010). Multi-scale research of patch patterns is one of the central directions of landscape ecology. Even though field surveys and remote sensing have been used to a greater extent in studies of patch patterns at plot and landscape scales, there is a lack of research on small-scale patchiness and its effect on ecosystem N and C accumulation. It would be pragmatic to identify signals for grassland state shifts by exactly discovering pertinent patch attributes and their specific variations along the entire stages of degradations. This would serve as an essential monitoring tool if it could be done by direct and simple vegetation measurements at small spatial scales.

Many studies have been conducted on species composition, biomass, and nutrient concentrations during the degradation succession of grasslands (Chen et al., 2013; Dong et al., 2013; Babel et al., 2014; Hopping et al., 2018). All the same, few studies have been conducted to provide information on the effects of patchiness on grassland ecosystem carbon and nitrogen storage which play vital roles in regional and global C and N cycles. This study aimed to examine the patchiness characteristics of four typical alpine grass species patches and their effect on ecosystem carbon and nitrogen storage. This work, thus, shows how a ground-based small-scale vegetation survey can provide easy-to-use ways for determining patch characteristics and effects of patchiness on grassland C and N storage.

Materials and methods

Study area

The study area is located in the alpine grasslands of the Qilian Mountains in Zhuaxixiulong Township in the Tianzhu Tibetan Autonomous County of Gansu Province of China. The area has a typical alpine climate and is usually cold and wet for most parts of the year. It also has weather conditions such as thin air with low oxygen concentrations, high solar and high ultraviolet radiation, and an annual temperature of about −4.0°C (Zhang et al., 2015). The site has big mountains with steep slopes (Yao and Zhen, 2017). Four typical alpine grass patches were selected, namely, Koeleria pers patch (KP), Leymus secalinus patch (LS), Leontopodium nanum patch (LN), and Stipa aliena patch (SA). The area has four typical alpine grassland types, viz, alpine swamp meadow, alpine meadow, alpine steep meadow, and alpine steep (Qin et al., 2014). A map indicating the study

FIGURE 1
Map indicating the study area and sampling location.

area and sampling location is shown in Figures 1, 2 is a picture of the four typical alpine grass species patches and a bare patch.

Field sampling

Field sampling was conducted along a transect that traversed the typical vegetation within the area. A total of 12 locations were selected among the KP, LS, LN, and SA patches with each having three locations. Locations with flat slopes of <4° were selected. The grasslands within these locations are used for grazing, usually from May to June and September to October. For each grassland type, three types of patches were delineated: intact vegetation patches (IGP), large stripped vegetation patches (LBP) with a diameter of 4–10 m, and medium stripped patches (MBP) with a

FIGURE 2
Picture of selected alpine grass species patches; **(A)** *Leontopodium nanum* **(B)** *Stipa aliena,* **(C)** *Leymus secalinus,* **(D)** *Koeleria pers,* and **(E)** the grassland showing a bare patch.

diameter of <1–3.5 m. A total of 12 sampling locations were established and 90 soil core samples were taken in each location encompassing the three different patches in the selected types of grasslands. In total, 1,080 soil samples were taken at depths 0–10, 10–20, 20–30, and 30–40 cm with a core sampler (5 × 5 cm). Sampling in each patch was conducted between the end of July and the middle of August when vegetation growth was at its peak. Soil bulk density was estimated using the same core sampler (undisturbed soil). A total of three 50 cm × 50 cm quadrats were randomly established in each patch type and above and below-ground biomass was taken. Patches with different sizes were measured along the transect in each sampling location and on each surface type, and cover fractions of the patches were then calculated. Ecosystem respiration was estimated using an automated soil CO_2 flux system (LI-800A, LI-COR Inc., Lincoln, United States). PVC collars (20 cm diameter and 15 cm height) were inserted into the soil to a depth of about 10–12 cm. Measurements were made among the four typical alpine grasslands with a total of 12 subplots within each patch surface. All measurements were made on sunny days.

Laboratory analysis

Soil samples were sent to the laboratory, air-dried, sieved *via* a wire mesh to remove unwanted particles such as roots and debris, and used for the determination of SOC and TN. Samples for below-ground biomass were washed in a fine wire mesh after which roots were then oven-dried and weighed. Oven-dried vegetation samples and root samples were grounded and sieved for analyzing organic C and TN. Organic C quantity in all samples was determined *via* dichromate oxidation using Walkley–Black acid digestion. TN in all the samples was determined by digestion and then tested using a flow injection analyses system (FIAstar, 5000, Foss Inc., Sweden) (Sparks et al., 1996).

Soil microbial biomass C and N were determined using the fumigation-extraction method (Wu et al., 1990). A total of 20 g of wet soil (dry weight basis) was fumigated by placing it in a sealed vacuum desiccator containing alcohol-free $CHCl_3$ vapor for 24 h. The fumigated base was repeatedly discharged in an aseptic, empty desiccator until the scent of $CHCl_3$ was no longer detectable, and then extracted with 80 ml of 0.5 M K_2SO_4 (soil: K_2SO_4 = 1:4) for 30 min. The extraction of non-fumigated soil was the same as that of fumigated soil. Soil microbial biomass C and N were calculated as the difference between total organic C and total N in the fumigated and non-fumigated extracts, respectively, with a conversion factor (KEC) of 0.38 and (KEN) of 0.45 (Jenkinson, 1988; Joergensen, 1996).

Estimation of SOC, TN, EC, and EN

The soil organic carbon and nitrogen were calculated as follows:

$$\mathrm{SOC} = \sum_{i=1}^{n} \rho \times (1 - \sigma\,\mathrm{gravel}) \times C_{SOC} \times \mathrm{Di},$$

$$\mathrm{TN} = \sum_{i=1}^{n} \rho \times (1 - \sigma\,\mathrm{gravel}) \times C_{TN} \times \mathrm{Di},$$

where SOC is soil organic C (kg m^{-2}), TN is soil total N stocks (kg m^{-2}), ρ is the soil bulk density (g cm^{-3}), σ gravel is the relative amount of gravel (% w/w), C_{SOC} is the soil organic C concentration (g kg^{-1}), C_{TN} is the soil total N concentration (g kg^{-1}), and Di is the soil thickness (cm) at depth i, i = 1. . . . . .4.

The plant and root carbon and plant and root nitrogen stocks were calculated as

$$\mathrm{PC/RC} = \mathrm{PB/RB} \times \mathrm{C}_{\mathrm{P/R}},$$

$$\mathrm{PN/RN} = \mathrm{PB/RB} \times \mathrm{N}_{\mathrm{P/R}},$$

where PC/RC is the plant/root C stocks, PN/RN is the plant/root N stocks, PB/RB is the plant/root biomass (g m^{-3}/kg m^{-2}), C $_{P/R}$ is the plant/root C concentration (g kg^{-1}), and N $_{P/R}$ is the plant/root N concentration (g kg^{-1}).

Total ecosystem carbon and nitrogen stocks (kg m^{-2}) were calculated as

$$\mathrm{EC} = \mathrm{SOC} + \mathrm{PC} + \mathrm{RC},$$

$$\mathrm{EN} = \mathrm{TN} + \mathrm{PN} + \mathrm{RN},$$

where EC is ecosystem C (kg m^{-2}), SOC is soil organic C (kg m^{-2}), PC is plant carbon (kg m^{-2}), RC is root carbon (kg m^{-2}), EN is ecosystem nitrogen (kg m^{-2}), TN is soil total nitrogen (kg m^{-2}), PN is plant nitrogen, and RN is root nitrogen (kg m^{-2}).

Data analysis

Data on gravel content, cover fraction, plant and root biomass, soil nitrogen, plant and root N, ecosystem carbon and nitrogen stocks, and soil physicochemical parameters were analyzed via a one-way ANOVA with the least significant difference at 5%. The relationship between ecosystem carbon and nitrogen with plant and root biomass and gravel content was analyzed via regression analysis. All statistical analyses were carried out using SPSS software version 21 (IBM Corp., Chicago, IL, United States). Principal component analysis was carried out to evaluate the effect of vegetation patchiness on ecosystem C and N. Figures and tables were drawn using Microsoft Office Word 365 and GraphPad Prism 6 (GraphPad Software, Inc., San Diego, CA, United States).

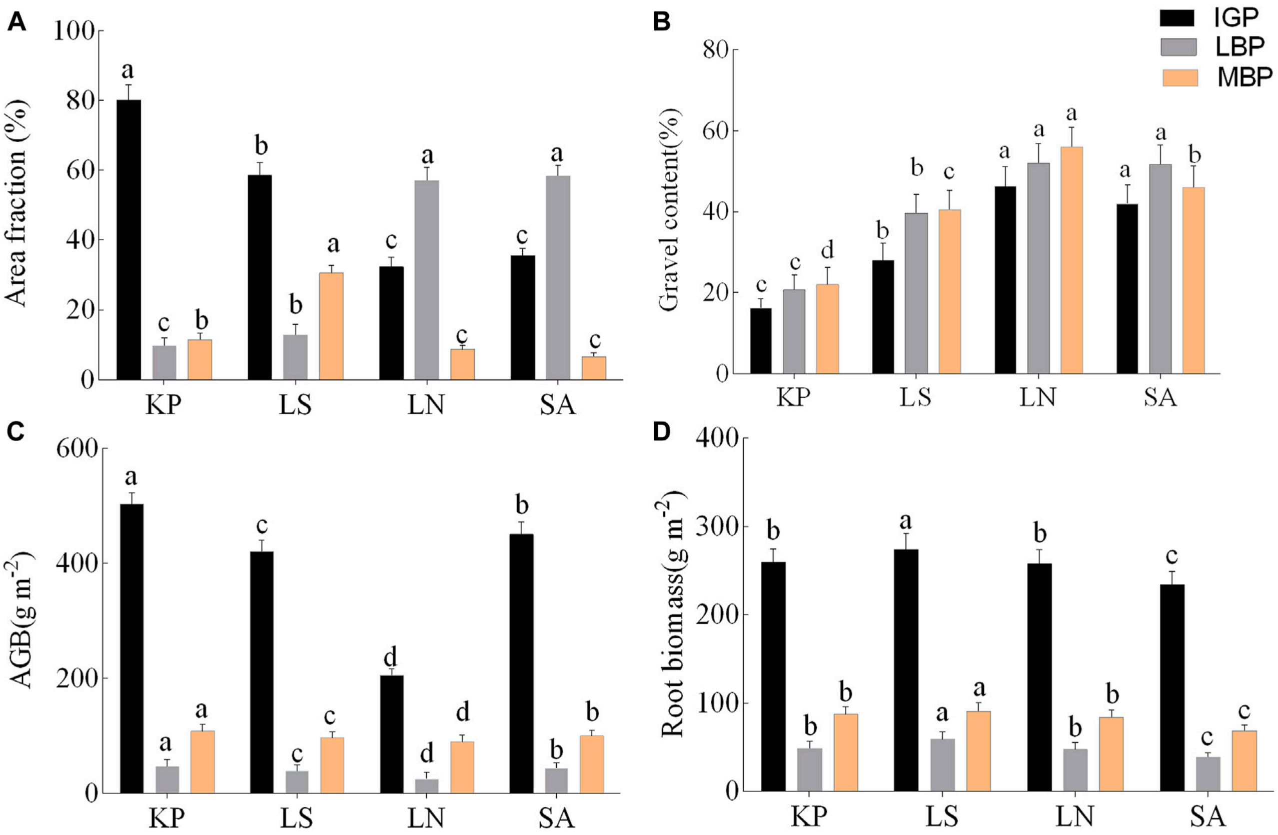

FIGURE 3
Cover fraction **(A)**, soil gravel **(B)**, plant biomass **(C)**, and root biomass **(D)** in each of the various patches of the four alpine grass species types. Bars with different letters show significance at $p < 0.001$. IGP; intact vegetation patch, LBP; large stripped vegetation patch, MBP; medium stripped vegetation patch, KP; Koeleria pers patch, LS; Leymus secalinus patch, LN; Leontopodium nanum patch, SA; Stipa aliena patch.

Results

Cover fraction of patch types, soil gravel, and plant biomass

Vegetation patterns and patch features varied amongst the various grassland types. The intact and stripped vegetation patches mosaic co-existed within the various grassland types. The average cover fractions of intact, large, and medium stripped vegetation patches constituted approximately 58–80%, 10–12%, and 11–30%, respectively, of the total area of KP and LS grass patches (Figure 3A). On the other hand, intact, large, and medium stripped vegetation patches contributed close to 34, 58, and 8%, respectively, of the total field of LN and SA grass patches (Figure 3A). In all, the KP patch recorded significantly low amounts of gravel content than the rest. For each of the selected grass types, the intact vegetation patch had less gravel content than those in stripped vegetation patches (Figure 3B). In each of the different patches, there were sharply varied productivity levels in all grass types. Intact vegetation patches recorded significantly higher biomass of both plants and roots than the rest of the patches (Figures 3C,D).

Ecosystem C and N storage and respiration

The intact vegetation patches in all the grassland types recorded higher SOC and TN stocks than the other patches (Figures 4A, 5A). In addition, the intact vegetation patches in all the selected grass types had significantly higher above-ground biomass C and N, root C and N, ecosystem carbon, and nitrogen than that of the large and medium stripped vegetation patches (Figures 4B–D, Figures 5A–D). Also, ecosystem respiration was higher in the intact vegetation patches than in the stripped ones. KP and LS grass patches recorded significantly high amounts of soil respiration as compared to the rest (Figure 6).

Soil C and N added approximately 78% and 83% of total ecosystem C in LN and SA, respectively, and 69% and 77% of total ecosystem N in LN and SA, respectively (Table 1). Above-

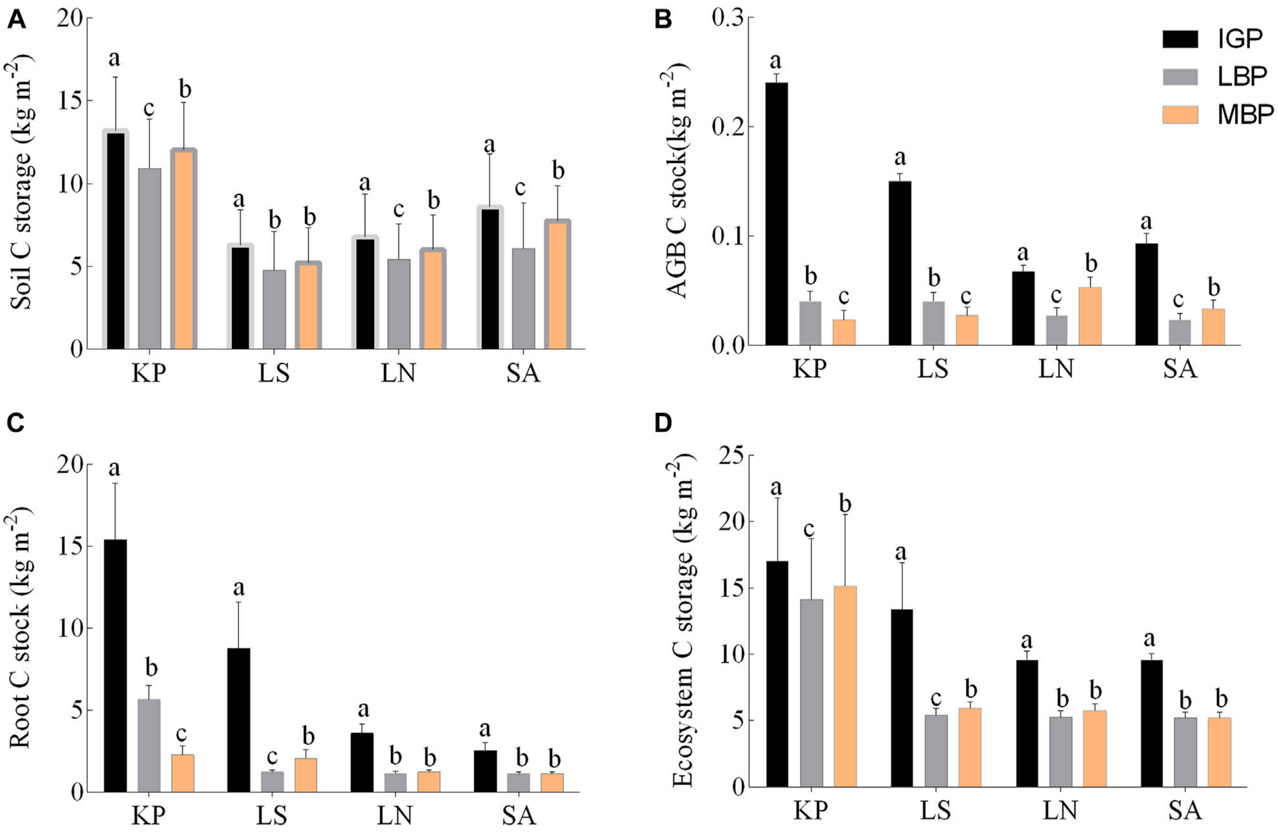

FIGURE 4
Soil organic carbon **(A)**, plant carbon **(B)**, root carbon **(C)**, and ecosystem carbon **(D)** in each of the selected patches. Bars with different letters show significance at $p < 0.001$. IGP; intact vegetation patch, LBP; large stripped vegetation patch, MBP; medium stripped vegetation patch, KP; Koeleria pers patch, LS; Leymus secalinus patch, LN; Leontopodium nanum patch, SA; Stipa aliena patch.

ground biomass contributed the lowest to ecosystem total C and N in all types of grasslands. Similarly, root C and N contributed closely to 38% for KP and LS, 21% and 29% for LN, and 15% and 22% for C and N in SA (Table 1).

Relationship between ecosystem C and N storage, gravel content, and vegetation productivity

The study indicated that ecosystem carbon and nitrogen had a strong relation with soil gravel and above and below-ground biomass. There was a significant negative correlation between ecosystem carbon and nitrogen and soil gravel content (Figures 7A,B). However, ecosystem carbon and nitrogen stocks had a positive correlation between plant biomass (Figures 7C,D) and root biomass (Figures 7E,F), indicating that vegetation productivity had an impact on ecosystem carbon and nitrogen storage. Principal component analysis (PCA) was conducted to examine the effects of vegetation patchiness on ecosystem C and N storage (Figures 8A,B). Principal component 1 (PC 1) explained 73.27% while principal component 2 (PC 2) explained 15.38% of the total variations. Principal components 1 and 2 explained 88.65% of the variance. All vegetation and soil parameters within the intact and medium grass vegetation patches were on the positive side of PC 1 except for the cover fraction in LBP and MBP and gravel. SOC, root, and plant C and N were strongly positively correlated with ecosystem C and N. Gravel content, cover fraction in LBP, and MBP were negatively correlated with ecosystem C and N. The KP patch had strong positive loadings while the LS patch had strong negative loadings on PC 1. On PC 2, all patches except the LS patch had strong positive loadings, indicating that vegetation patchiness strongly influenced ecosystem C and N storage.

