




# A framework for sustainable management of ecosystem services and disservices in perennial grassland agroecosystems

SHISHIR PAUDEL <sup>1,2,†</sup> ADAM B. COBB <sup>1</sup> ELIZABETH H. BOUGHTON <sup>3</sup> SHERI SPIEGAL,<sup>4</sup>  
 RAOUL K. BOUGHTON,<sup>5</sup> MARIA L. SILVEIRA,<sup>5</sup> HILARY M. SWAIN,<sup>6</sup> RYAN REUTER,<sup>7</sup>  
 LAURA E. GOODMAN,<sup>1</sup> AND JEAN L. STEINER<sup>8,9</sup>

<sup>1</sup>Department of Natural Resource Ecology and Management, Oklahoma State University, Stillwater, Oklahoma 74078 USA

<sup>2</sup>Phipps Conservatory and Botanical Gardens, Pittsburgh, Pennsylvania 15213 USA

<sup>3</sup>Archbold Biological Station's Buck Island Ranch, Lake Placid, Florida 33852 USA

<sup>4</sup>US Department of Agriculture–Agriculture Research Service (USDA-ARS), Jornada Experimental Range, Las Cruces, New Mexico 88003 USA

<sup>5</sup>Range Cattle Research and Education Center, University of Florida, 3401 Experiment Station, Ona, Florida 33865 USA

<sup>6</sup>Archbold Biological Station, Venus, Florida 33960 USA

<sup>7</sup>Department of Animal Science, Oklahoma State University, Stillwater, Oklahoma 74078 USA

<sup>8</sup>Grazinglands Research Laboratory, USDA-ARS, El Reno, Oklahoma 73036 USA

<sup>9</sup>Department of Agronomy, Kansas State University, Manhattan, Kansas 66502 USA

**Citation:** Paudel, S., A. B. Cobb, E. H. Boughton, S. Spiegel, R. K. Boughton, M. L. Silveira, H. M. Swain, R. Reuter, L. E. Goodman, and J. L. Steiner. 2021. A framework for sustainable management of ecosystem services and disservices in perennial grassland agroecosystems. *Ecosphere* 12(11):e03837. 10.1002/ecs2.3837

**Abstract.** Increasing demand for agricultural products is driving grassland management intensification with subsequent impacts on ecosystem services and disservices. Key questions related to grassland production as well as environmental and social concerns must be addressed to ensure sustainability. We propose a unified perspective, addressing numerous trade-offs and synergies between grassland ecosystem services and disservices, and considering an array of ecological and human consequences associated with history and ongoing shifts in management strategies. Much of our discussion utilizes evidence from humid grasslands; however, our examples and recommendations have global implications for the future of grassland management. We characterize four categories of ecosystem services and disservices (provisioning, supporting, regulating, and cultural) provided by perennial grasslands that are extensively managed (low or no input, never cultivated) or intensively managed (high-input, cultivated). We explore a range of potential outcomes following transition from extensive to intensive agroecosystems around the globe. Additionally, we suggest specific research priorities to better evaluate ecosystem services and disservices across management intensities. Finally, we highlight potential benefits of landscape mosaics that include grasslands across a continuum of extensive to intensive strategies.

**Key words:** biodiversity; conservation and production; extensively managed; greenhouse gases; intensively managed; pasture; rangeland; semi-natural; trade-offs.

**Received** 20 April 2021; revised 11 June 2021; accepted 29 June 2021. Corresponding Editor: Ginger Allington.

**Copyright:** © 2021 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** paudelshishir@gmail.com

## INTRODUCTION

Ecosystems and humans are inexorably linked (Daily 1997, MEA 2005) as ecosystems services

(Box 1) are essential for human welfare (Costanza et al. 1997; see Box 1 for definitions of bolded words). Grassland ecosystems, particularly perennial grasslands, provide an array of benefits to

**Box 1.****Glossary and definition of main terms (adapted from Allen et al. 2011).**

**Ecosystem service:** Benefits (commodity and non-commodity) humans obtain from ecosystems that support survival and quality of life (Costanza et al. 1997, MEA 2005). Ecosystem services group into four categories:

1. *Provisioning services*, such as food, fiber, and fuel.
2. *Supporting services*, such as biodiversity, soil structure, and nutrient cycling.
3. *Regulating services*, such as climate regulation, freshwater and flood regulation, pollination, and disease and pest control.
4. *Cultural services*, such as recreation, esthetics, spiritual value, and education.