Variations in soil physicochemical parameters

Soil bulk density was lowest in the intact vegetation patches than in the medium and large stripped vegetation patches across all grassland types. Soil TP, TK, and AP were highest in the intact

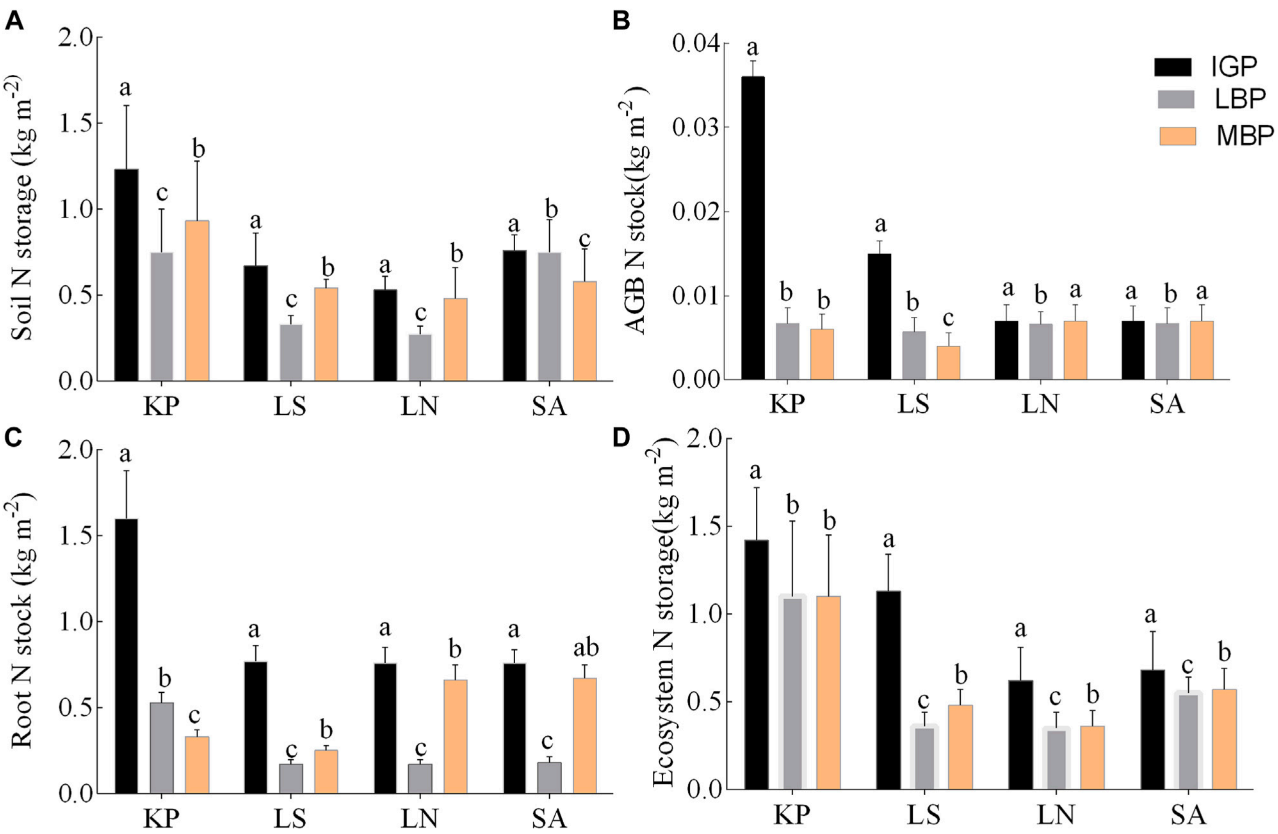

FIGURE 5
Soil total nitrogen **(A)**, plant nitrogen **(B)**, root nitrogen **(C)**, and **(D)** ecosystem nitrogen storage in the selected patches. Bars with different letters show significance at $p < 0.001$. IGP; intact vegetation patch, LBP; large stripped vegetation patch, MBP; medium stripped vegetation patch, KP; Koeleria pers patch, LS; Leymus secalinus patch, LN; Leontopodium nanum patch, SA; Stipa aliena patch.

vegetation patches than in the medium and large stripped vegetation patches within all the selected grassland types and decreased with increasing depth. Soil AK did not follow a similar trend as that of TP, TK, and AP; it varied across the selected patches. The KP grass patch recorded the highest values of soil TP, TK, AP, and AK than the rest of the grassland types. It equally recorded the lowest value of soil bulk density. Similarly, soil MBC and MBN were equally higher in the vegetation patch than in the medium and large stripped vegetation (Table 2).

Discussion

Factors responsible for vegetation patchiness

The alpine grassland in the QTP is composed of three defined attributes which are vital for its ecosystem's grassland sequence: a mattic epipedon layer (Dai et al., 2020), an active permafrost layer (Yin et al., 2017), and a non-uniform rainfall distribution (You et al., 2014). These distinct attributes lead to a unique eco-hydrological process (Wang et al., 2012). These features can increase the degradation of alpine grasslands in the QTP. They could also lead to the expansion of bald patches via the destruction of the mattic epipedon layer at the interface between bald and vegetation patches (Chen et al., 2017) to form desertification lands and thermokarst lakes (Wang et al., 2018).

In arid regions, self-organized patchiness is the resultant effect of positive feedback between vegetation growth and water availability (Chen et al., 2017). Higher vegetation density enhances water infiltration and lowers its evaporation (Qin et al., 2019). On the Qilian Mountains, alpine swamp meadow and alpine meadow grasslands are primarily located within sub-stable and transition permafrost fields which have high soil moisture and low temperature while alpine steppe meadow and alpine steppe grasslands are mainly situated in unstable permafrost and seasonal frozen soil areas which have low soil moisture and high soil temperature (Wang et al., 2016). The modification of soil hydrothermal attributes induced by surface

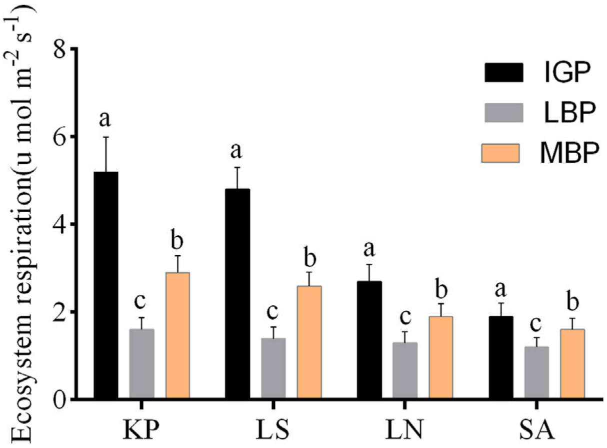

FIGURE 6
Ecosystem respiration of the various grass species patches. Bars with different letters show significance at $p < 0.001$. IGP; intact vegetation patch, LBP; large stripped vegetation patch, MBP; medium stripped vegetation patch, KP; Koeleria pers patch, LS; Leymus secalinus patch, LN; Leontopodium nanum patch, SA; Stipa aliena patch.

permafrost-free thaw processes (You et al., 2017) may account for the form and patchiness of the vegetation. In addition, the major kind of land use of the alpine grassland is grazing which also serves as a habitat for wild mammals. The overall effect of grazing, trampling by livestock, and burrowing activities of small mammals are regarded to be contributing factors to the formation of patchiness (Gao et al., 2010; Qin et al., 2018). Soil texture and topography can alter the redistribution of soil water content and hence affect vegetation patterns (Hais et al., 2016; Zhang and Yao, 2016). Therefore, soils with drier surfaces are not optimal for the survival of continuous vegetation patches (Qin et al., 2015; Chen et al., 2017).

Effects of patchiness on ecosystem C and N storage

The results of the study indicated that patchiness in the typical alpine grass species led to a considerable decrease in ecosystem carbon and nitrogen storage which are in agreement with studies by Yi et al. (2016) and Zhang et al. (2019). The increasing soil output via erosion exceeds the input of organic matter which may have accounted for the decline in ecosystem carbon and nitrogen storage. This is so because stripped vegetation patches result in increased erosion and gravel content in the soil which is not useful for vegetation growth (Chen et al., 2017). There were significant variations in the decline of ecosystem carbon and nitrogen within the selected patches. Furthermore, there was a substantial decline in ecosystem carbon and nitrogen in KP and LS than in LN and SA (Figure 4D, Figure 5D). The results indicated that ecosystem carbon and nitrogen distribution and storage are mainly reliant on the form and structure of the vegetation. Close to 62% of ecosystem carbon and nitrogen was found in the soil and 38% in vegetation for KP and LS. On the other hand, more than 80% of ecosystem carbon and nitrogen was found in the soil while less than 20% in vegetation for LN and SA. Studies have shown that alpine grassland ecosystem C is highly vulnerable with a significant quantity of easy cycling carbon but has a lesser quantity of resistant carbon (Chen et al., 2016b). Vegetation degradation leads to increased organic matter decomposition rates as a result of limited moisture and greater availability of oxygen (Wu et al., 2012; Chen et al., 2017). It is a fact that vegetation productivity impacts ecosystem carbon and nitrogen greatly (De Deyn et al., 2009; Zhang et al., 2019) and our findings are consistent with this fact. Our findings show there was a significant positive correlation between ecosystem carbon and nitrogen and plant and root biomass (Figures 7C–F). The decomposition of litter is considered the major source of soil C and N. A substantial decrease in vegetation production due to patchiness accounted for the decline of ecosystem carbon and nitrogen storage. However, there was a significant negative correlation between ecosystem carbon and nitrogen and soil gravel content (Figures 7A,B). These results are in sync with previous studies (Qin et al., 2015; Qin et al., 2018). Also, the results indicate there were significantly high levels of gravel in stripped vegetation patches compared to that of intact vegetation patches (Figure 3B) which are consistent with the findings by Qin et al. (2015). The literature shows that most of the alpine grasslands of QTP have thin soils and contain a significant

TABLE 1 Distribution of ecosystem carbon and nitrogen among soil and vegetation.

Patch type	Ecosystem carbon distribution (%)			Ecosystem nitrogen distribution (%)		
	Soil	AGB	Root	Soil	AGB	Root
KP	65.96	0.44	33.6	61.37	0.77	37.86
LS	62.41	0.68	36.91	60.49	0.89	38.62
LN	78.38	0.55	21.07	69.75	0.89	29.36
SA	83.80	0.49	15.71	77.05	0.74	22.21

KP; Koeleria pers patch, LS; Leymus secalinus, LN; Leontopodium nanum patch, SA; Stipa aliena patch, AGB; Aboveground biomass.

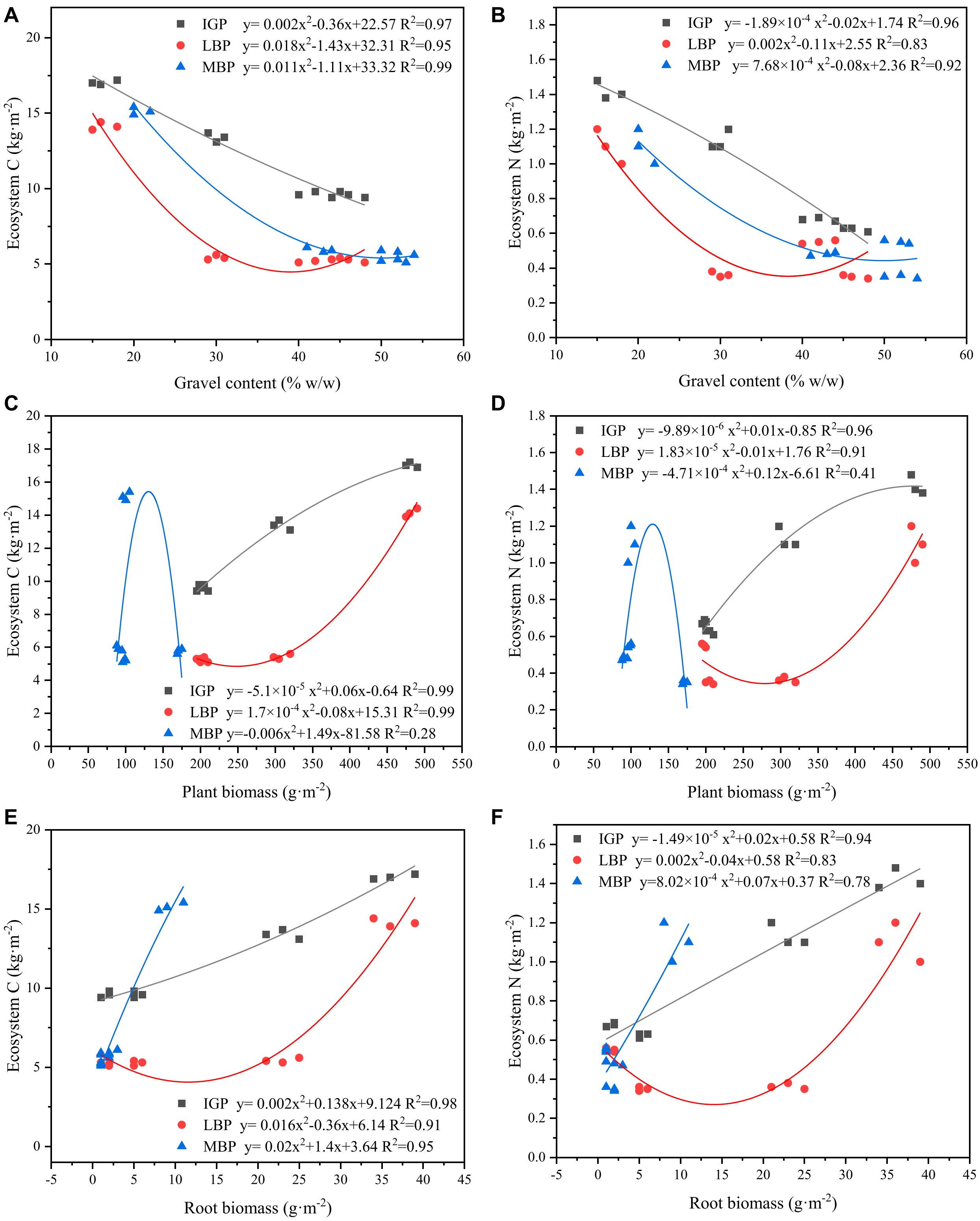

FIGURE 7
Relationship between ecosystem carbon **(A)** and nitrogen storage **(B)** with gravel, ecosystem carbon **(C)** and nitrogen storage **(D)** with plant biomass and ecosystem carbon **(E)** and nitrogen storage **(F)** with root biomass. $p < 0.001$. IGP; intact vegetation patch, LBP; large stripped vegetation patch, MBP; medium stripped vegetation patch.

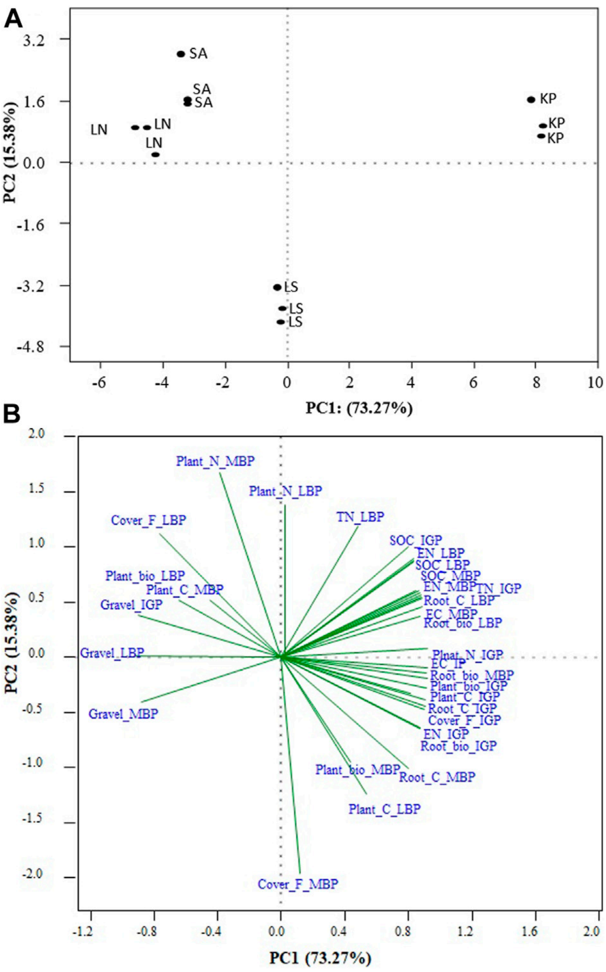

FIGURE 8
Principal component analysis **(A)** score plot and **(B)** biplot based on the effect of grassland patchiness on ecosystem C and N storage in four typical alpine grass species patches. KP; Koeleria pers patch, SA; Stipa aliena patch, LN; Leontpodium nanum patch, LS; Leymus secalinus patch. Cover F LBP; cover fraction in large stripped patch, Cover F IGP; cover fraction in intact grass patch, Cover F MBP; cover fraction in medium stripped patch, SOC IGP; soil organic carbon in intact grass patch, SOC LBP; soil organic carbon in large stripped patch, Plant bio IGP; plant biomass in intact grass patch, Plant N IGP; plant nitrogen in intact grass patch, EN IGP; ecosystem nitrogen in intact grass patch.

quantity of gravel (Qin et al., 2015). Grassland soils contain a significant amount of soil organic carbon and total nitrogen in the topsoil and for that matter, ecosystem carbon and nitrogen are susceptible to soil erosion once the soil is exposed (Nie et al., 2013; Liu et al., 2012). As soon as the topsoil is carried away by water and wind erosion, ecosystem carbon and nitrogen are lost (Lin et al., 2014). During the growing season, runoff is capable of carrying away significant nutrients and top tiny pieces of soil due to less plant biomass in stripped vegetation patches (Bertol et al., 2003). This leads to the expansion of stripped vegetation patches and its resultant effect on vegetation productivity, hence, is a decline in ecosystem carbon and nitrogen storage. Bald patches facilitate the establishment of biological and physical crusts (Assouline et al., 2015). The bald patches reduce water infiltration ability and worsen water stress of the remaining vegetation (Thompson et al., 2010). Degraded grasslands are extremely fragmented with the area of grassland patches endlessly reducing while their spatial isolations increase (Krauss et al., 2004). Habitat fragmentation is a threat to biodiversity and leads to a reduction in species richness within small and isolated habitat patches (Ouborg et al., 2006). Large intact vegetation patches are certainly a vital key for the maintenance of some vital ecological processes (Watson et al., 2018) and biodiversity conservation (Gibson et al., 2011). Nonetheless, Wintle et al. (2018) indicated that several species could be lost if small, isolated patches of remnant habitats were ignored and conservation efforts centered mainly on large, intact, and highly connected areas. The make-up and functionality of the soil microbiome are governed by soil abiotic factors such as pH, texture, and nutrient and moisture availabilities (Maestre et al., 2012; Maestre et al., 2015; Ochoa-Hueso et al., 2018), which are susceptible to soil erosion. Erosion is regarded to negatively affect microbial biomass abundance, and make-up by modifying natural soil features and taking away the vegetation protective cover (Mabuhay et al., 2004; Li et al., 2015; Hou et al., 2014). Successively, all of these modifications may change the turnover and availability of soil nutrients and soil functionality.

To combat degradation and promote restoration, socio-ecological solutions are required. Increasing grassland awareness in global policy; generating standardized degradation indicators; leveraging scientific innovation for effective restoration at regional and landscape sizes; and improving information transfer and data sharing on restoration experiences are all important measures. The possible ecosystem service trade-offs in degraded and regenerated grasslands can be balanced by systematic assessment and common awareness of stakeholder needs. Integrating these efforts into a sustainability strategy will help to slow degradation and improve restoration success, while also protecting the socioeconomic, cultural, and ecological benefits that grasslands bring (Bardgett et al., 2021).

To improve the assessment of grassland deterioration and propose unique methods for restoration and sustainable grassland management, environmental research innovations must be created and implemented. Remote sensing advances on a global and regional scale have the ability to assess the extent and condition of grasslands and inform the spatial targeting of large-scale restoration operations. For example, maps of general degradation indicators, such as primary productivity, standing biomass, soil moisture, phenology, and soil organic carbon (Bardgett et al., 2021; Schweiger et al., 2018) could be combined with spatial information on climate, edaphic, and socio-economic data to identify national and global patterns

TABLE 2 Variation of soil physicochemical parameters within the selected patches.