**Ecosystem disservices:** Undesirable outcomes of ecosystem functions that negatively affect humans or the environment, such as air pollution, greenhouse gas emissions, soil erosion, freshwater contamination, allergies, diseases, and economic losses. These are also sorted into the same four categories as ecosystem services.

**Extensive (native) grasslands:** Grasslands where majority of vegetative ground cover (>60%) is composed of indigenous species of grasses and forbs and generally comprised of diverse species, that can be perennial, annual, or biennial and managed (low or no input) by humans for livestock grazing. Ecological processes in these extensive grasslands are primarily determined by natural processes, species interactions, and site characteristics (Dixon et al. 2014).

**Intensification:** Intensification is a result of technological progress, including cultivation of grass species, improvements in knowledge, management, mechanization, and herbage and animal breeds. Commonly, there is also a change in inputs such as fertilizers, feed, herbicides, and technical assistance from veterinarians and contractors. Technological progress leads to changes in the utilization of forage and grasslands and leads to higher yield per ha and per unit labor, and to changes in various emissions (Oenema et al. 2014).

**Intensively managed (cultivated) grasslands:** Grasslands/pasturelands specifically altered for agriculture reasons (grazing, hay, food, or fuel production), typically composed of a single or few plant species (native or non-native) that are regularly amended with various agrochemicals. These grasslands can be directly cultivated from native systems or planted following other land use patterns, such as cropping. These grasslands are also referenced as human-created cultural grasslands (Dixon et al. 2014).

**Monoculture grasslands:** Grasslands composed of a single grass or forb (native or non-native) species exclusively planted for forage or feedstock or biofuel production.

**Perennial grasslands:** Broadly representing the majority of global grasslands, such as pastures and hayfields that are dominated by perennial grasses, legumes, and forbs with extensive rhizomatous structure (Blair et al. 2014, Dixon et al. 2014); these dominant plant species are widely utilized for ruminant grazing, forage production, and feedstock for biofuel. They can be native or cultivated.

**Pastures:** Grasslands covered with grass, legumes, and other forbs that are exclusively used for ruminant grazing.

**Synergy:** A situation where enhancing one category of ecosystem service can also improve another category of service. For example, improving the supporting service of biodiversity may also improve the cultural service of landscape beauty (see Raudsepp-Hearne et al. 2010).

**Trade-off:** A situation where beneficial changes (quality and/or quantity) in one category of ecosystem service causes an undesirable change in another service. For example, while increased agrochemical use may increase provisioning services, agrochemicals can negatively impact water quality.

humankind (Asbjornsen et al. 2014, Steiner et al. 2014, Franzluebbers and Steiner 2016), including meat, milk, and fiber via livestock production, and many other vital and often unrecognized services such as climate regulation, soil conservation, biodiversity, natural medicine, tourism, cultural, and societal benefits (Daily 1997). However, most grasslands are under increasing pressure due to growing global demand for animal

products (White et al. 2000, O'Mara 2012, Blair et al. 2014). Specifically, temperate native grasslands are among the most at risk ecosystems globally (Carbutt et al. 2017, Comer et al. 2018). Due to the importance of perennial grasslands, appropriate management is critical for ecosystem services sustainability (Tilman et al. 2001).

In the mid-twentieth century, grassland management shifted rapidly toward **intensification**

of agroecosystems and a considerable portion of native and semi-native perennial grasslands that were previously extensively managed (no or low-input; Bengtsson et al. 2019), hereafter referred to as extensive grasslands (Fig. 1), were converted to intensively managed grasslands or pastures, hereafter referred to as cultivated grasslands (Allen et al. 2011). This occurred predominantly across agricultural landscapes in humid to mesic temperate and subtropical and tropical regions (White et al. 2000); however, semiarid grasslands are increasingly managed with similar intensification strategies (Zhou et al. 2019a). These cultivated grasslands are often composed of monoculture or low-diversity stands (Fig. 1), resulting from plowing and sowing agriculturally developed forage followed by substantial inputs, intended to enhance livestock production. Particularly in North America and Europe, several productive introduced perennial grasses, such as ryegrass (*Lolium* spp.), tall fescue [*Lolium arundinaceum* (Schreb.) Darbysh], Canada bluegrass (*Poa compressa* L.), Guinea grass (*Panicum*