	Patch type	Soil depth	BD (g/cm³)	TP (g/kg)	TK (g/kg)	AP (mg/kg)	AK (mg/kg)	MBC (mg/kg)	MBN (mg/kg)
KP	IGP	0–10 cm	0.68 ± 0.05f	1.18 ± 0.03a	16.72 ± 0.26a	27.36 ± 0.54a	340.18 ± 8.05c	507.23 ± 10.51a	18.65 ± 0.54a
	LBP		0.91 ± 0.02b	0.56 ± 0.04e	12.23 ± 0.19d	16.48 ± 0.45e	328.46 ± 9.15d	302.41 ± 9.53e	16.21 ± 0.35d
	MBP		0.85 ± 0.04c	0.79 ± 0.02b	16.43 ± 0.08a	26.08 ± 0.25b	385.38 ± 7.45a	485.25 ± 10.14b	17.28 ± 0.21b
LS	IGP		0.70 ± 0.04e	1.15 ± 0.05a	15.78 ± 1.02b	26.79 ± 0.35b	312.48 ± 6.55e	401.25 ± 9.25c	16.11 ± 0.15d
	LBP		0.87 ± 0.05c	0.50 ± 0.04f	11.01 ± 0.12e	16.21 ± 0.55e	309.69 ± 8.15e	290.52 ± 6.34f	13.21 ± 0.19f
	MBP		0.80 ± 0.03d	0.73 ± 0.03c	15.42 ± 0.14b	25.38 ± 0.15c	330.29 ± 9.35d	340.13 ± 9.54d	14.87 ± 0.08e
LN	IGP		0.74 ± 0.05e	1.12 ± 0.06a	15.48 ± 0.08b	26.11 ± 0.18b	378.06 ± 9.55b	301.48 ± 8.24e	13.41 ± 0.17f
	LBP		0.89 ± 0.06c	0.49 ± 0.07f	12.11 ± 0.14d	16.15 ± 0.25e	311.49 ± 6.75e	210.22 ± 6.44h	9.67 ± 0.26h
	MBP		0.82 ± 0.04d	0.68 ± 0.03d	14.47 ± 0.12c	25.84 ± 0.15c	342.69 ± 9.35c	250.75 ± 7.14g	11.54 ± 0.15g
SA	IGP		0.76 ± 0.03e	1.13 ± 0.04a	15.69 ± 0.07b	25.96 ± 0.33c	309.19 ± 7.35e	402.57 ± 10.64c	16.79 ± 0.37c
	LBP		0.99 ± 0.05a	0.50 ± 0.02f	11.10 ± 0.09e	15.89 ± 0.25f	289.79 ± 6.78f	290.65 ± 7.84f	10.61 ± 0.09g
	MBP		0.89 ± 0.02c	0.69 ± 0.03d	15.54 ± 0.11b	24.89 ± 0.23d	311.65 ± 8.65e	320.46 ± 10.61e	14.71 ± 0.11e
KP	IGP	10–20 cm	0.71 ± 0.06f	0.69 ± 0.02a	16.34 ± 0.09a	18.68 ± 0.35a	249.19 ± 5.35a	420.51 ± 11.74a	15.11 ± 0.18a
	LBP		0.92 ± 0.05b	0.39 ± 0.03e	11.15 ± 0.12d	10.48 ± 0.15e	215.48 ± 4.55e	280.43 ± 7.34c	13.16 ± 0.13c
	MBP		0.84 ± 0.03d	0.45 ± 0.04d	16.35 ± 0.15a	16.59 ± 0.25b	240.79 ± 6.25b	325.41 ± 9.74b	14.98 ± 0.22b
LS	IGP		0.76 ± 0.06e	0.64 ± 0.07b	15.31 ± 0.08b	16.57 ± 0.64b	239.29 ± 8.64b	310.65 ± 9.84b	13.45 ± 0.14c
	LBP		0.93 ± 0.03b	0.32 ± 0.06f	12.42 ± 0.05c	10.48 ± 0.25e	210.71 ± 5.25f	205.47 ± 6.24d	10.13 ± 0.07e
	MBP		0.83 ± 0.05d	0.42 ± 0.08d	15.14 ± 0.07b	16.48 ± 0.45b	221.21 ± 6.45d	280.62 ± 7.84c	12.79 ± 0.15d
LN	IGP		0.79 ± 0.03d	0.60 ± 0.06c	15.28 ± 0.12b	18.57 ± 0.60a	239.29 ± 7.64b	215.44 ± 6.34d	10.22 ± 0.05e
	LBP		0.96 ± 0.02a	0.29 ± 0.04f	12.45 ± 0.05c	10.35 ± 0.25e	210.71 ± 6.25f	180.73 ± 7.16f	7.23 ± 0.03g
	MBP		0.88 ± 0.04c	0.39 ± 0.06e	15,18 ± 0.04b	16.59 ± 0.15b	230.71 ± 9.15c	198.25 ± 6.21e	9.28 ± 0.01f
SA	IGP		0.81 ± 0.04d	0.61 ± 0.07c	15.23 ± 0.08b	15.98 ± 0.61b	232.29 ± 6.64c	298.45 ± 8.74c	12.81 ± 0.14d
	LBP		0.95 ± 0.07a	0.31 ± 0.04f	12.48 ± 0.11c	11.52 ± 0.25d	209.71 ± 4.25f	199.14 ± 7.11e	9.22 ± 0.05f
	MBP		0.89 ± 0.06c	0.42 ± 0.06d	15.12 ± 0.06b	14.79 ± 0.45a	230.71 ± 6.45c	205.66 ± 5.24d	11.95 ± 0.12d
KP	IGP	20–30 cm	0.82 ± 0.01d	0.50 ± 0.05a	16.19 ± 1.05a	14.68 ± 0.50a	219.29 ± 8.34a	304.11 ± 8.75a	9.65 ± 0.07a
	LBP		0.93 ± 0.04b	0.37 ± 0.02c	11.02 ± 0.08c	10.49 ± 0.37b	201.29 ± 5.24d	190.34 ± 6.22c	6.83 ± 0.03e
	MBP		0.88 ± 0.05c	0.42 ± 0.05b	16.09 ± 0.07a	13.59 ± 0.25a	211.71 ± 7.25c	258.67 ± 7.13c	7.21 ± 0.08d
LS	IGP		0.83 ± 0.04d	0.49 ± 0.05a	15.12 ± 0.06b	14.58 ± 0.49a	215.29 ± 6.64b	275.81 ± 7.33b	9.86 ± 0.05a
	LBP		1.02 ± 0.01a	0.30 ± 0.07d	10.12 ± 0.11d	9.79 ± 0.25bc	199.31 ± 7.15c	180.72 ± 5.24d	6.92 ± 0.03e
	MBP		0.89 ± 0.04c	0.39 ± 0.04b	15.08 ± 0.02b	13.59 ± 0.35a	210.41 ± 8.35c	190.46 ± 6.14c	7.42 ± 0.05d
LN	IGP		0.84 ± 0.06d	0.41 ± 0.02b	15.12 ± 0.09b	14.58 ± 0.41a	216.29 ± 5.64b	185.67 ± 6.74d	8.23 ± 0.09b
	LBP		1.21 ± 0.09a	0.27 ± 0.05e	10.23 ± 0.15d	9.49 ± 0.25bc	198.11 ± 6.15e	136.81 ± 5.12 fg	6.43 ± 0.03e
	MBP		0.91 ± 0.02b	0.30 ± 0.03d	15.11 ± 0.05b	13.69 ± 0.15a	210.31 ± 7.35c	149.62 ± 5.34f	7.01 ± 0.02d
SA	IGP		0.91 ± 0.06b	0.42 ± 0.03b	15.10 ± 0.08b	13.79 ± 0.42a	213.49 ± 8.34bc	199.48 ± 4.84c	9.79 ± 0.04a
	LBP		1.26 ± 0.07a	0.29 ± 0.06e	11.21 ± 0.04c	9.19 ± 0.25c	200.21 ± 5.55d	150.18 ± 3.69f	6.58 ± 0.01e
	MBP		0.96 ± 0.02b	0.33 ± 0.02d	15.08 ± 0.13b	13.29 ± 0.45ab	209.51 ± 8.45c	168.44 ± 5.58e	7.93 ± 0.06c

KP; Koeleria pers patch, LS; Leymus secalinus, LN; Leontopodium nanum patch, SA; Stipa aliena patch, IGP; intact grass patch, MBP; medium stripped grass patch, LBP; large stripped grass patch, BD; bulk density, TP; total phosphorus, TK; total potassium, AP; available phosphorus, AK; available potassium, MBC; soil microbial biomass, MBN; soil microbial biomass nitrogen. Means with standard error, figures with different letters show significant difference.

of grassland degradation and pinpoint locations where restoration efforts could have the greatest impact.

The accumulation of SOC with grassland development promotes ecosystem nitrogen retention, resulting in the accumulation of soil total nitrogen. The increased vegetation biomass and decreased soil erosion in long-term vegetation restoration lead to an increase in above-ground and underground carbon inputs, which may be the main factors contributing to soil carbon and nitrogen sequestration (Bardgett et al., 2021). Paddock-scale measurements over 10 years with variable weather conditions in Switzerland also highlighted the need to minimize fallow periods following sward renewal to avoid carbon losses (Ammann et al., 2020). McNally et al. (2015) estimated that increased root mass and rooting depth for a sward with seven species compared with conventional ryegrass/clover could increase soil carbon inputs to a depth of 0.3 m by up to

1.2 tC ha^{-1}. Moderate grazing, dung returns, introducing legumes, increasing sward diversity rotational grazing, and lower grazing or cutting intensity can minimize carbon losses, maintain carbon stocks, and mitigate greenhouse gas emissions (Wang and Fang, 2009; Whitehead, 2020).

Effect of stripped vegetation on soil physicochemical properties

Stripped vegetation could cause micro-climate features such as soil temperature, water, availability of light, airflow, and nutrients, affect plant physiological processes, and finally influence the growth of individual plant communities (Anderson and Leopold, 2002). The micro-climate is modified by stripped vegetation which in turn influence above and below-ground productivity and soil microbial decomposers, which may finally affect soil chemical properties (Sariyildiz, 2008). Our results show that soil TP, TK, and AP were higher in vegetation patches than in the medium and large stripped vegetation patches. The decreased litter decomposition in the large stripped vegetation patches could account for the reduction in soil P and K. Furthermore, the decrease in litter/root decomposition and the enhanced nutrient volatilization in large stripped vegetation patches tend to decrease soil P, K, and N concentrations (Scharenbrock and Bockheim, 2008). The results of this study are in line with that of Zhou et al. (2017). The lower plant biomass and its attendant low SOC in the stripped vegetation patches could account for the low MBC and MBN. Soil erosion takes away the top fertile soil and nutrients which support microbial habitats and soil ecosystem services resulting in a reduction in productivity (Van Oost and Bakker, 2012; FAO, ITPS, 2015). Grassland degradation can influence soil microbes in several ways. It often decreases SOC greatly (Liu et al., 2018), which in turn decreases microbial abundance and subdues soil microbial activity.

Conclusion

The research examined the features of grassland patches and estimated the effects of patchiness on ecosystem carbon and nitrogen storage via a field survey. The results indicated that there were variations in patchiness among the different typical alpine grass species patches. Our results suggested that stripped vegetation patches led to an increase in soil gravel content. Also, patchiness led to a substantial decline in ecosystem carbon and nitrogen. The reduction in plant biomass input and the increase in soil erosion due to stripped vegetation patches accounted for the vast decline in ecosystem carbon and nitrogen.

Data availability statement

The raw data supporting the conclusion of this article will be made available by the authors, without undue reservation.

Author contributions

TA, WC, and SH formulated the idea and designed the study. TA and SH performed the fieldwork. TA, CW, WL, and FS performed the data analysis. TA wrote the manuscript and RO and CW revised the manuscript with advice from all authors. All authors contributed to the manuscript and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher’s note

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Where and why to conserve grasslands socio-ecosystems? A spatially explicit participative approach

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Grasslands of southern South America are being replaced by annual crops and forest plantations. The environmental and social consequences of this expansion generate the need for its regulation. If a conservation policy were established, it would be critical to define which areas would have priority for conservation. Multi-criteria analysis techniques are useful tools in territorial planning processes since they allow incorporating diverse and even opposing opinions and objectives. We present a methodological approach to define the Grasslands' Conservation Value (GCV) from a spatially explicit territorial diagnosis, based on multiple criteria and incorporating explicitly and quantitatively the valuations and opinions of stakeholders. The study was developed as part of the strategy of a public inter-institutional entity to contribute in defining grasslands conservation policies. The methodological approach included workshops in which the definitions of the conservation criteria and their weighting were agreed upon. Definitions were based on a multidimensional technical characterization of the territory through indicators, for which the information used was compiled, analyzed, shared, and synthesized. Based on multi-criteria analysis, each of 12 stakeholders' groups representatives established the individual weighting of the criteria for determining the GCV and then, established a consensus weighting. The GCV was mapped by integrating territorial diagnosis of these criteria with the weightings carried out by the stakeholders. The degree of agreement among stakeholders in the differential valuation of the ecological criteria was high for 8 of the 12 stakeholders (Pearson's correlation coefficients >0.92), showing a high agreement between their opinions and those resulting from the group consensus. In all cases, the agreement about the spatial variation of conservation value was higher than on the criteria weights (Pearson's correlation coefficients ≥0.92 for 10 stakeholders). Furthermore, the sites with lower values in the consensus map corresponded mostly to those sites with lower agreement among stakeholders. The proposed methodology allowed the incorporation of different perceptions not only in the definition of conservation criteria but also in their prioritization, in a transparent and auditable process. This could contribute to the implementation of future regulations that restrict the replacement of grasslands, increasing the legitimacy of territorial planning processes.

KEYWORDS

territorial planning, decision-making, socio-ecological systems, multicriteria analysis, stakeholders, ecosystem services, remote sensing, GIS

1 Introduction

Temperate grasslands are one of the most threatened biomes (Sala, 2001; Carbutt et al., 2017) with one of the highest habitat losses and the smallest protected area at global scale (Hoekstra et al., 2005). During the last decades, land-use changes determined the loss of extensive areas of native grasslands in South America (Paruelo et al., 2006; Baldi and Paruelo, 2008; Hansen et al., 2013; Salazar et al., 2015). This process is part of a global trend where many factors interplay to determine these changes (Geist and Lambin, 2002; Modernel et al., 2016; Volante et al., 2016). Among them, land grabbing processes, commodities prices, and technological changes have been identified as major drivers (Borras et al., 2012; Rulli et al., 2013). In particular, the temperate grasslands of southern South America -Río de la Plata Grasslands region-represent one of the most extensive grassland ecosystems in the Neotropics (Soriano et al., 1992). In this region, the area of native grasslands was reduced by 19.4% between 2000 and 2019 (Mapbiomas Pampa, 2021). In the Uruguayan portion two type of transformations took place. On the one hand, an increase in the area devoted to annual crops (mainly soybean) and, on the other, an expansion of forest plantations (mainly Eucalyptus and Pinus) (Baldi and Paruelo, 2008; Vega et al., 2009; Oyarzabal et al., 2019; FAO, 2020). The environmental and social consequences of this process (Brazeiro et al., 2008; Piñeiro, 2010; Eclesia et al., 2012; Texeira et al., 2015) highlighted the need to regulate agricultural and forestry expansion (Paruelo et al., 2006). In fact, a Law that regulate forest plantations expansion is current under debate in the Uruguayan Congress (Parlamento del Uruguay, 2021).

If a conservation policy for natural grasslands were established, it would be critical to define which areas would have a priority for conservation. The criteria for assigning a high conservation value in an area were, historically, associated with the biodiversity preservation (Margules and Usher, 1981; Daniels et al., 1991; Scott et al., 1993; Humphries et al., 1995; Margules and Pressey, 2000; Egoh et al., 2007), which was the accepted overall objective of conservation policies for decades (Callicott et al., 1999). Recently, a more general concern for maintaining the capacity of ecosystems to sustain and regulate processes (e.g., nutrient and water dynamics, and carbon balance) has gained consensus (Goldman et al., 2008; Naidoo et al., 2008). Such concern is clearly related to the link between ecosystem functioning and the Ecosystem Services (ES) supply (Fisher and Turner, 2009; Haines-Young and Potschin, 2010). Noss (1990) provide an integrative view of the biodiversity concept including not only compositional aspects but also structural and functional dimensions at different levels of organization, from genes to landscapes. Even considering a broader definition of biodiversity and including other ecological criteria it is critical to also consider the human component and its interaction (Collins et al., 2011). In many cases, conservation planning failed due to insufficient consideration of social, economic, cultural, or institutional aspects (Ban et al., 2013). To identify which criteria related to the human dimension are important, why they are important, and how they should be quantified, integrated, and interpreted has proven a challenge (Pacheco-Romero et al., 2020). In this context, the subject of conservation should be the socio-ecosystem (Berkes et al., 2000) and given that the conservation value is linked to the capacity to provide ES (Eastwood et al., 2016), it should be characterized at the level those services are provided, the landscape. At this level occurs the most intense interactions between people and nature, consequently the composition and configuration of a landscape deeply affect and are affected by human activities (Wu, 2013).

Another critical aspect when a conservation policy is planned is who will determine the priority areas for conservation. As both the representativeness of the stakeholders and their ability to influence the results of the process increase, legitimacy in the implementation of these results is likely to increase as well (Reed, 2008; Aguiar et al., 2018). In turn, successful implementation of the results will depend on conservation interventions that are ecologically appropriate and socially acceptable (Ban et al., 2009; Dudley and Stolton, 2010). In this sense, stakeholder's participation in the prioritization of conservation needs is key to increasing the legitimacy and transparency of decisions. To incorporate the opinions and visions of the different stakeholders is a major challenge, as the process is influenced by the social (Auer et al., 2020) and symbolic (Benn and Jones, 2009) capital of the stakeholders and by the power relationships among them (Reed, 2008; Sterling et al., 2019). Furthermore, given that decisions are based on the interaction between values, interests, emotions (Levine et al., 2015) and available evidence (Sterling et al., 2017), specific methods are needed that consider this complexity of factors (Mukherjee et al., 2018). One way to do this is to explicitly separate the objective and subjective components of this process. For this, is critical to generate mechanisms to make explicit and document both, the criteria that are considered to determine the conservation value and how they are spatially applied, as well as the different perceptions of stakeholders involved in the process.

Multi-criteria analysis techniques are very useful tools in territorial planning processes, since they allow diverse opinions to be considered and the coexistence of opposing objectives or visions (Saaty, 1977, 2014; Saaty and Peniwati, 2008). This method makes it possible to quantify, record and document systematically the different opinions, bringing transparency to the decision-making process. However, many of the studies that use these techniques for conservation-related decision-making do not involve stakeholders in the formulation of criteria and weight them based on hierarchies defined by experts, instead of collecting stakeholder concerns (Esmail and Geneletti, 2018). In turn, often some techniques are used to reduce the variability of stakeholder weightings (Proctor and Drechsler, 2006), which does not allow assessing the degree of agreement among them. The studies linked to the prioritization of conservation areas in Uruguay, were based exclusively on ecological aspects and weighting of criteria was defined by experts (Bilenca and Miñarro, 2004; Soutullo et al., 2013; di Minin et al., 2017; Brazeiro et al., 2020).

In this article we present and apply a novel methodological approach to characterize the Grasslands' Conservation Value (GCV) from a spatially explicit territorial diagnosis based on multiple criteria (ecological and socioeconomic) and incorporating explicitly and in quantitative terms the assessments and opinions of stakeholders. From the results of the process, we quantify the degree of agreement among stakeholders both in the differential assessment of the criteria and in the spatial variation of the conservation value. We also evaluate which criteria contribute to the differentiation of the assessments. The analyses were performed in the South-Central region of Uruguay, in the Río de la Plata Grasslands, which is undergoing profound land-use and land-cover changes. The process was carried out as part of the strategy of a public inter-institutional entity to contribute to the definition of grassland conservation policies.

2. Methods

2.1 Case description and study area

As part of the concern on the sustainability of cattle production on native grasslands, the Ministry of Livestock, Agriculture and Fisheries of Uruguay set up in 2012 the Board of Livestock on Natural Grasslands ("Mesa de Ganadería sobre Campo Natural", MGCN for its acronym in Spanish). The MGCN is a public inter-institutional entity whose objectives are aimed at the dynamic conservation of grasslands. It includes different institutions: representatives of the research and development system, rural extension, farmers' associations, non-governmental organizations, international cooperation institutions, and governmental agencies (Supplementary Table S1) (MGCN, 2021). In a context of growing concern about the transformation of grasslands into croplands and forest plantations, the MGCN initiated in 2017 action aimed to make a spatially explicit territorial diagnosis and to characterize the conservation value of grasslands of the South-Central region of Uruguay (Panario, 1987; Panario et al., 2014). This pilot area was selected by the stakeholders given its vulnerability to grassland losses. It has undergone major changes in land-use and is currently seriously threatened by the installation of a new pulp mill (http://upmpasodelostoros.com) that promotes future forestry production projects.