*maximum* Jacq.), and bahiagrass (*Paspalum notatum* Flueggé) were planted as a strategy to increase forage yields (Williams and Baruch 2000) and to meet a range of other objectives including improved agronomic traits, resilience to environmental stresses, grazing tolerance, and resource-use efficiency (Williams and Baruch 2000, Barney and DiTomaso 2008). In most instances, these species, especially when fertilized, are highly productive (Williams and Baruch 2000, Havstad et al. 2007). Indeed, a recent global meta-analysis reported a 20% increase in yield from intensification (i.e., substantial agrochemical inputs to enhance production) (Beckmann et al. 2019). Clec'h et al. (2019) reported productivity was ~487% (t DM/ha) greater in cultivated pastures compared to extensively managed pastures in Switzerland. These intensive plantings often resulted in a landscape mosaic of both extensively managed systems and cultivated grasslands. Because grasslands can be altered to different extents, it is important to recognize that grassland intensification can be

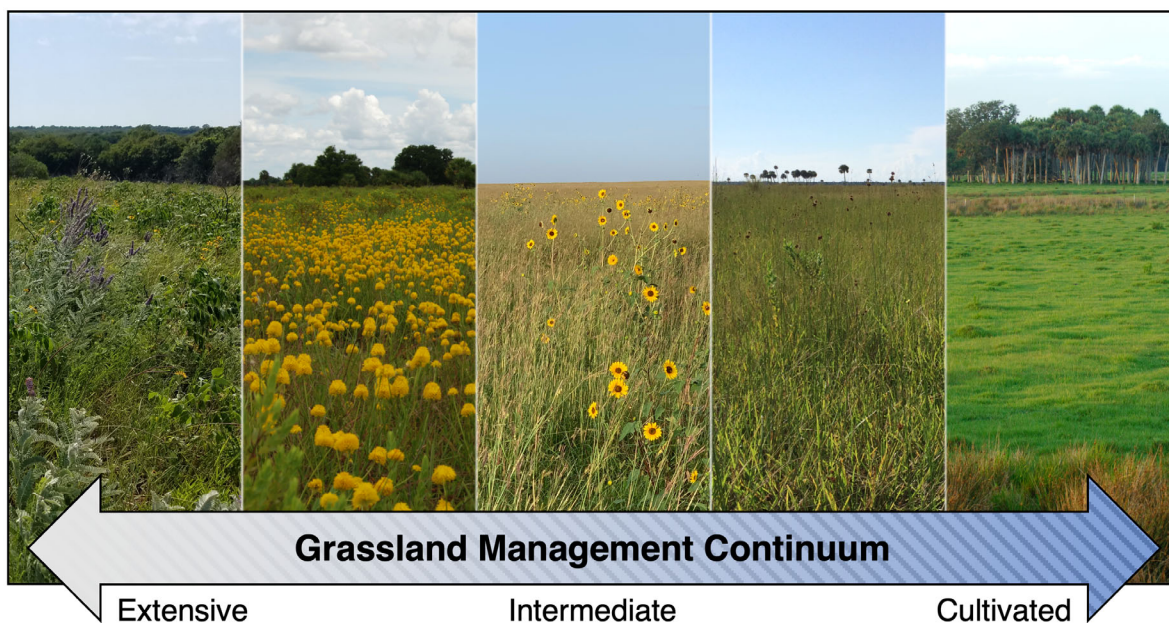


Fig. 1. Pictures representing the grassland management continuum. There are few published comparisons of multiple ecosystem services and disservices provided by extensive, intermediate, and cultivated grasslands. However, understanding multifunctional outcomes, trade-offs, and synergies associated with these management strategies are critical for the conservation of native grassland species and sustainable use of cultivated grasslands.

viewed as a continuum rather than a categorical ranking, although we primarily refer to two categories of classification, intensive and extensive, for comparison purposes (Fig. 1). Intensification strategies such as mechanical soil disturbance, over-seeding, irrigation, and fertilization are increasingly being utilized and assessed for grasslands in arid and semiarid systems, including in western and northern China (Gang et al. 2018, Zhou et al. 2019a), Argentina (Paredes et al. 2018), and South Africa (O'Connor 2005).

Intensive management of grasslands, aiming to support economically viable livestock production, is reported to provide enhanced provisioning services, such as increased forage production (Adler et al. 2009; Appendix S1: Table S1), stocking rate (Swain et al. 2013; Appendix S1: Table S1), and economic benefits (Isselstein et al. 2005, Dong et al. 2007). Indeed, cultivated grasslands are a necessary component of economically viable livestock operations in many landscapes (e.g., subtropical ranches in central Florida, USA; Swain et al. 2013). In addition, as these cultivated grasslands became established in the landscape, they continue to provide habitat for specific wildlife species (Morrison and Humphrey 2001), landscape and grassland habitat connectivity, and store carbon (Silveira et al. 2014), providing more services than the majority of annual crop production systems (Asbjornsen et al. 2014, Werling et al. 2014). Compared to extensive grasslands, cultivated grasslands typically require greater inputs such as fertilizer, irrigation, herbicides to control undesirable plants, specialized livestock breeds, and livestock control through additional fencing (Auclair 1976, Isselstein et al. 2005, Suttie et al. 2005). Researchers, conservation agencies, and practitioners have raised concerns about biodiversity conservation and environmental sustainability of cultivated grasslands, compared to extensively manage native grasslands (Tilman et al. 2001, 2002), as intensification may lead to loss of biodiversity, ecological functions, and other important ecosystem services in agricultural landscapes (Landis 2017).

Previous studies suggest substantial ecological and environmental trade-offs to managing grasslands primarily for agricultural production and provisioning services, compared to managing with the goal of maintaining multiple ecosystem services (Bennett et al. 2009). Since one of the

main drivers of grassland intensification is to increased livestock production, there may be more ecological and environmental trade-offs in cultivated grasslands (where the focus is primarily provisioning services) compared to extensive systems (Isselstein et al. 2005, Gardiner et al. 2010, Power 2010, Lemaire 2012, Van Vooren et al. 2018). Some examples of ecological and environmental trade-offs observed in cultivated grasslands that are grazed and utilized for livestock production may include: loss of wildlife, pollinators, and overall species diversity (Planteux et al. 2005, Asbjornsen et al. 2014, Davidson et al. 2020); poor downstream water quality due to persistent soil alterations from past fertilization practices (Capece et al. 2007, Swain et al. 2013); increased bare ground from overgrazing and trampling (e.g., Akiyama and Kawamura 2007, Blair et al. 2014); and loss of soil quality from compaction and changes to soil microbial communities (Tschardt et al. 2005, Hickman et al. 2006, Searchinger et al. 2008, Lemaire 2012). These potential undesirable outcomes that directly or indirectly undermine human well-being are referred to as ecosystem disservices (Zhang et al. 2007, Shackleton et al. 2016). Grassland intensification may also lead to environmental problems associated with agrochemical (e.g., fertilizers and herbicides) applications (Power 2010, Asbjornsen et al. 2014). Such agrochemical use in grassland management, in some instances, can also have indirect effects beyond grassland ecosystem boundaries, such as degrading downstream water quality (Rabalais et al. 2002, Tilman et al. 2001). For example, Owens et al. (1994) reported groundwater  $\text{NO}_3\text{-N}$  concentrations beyond USEPA potable water standards in watersheds connected to fertilized monoculture grass pastures that were grazed by beef cattle, compared to similar pastures where inter-seeded alfalfa was utilized to enhance soil fertility. These differences in nutrient concentration in drainage water also vary with the timing of nutrient applications and stocking rates (Julian et al. 2017, Nash et al. 2019). Julian et al. (2017) reported a significant reduction in nutrient loading in catchment areas, after reducing the number of dairy cattle and sheep in grazing pastures. Nash et al. (2019) reported a greater proportion of nutrients exported into drainage areas from poorly managed, high-input grazing pastures

compared to drainage connected to pastures with carefully timed fertilizer applications.

Despite the emerging ecosystem services and disservices framework (see Power 2010, Bengtsson et al. 2019), few empirical studies present side-by-side comparisons for a broad range of ecosystem services, trade-offs, synergies, and disservices provided by extensive vs. cultivated grasslands. Studies focusing on a wide array of both ecosystem services and disservices related to cultivated perennial pastures are particularly scarce (Power 2010, Shackleton et al. 2016). Existing studies overwhelmingly address a few specific ecosystem functions and are concentrated in humid to mesic temperate grasslands of North America, Europe, or Australia (see Appendix S1: Table S1) with little work in the humid grasslands of the subtropics or tropics. Historically, few arid and semiarid grassland systems experienced intensive management and changes in ecosystem services in response to intensification have not been widely studied (White et al. 2000, Briske et al. 2015, Zhou et al. 2019b).