The South-Central region, with 2.3 million hectares, is characterized by gentle hills with soils originated from granitic bedrock and quaternary sediments (Panario et al., 2014). The climate is humid temperate, the average annual temperature is 17°C and the average annual precipitation varies between 1,100 and 1,200 mm per year (INUMET, 2021). Native grasslands, devoted to livestock production, occupied 42% of the South-Central region, annual crops lands (mainly soybean, corn, and winter crops) 54% and forest plantations the remaining 4% (Baeza et al., 2019) (excluding urban areas and water bodies). Two native grasslands communities are present in this region (Lezama et al., 2019). The first one corresponded to sparsely-vegetated grasslands. This community is characterized by meso-xerophytic species and includes stands with shallow or very shallow soils. It has two variants (sub-communities) in the study area, one of them is characterized by *Stenachaeniumcampestre-Andropogon ternatus* and the other one by *Aira elegantissima-Micropsisspathulata* (Lezama et al., 2019). The second plant community corresponds to densely-vegetated grasslands dominated by mesophytic species, encompassing stands with high plant cover values (near 100%) that occupied medium and deep soils. Again, this community present two variants in the region, one characterized by the presence of *Chevreuliasarmentosa-Danthonia* montevidensis and the other by *Lolium multiflorum-Nassellacharruana* (Lezama et al., 2019).

2.2 Methodology for determining the conservation value

The methodological approach included: 1) three workshops in April, May, and June 2017 in which the definitions of the conservation criteria and their weighting were agreed upon, and 2) technical work where the information to be used was prepared, analyzed, and synthesized (Figure 1). The workshops were convened by the MGCN as part of its regular meetings. Participants

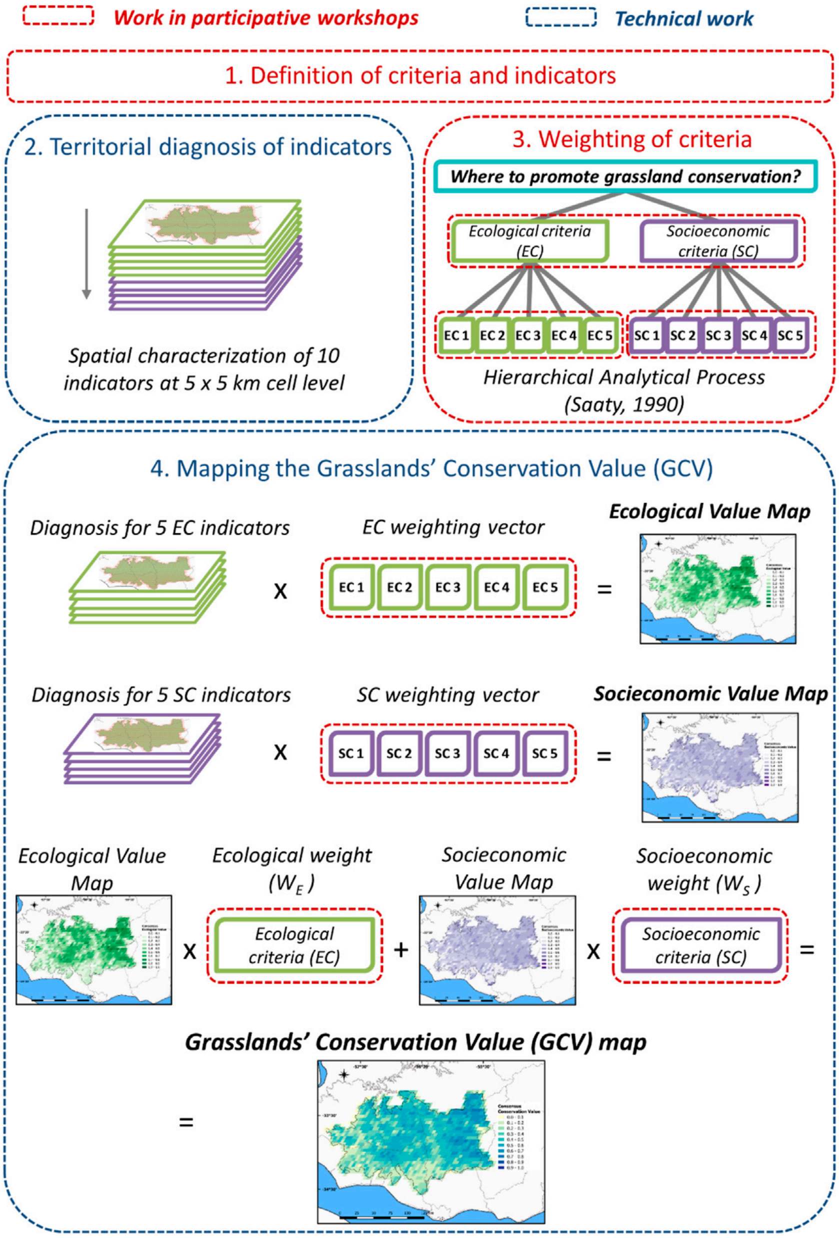


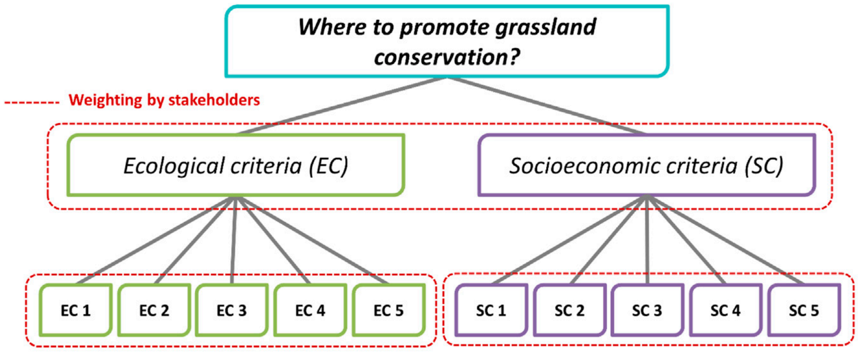
FIGURE 1

Methodological steps for defining the Grasslands' Conservation Value (GCV). The size of the boxes does not represent the relative importance of each stage in the process.

included representatives of the different organizations of the MGCN (each of the stakeholders has a representative on the MGCN, Supplementary Table S1) and the technical team (the authors of this article). Although the three workshops were attended by most of the representatives, there were some who participated in only 1 or 2 of the workshops. In the first workshop the criteria and indicators to be included in the territorial diagnosis were presented and discussed. The weightings of the ecological and socioeconomic criteria were carried out in the second and third workshop, respectively.

2.2.1 Criteria and indicators for the socio-ecological diagnosis

The first step included the definition of the criteria on which the conservation value was to be determined (Figure 1). The criteria corresponded to both biophysical and human components of the socio-ecological system. Before the first workshop, the members of



	Criterion	Indicator		Criterion	Indicator
EC 1	Protected areas	Presence / Absence	**SC 1**	Farm size	Median cadastral plot
EC 2	Faunal diversity	Potential mean species richness of mammals, birds, amphibians, reptiles, and fish.	**SC 2**	Family farming	% of grasslands on family farms
EC 3	Functional diversity	Shannon index of Ecosystem Functional Types	**SC 3**	Grasslands carrying capacity	Cattle carrying capacity
EC 4	Grasslands' area	% of grasslands	**SC 4**	Infrastructure	Km of road
EC 5	Grasslands' Ecosystem services supply	% of grasslands withouth negative trends in Ecosystem Services Supply Index	**SC 5**	Population	Rural population density of the census segment

FIGURE 2
Hierarchical structure used to determine the Grasslands' Conservation Value (GCV). The question to be answered is which cells (5 x 5 km) have higher conservation value. The criteria to answer that question were grouped into two categories: ecological (EC 1 to EC 5) and socioeconomic (SC1 to SC5), which were characterized by a spatially explicit diagnosis of their indicators. Each dotted red box encloses the elements that the stakeholders compared in the three weightings carried out. Each comparison gives rise to a weighting vector representing the relative importance of each element with respect to the others, whose sum is equal to 1.

the MGCN, in the context of their regular meetings, worked on identifying important criteria to determine the GCV. A first list of criteria resulted from these meetings, and it was provided to the technical team. Indicators for these criteria were derived mainly from two sources, scientific articles and information from public institutions. In the first workshop, based on this proposal, the technical team, based on the previous work of the stakeholders, presented a first proposal of criteria to be included in the socio-ecological diagnosis. Each criterion was characterized by different indicators. Such indicators had to be spatially explicit to geographically discriminate areas with different conservation value. In turn, each indicator was evaluated by the members of the MGCN according to its relevance, source, and scale. Based on the comments of the workshop participants, the criteria and indicators considered were incorporated, modified, or discarded. Some new criteria were incorporated upon the comments of the attendants. A total of 34 indicators corresponding to 15 criteria were mapped and integrated into a Geographic Information System (Quantum GIS software) (Supplementary Table S2). Each indicator was summarized at a spatial resolution of 5 km (Figure 1) and scaled to the range (0–1) to make them comparable, using the following equation:

$$Xi\,scaled = \frac{Xi - X\min}{X\max - X\min} \qquad (1)$$

Where X_i *scaled* corresponds to the scaled value of indicator X for cell i, X_i is the value taken by indicator X in cell i, $X_{\min}$ is the minimum value taken by indicator X among all cells and $X_{máx}$ is the maximum value taken by indicator X. For each criterion, a single indicator was selected, and correlation analyses were performed between the indicators in each group to rule out redundancies among them (Supplementary Figure S1). In those cases where Pearson correlation coefficient between two indicators was greater than 0.65, only one of them was conserved (e.g., floristic diversity was excluded because it presented a high correlation with the proportion of grasslands, $r = 0.98$).

As a result, a final set of 10 criteria was agreed in the second workshop (Figure 1). The criteria were divided into two groups (ecological and socioeconomic). In the first group, 5 Ecological Criteria (EC) were included, characterized through 5 indicators (Figure 2, Supplementary Table S3, Supplementary Figure S2):

- EC1: Protected areas and priority sites for conservation, characterized by the presence/absence of both a protected area and areas integrated into the network of priority sites to be incorporated according to a plan proposed by the National System of Protected Areas (SNAP, 2015).

- EC2: Faunal diversity, characterized through 5 maps of potential species richness for mammals, birds, reptiles, amphibians, and fishes in ~66,000 ha cells for all of Uruguay (Brazeiro et al., 2008). A potential faunal diversity index was determined as the sum of the 5 specific richnesses summarized at the 5 × 5 km cell level.
- EC3: Functional diversity, characterized through the Ecosystem Functional Types (EFT) diversity. The EFT (Paruelo et al., 2001) result from combining three attributes of the annual dynamics of remotely sensed vegetation indices: the annual mean, the intra-annual coefficient of variation, and the moment of year of peak productivity. This approach allows to infer the degree of productive diversity. From the annual dynamics of the Enhanced Vegetation Index (EVI, derived from MODIS sensor images, product Mod13q1 with a spatial resolution of 250 m and a temporal resolution of 16 days), the EFTs were obtained for the year 2015. Four fixed levels were generated for the three attributes that were then combined to generate a map of EFTs (Alcaraz-Segura et al., 2013). The 250-m pixels corresponding to grasslands (identified from the EC4 land cover map corresponding to the same year) were excluded, and the Shannon Index was calculated to describe the functional diversity of the grassland surroundings.
- EC4: Remaining grassland area (proportion), obtained from a land-cover map for 2015, with a spatial resolution 30 m (Baeza et al., 2019).
- EC5: Grasslands' ecosystem services supply, determined by trends in the Ecosystem Services Supply Index (ESSI), a synoptic indicator that estimates and maps supporting and regulating ecosystem services related to water and carbon dynamics derived from remote sensing data (Paruelo et al., 2016). The support for using ESSI as a proxy of ecosystem service supply is based on its ability to explain between 48 and 66% of the variability of four ecosystem services estimated from empirical data or mechanistic models: groundwater recharge and avian richness in Dry Chaco forests and soil organic carbon and evapotranspiration in Río de la Plata Grasslands (Paruelo et al., 2016). It is based on two attributes of vegetation index annual dynamics, the annual mean (VI_{MEAN}, a proxy of total C gains) and the intra-annual coefficient of variation (VI_{CV}, an indicator of seasonality): $ESSI = VI_{MEAN} * (1—VI_{CV})$. Those sites where annual productivity is higher and more seasonally stable would have a higher ES supply. From the annual dynamics of EVI (derived from MODIS sensor images, product Mod13q1 with a spatial resolution of 250 m and a temporal resolution of 16 days), the annual ESSI values were obtained, and their trend was estimated during the period 2000–2015. Since the criterion aimed to capture the ecosystem services supply provided by grasslands in a cell, the proportion of pixels corresponding to grasslands (identified from the EC 4 mapping) without negative ESSI trends (i.e., where the ecosystem services supply has been maintained or increased) was calculated with respect to the total number of grassland pixels in the cell.

In the second group, 5 Socioeconomic Criteria (SC) were included, characterized through 5 indicators (Figure 2, Supplementary Table S4, Supplementary Figure S3):

- SC1: Farm size, characterized through the median of cadastral plots (Dirección Nacional de Catastro, 2017).
- SC2: Family farming, whose indicator was the proportion of grasslands in family farms with respect to the total area of grasslands in the cell. One of the stakeholders (representative of The Rural Development office of the Ministry of Livestock, Agriculture and Fisheries) provided the information of the family farms, protecting the identity of the owners.
- SC3: The grasslands carrying capacity was estimated as follows: $CC = \frac{ANPP*HI}{AIC}$ where, CC is the carrying capacity ($heads*ha^{-1}$), ANPP corresponds to the Aerial Net Primary Productivity ($kg*ha^{-1}*yr^{-1}$), HI represents the Harvest Index (kg consumed/kg produced), and AIC is the is the Annual Individual Consumption ($kg\ consumed*head^{-1}*año^{-1}$). The ANPP was estimated from remotely sensed data (EVI derived from MODIS sensor images, product Mod13q1 with a spatial resolution of 250 m and a temporal resolution of 16 days) using the Monteith model (Monteith, 1972; Piñeiro et al., 2006; Grigera et al., 2007; Paruelo et al., 2019). Mean annual ANPP for remnant grasslands, identified in the EC4 mapping, for the period 2000–2015 was estimated at a spatial resolution of 250 m. The HI was estimated from ANPP using a function proposed by Golluscio et al. (1998) and for annual individual consumption a value of 2,774 kg per year was taken as a reference, suggested by experts from the "Instituto Plan Agropecuario", a public cattle extension institution and member of the MGCN (Supplementary Table S1).
- SC4: An index of infrastructure of each cell was characterized through the sum of the kilometers of road of the official national road network (Ministerio de Transporte y Obras Públicas, 2017).
- SC5: Population, characterized by the rural population density reported in the National Census of Population, Housing and Households (Instituto Nacional de Estadísticas, 2011). The most detailed spatial resolution available corresponds to the census segment.

For the EC, stakeholders agreed that the relationship between the values of each indicator and the contribution to conservation value was positive (i.e., higher values of each indicator contribute to a higher conservation value). In the case of the SC, although

TABLE 1 Example of pairwise criteria comparison and obtaining the weighting vector corresponding to the ecological criteria. The row and column headings contain the criteria compared by the stakeholders using the Saaty scale in italic cells. Once the preferences had been assigned, the geometric mean was calculated for each row of the matrix and the geometric means of all the rows were summarized. The weighting value (relative importance) of each criterion was obtained by dividing its geometric mean (A) by the sum of the geometric means of all rows (7.52). These values determine the weighting vector (C), which indicates the relative importance of each criterion. The last row (B) is used to calculate the consistency level of the matrix.

Ecological Criteria (EC)	EC1	EC2	EC3	EC4	EC5	Geometric mean (A)	Weighting vector (C)
EC1: Protected areas	*1*	*1*	*3*	*1/7*	*1/5*	0.61	0.08
EC2: Faunal diversity	*1*	*1*	*3*	*1/5*	*1/3*	0.72	0.10
EC3: Functional diversity	*1/3*	*1/3*	*1*	*1/7*	*1/5*	0.32	0.04
EC4: Grasslands' area	*7*	*5*	*7*	*1*	*5*	4.15	0.55
EC5: Grasslands' Ecosystem services supply	*5*	*3*	*5*	*1/5*	*1*	1.72	0.23
Sum (B)	14.33	10.33	19.00	1.69	6.73	7.52	

the stakeholders agreed that these were important criteria to include, they had different opinions regarding the relationship between the values of each indicator and their contribution to the GCV. These discrepancies required prior agreement, as opinions on weighting depends on the direction in which each indicator contributes to the GCV. For 4 of the 5 criteria, the relationship was positive, while for SC1, it was negative: those cells with smaller median size of cadastral plots would have a higher GCV than those with larger median size. Therefore, this indicator was incorporated into the GCV estimation as its complement (1- SC1 scaled). More details on the criteria and indicators considered is presented as supplementary material (details of the indicators calculated for the ecological and socioeconomic criteria are shown in Supplementary Table S3 and Supplementary Table S4, respectively, while the indicators maps are shown in Supplementary Figure S2 and Supplementary Figure S3).

2.2.2 Weighting of criteria

The weighting of the criteria was based on a multi-criteria analysis method, the Analytic Hierarchy Process (Saaty, 1990, 2014). To establish the relative importance of each criterion, the participants make pairwise comparisons of each criterion with respect to the rest using the Saaty scale (Saaty, 1977). The assignment of preferences was established by comparing the importance of the criterion in each row with respect to the criterion in each column in a square matrix (Table 1) through the scale whose values range from 1 to 9 and establish the following priorities:

1 = Equally important
3 = Moderately more important (and conversely 1/3 is moderately less important)
5 = Strongly important (1/5 strongly less important)
7 = Very strongly important (1/7 very strongly less important)
9 = Extremely more important (1/9 extremely less important)

2, 4, 6, 8 correspond to intermediate values that can be used to resolve compromise situations.

The method provides a measure of the degree of weighting consistency called Consistency Ratio (CR), which indicates to what extent the preferences were assigned through an informed and coherent judgment (Saaty, 1990, 2014). To this, the comparison matrix must comply with 3 properties: reciprocity (e.g., if criterion A is moderately more important than B, then B must be moderately less important than A), transitivity (e.g., if criterion A is more important than B and B is more important than C, then A must be more important than C), and proportionality (e.g., if A is moderately more important than B and B is moderately more important than C, then A must be extremely more important than C). A matrix with CR ≤ 0.10 implies accepting up to 10% of the inconsistency that would have been obtained by chance. If the ratio is much higher than 0.1, the judgments are unreliable because they are too close to randomness (Saaty, 1990, 2014) (see supplementary material for details on consistency analysis).

Based on the hierarchical scheme proposed, the stakeholders made three comparisons (Figure 2). The first one took place during the second workshop, after we presented the results of the ecological indicators diagnosis. Each of the 12 participants compared the 5 ecological criteria with each other using the Saaty scale. Based on the individual preferences a consensus matrix comparison was agreed in a plenary session. This allowed us to calculate an individual weighting vector (anonymous) that summarizes the relative importance that each stakeholder assigned to the ecological criteria and a consensus weighting vector. We also calculated the consistency of each weighting. The second comparison was carried out in the third workshop, after we presented the results of the socioeconomic indicators diagnosis. Each of the participants compared the 5 socioeconomic criteria with each other using the Saaty scale. In this instance, due to the stakeholders' own dynamics during the workshop, we did not have the individual weightings, but they only registered the consensus weighting of the socioeconomic indicators as agreed in the plenary session. Finally, the relative importance of the ecological criteria with respect to the socioeconomic criteria was determined in plenary session and by consensus. Because at this hierarchical level there is only one pair of elements to compare, we asked them to directly assign a relative importance value. They had to distribute the 100% of the relative importance between the ecological and socio-economic criteria, ecological weighting (W_E) and socio-economic weighting (W_S), respectively.