Understanding multifunctional outcomes associated with these distinct systems is critical for conservation of native grassland species and sustainable use of cultivated grasslands, especially under ongoing global changes and increasing anthropogenic threats (e.g., land use changes, shifting fire regimes, overgrazing, invasive species, and woody encroachment) (Fargione et al. 2009, Blair et al. 2014, Gaskin et al. 2020). However, we have limited information on contrasting ecosystem services provided by extensively managed vs. cultivated grasslands. Here, we propose utilizing a framework of ecosystem services and reduced ecosystem services (or increased disservices) across the continuum of extensively managed to cultivated grasslands to better elucidate parameters of sustainable perennial grassland management. This synthesis creates a foundation for future research in agroecosystems to examine influences of specific management tools (e.g., fire and grazing) and global changes (e.g., drought and invasive species) in terms of their influence on extensively managed or intensively managed cultivated grassland ecosystem services and disservices.

We aim to improve grassland outcomes assessment and management by further developing the framework of four categories of ecosystem

services (Box 1; provisioning, supporting, regulating, and cultural) defined by the Millennium Ecosystem Assessment (MEA 2005) and disservices (see Shackleton et al. 2016) in extensive and cultivated grassland systems utilized for livestock production. Identifying and addressing key knowledge gaps (Box 2) in research literature will expand application of this framework and improve future decision making. For each category of ecosystem services, we (1) briefly review how extensive and cultivated perennial grasslands provide ecosystem services, (2) outline potential decreasing ecosystem services (or increasing ecosystem disservices) and key knowledge gaps associated with both extensive and cultivated grasslands, and (3) describe specific future research needs to address knowledge gaps and support sustainable grassland management. Identifying ecosystem services and disservices and their influence on agricultural production, rural livelihoods, environmental quality, and climate mitigation are critical steps toward sustainable management of grassland agroecosystems.

## PROVISIONING SERVICES AND DISSERVICES

Perennial grasslands (both extensive and cultivated) provide several provisioning services that improve human well-being, including livestock forage (aboveground biomass) to create food (meat and milk), fibers (leather and wool), and energy, as well as medicinal resources (Havstad et al. 2007, Asbjornsen et al. 2014). We first briefly describe these provisioning services and then outline potential trade-offs and synergies of both extensive and cultivated grassland management strategies (Table 1).

### *Livestock forage and food*

Forage production is the primary use and economic value of grass-based farming systems in the United States and other parts of the world, with global implications for livestock production (Franzluebbers and Steiner 2016, Steiner et al. 2009). The amount and quality of forage production at the local scale drives regional and global supplies of agricultural commodities and food security. Therefore, sustainable forage production is vital to satisfy increasing global demand for meat and dairy. Yet, grassland management practices and types (e.g., extensive vs. cultivated)

**Box 2.****Summary of key knowledge gaps for comparison of extensive vs. cultivated perennial grasslands across categories of ecosystem services and disservices.***Provisioning services*

Knowledge gap 1: Forage production and efficiency (optimization) across a continuum of grassland management systems.

Knowledge gap 2: Medicinal plant loss (ethnobotany) due to grassland management.

*Supporting services*

Knowledge gap 3: Multi-trophic consequences (cascade) of grassland conversion, including shifts in belowground processes and microbial community dynamics. Additionally, the relative importance of plant diversity *vs.* other factors such as fertilization, irrigation, grazing management, and introduction of invasive earthworms.

Knowledge gap 4: Comparing soil quality and nutrient cycling dynamics across management strategies and in relation to climate and edaphic conditions, at various scales from local, to regional, and cross-continental.

*Regulating services*

Knowledge gap 5: Net GHG (CO<sub>2</sub> equivalents) and long-term soil carbon storage, in relation to grazing intensity and emissions during conversion. Historic grassland conversion “carbon debt” as well as ongoing outcomes associated with fertilization of cultivated perennial grasslands.

Knowledge gap 6: Pollinator diversity and abundance associated with grassland management.

Knowledge gap 7: Freshwater quality associated with grassland across the management continuum, including downstream and watershed scales.

Knowledge gap 8: Biotic regulation of pests before and after grassland conversion. Estimations of the economic values of restoration or management of intensive pastures and native grasslands.

*Cultural services*

Knowledge gap 9: Human outcomes in relation to grassland conversion across diverse landscapes and global regions.

are likely to dictate the quantity and quality of forage and livestock production. Previous studies suggest cultivated grasslands with regular use of fertilizers and associated intensive management tend to improve both biomass and livestock production, compared to extensive systems (Isselstein et al. 2005, Griffith et al. 2011; see Appendix S1: Table S1). Indeed, Griffith et al. (2011) reported ~12.5–21.5% greater aboveground production in cultivated grasslands compared to extensively managed grasslands in the Great Plains, USA. In southern Brazil, Dick et al. (2015) reported double yields of milk and meat in cultivated pastures compared to extensive pastures. Greater forage production in cultivated grasslands enables higher stocking rate and increased weight gain in livestock. Accounting for inputs and outputs, intensive management of grasslands on at least a portion of ranching land is often advantageous or necessary for profitability (Alcock and Hegarty 2006, Swain et al. 2013). For instance, Dong et al. (2007) reported higher

total revenues, output:input ratios (i.e., the recovery of investment in the managed production system), and net economic benefits from cultivated grasslands, compared to extensive native grasslands.

Comparing production from cultivated vs. extensive native grasslands is not straightforward, because forage quality and quantity vary by plant species, season, inputs, and local environmental conditions. In many livestock production systems, provisioning services provided by extensive and cultivated grasslands complement each other as cattle are rotated seasonally between the two grassland types (Swain et al. 2013). Moreover, rural economics and prosperity require us to examine ecosystem services in a framework that bundles provisioning and environmental quality (Dumont et al. 2018), and we propose forage provisioning is the foundation for all feasible grassland management strategies. Since there are limited data on a gradient from primarily extensive to mostly cultivated grasslands and most

Table 1. Four categories of ecosystem services—with specific services and examples within each category—provided by extensive and cultivated (intensive) grasslands.

Ecosystem services	Specific services	Ecosystem service outcomes		Remarks and references
		Extensive	Intensive	
Provisioning services	Forage and biofuel production	–	+	In most cases, cultivated grasslands produced higher amount of biomass for forage and biofuel (Griffith et al. 2011)
	Forage quality	–	+	Cultivated pastures provide better quality forage with higher crude protein and fiber (Fiems et al. 2002)
	Milk and meat production	–	+	Generally, converted grasslands support higher stocking density, producing more milk and meat (Dick et al. 2015). However, outcomes may vary with quality of forage production (Bengtsson et al. 2019)
	Fiber and wool production	+/-	-/+	Fiber production benefits associated with extensive grasslands (Ryder 1983). However, wool production benefits associated with intensive management, due to increased stocking rates (Saul et al. 2011)
	Economic gain	–	+	Economic gain from forage, meat, and dairy production is substantially greater from converted grasslands, compared to extensively managed systems (Dong et al. 2007)
	Medicinal resources	+	–	Many rural people depend on herbal medicine collected from extensive native grasslands (Bengtsson et al. 2019)
	Supporting services	Biodiversity	+	–
Soil health		+	–	Species-rich extensive pastures support highly diverse soil microorganisms, including mycorrhizal fungi, supporting well-drained soils with higher aggregate stability (van der Heijden et al. 1998, Wilson et al. 2009)
Regulating services	Hydrology and freshwater	+	+	Both pasture types support aquifer recharge, increase nutrient retention, reduce sediment transport, and improve water infiltration (Fargione et al. 2009, Asbjornsen et al. 2014)
	Water quality	+	–	Reduced water quality near converted grasslands, due to nutrients (e.g., N & P) and additional chemical runoff (Saarijärvi et al. 2007). Intensive management may alter hydrology and agrochemical inputs increase nutrient leaching, degrading water quality (Tilman et al. 2001, Power 2010)
	Climate regulation	+	+/-	Perennial grasslands, regardless of management strategy, retain substantial amount of soil carbon (Conant et al. 2001). With intensification, converted pasture may release greater amount of N <sub>2</sub> O and CH <sub>4</sub> that have the capacity to offset carbon sequestration, increasing global climate change (Soussana et al. 2010)
	Pollination	+	-/=	In general, converted pastures lack diverse flowering forbs, reducing pollinator resources, with reduced pollination services in surrounding areas. However, extensive pastures are typically rich in flowering forbs and offer better habitat for pollinators, increasing pollination services (Hoehn et al. 2008, Albrecht et al. 2012)
	Weed and pest control	+	–	Extensive grasslands are more resilient to weeds and pests than intensive pastures (Letourneau et al. 2011, Finn et al. 2013). Conversion of extensive pastures to intensive systems, leads to decreased weed and pest control services (Hauck et al. 2014)
	Cultural services	Esthetic	+	+/=
Recreation/ Hunting		+	-/=	With habitat variety, extensive pastures may provide better recreation opportunities such as hiking, bird watching, and hunting than converted pastures (Hahn et al. 2018)
Culture and heritage		=	=	Linkages between management strategy and culture or heritage is lacking, but both extensive and converted pastures provide opportunities for, family, community, and social coherence among ranchers, especially in rural areas
Education and scientific study		+	+	Both styles of management contribute to important ecological theories, including productivity–diversity relationships (Tilman et al. 2001)