2.2.3 Conservation value estimation and mapping

The area was divided into 1,217 cells of 5 × 5 km (Figure 3). Each of these cells represents the entity to which a conservation value will be assigned. The size of the cell was defined based on two criteria: 1) at this resolution (2,500 ha) basic attributes of the landscape (represented elements, configuration and structure) can be characterized (Baldi et al., 2006; Baldi and Paruelo, 2008), and 2) such grain is in between the resolution of coarser (e.g., faunal diversity, human population) and finer (e.g. remaining patches of grassland, supporting and regulating ecosystem services supply) available information. As some of the criteria (e.g., supporting and regulating ecosystem services supply, grasslands carrying capacity, functional diversity) were quantified from such spectral data derived from the MODIS (Moderate Resolution Imaging Spectroradiometer) sensor on board the Terra satellite (Earth Observation System - NASA), the cells of the grid were adjusted to the pixels of the satellite images.

The GCV was determined by integrating the territorial diagnosis of ecological and socioeconomic indicators at the landscape level (5 × 5 km cells), with the weightings carried out by the stakeholders. To incorporate the diagnostic value of the indicators, stakeholders agreed on how each would contribute to conservation value. For 9 of the 10 indicators, a higher diagnostic value corresponded to a higher conservation value (e.g., Faunal diversity, presence of protected areas, carrying capacity, etc.). On the other hand, for the field size criterion, they agreed that higher median area of cadastral parcels would result in a lower conservation value. This was contemplated by performing an inverse scaling for this indicator (Equation 1). First, we determined: 1) the Ecological Value (EV) in each cell (Equation 2), which integrates the diagnostic value of the ecological indicators with the weighting of the ecological criteria by the stakeholders (12 individual weighting vectors and 1 consensus weighting vector) and 2) the Socioeconomic Value (SV) in each cell (Equation 3), which integrates the diagnostic value of the socioeconomic indicators with the weighting carried out in the group consensus. Finally, both values (EV and SV) were integrated together with their weighting (agreed upon in plenary) to obtain the Grasslands' Conservation Value (GCV) (Equation 4). The three values corresponding to group consensus (EV, SV, and GCV) and the 12 individual EV were mapped.

The EV of each cell (n = 1,217) was determined through the following equation:

$$EV_{i_1^{1217}} = \sum_{j=1}^{5} EC_{ji} * W_{ECj} \tag{2}$$

Where, EVi corresponds to the Ecological Value of the cell i, j represents the ecological criteria, EC_{ji} represents the scaled diagnostic value of the indicator describing ecological criterion j for cell i obtained in the territorial diagnosis and W_{EC} represents the weighting of criterion j defined in the weighting vector of the ecological criteria.

The SV of each cell (n = 1,217) was determined through the following equation:

$$SV_{i_1^{1217}} = \sum_{k=1}^{5} SC_{ki} * W_{SCk} \tag{3}$$

Where, SV corresponds to the Socioeconomic Value of the cell i, k represents the ecological criteria, SC represents the scaled diagnostic value of the indicator describing socioeconomic criterion k for cell i obtained in the territorial diagnosis and W_{SC} represents the weighting of criterion k defined in the weighting vector of the socioeconomic criteria.

Finally, the conservation value was determined by the weighted sum of EV and SV by their weights (higher hierarchical level) through the following equation:

$$GCV_{i_1^{1217}} = EV_i * W_E + SV_i * W_S \tag{4}$$

Where, GCV_i corresponds to the Grasslands' Conservation Value of cell i, W_E represents the ecological value of cell i, W_E its weighting value (upper level of the hierarchical scheme), SV corresponds to the socioeconomic value of cell i and W_s its weighting value (upper level of the hierarchical scheme).

2.3 Data analysis and synthesis

The degree of agreement among stakeholders was assessed through two complementary analyses. First, the degree of agreement in both the assessment of the criteria and the mappings was evaluated through correlation analysis (Pearson correlation coefficient, Sokal and Rohlf, 2009), and both analyses were compared to assess the extent to which dissent in the weightings translated into dissent in the maps. Second, from the 12 EV mappings, the Coefficient of Variation (EV_{CV}) was calculated in each of the cells and a map of the degree of agreement in the EV as a complement of the EV_{CV} ($1—EV_{CV}$) was obtained to identify spatially explicit consensus and disagreement.

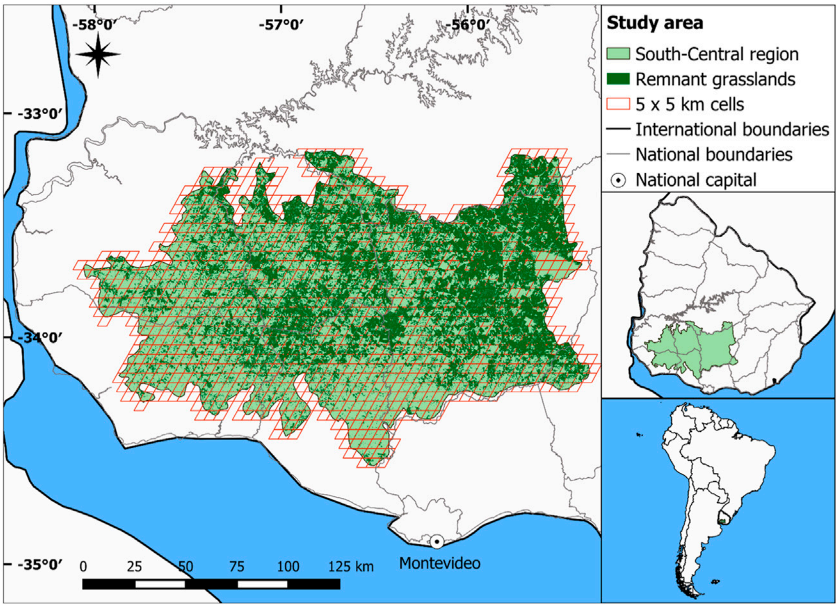


FIGURE 3
Study area. The conservation value has been determined for each cell of 5 x 5 km.

3 Results

3.1 Ecological value weightings and mapping

The ecological criteria most highly valued according to the group consensus weighting vector were, in decreasing order of importance, the proportion of grasslands (W_{EC4} = 0.55) and the level of supply of supporting and regulating ecosystem services (W_{EC5} = 0.23), followed by faunal biodiversity (W_{EC2} = 0.10), protected areas (W_{EC1} = 0.08) and finally functional diversity (W_{EC3} = 0.04) (Figure 4). The criteria comparison matrix, from which this weighting vector was derived, was consistent (CR = 0.10). As for the individual weights the most highly valued criteria were also the proportion of grasslands and the level of ecosystem services provided by the grasslands and were, in turn, those with the most variable weights among participants (W_{EC4}: mean = 0.44 and SD = 0.19; W_{EC5}: mean 0.26 and SD = 0.12) (Figure 4). Of the 12 individual comparison matrices, 6 were consistent (CR≤0.10 for participants 2, 5, 7, 9, 10, and 12); while of the remaining 6, 3 presented values close to the suggested threshold (CR = 0.17 for participant 1, CR = 0.11 for participant 6 and CR = 0.12 for participant 11) and the other 3 presented higher values (CR = 0.26 for participant 3, CR = 0.27 for participant 4 and CR = 0.41 for participant 8). The individual weighting vectors and their CR are reported in the supplementary material (Supplementary Table S5).

A total of 73% of the correlations between the individual priority vectors were positive, of which 75% presented correlation coefficients greater than 0.58 and 50% greater than 0.9 (Figure 5). In contrast, 27% of the comparisons presented negative correlation coefficients, of which 50% presented values lower than −0.58 (Figure 5). Higher positive correlation coefficients indicate that the criteria weighting ranking between two stakeholders is similar. More negative coefficients indicate opposite weighting rankings between two stakeholders, while those close to 0 represent different rankings. In this sense, stakeholders P6 and P8 presented negative correlation values with the majority of stakeholders, indicating the lowest degree of agreement (Figure 5). The degree of correlation between each priority vector and the consensus vector was greater than 0.92 for 8 of the 12 stakeholders, showing a high degree of similarity between their rankings and the one resulting from the group consensus (Figure 5). Two of the remaining stakeholders presented positive but lower values (P5 = 0.64 and P7 = 0.44) and the other two negative values (P6 = -0.19 and P8 = -0.63).

Regarding the degree of spatial agreement, the correlations between the 12 individual maps and the consensus map was higher or equal than 0.92 for 10 of the 12 stakeholders and for the remaining two it presented values of 0.61 (P6) and 0.66 (P8) (Figure 5). In all cases, the degree of agreement in the maps was higher than in the individual weigthings of criteria, even for the two stakeholders with a low degree of agreement in the individual weigthings of criteria. The dissent of these stakeholders in the weighting of criteria was not reflected in a dissent in the spatial

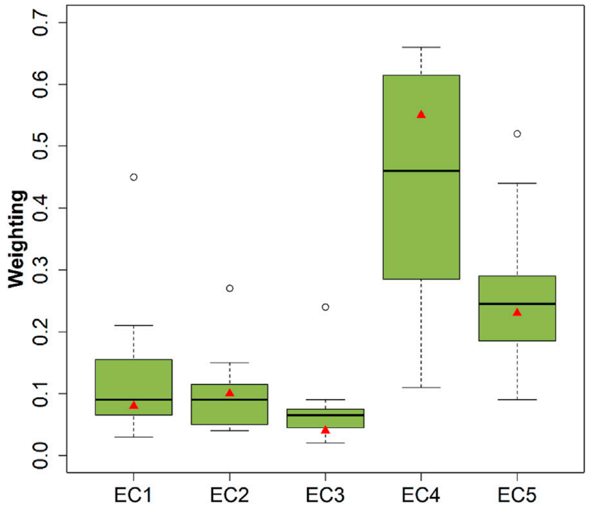


FIGURE 4
Distribution of the weighting values of the 12 individual stakeholders for each of the ecological criteria (EC1: Protected areas, EC2: Faunal diversity, EC 3: Functional diversity, EC4: Remaining grassland area, and EC5: Supporting and regulating ecosystem services supply). In each box, the horizontal black line represents the median, the extremes the quartiles (q1 and q3), the whiskers correspond to 1.5 of the interquartile range and the empty points are outliers. The red triangles represent the weights of the consensus vector.

ecological value. In turn, the cells with the lowest EV in the consensus map (Figure 6A), mostly coincide with those cells with the lowest degree of agreement in EV (Figure 6B).

3.2 Socioeconomic value weighting and grasslands conservation value mapping

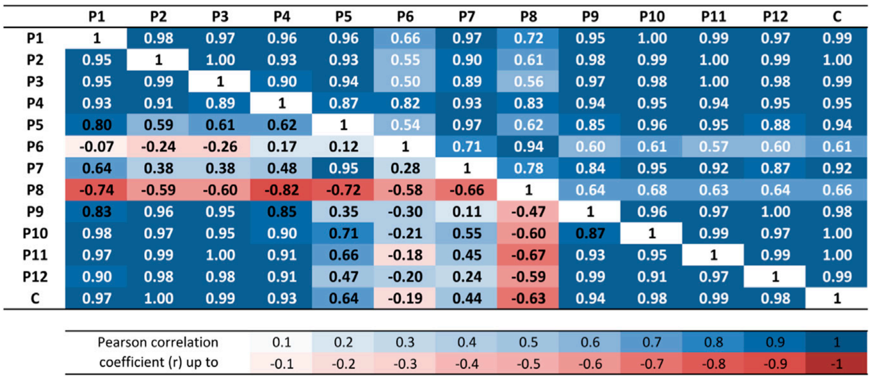
The socioeconomic criteria most highly valued according to the group consensus weighting vector were, in decreasing order of importance, grasslands carrying capacity (W_{SC3} = 0.51) and grasslands on family farms (W_{SC2} = 0.25), followed by population (W_{EC5} = 0.12), farm size (W_{EC1} = 0.08) and finally infrastructure (W_{EC4} = 0.04). The criteria comparison matrix from which this weighting vector was derived was consistent (CR = 0.03). These results combined with the diagnosis of socioeconomic criteria determined the consensus mapping of socioeconomic value (SV, Figure 7B). The weighting of ecological criteria (W_E) to socioeconomic criteria (W_S), as determined by group consensus (top level of the hierarchical scheme, Figure 2), was 0.7 and 0.3, respectively. The consensus EV and SV maps weighted by these values determined the GCV map (Figure 7). The consensus EV ranged from 0.07 to 0.84 and the most frequent values were low (21.7% of the area had values between 0.1 and 0.2) (Figures 7A,D). The consensus SV varied between 0.002 and 0.65 and was more homogeneous than the EV, with 73% of the values between 0.3 and 0.5 (Figures 7B,E). The consensus GCV varied between 0.06 and 0.71 and the spatial pattern was similar to that of the EV, but with a higher frequency of average values, since 24.8% of the area had conservation values between 0.4 and 0.5 (Figures 7C,F).

4 Discussion

Participatory evaluation and decision-making processes face the challenge of incorporating all opinions considering the power relations established among stakeholders (Felipe-Lucia et al., 2015). In this article we presented the development and implementation of a method to quantify the conservation value of natural grasslands based on objective criteria and incorporating the participation of the stakeholders involved. The methodology allowed the incorporation of different perceptions not only in the definition of conservation criteria but also in their prioritization, in a transparent and auditable process. It also made it possible to evaluate the degree of agreement among participants both in the prioritization of criteria and in the grasslands' conservation value spatial variation.

An *a priori* and inclusive definition of the criteria to be considered and a critical evaluation of the quality of the data was essential to accommodate all views and interests. The inclusion or exclusion of a criterion in the construction of the conservation value was based on the one hand, on the perception and justification of its importance by the technical team and, at least, one of the stakeholders. On the other hand, the quality of the data was particularly considered. In this sense, spatially explicit data, based on documented sources and with access to metadata were privileged. The scale (extension and resolution) of the information was a key aspect in selecting the data. In this sense, only information that was larger than the area of study was included. Although we tried to include data with a more detailed resolution than that of the defined cells (2,500 ha) to carry out aggregation processes, this was not always possible. In the case of two criteria considered particularly important by some stakeholders (faunal diversity and population density) the basic information was at a coarser resolution. In these cases, we had to downscale the grain of the original information layers. To each cell we assigned the value of the object containing it or an area-weighted average in those cases where the cell overlapped with more than one unit. The lack of spatially explicit information or the availability of information with limited spatial detail highlights the need for the science and technology system to generate more detailed information for the criteria that are important to stakeholders.

The criteria selected to represent the biophysical dimension of the socio-ecosystems sought to cover, at the landscape level, the three dimensions of biodiversity proposed by (Noss, 1990).



	P1	P2	P3	P4	P5	P6	P7	P8	P9	P10	P11	P12	C
P1	1	0.98	0.97	0.96	0.96	0.66	0.97	0.72	0.95	1.00	0.99	0.97	0.99
P2	0.95	1	1.00	0.93	0.93	0.55	0.90	0.61	0.98	0.99	1.00	0.99	1.00
P3	0.95	0.99	1	0.90	0.94	0.50	0.89	0.56	0.97	0.98	1.00	0.98	0.99
P4	0.93	0.91	0.89	1	0.87	0.82	0.93	0.83	0.94	0.95	0.94	0.95	0.95
P5	0.80	0.59	0.61	0.62	1	0.54	0.97	0.62	0.85	0.96	0.95	0.88	0.94
P6	-0.07	-0.24	-0.26	0.17	0.12	1	0.71	0.94	0.60	0.61	0.57	0.60	0.61
P7	0.64	0.38	0.38	0.48	0.95	0.28	1	0.78	0.84	0.95	0.92	0.87	0.92
P8	-0.74	-0.59	-0.60	-0.82	-0.72	-0.58	-0.66	1	0.64	0.68	0.63	0.64	0.66
P9	0.83	0.96	0.95	0.85	0.35	-0.30	0.11	-0.47	1	0.96	0.97	1.00	0.98
P10	0.98	0.97	0.95	0.90	0.71	-0.21	0.55	-0.60	0.87	1	0.99	0.97	1.00
P11	0.97	0.99	1.00	0.91	0.66	-0.18	0.45	-0.67	0.93	0.95	1	0.99	1.00
P12	0.90	0.98	0.98	0.91	0.47	-0.20	0.24	-0.59	0.99	0.91	0.97	1	0.99
C	0.97	1.00	0.99	0.93	0.64	-0.19	0.44	-0.63	0.94	0.98	0.99	0.98	1

Pearson correlation coefficient (r) up to	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9	1
	-0.1	-0.2	-0.3	-0.4	-0.5	-0.6	-0.7	-0.8	-0.9	-1

FIGURE 5

Below the diagonal: correlations between the weighting vectors resulting from comparing the ecological criteria among the 12 participants (P1 to P12) and the group consensus (C); values correspond to Pearson's correlation coefficient (white values indicate significant correlations, *p* value < 0.05). Above the diagonal: correlations between the Ecological Value (EV) maps of the 12 participants (P1 to P12) and the group consensus (C); values correspond to Pearson's correlation coefficient (white values indicate significant correlations, p value< 0.001).

Thus, aspects related to composition (EC2: potential species richness), structure (EC4: proportion of remaining grassland area) and functioning (EC3: diversity of ecosystem functional types) were included. Along with the biophysical aspects, two aspects related to the interaction between the biophysical and human dimensions were considered (Pacheco-Romero et al., 2020): the presence of protected areas and the change in the supply of regulating and support Ecosystem Services. The criteria associated with the human dimension partially captures the aspects pointed out by Pacheco-Romero et al. (2020). The influence of these criteria in defining conservation value was more controversial than in the case of biophysical aspects. In fact, for some of the criteria the participants disagreed not only on the weight but also on the direction of the influence (positive or negative) on the contribution to the conservation value of grasslands. These disagreements in the direction of influence of the indicators promote major changes in weighting. For example, if a certain stakeholder considered that infrastructure (SC4) was a particularly important criterion and in turn that those areas with a lower degree of infrastructure (SC4) should be those with a higher conservation value, when an inverse (positive) direction was agreed upon for this indicator, the weighting assigned to it was naturally reduced.

Although in study case presented, consensus weights were achieved in the absence of conflict, we consider that there are risks associated with reducing the opinions of multiple stakeholders in a single weighting. There is no consensus in the literature on how to reduce variability in the weights; and the commonly used reductions (some measure of central tendency such as average, median or mode), imply not only that information is lost but also that stakeholders whose weights are very different from the agreed weighting may no longer wish to participate in the process (Proctor and Drechsler, 2006). In this sense, we consider that the most valuable aspect of the method we presented is the possibility of assessing the degree of agreement among stakeholders both in the perception of the criteria (Figure 4, Figure 5) and in the spatial variation of the conservation value (in this case, the ecological value, Figure 6B). Moreover, these aspects were documented and are available to be consulted and discussed in an iterative process. Due to the particular characteristics and dynamics of the MGCN, we did not have the individual priority vectors for the socioeconomic criteria and therefore have not been able to generate individual maps of socioeconomic value (or conservation value), which would be very important to be able to document the degree of agreement on socioeconomic value and its impact on the final GCV. Where and why to conserve grasslands in South-Central region of Uruguay, was associated, according to the stakeholders of the MGCN, mainly, to two criteria. The GCV map resembles the distribution of remnant grasslands (Figure 3, Figure 7C). This is because among the ecological criteria, the area occupied by remanent grasslands was the most important according to group consensus ($W_{EC4} = 0.55$, Figure 4). The second most weighted criterion by consensus was Grasslands' supporting and regulating ecosystem services supply ($W_{EC5} = 0.23$, Figure 4), which takes positive values where there were grasslands and zero where there were no grasslands. At the same time, the weighting of the ecological criteria was higher than that of the socioeconomic criteria ($W_E = 0.7$). This implies that those landscapes with few remnant grasslands would not have conservation priority. In this sense, stakeholders raised the possibility of replicating the methodology to answer a different question, which are the areas with the highest restoration priority? In such case a lower proportion of native grasslands and its connectivity would have a greater importance.