Note: Outcomes of pasture management strategies: increasing services (+), decreasing services (–), and no obvious differences between types (=).

studies work in one grassland type, the effects of intensification on quantity and quality of forage and livestock production are difficult to conclude. More assessments of forage and livestock productivity and input:output ratios in extensive and cultivated grasslands, and the continuum of practices spanning those categories are needed at various scales to improve sustainable grassland management and ranching strategies (see Box 2; Knowledge gap 1).

In addition to forage, perennial grasslands provide other important resources such as bioenergy feedstock and animal co-products utilized in downstream manufacturing (e.g., textiles, leather, tallow; Ryder 1983). Some extensive grasslands are important sources of medicinal and food plants particularly in developing countries, such as those across Africa, with substantial economic outcomes (O'Connor 2005, Bengtsson et al. 2019). Unfortunately, we have limited scientific information on the supply of medicinal and food plants from extensive and cultivated grasslands (see Box 2; Knowledge gap 2).

## SUPPORTING SERVICES AND DISSERVICES

Perennial grasslands also provide non-commodity outputs such as biodiversity, habitat, soil quality, and nutrient cycling. We briefly describe these supporting services and outline trade-offs and synergies related to grassland management strategies (Table 1).

### *Biodiversity and habitat*

Plant species diversity can have enormous beneficial effects on ecosystem processes and stability (Tscharntke et al. 2005). In particular, high diversity plant communities tend to reorganize quickly after disturbances (Loreau et al. 2003), are relatively resilient to insects, pests, and weeds (Letourneau et al. 2011, Finn et al. 2013, Hautier et al. 2018, Bengtsson et al. 2019, Hanisch et al. 2020), and provide stable production and soil quality in variable weather (van der Heijden et al. 1998, Isbell et al. 2017, Wagg et al. 2017, Chen et al. 2018, Leff et al. 2018). Therefore, maintaining vegetation diversity on a landscape is critical for long-term sustainability of ecosystems and the services they provide. Extensively managed perennial grasslands, in particular, harbor a rich diversity of plants (Fig. 1), provide

habitat for birds and insects, supply genetic resources, and are of substantial conservation value (White et al. 2000, Noss 2012, Werling et al. 2014, Ohwaki, 2019, Zografou et al. 2020).

Managing grasslands intensively often reduces supporting ecosystem services, including biodiversity (Plantureux et al. 2005). Although some intensive pastures show greater carrying capacity for particular taxa (Crested Caracara: Morrison and Humphrey 2001; and spider and ground beetle: Albrecht et al. 2010) and harbor similar numbers of birds and insect herbivores (Werling et al. 2014), there are clear trade-offs with supporting services following intensification. For example, in the Midwestern United States, Werling et al. (2014) reported significantly higher plant and predatory arthropod richness in native prairies compared to adjacent cultivated monoculture. Boughton et al. (2019) showed that more intensely managed ranches had a greater potential for ecosystem disservices in the context of wetland restoration projects such as increased cover of non-native plants, abundant mosquitoes, and lower amphibian abundance. Furthermore, native perennial grasslands preserve plant genetic diversity by harboring unique seed banks (Minns et al. 2001), and species genetic diversity is key for adaptation to adverse environments and increased resistance to pests and diseases (Zhang et al. 2007).