Though the stakeholders involved in the processes included the academia, conservation NGOs and ranchers' associations, the focus was on conservation issues. In temperate and sub-humid grasslands, the exclusion of grazing does not necessarily lead to grassland

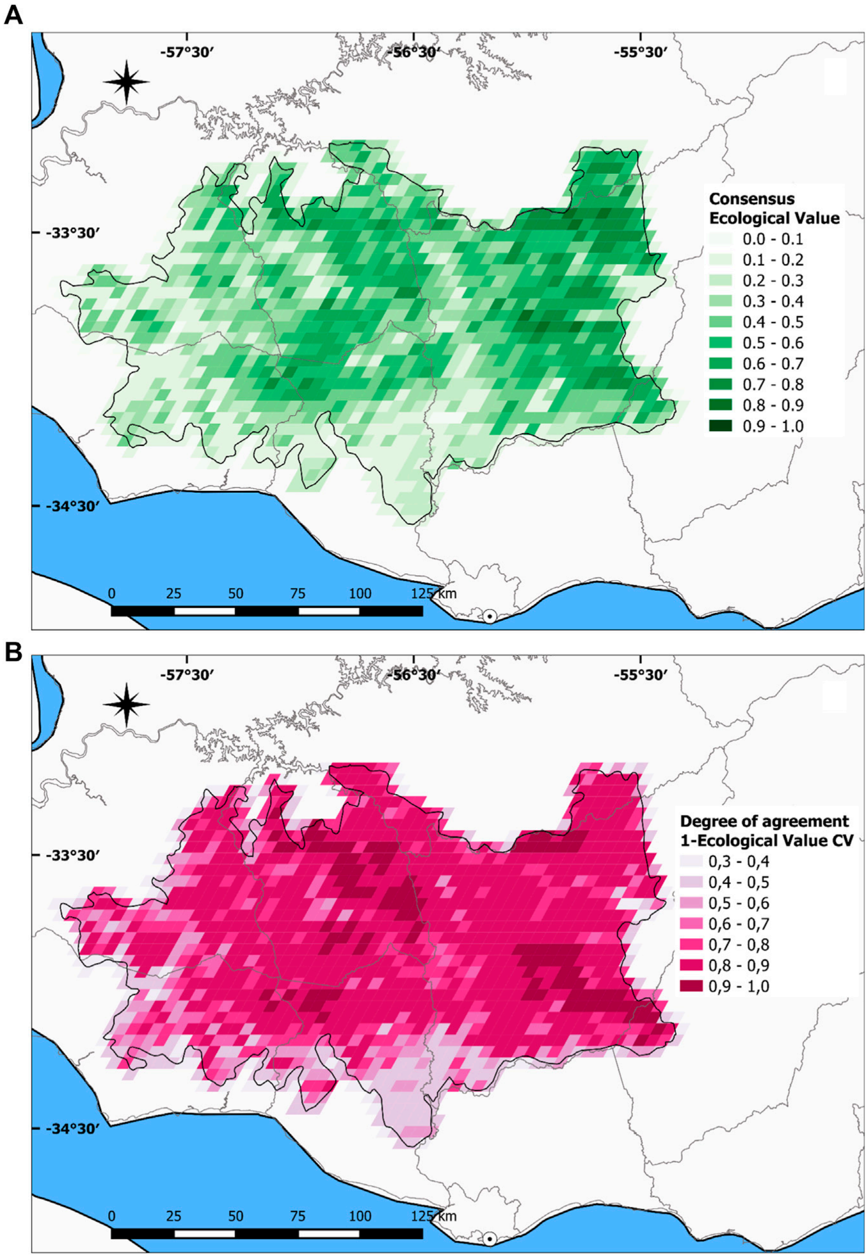


FIGURE 6
Consensus Ecological Value (EV) map **(A)**. Complement of the coefficient of variation of the 12 individual Ecological Value (EV) maps **(B)**.

conservation (Lunt et al., 2007; Cingolani et al., 2008; Gallego et al., 2020). In similar ecosystems, there is evidence that grazing prevents the accumulation of standing dead biomass, increasing light availability and consequently species richness and productivity (Rodríguez et al., 2003; Altesor et al., 2005; Overbeck et al., 2007). In turn, these compositional benefits are reflected in an increase in the supply of supporting and regulating ecosystem services (Gallego et al., 2020). Therefore, grasslands play a key role in supplying both provisioning (meat, wool, water supply) and regulating services (pollination, C sequestration, hydrologic regulation) (Yahdjian et al., 2015). In this sense, the participants weighted the criteria considering that a higher conservation value would imply a restriction for the transformation of grasslands to other land uses, but it would be compatible with cattle production. Thus, a high conservation value would not necessarily imply carrying out strict conservation activities. It is important to note that those stakeholders linked to activities that imply the replacement of grasslands (forestry industries, agricultural companies, for example) were not represented in the MGCN.

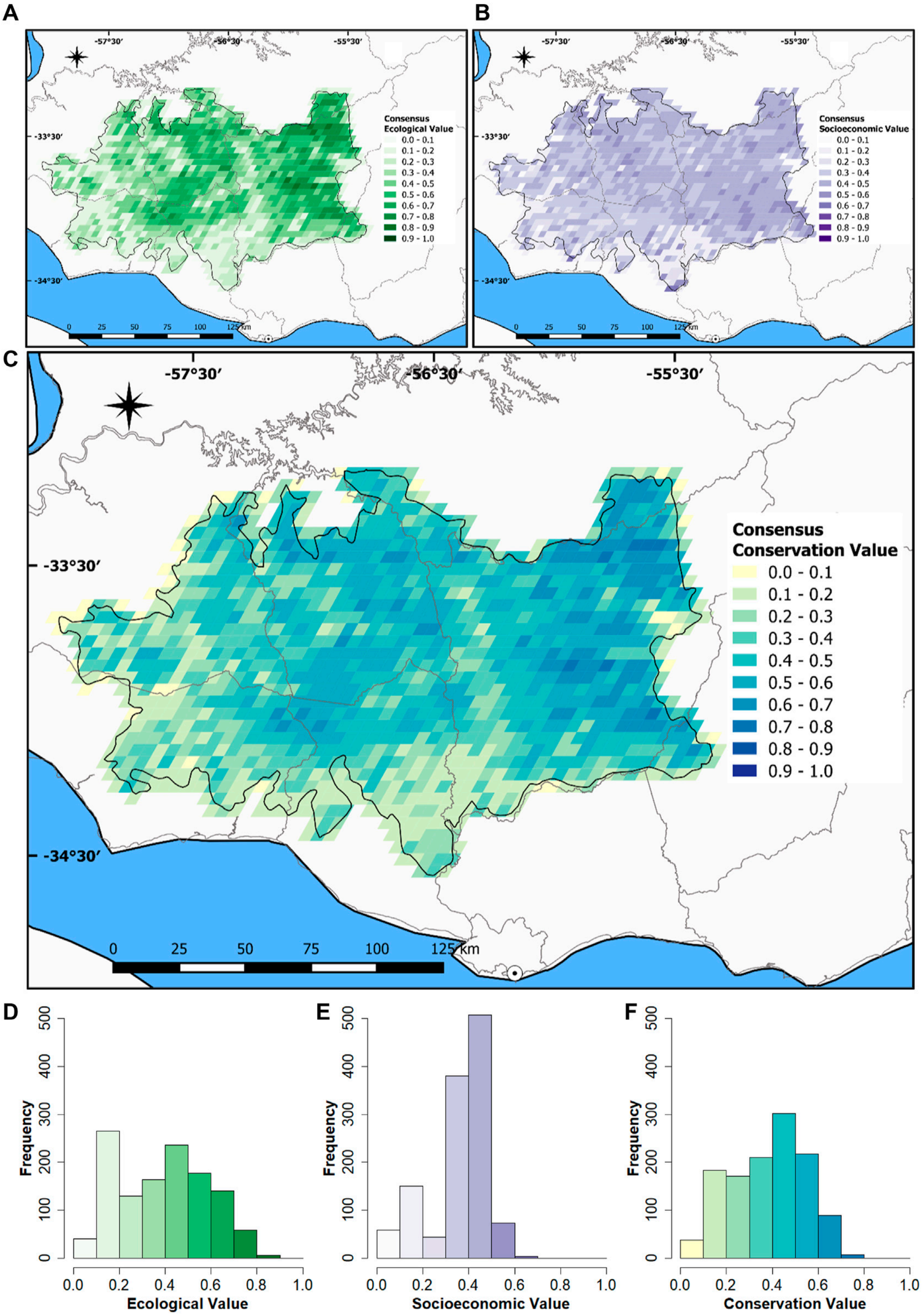


FIGURE 7
Consensus maps and histograms of Ecological Value (EV) **(A and D)**, Socio-economic Value (SV) **(B and E)** and Grasslands' Conservation Value (GCV) **(C and F)**.

The degree of agreement on the prioritization of conservation areas was greater than on the prioritization of criteria, even for participants with a low degree of agreement on the prioritization of criteria. This highlights an important emerging property of the process: the need to postpone the dispute of visions on particular criteria until the results are seen. Some stakeholders differed sharply in the weighting of the presence of protected areas in defining the conservation value. However, given the scarce presence of protected areas in the territory, marked differences in weighting had a low effect on the resulting conservation values. This underscores the importance of postponing discussions and consensus-building until a clear idea of the practical consequences (in this case the GCV assigned) is obtained. The effort to avoid conflicting positions on the importance of each of the criteria should be concentrated on those that have the greatest impact on the final result.

The territorial diagnosis process carried out set the basis to explore the consequences of different scenarios of conservation, transformation, and/or restoration of grasslands areas on critical dimension of the environmental footprint of human activities. Different scenarios of land-use and land-cover can be evaluated in terms of Ecosystem Services supply, natural habitat preservation, functional diversity, and economic output. Aside from its applications, the process was important in itself because it allows the stakeholders to have a clear idea of the dimensions involved in a zoning exercise and to identify gaps in data and conceptual models. Moreover, the methodology implemented not only make visible the range of visions on grassland conservation but also set a productive arena where to discuss alternatives. This could contribute to enrich the decision-making process in the implementation of future regulations restricting grasslands substitution, increasing the legitimacy of territorial planning processes.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary Material, further inquiries can be directed to the corresponding author.

Ethics statement

Ethical review and approval was not required for the study on human participants in accordance with the local legislation and institutional requirements. Written informed consent for participation was not required for this study in accordance with the national legislation and the institutional requirements.

Author contributions

JP, LS, and AA contributed to conception and design of the study. LS and FG organized the database. JP, LS, AA, and FG carried out the field work (participative workshops). LS performed the statistical analysis and wrote the first draft of the manuscript. All authors contributed to manuscript revision, read, and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Publisher's note

Supplementary material

The Supplementary Material for this article can be found online at: https://www.frontiersin.org/articles/10.3389/fenvs.2022.820449/full#supplementary-material

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Veld restoration strategies in South African semi-arid rangelands. Are there any successes?—A review

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Rangeland deterioration is a major challenge faced especially by communal farmers in most of the developing countries including South Africa. The high population of people and livestock exert pressure on the rangeland leading to deterioration which results to economic loss, due to a reduction in agricultural activities such as livestock production. The rehabilitation of degraded lands has substantial returns from an environmental, economic and social perspective. Except for the powerful economic justification, initiation of restoration and rehabilitation of lands is still required to address the continuing land degradation across the world. To gain an insight on the impact of rangeland degradation, the basic restoration strategies need to be assessed and implemented. In this review, we have highlighted an overview of rangeland degradation in South Africa; Livestock dependency in rangelands; causes and consequences of rangeland degradation which include the economic impact of rangeland degradation; and rehabilitation strategies. Soil, climate, grazing management are some of the major factors to consider when adopting the veld restoration strategies. In South Africa, all restoration methods can be practiced depending on the area and the nature of degradation. Moreover, past land use system records and rehabilitation resources such as material and skilled labour can be required to have a successful rangeland rehabilitation.

KEYWORDS

rangeland rehabilitation, rangeland deterioration, ecosystem, livestock, economy

1 Introduction

Generally, rangelands are commonly denoted as pristine or natural ecosystems primarily inhabited by a diversity of vegetation that includes forbs, natural grasslands, and shrubs or trees, which are suitable for livestock grazing and wildlife (Allen et al., 2011; Zerga, 2015). About 25% of the total land surface worldwide is natural arid and semi-arid rangelands (Liebig et al., 2006; Alkemade et al., 2013). Rangelands have the most land re-sources in Africa, accounting for approximately 65% of the total land surface, as demonstrated by Nalule (2010), and provide a variety of ecologically, culturally, biologically and socioeconomically beneficial goods and services (Asner et al., 2004; Liebig et al., 2006; Mussa et al., 2016).

Typically, rangelands play a critical role as a primary source of feed for both livestock and wildlife (Moyo and Swanepoel, 2010). Nonetheless, rangelands provide other secondary resources such as medical plants, firewood, wild foods and support livelihoods through the provision of essential foods such as milk and meat as sources of nutrients (Mannetje, 2002; Zerga, 2015). The provision of animal products helps smallholder farmers to generate income and also improve household nutrition through sales and consumption of those animal products (Asner et al., 2004). According to Abusuwar and Ahmed (2010), herbivore productivity is generally considered poor in communal grazing systems due to rangeland degradation caused by the heavy grazing, availability of the low-quality pioneer species, invasiveness of unwanted species, climate change and sub-optimal resource use activities.

The impact of land degradation is found to be the major challenge in rangelands world-wide (Palmer et al., 1997). As documented by United Nations Environment Program, 1992, approximately 7–14 million square kilometers of global land is affected by land degradation and an estimation of about 75% of the world`s grazing land has already deteriorated to the point where it has lost a minimum of 25% of its animal carrying capacity (Harrison & Pearce, 2000; Moyo et al., 2013). According to Reynolds et al. (2007) and Myburgh (2013), it has been estimated that about 15%–25% of semi-arid areas have been significantly degraded, which means that soils have been exposed to severe climatic conditions and significant erosion has occurred, allowing nutrients to run off the land surface. Every year, approximately 25,000 ha of agricultural land surface become too degraded for crop production (UNEP, 1992). According to Donald and Jay (2012), reduced food security, famine, and hunger are some of the effects of increased land degradation and drought. The influence of land degradation is greatest in the world's arid and semi-arid areas (Snyman and Du Preez, 2005). All over the world, the problem of rangeland degradation is well documented and proven that these rangelands are more susceptible to degradation over time (Palmer et al., 1997; Hoffman and Todd, 2000; Mekuria and Aynekulu, 2013). Due to the increasing of human population (3.2 billion) around the world, the loss of biodiversity and ecosystems can normally lead to a delay in the development of sustainable goals (Scholes et al., 2018; Mani et al., 2021). Gibbs et al. (2015) indicated that almost one to six billion hectares of world land are highly degraded.

An estimated 25% of South Africa's natural arid and semi-arid rangelands are already degraded (Kellner and de Wet., 2021). Hoffman and Ashwell (2001) stated that poor grazing practices, the inappropriate use of fire, and poor soil conditions such as erosion and salinization cause land degradation. Furthermore, urbanization, mining and deforestation by clearance of woody plants, and other land use types lead to land degradation in these areas (Tizora et al., 2016). Overgrazing of sub-Saharan grasslands can be considered a form of natural resource disturbance, and is partly blamed for desertification (IFPRI, 2003).

For improved and sustainable livestock production and continued provision of other eco-system services, restoration technologies must be applied to combat deterioration in rangelands, particularly those that cannot recover easily. The fact that preserving existing habitats is insufficient to ensure the survival of the biotic community and that damaged systems often do not return to their form by natural successional processes in a reasonable amount of time in arid and semi-arid environments has made restoration an utter necessity (Van den Berg, 2002). According to Ravera (1989), reclamation of an ecosystem is usually complicated and very expensive to acquire, and a complete recuperation is unlikely be-cause certain ecosystem components may have been damaged during the degradation process. For sustainable livestock productivity, soil conservation and biodiversity in conventional agricultural systems, Kavana et al. (2005) proposed that modern scientific knowledge and traditional resource management should be complementary. Restoration objectives derived from geomorphological and ecological imperatives can be a scientific perspective (Kondolf, 1998). McDonald et al. (2004) reported that restoration is more of a method of altering the biophysical environment than a concept, and it captures the relationship between scientific definitions and social objectives. Landowners, administrators, and scientists have used a wide range of restoration methods in conservation and agriculturally managed areas all over the world. Bush clearing, reseeding, prevent erosion, grazing management practices, and some of the methods applied when restoring the rangelands (Liniger et al., 2011). The actual aim of rehabilitation is to restore an ecosystem to its natural state. Saco et al. (2006) indicated that the usual common aim in the rangelands is to promote palatable productive perennials grass species as they are beneficial to animal and other positive environmental output. One of the major obstacles to reduce land degradation and improve rangeland productivity, as well as promote the adoption of sustainable land management among agro-pastoral and pastoral communities, is a lack of rangeland management awareness and skilled rangeland management practitioners (Liniger et al., 2011). Even though the information on causes and consequences of rangeland degradation in the world and South Africa is available in literature, the best methods to rehabilitate the land can depend on the type of land degradation and management technique and or approached used. As a result, this review, describes the major causes of rangeland degradation and their effects; success and challenges of site-specific rehabilitation methods in degraded rangelands of South Africa are evaluated.

2 Livestock dependency in rangelands

The small-scale farmers' farming system has developed over time and is now managed by a complex cultural and social organization whose methods and needs are poorly understood by outsiders of the system (Abate, 2006). In arid and semi-arid areas, livestock production is the mainstay of the farming systems in both rural areas and ruminants are reared for a variety of reasons, such as meat, milk, manure, hides, cultural practices, and security purposes (Quirk, 2000). According to FAO (2009), ruminants are the most common users of rangelands, putting a strain on the biodiversity and natural resources. Over some years, the use of extensive grazing animal systems has shown that the animals tend to use a diverse range of grasses as their primary source of feed and impose variable pressure on the ecosystems (Bati, 2013). Rust and Rust (2013) argued that the majority of ruminant livestock populations around communal grazing lands in Southern Africa are dependent mainly on natural vegetation as a primary source of forage to meet their nutrient needs. In general, natural vegetation such as forbs, grasslands and browse species provide nutrients that are essential for ruminants feeding on extensive production systems (Bati, 2013). Rangelands as a whole can be considered the cheapest source of feed (Ismail et al., 2014), due to their capacity to feed a large number of livestock and their ability to meet the animal nutrients requirements. According to Mary-Howell and Martens (2008), there is spatial variation in the quantity and quality of forage and nutrients provided by rangelands. Assessment of nutritive value and estimating the carrying capacity of communal rangelands in arid and semi-arid areas is critical for designing effective livestock development interventions. This will encourage competitive livestock production while maximizing the use of local rangelands.

However, livestock production in many communal grazing areas of South Africa has been negatively affected by rangeland deterioration caused by overgrazing that leads to a loss of palatable grass species, and bush encroachment. These results in reduced herbaceous biomass which is dominated by low grazing value grasses that limit livestock productivity (Ward, 2005). Due to a limited information about livestock and grazing management, small-scale rural farmers are facing severe profitability constraints from livestock development on communal rangeland. Rangeland practitioners have a pressing need to improve the nutritional status of pastures in order to boost animal production, especially in areas where animal products are in high demand and where people's livelihoods are at risk, such as in developing countries (Boval and Dixon, 2012).

3 Rangeland degradation in South Africa

There are several definitions of rangeland degradation. Conacher and Conacher. (1995) defined land degradation as a process whereby biophysical environmental values are negatively affected by the contribution of human-induced processes on the land. Han et al. (2008) describe rangeland degradation as a decrease in plant height, forage production, vegetative protection, and grass diversity. Ndandani (2014) emphasizes that there is no single distinguishable description of land degradation, but all the meanings explain how various land resources (water, air, soil, and vegetation) have deteriorated from satisfactory to unsatisfactory conditions in the supply of ecosystem services. For example, rangeland degradation resulted in the transition from a favorable palatable perennial grass-dominated regime to an encroachment of unpalatable woody plants, shrubs and/or grasses (Snyman, 2004; Hare et al., 2020).

Rangeland degradation is still a major concern across Sub-Saharan Africa as it results in a drop in environmental quality and productivity, such as loss of cover, change in species composition, alien plant invasions, bush encroachment, and deforestation (Hoffman and Todd, 2000; Palmer and Ainslie, 2006; Jama and Zeila, 2005). Increases in woody cover are thought to affect 10%–25% of rangelands worldwide (Reynolds et al., 2007). Densification is expected to grow at a rate of 0.5%–2% per year globally (Cho and Ramoelo, 2019). The studies by O'connor et al. (2014) highlight that the state of woody species changes has moved from 0.13% to 1.28% per year. The arid and semi-arid rangelands of Sub-Saharan Africa, which are vital for livestock production, have been steadily transforming for the past few years and are now under pressure due to mismanagement of the rangelands (United Nations Environment Program, 1992). Increased hunger or starvation, food shortages, and decreased livestock production are other consequences of rangeland degradation (Al-bukhari et al., 2018). Rangeland ecosystem degradation poses a serious challenge to the African population, threatening communal societies and economies, as well as sustainable animal production (Darkoh, 2003; Wassie et al., 2020).

Even though rangeland deterioration is a global problem, it is particularly acute in Southern Africa's communal grazing lands (Hoffman and Todd, 2000; Moyo et al., 2013). With an estimation of 60% of South African land being degraded (Bai and Dent, 2007), 91% of this land degradation is due to desertification (Hoffman and Ashwell, 2001), as a result of overgrazing (Snyman and Du Preez, 2005). Le Roux et al. (2007) indicated that 70% of the South African land surface is affected by erosion, which causes a severe consequence on soil fertility and will result in lower soil productivity due to the different intensity of soil erosion. Belayneh and Tessema (2017) also pointed to bush encroachment as one of the factors behind rangeland degradation. In South Africa, rangeland management is

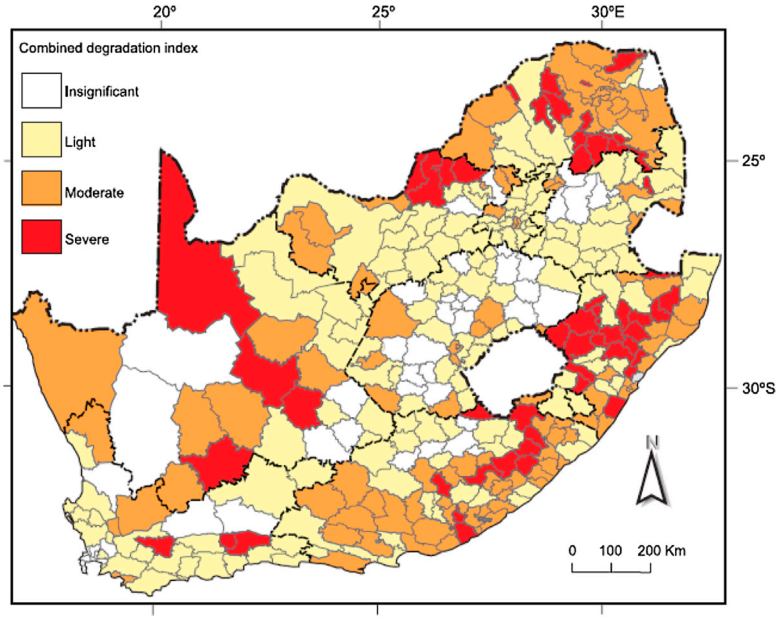

FIGURE 1
Combined degradation index of South African rangeland degradation, darker shading indicates areas with severe degradation. Adopted from Hoffman et al. (1999), Meadows and Hoffman (2002).

different in commercial livestock farms, wildlife (game) farmlands and communal areas, which are mainly found in the former "homelands" communal areas. Tokozwayo (2016) argued that communal production systems tend to be known for their composite nature since many individuals share the resources. Nevertheless, Moyo et al. (2013) stressed that in semi-arid of South Africa mismanagement of the rangelands has drastically reduced the capacity of the communal rangelands to produce sufficient livestock food. Also, a research study conducted by Ravhuhali et al. (2021) support that most of the communal grazing areas of South African rangelands, such as North-West province, are not well managed. Furthermore, Tefera et al. (2010) argued that poor grazing management has a negative impact on grazing rangelands, with the most desirable and high-grazing-value species being largely replaced by low-grazing-value and less desirable species. While, the study conducted by Meadows and Hoffman (2003) highlights that it is not only mismanagement that negatively affects South African rangelands, there are other environmental attributes that contribute to negatively impacting areas of the country that are already severely degraded, such as future precipitation changes coupled with other changes in climatic variables. The South African National Report on Land Degradation (NRLD, Wessels et al., 2007) indicates that the severity of rangeland degradation is predominantly confined largely to communal lands and small patches of commercial lands, although not all parts of the communal lands are degraded. Again, Wessels et al. (2007) stated that communal areas are characterized by increased human and animal populations, bush encroachment, overgrazing, climatic change, soil erosion, excessive wood removal, loss of more palatable grazing species, and drought are among the well-known and are thus significantly regarded as degraded. However, mapping and quantification of the extent of the problem are hampered by a weak database. Erosion is considered a pernicious threat to the productivity of the land and to water resources (Critchley and Netshikovhela, 1998). Below, Figure 1 represents South African land degradation with a combined degradation index.

3.1 Causes of rangeland degradation

3.1.1 Bush encroachment and alien plant invasion (Woody densification)

In South Africa, bush encroachment occurs when there is a rise in the abundance of woody plants in previous grassland regions especially in semi-arid areas (Magandana, 2016), which is accompanied by changes in the herbaceous cover and composition of the natural vegetation (Safriel, 2009). The rapid spread of woody densification and invasion of woody plant species in arid and semi-arid rangelands of South Africa has been well established as a frequent form of rangeland degradation (Mussa et al., 2016). Msiza and Ravhuhali (2019) argued that rangeland vegetation alters from herbage to woody plants as the bush encroaches, resulting in the rise of bare patches

FIGURE 2
Bush encroachment, spread of acacia species around North West province of South Africa. Photo taken by H. S. and K. E.

in the area and a decrease in herbage cover. In the North West province of South Africa, the spread of acacia species has been noted to be the one encroaching the land in semi-arid zones (Figure 2) (Msiza and Ravhuhali, 2019). Woody vegetation expansion decreases the relative amount of forage grasses, and rangeland carrying capacity with adverse effects on animal productivity (Al-bukhari et al., 2018). Reduction of forage and grasses decrease grazing capacity and livestock carrying capacity, as demonstrated by Long et al. (2010). The grazer carrying capacity can be reduced by up to 89% in severe cases (de Klerk, 2004).

Several authors have reported the worldwide challenges of densification such as threatening the herbaceous layer, and weakening the ecosystems services (Asner and Heidebrecht, 2003; Wigley et al., 2010; Reich et al., 2019). Despite the fact that woody densification does not reduce primary production, it meets the IPBES definition of degradation by reducing certain ecosystem services and biodiversity over time (Díaz et al., 2019). The effects of woody densification on carbon stocks are mixed, and the findings are inconclusive. According to Berthrong et al. (2012), most sites lose soil organic carbon, but this is compensated for by aboveground carbon gains. Gebeyehu et al. (2019) found a decrease in carbon stocks in heavily disturbed areas when compared to the less disturbed sites, and this might have been due to the fact that woody encroachment normally increases the amount of carbon stored in the ecosystem as influenced by the amount of above-ground biomass.

The causes of woody densification is unknown, but it is thought to be heavy grazing, which causes grass loss thereby decreasing the potential of rangeland fires, which reduces competition between grasses and woody plants. At the end woody plants will outcompete the grasses. Furthermore, there is also mounting evidence that increased atmospheric CO_2 fertilization effects, which favour C3 tree growth more than C4 grasses thus aiding densification of woody species (Kgope et al., 2010; Higgins and Scheiter, 2012). In areas such as natural dense sites, there is an increased CO_2 which normally contributes to the increase of woody species as this is due to better climatic conditions associated with greenhouse gas concentration and nitrate availability in the soil (Huang et al., 2007).

Invasive alien species have increased by 71% between 2006 and 2016 (O'Connor and van Wilgen 2020), are known for their negative impact on biodiversity and rangeland production (Ntalo et al., 2022) and as a result of that, they contribute to economic or financial loss around the world as they are the drivers of environmental changes (Richardson et al., 2014; Shackleton et al., 2014; Stanford et al., 2017). Though the beneficial effects of some of these alien species are observed, Shackleton et al. (2017) indicated that these species can have harmful effects on social ecological systems. The spread of alien species threatens livestock productivity due to their negative impact to the environment (Ntalo et al., 2022), and also affects the water supply (Ravhuhali et al., 2021). O'Connor and van Wilgen (2020) highlighted that the densification of woody species such as *Prosopis* spp., *Acacia mearnsii,* and *Pinus* spp., can reduce the herbaceous layer (reduce carrying capacity), leading to lower animal productivity.

3.1.2 Overgrazing

Rangelands in large parts of grazing areas in developing countries are not properly managed (Ravhuhali, 2018). Jeddi and Chaieb (2010) indicated that the grazing systems practised in

FIGURE 3
Aristida species, less palatable grass species. Photo taken by H. S. and K. E.

communal areas such as continuous grazing are the most common causes of communal rangeland degradation. Excessive heavy grazing has frequently been blamed for the resultant decline in biodiversity in arid and semi-arid regions. Overgrazing is a huge threat in most parts of South Africa's rangelands, and according to Smit (2003), is one of the major causes of woody densification (bush encroachment). It is believed that the increased bush encroachment in the savannahs of Africa has been caused by the removal of wildlife animals and replacement by domestic livestock which mainly graze than browse. Furthermore, communal areas have high stocking densities (Owen-Smith, 1989), which lead to poor grazing management (Smit, 2003). Barac (2003) and Van den Berg (2007) argued that excessive overgrazing leads to soil cover (top soils) exposure to runoff, compaction of soils, soil erosion, decrease in carrying capacity, and changes in species composition as well as bush encroachment. Ravhuhali (2018) stressed that overgrazing pressure leads to subsequent changes in botanical composition, species diversity and soil moisture properties. Overgrazing pressure, which occurs in tandem with an increase in livestock and human population, has been reported to result in an increase in less palatable grass species, and woody plant species in communal rangelands (Chipika and Kowero, 2000; Kraaij and Ward, 2006). Figure 3 below presented semi-arid area located in North West province South Africa which is infested with less palatable grass species such as *Aristida* spp.

In addition, domestic livestock grazing on local communal grazing areas has a negative effect on soil, hydrology, and local vegetation (Ibanez et al., 2007). According to Saini et al. (2007), negative impacts of poor livestock grazing systems result in a loss of plant cover, diversity, and productivity, topsoil disruption, and soil compaction because of animal trampling, resulting in decreased water penetration and increased erosion (Figure 4), aggravating the effects of drought (Taube et al., 2013; Tesfahunegn, 2018). According to Sullivan and Rohde (2002), animals selectively graze plants according to their dietary preferences (palatable herbaceous plants), resulting in an increase in unpalatable herbaceous plant species (pioneers, annual plants, and bushes), and leading to a reduction in species richness (Figure 3). Grazing pressure has resulted in a decline in rangeland condition around the world, as well as a decrease in forage quality and quantity (Kirkman and de Faccio Carvalho, 2003).

3.1.3 Climate change

The challenges of biodiversity and climate change are global problems with complex causes that vary in different parts of the world (Lüscher et al., 2014). Climate change is the primary driver of rangeland dynamics in both arid and semi-arid regions, particularly in Africa (Bloor et al., 2010; UNCCD, 2015). Changes in vegetation diversity, soil profiles, hydrological cycles, and rangeland water patterns all lead to land degradation, and all of these are the results of climate change (Hopkins and Del Prado, 2007). As the rangelands are affected by climate change, farming and grazing systems are also altered as a response to the increased precipitation variability and intensity of floods and droughts, particularly in semi-arid and arid regions (Nicholson, 2000; Mussa et al., 2016). According to Zerga (2015) and Fereja (2017), climate change had vast negative impacts on the rangelands, which include a decrease in plant diversity, topsoil, water scarcity and enhanced rangeland deterioration. In recent years, South Africa, has experienced increased drought frequency and severity that lead to approximately 10% of soil moisture decline across most semi-arid regions (Hermans and

FIGURE 4
Photo displaying soil erosion and bare patches in some grazing area around semi-arid area in North West province of South Africa. Photo taken by H. S. and K. E.

McLeman, 2021) and with the high temperatures drawing salt to the soil surface (Ramamurthy and Pardyjak, 2011). Because of frequent droughts in Africa, notably in South Africa most woody cover has been enhanced due to its high ability to survive extreme temperature, which is more unfavourable to grasses and other herbaceous species (Teague and Smit, 1992). Ward et al. (2014) stressed that the growth of woody plant trees in South Africa is favoured by the increased levels of atmospheric (CO_2) accumulated in the area. The high growth of C3 plants (trees) versus the C4 (grasses) serves as evidence that the increased levels of atmospheric CO_2 in semi-arid environment plays a huge role in bush encroachment (Ward, 2010). According to Wigley et al. (2010) the increased concentration levels of atmospheric CO_2 in a given environment tend to lead to high biomass of the roots which normally causes the rapid re-growth of C3 (woody trees) plants after the above-ground biomass has been disturbed by various factors such grazing, fire as well as other anthropogenic factors.

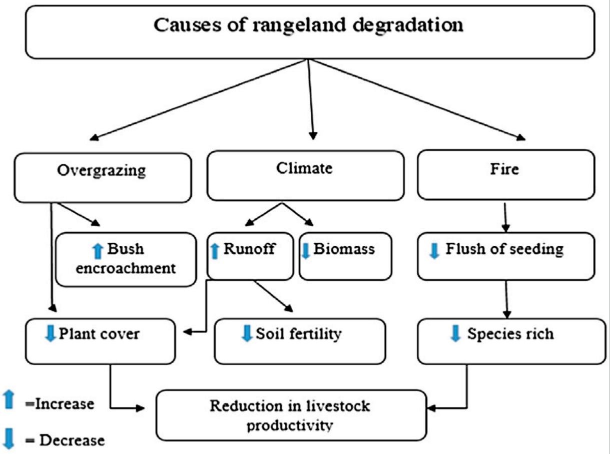

FIGURE 5
The schematic presentation of the process of degradation. Adopted from Ravhuhali (2018).

4 Impacts of rangeland degradation

The impacts of rangeland degradation are presented in Figure 5. Rangeland degradation has a significant impact on the livelihoods of inhabitants of communal areas and the economy of South Africa due to its deleterious impact on rangeland condition (Rouget et al., 2006), soil profile (Mekuria et al., 2007), and livestock productivity (Kwon et al., 2015). These communal area inhabitants tend to lose their livestock assets and become destitute. As a result, the local population normally experiences food insecurity, and the government has to provide assistance to maintain food security and sustain livelihoods through alternative sources of revenue diversification and other sources of money (Teshome and Ayana, 2016). Solomon et al. (2007) indicated that in other countries such as Ethiopia, this leads to poverty and tribal disputes over grazing land and water supplies in the long term. In addition, bush encroachment has been shown to affect 10–20 million hectares of agricultural productivity and biodiversity (Ward, 2005) and has emerged as one of the top perceived rangeland problems in about 25% of South Africa's districts (Hoffman et al., 1999).

Most farmers normally prioritise livestock more than the resources available to sustain the livestock. Due to the unregularly usage of rangelands, high stocking rates can result in plant cover and species diversity reduction, leading to rangeland degradation which will negatively affect animal production (Ravhuhali, 2018). Rangeland degradation can result in a depletion in soil quality (Nutrients loss, poor soil structure, soil compaction, unbalancing of elements, high salination and acidity) due to human and climate change (Eswaran et al., 2001; Mekuria et al., 2007). Eswaran et al. (2001) highlighted that there is a severe economic impact in most parts of semi-arid zones through nutrient depletion as a form of rangeland degradation. These nutrients leaching from the land can affect plant growth and yield.

Rangeland degradation can alter the species composition of the herbaceous layer. Through overgrazing, the grass species diversity declined, followed by infestation of unpalatable pioneer species and some invasive non-native species in a space of perennial and high grazing value grass species (Huxman et al., 2005; Wheeler, 2010), and this can affect the sustainability of ruminant animal farming (Nenzhelele, 2017).

Due to the increasing population globally, the demand for animal products tends to increase. The biggest threat of rangeland degradation lies in the sustainability of livestock. The reduction of animal production normally happens as a result of land degradation (lack of palatable and more nutritious grass species). The number of livestock, animal gains, low reproductive rate, and more mortality are some of the rangeland degradation highlights (Tesfa and Mekuriaw, 2014).

5 Rehabilitation of the degraded rangelands in South Africa

Understanding the conservation of existing ecosystems is insufficient to secure the future of the world population (Yirdaw et al., 2017). Degraded ecosystems in semi-arid areas often do not improve under the natural process of succession within short periods of time to a potential that can be utilized for livestock production (Van den Berg, 2002). Kellner (2000) and Tuffa et al. (2017) stressed that restoration is a possible intervention once vegetation transitions and rangeland conditional states tend to cross the threshold limitations for natural recovery. Several authors have described rangeland improvement efforts using various terminology, such as reinforcement, rehabilitation, reclamation, re-vegetation, and restoration (Le Houerou, 2000; Bainbridge, 2003). Most of these terms are used to characterize restoration ecology in the context of the current review.

The ecological restoration is known as the process of maintaining, conserving and repairing the world's ecosystems (Schlesinger et al., 1999) after they have been degraded, damaged, or destroyed (Bainbridge, 2007). Harris et al. (1996) stressed that ecological restoration is the process of restoring the diversity and dynamics of indigenous ecosystems to their original condition before any decline. Ecological restoration may require considerable investments in decision support tools and associated outlines or frameworks that can help to ensure and guarantee that the technique is successful and that the restoration goals are accomplished. Restoration techniques are required worldwide, notably in Africa's communities in order to restore the communal rangelands' structure and functions. These restoration techniques can help with social, economic and environmental problems not only in South Africa, but also around the world. Rangeland restoration may help local communities adapt to land degradation, desertification problems and climate change by providing alternative food security in Sub-Saharan regions (Mureithi et al., 2016).

To ensure proper rehabilitation of degraded rangelands, we need to understand how they functioned before they were degraded, and then use this knowledge to reinstate essential processes that are highly needed (Fayiah et al., 2020). Generally, there are two types of restoration depending on the degree of damage, which include passive and active restoration. According to Kauffman et al. (1997), active restoration means manipulation of biota through reintroducing animal or plant species that have extirpated from an area, while passive restoration means the restoration of degraded ecosystems by removing anthropogenic perturbations that are causing degradation. For effective rehabilitation of the rangeland, we can use numerous active restoration practices such as direct seeding, reseeding, or passively by allowing the progression of natural regeneration. In addition, water and soil conservation measures, water harvesting, surface scarification, grazing/livestock management, control of bush encroachment and the use of controlled fires (Figure 6) (Li et al., 2011) are other active restoration activities. The following are some of the most frequently utilized approaches for rehabilitation of degraded rangelands.

5.1 Management of bush encroachment (the removal of encroached trees and invasive species)

Bush encroachment has received increased attention recently, notably in South Africa, and it is now one of the

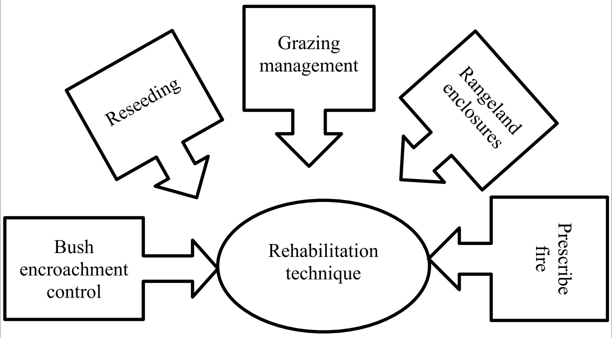

FIGURE 6
A diagram showing some of the techniques when rehabilitating the rangeland. Adopted from Li et al. (2011).

most prevalent forms of rangeland degradation all over the world (O'connor et al., 2014). Because it is one of the most prominent factors of degradation in rangelands, it is important to control bush encroachment and rehabilitate the rangeland to its normal form. According to Angassa and Oba (2008) and Mussa et al. (2016), bush encroachment control is described as a method of reducing and suppressing the excessive spread of invasive woody plant community structures and shifting the rangeland vegetation from woody tree domination to herbaceous vegetation in order to create a suitable habitat for grazers. To accomplish this, we can employ a variety of ways of controlling bush encroachment that are well known, viz, mechanical, chemical, and biological technique. Nevertheless, for a better degraded rangeland rehabilitation, integrated approaches are recommended (Belachew and Tesema, 2015).

One of the studies conducted in South Africa, it shows that with the appropriate management and control of woody encroachment and alien plant invasions, the ecosystems can be rehabilitated to its normal form (Stafford et al., 2017). The same authors stressed that the removal of woody plants community will likely decrease the amount of atmospheric CO_2 in an ecosystem since the woody plants are a significant carbon sink. Several authors in South Africa have investigated various techniques to restore heavily encroached rangelands and those invaded by alien plants, and they include the use of fire (Trollope, 1974; Kraaij and Ward, 2006), chemicals (Wigley et al., 2010), and competent grazing management (Lesoli et al., 2013). The study by Smit et al. (2016) revealed that the application of high intensity fire treatments reduced the tree species by up-to 70% in Kruger National Park. Gordijn (2010) recommended one burn every 2–4 years for the best output through the use of fire on the encroached areas. Debushing through mechanical is one the most affordable bush encroachment control done by farmers around semi-arid areas of South Africa. Most of the famers around North West province are applying this particular methods in controlling bush encroachment (Figure 7). Kellner and de Wet. (2021) also found that introducing different restoration treatments (which include clearing, soil disturbance, brush packing and reseeding (CSRSBP); clearing and brush packing (CBP); and clearing, brush packing and reseeding (CRSBP) increased the carrying capacity of some selected rangelands in South Africa. However, there are some significant risks in terms of attaining the ecosystem service benefits from rangeland restoration techniques. Although there are numerous risks, the benefits from restoring rangeland affected by bush encroachment and alien plant invasions depends on the subsequent land use and land use practices (Lesoli et al., 2013; Stafford et al., 2017). Ultimately, proper management of bush encroachment and invasive alien plant species can deliver significant ecosystem services benefits that surpass costs of restoration.

In addition, to be successful in rangeland restoration initiatives, indigenous traditional knowledge of the local community should be included, as well as the promotion of awareness and an integrated strategy by rangeland practitioners (Patel, 2011; Tessema et al., 2011). Alien invasion and bush encroachment problem has become a major concern in African rangelands, as well as in South Africa, notably in the Savannah biome rangelands, it transforms grasslands into shrublands by competing with herbaceous fodder and reducing the stocking rate (Abule et al., 2007; Angassa and Oba, 2008). Controlling the bush encroachment can assist in establishing a grazing area with palatable herbaceous species for the livestock, and if done consistently, it can help stabilize rangelands and reduce the negative consequences of future feed and food shortages. The combined actions of regulating fire, controlling grazing and cutting can prevent woody species succession (Sawadogo et al., 2002; Milton, 2004). Mussa et al. (2016) stressed that herbaceous vegetation generates more feed as the number of woody species declines.

5.2 The use of invasive species such as prickly pear to arrest the top soil loss

Species such prickly pear is one of the invasive species that normally disturb the vegetation due to its contribution to the reduction of carrying capacity and, most importantly, causing injuries to people and some livestock (Walters et al., 2011). They are also known for hampering livestock movement due to their thicket form. The invasiveness of this species can result in social and ecological costs (Shackelton et al., 2017; Pyšek et al., 2020; Seebens et al., 2021). In semi-arid regions, prickly pear especially its spines can be regarded as an excellent rangeland restoration, rehabilitation plant and can be used in the recovery of degraded and dry lands (Neffar et al., 2013). In South Africa, the role of prickly pear as a biological resource for adaptation in poor environmental conditions because of its resistance to dry lands has been reported (Habibi et al., 2009; Neffar et al.,

FIGURE 7
Mechanical method of controlling bush encroachment in communal grazing areas around North West province of South Africa. Photo taken by H. S. and K. E.

2013). This phenomenon is supported by findings of Singh (2004) that these invasive species have an ability to strengthen poor soils subjected to erosion and erratic rainfalls of arid zones. Apart from being an alien species, prickly pear has become a dominant plant in most countries, it spreads aggressively by anchoring top soils from degrading due to adverse climatic conditions (Milton and Dean, 2010; Sipango et al., 2022). In most semi-arid and arid regions, the use of prickly pear plants, which are salt tolerant and adapt to different soils makes them an ideal plant for sustainable agriculture production (Singh et al., 2014). Prickly pear adapt in poor degraded soils and facilitate the reduction of soil erosion (Sipango et al., 2022). This invasive plant species uses its extensive deep root stem to survive in severely degraded soils with a limited or no nutrient supply (Snyman, 2006; Sipango et al., 2022). Cactus species is well known as an invasive species which are defined as one of the non-native aliens that are harmful to the ecosystem [Convention on Biological Diversity (CBD), 2008; Pejchar and Mooney, 2009]. In South Africa, studies reported that cactus availability play an important part in the control of top soil erosion and degradation (Van Wilgen and Scott, 2001; Pejchar and Mooney, 2009).

5.3 Rangeland re-vegetation and reseeding

Introducing seed techniques in rangelands is extremely useful (Tessema et al., 2011), and very important for areas that have experienced prolonged veld degradation to fill up the bare patches. Degraded rangelands have been successfully rehabilitated in a short period of time by introducing native grasses that are well-adapted to the harsh environment of that area (Snyman et al., 2013), and this has also enhanced the necessary habitat for many local animals, which tends to improve animal production (Palmer and Ainslie, 2005; Opiyo et al., 2011). Several authors advocated for the use of grass reseeding as a cost-effective and successful rehabilitation technique for degraded rangelands, particularly in Africa, because most African countries are still underdeveloped, and the lower the cost, the higher the chances of its widespread use (Van Den Berg and Kellner, 2005; Mganga, 2009; Tilahum et al., 2017). Successful reseeding/re-vegetation, on the other hand, has been shown to be dependent on factors such as weed control, seedbed preparation, seed pre-treatment for improving germination and climatic conditions (rainfall, temperature and humidity) (Mganga, 2009). Snyman (2003) stressed that semi-arid rangelands, which have retrogressed beyond a certain threshold and cannot be rest-covered, can only be repaired by mechanical inputs in order to assist the re-establishment of rangeland vegetation. This is because most of these areas have already been severely damaged, and natural succession processes will make recovery difficult or practically impossible.

However, there are some studies conducted in South Africa where degraded rangelands have successfully recovered by the use of proper re-vegetation and rotational grazing, and high forage production and wood density reduction were observed (Bolo et al., 2019). Furthermore, due to their establishment rate and frequency over three seasons, Kellner and de Wet (2021) recommend restoration of degraded semi-arid rangelands by over sowing forage species such as *C. ciliaris* and *A. pubescens* in a sandy soils (8%–42%, respectively), and *D. eriantha*, and *C. gayana* (30%–64%, respectively) when the soils have more silt and clay. These species were also supported by Msiza et al. (2021). Knowing the soil type of the certain area assists in choosing the grass species that are well adapted to the environment and significantly reduce the over-sowing expenses, making this rehabilitation approach more accessible to land managers.

5.4 Grazing management (resting of the overgrazed areas)

Rangeland grazing management techniques are mostly focused on balancing livestock numbers with forage availability, equal distribution of animals in the veld, sustaining vegetation by alternating grazing periods and rest times, and utilizing the most suitable livestock (Mussa et al., 2016). In semi-arid areas, veld degradation is linked to poor livestock management, so it is critical to improve grazing management strategies in relation to the amount and kind of livestock, as well as the type of vegetation, in order to maintain productive and healthy rangelands (Mitchell et al., 2009; Ash et al., 2011). According to previous studies documented in South African degraded rangelands, the reduction of livestock numbers and controlled grazing activities optimize the grazing pressure in the veld and improve the chances of rangeland restoration. Woodfine (2009) corroborates the findings of that proper grazing management in degraded rangeland has great potential to restore and protect the biodiversity of the degraded area, as well as enhancing the processes and functions of the ecosystem. On the effect of precipitation and grazing-induced degradation on vegetation productivity, the same authors found that the normalized difference vegetation index of degraded areas were between 1.4% and 20% lower than non-degraded areas. Furthermore, Harmse et al. (2020) stressed that rotational grazing is one of the techniques successfully used to restore the degraded rangelands of South Africa.

Sankaran et al. (2005) stressed that a proper understanding of the effects of grazing management systems on vegetation ecosystem dynamics is required to maintain optimum carrying capacity and species diversity, since changes in species composition has a substantial impact on animal production sustainability. Grazing management is the best strategy for rehabilitating degraded rangelands in areas with poor vegetation cover, overgrazed, and have degraded soils, and this is considered the most promising initiative for restoring degraded rangeland (Woodfine, 2009), since it enhances the vitality of mature perennial grasses. Neely et al. (2010) argued that knowing the grazing history and ecological variation can assist when practicing timely grazing management and can enhance a positive impact on rangeland condition, as well as the functioning of dry-land hydrological systems and the restoration of biodiversity in the ecosystem.

5.5 Manipulation of the rangeland to improve livestock distribution

South Africa is a semi-arid nation and characterized by prolonged drought periods (Rountree et al., 2000) that have a negative impact on rangeland vegetation and soils. Interventions which involve manipulation of the distribution of watering points, shaded and rested areas, forage and mineral salts can be initiated to improve veld condition (Vaniman et al., 2004; Kapu, 2012). Animals are obviously attracted to water in arid areas, however the supplementation of salt and mineral was reported to have mixed results (Ganskopp, 2001; Vaniman et al., 2004). Even though veld recovery might become extremely difficult if soil quality deteriorates, the distribution of mineral salt and watering developments and fencing has been used successfully to improve veld conditions in arid regions. Mineral salt and major watering points such as water holes, troughs and dams can be strategic initiatives needed to limit and reduce grazing pressure in certain areas of the rangeland in arid regions (Porath et al., 2002). Mapiye et al. (2008) added that rangeland managers can manipulate South African rangelands and livestock productivity by using an appropriate planned fire type, season and burning frequency. However, prescribed burning must be integrated with other grazing management techniques in order to improve livestock distribution.

5.6 Rangeland enclosures

Rangeland enclosures halt grazing for a certain period, and is a common strategy that has been successfully examined in the rehabilitation of damaged rangelands (Mohammed et al., 2016). Based on their experience in various locations in Ethiopia, Mussa et al. (2016) found that rangeland enclosures are a good structure for rangeland restoration, as long as they completely specify their users, resource restrictions, and realistic norms originating locally. In South Africa, Bolo et al. (2019) and Treydte et al. (2021) highlighted that this can be an ideal method for improving vegetation regeneration and promoting land restoration for degraded lands than open grazing of rangelands. Milton et al. (1998) and Verdoodt et al. (2009) added that this can transform degraded rangeland to its productive stage, with an increased seedling proportions and the stimulation of high palatable forage density with the great chances of enhancing livestock production in South Africa. Gidey and Van der Veen, (2014) in Ethiopia and Nyberg et al. (2015) in Kenya reported similar results. However, if scientific and indigenous knowledge are not integrated, bush encroachment will become a major threat in these enclosures over time, as compared to more regular grazing rangelands (Ayana, 2005; Angassa, 2007).

5.7 Prescribed fire

Fire is a phenomenal force that influences the ecological process in woodland and grassland systems throughout the world, notably in African savannah biomes (Higgins et al., 2000; Hamman et al., 2011). Prescribed fires have a history of maintaining the diversity of grassland ecosystems in semi-arid regions by creating the vegetative composition of rangelands (Williams, 2003; McGranahan & Kirkman, 2013). Tefera et al. (2010) stressed that the main role of prescribed fires on rangeland is to suppress undesirable grasses, woody species, clearing, and controlling pests and wildfires to enhance desirable grasses' ability to regenerate, because through fire, unwanted seeds and trees can be destroyed when exposed to lethal temperatures. Fire is also known to remove dead plant materials on the rangeland and, because of this, can produce several benefits, such as an increase in grass nutritional quality, palatability and availability, as well as improving new grass growth (Croft et al., 2015).

In the South African rangeland, Mapiye et al. (2008) reported that controlled fires play a beneficial role in enhancement of proliferation of high quality forages through preventing the spread of undesirable C3 (woody plants) plants. However, fires can also remove desirable and palatable plant species if not carefully planned in advance and prepared appropriately according to seasons (summer and late autumn). This malpractice leaves behind the non-palatable big stemmed woody plant species, which tend to lead to rangeland degradation. Similarly, in the South African rangelands, early winter burns has been found to leave soil cover exposed to erosion and insolation throughout the winter season (Trollope et al., 1989), which lead to severe erosion and compaction with the first coming rainfall. Although, there is a lot of information regarding the positive effects in the use of fire as a management tool in South African savannah rangelands, the information needed to carry out specific prescribed burns is often disjointed (Mapiye et al., 2006). Van Langevelde et al. (2003) stressed that throughout the post-fire growth season, post-burned grassland vegetation had a higher aboveground nutrient content than unburned vegetation. Again, Coppock et al. (2007) and Gebru et al. (2007) reported similar results, on investigations conducted in Southern Ethiopia rangeland using fire to burn the land, and the vegetation cover of highly valuable grass (*Themeda triandra*) had increased from 18% to 40% of basal cover and the quantity of bare ground was drastically reduced after burning. The burning strategy, when combined with other suitable rangeland management strategies, can successfully minimize bush encroachment and increase forage production and quality for grazing animals. Government guidelines in South Africa recommend burning immediately after the first springs to improve the removal of amassed moribund and unwanted materials. Generally, without fire, organic waste and litter would accumulate, thus increasing tree density and eventually leading to woodland biomes.

6 Economic cost of rehabilitation techniques

Historically, economic development in most countries is based on the exportation of natural resources, particularly land resources (Worlanyo and Jiangfeng, 2021). Globally, land degradation has been the greatest threat, posing a major economic challenge for farmers (Zhao et al., 1991; Utuk and Daniel, 2015; Megerssa and Bekere, 2019). Degradation is hampering the developing world economically, and this is because of high human population pressure on land. Restoration of degraded lands is a positive return action from both an environmental and an economic and social standpoint (Arneth et al., 2001). The case study of Nkonya et al. (2016) reported that the money invested in land restoration yields high economic returns over the years. Except for the powerful economic justification, initiation of restoration and rehabilitation of lands is still required to address the continuing land degradation across the world (Mirzabaev et al., 2019; Hermans and McLeman, 2021).

Some of the main specific barriers to the restoration of degraded lands are a lack of financial benefit, prohibitive adoption costs, and a lack of knowledge (Mirzabaev et al., 2019). When compared to other approaches with no system baseline, spatial prioritization of restoration efforts could deliver benefits in biodiversity conservation and carbon storage at significantly lower costs (Strassburg et al., 2019). When land is restored, farmers breed animals at a high rate for economic considerations (Hermans and McLeman, 2021). It was reported that small camp erection by farmers has key implications caused by the cost of fencing (Hobbs and Harris, 2001). In the near future, the economic implications should be weighed against the future of rich biodiversity and the introduction of ideas that government subsidies to farmers should be reconsidered to lower the cost of these rehabilitation techniques on degraded lands (Cupido, 2005). It was discussed that economic and technical factors have an impact by hindering the effective restoration of degraded areas (Milton et al., 2003). Aside from financial suggestions, veld restoration may be hampered by a scarcity and lack of palatable grass seeds (Aronson et al., 2010).

The availability of funds for the seed companies to produce indigenous seeds rely on governments land care entities and these entities can fund research based on restoration techniques. The study highlighted that if the financial investments in rehabilitation techniques are not justified; veld restoration could be funded by ecosystem services (Mugido, 2011). Restoration of degraded lands is not only ecological, hydrological, and the focus of research; sound investigation rules and information are required to improve the success of restoration economically and practically (Hobbs and Harris, 2001). Furthermore, the rehabilitation cost depends on the density of space in that particular area, and rehabilitation costs are complex processes that involve economic implications (Spurgeon, 1999). Therefore, projects such as Land Redistribution (LRAD), Comprehensive Agricultural Support Package (CASP), Succulent Karoo ecosystem planning and local governments (SKEP) should be used as vehicles to reduce these challenges facing degraded veld by way of creating jobs in these regions through establishing indigenous seed farms (Esler and Kellner, 2001).

It was discussed that since degraded lands cannot contribute effectively to sustained economic development, land restoration is the best option to increase the chance of attaining sustainability and improve economic returns for farmers (Brown and Lugo, 1994). In this context, establishing a financial mechanism for compensating land users and improving ecosystem delivery could increase investment in land restoration and rehabilitation, and redirecting misdirected subsidies is a serious approach that must be taken (Wilson and Lovell, 2016). The cultivation of sustainable lignocellulosic energy plants provides economic returns while playing a part in the rehabilitation and restoration of degraded lands (Mentis, 2020). Even though the economic benefit of restoration, is higher than the cost of restoration land restoration could provide an economic return (WRI, 2017), more investments at the global level stage (Bakshi et al., 2014).

7 Summary

The best method for rangeland restoration is based on several factors, such as soil, climate and grazing management. Understanding rehabilitation strategies on degraded rangelands is critical for existing ecosystems in order to ensure the survival of living organisms. In South Africa, all restoration methods can be practiced depending on the area and the nature of degradation. Ecological restoration may need considerable capital injection, skilled labour, in decision support tools and the integration of other stakeholders that can help to ensure and guarantee that the technique is successful and that the restoration goals are accomplished. In order to have better rangeland rehabilitation programs, there should be records of the past land use system, and these records are needed to reinstate essential processes for successful rangeland restoration.

Author contributions

Conceptualization, HSM, NHM, NS, KER, HKM, and BM; Validation, HSM, NHM, NS, KER, HKM, and BM; Data curation, HSM, NHM, NS, KER, HKM, and BM; Writing—original draft preparation, HSM, NHM, NS, and KER; Writing—review and editing, HSM, NHM, NS, KER, HKM, and BM; Visualization, HSM, KER, and NS; Supervision, KER, HKM, and BM. All authors have read and agreed to the published version of the manuscript.

Conflict of interest

Publisher's note

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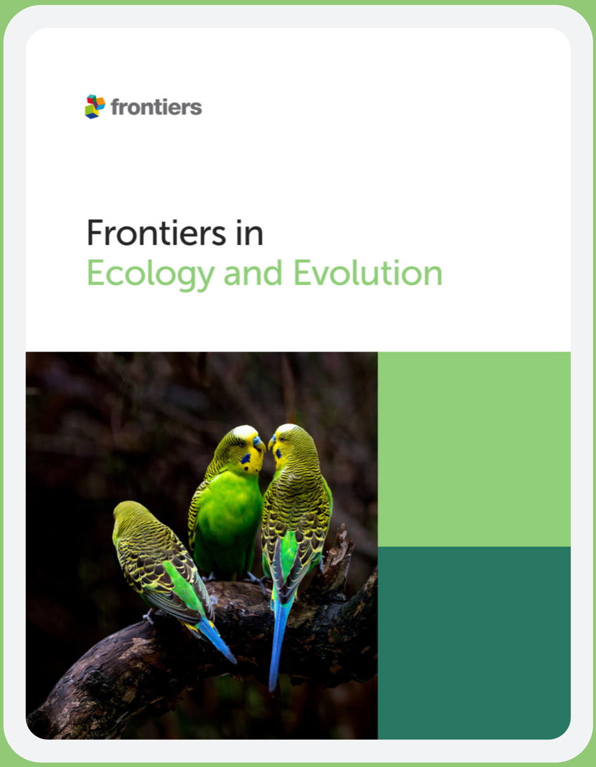

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