Reduced supporting services may also affect several regulating and cultural services (Swain et al. 2013, Dumont et al. 2018). Previous studies suggest that grassland intensification led to substantially decreased bird populations across the UK, US Great Plains, and Germany (Vickery et al. 2001, Hickman et al. 2006, Hernández et al. 2013, Gossner et al. 2016). Hickman et al. (2006) found ~70% lower average bird abundance and diversity in cultivated old world bluestem (*Bothriochloa ischaemum*) grasslands compared to extensively managed native systems. They concluded that decreased bird abundance and diversity in cultivated grassland were driven by reduced abundance of arthropods. Hernández et al. (2013) highlighted declining northern bobwhite quail (*Colinus virginianus*) populations as well as other bird species across the United States, following widespread intensification of native grasslands with non-native grass species across agriculture landscapes. Reduced plant



diversity reduces nesting sites and seed resources for granivorous birds, increasing supporting disservices (Vickery et al. 2001). Presumably, reduced biodiversity at lower trophic levels impacts other species across the system. Such comprehensive assessments of multidirectional consequences of grassland management on biodiversity are missing, particularly regarding landscape-scale influences over time (Box 2; Knowledge gap 3). Therefore, landscape context and configuration surrounding grassland fragments, either cultivated or extensive, must be considered when assessing management intensity impacts on biodiversity (Landis 2017, Pejchar et al. 2018).

#### *Soil quality and nutrient cycling*

Both extensive and cultivated perennial grasslands are known to enhance soil health (see <https://www.nrcs.usda.gov/wps/portal/nrcs/main/soils/health/>), store carbon, accumulate nitrogen and phosphorus, and support abundant soil organisms, including microbial communities (Wilson et al. 2009). All these characteristics are critical for maintaining soil and grassland productivity. However, grassland intensification may have variable impacts on soil fertility and ecosystem resilience. In particular, intensive management may bring changes in soil fauna and microbial abundance, resulting in reduced soil quality with potential negative consequences on multiple soil-related services, including carbon storage and nutrient leaching (Asbjornsen et al. 2014, Egan et al. 2018). Depending on a number of factors, particularly grazing management and fertilization, intensification strategies can lead to relatively greater soil carbon (Conant et al. 2001, Poeplau et al. 2018). However, relatively low plant species diversity is often associated with intensively managed grasslands, and lower plant diversity has been linked with declining soil organic carbon across global grasslands (Chen et al. 2020). Indeed, Yang et al. (2019) reported 70% greater soil carbon storage in diverse grasslands compared to monoculture, following restoration of abandoned agricultural fields. Cline et al. (2018) and Wagg et al. (2019) reported increased nutrient cycling in diverse grasslands compared to less diverse system. Similarly, Wang et al. (2006) found greater microbial N and C in cultivated than extensive grasslands. In contrast, McSorley and Tanner (2007) reported marginal

effects of grassland intensification on soil nematodes richness and abundance in southcentral Florida, USA. Use of chemical inputs can negatively affect soil microbes in grasslands systems (Sankaran and Augustine 2004, Benizri et al. 2015, Wang et al. 2018); however, this is not universal, as optimized inputs can also increase microbial abundance and activity in grasslands (Wilson et al. 2009, Zhou et al. 2019b). Nevertheless, monoculture in cultivated grasslands may not provide sufficient soil microorganism habitat, diverse residue inputs, or soil aggregation (see Sanderson et al. 2004). However, we have limited information to draw universal conclusions and need additional research to clarify the influence of plant diversity, relative to other drivers, on soil processes, especially in managed pastures in different climate regions (Box 2, Knowledge gap 3).

Extensive grasslands with diverse native graminoids and legumes may increase soil nutrient pools, particularly plant-available N, through quality litter inputs (Sanderson et al. 2004). Cultivated grasslands can also be over-seeded with legumes (e.g., *Medicago falcata*) to provide similar benefits (Zhou et al. 2019a). Effects likely vary with location, climate, plant community, and litter decomposition rates, making global patterns elusive (Box 2, Knowledge gap 4). Nevertheless, shifts in the local soil microbial community and soil structure following intensification and associated poor management practices (e.g., overgrazing) may lead to greater supporting disservices, such as greater bare ground and decreased soil aggregate stability (Blair et al. 2014). These changes have been particularly pronounced in arid grasslands (e.g., Sahel region, Africa) where pasture intensification followed by overgrazing led to substantial soil compaction and bare ground (Mortimore and Turner 2005). Due to variation in climate and edaphic conditions, a global network of extensive and cultivated grassland research sites is needed to compare soil, microbial, and nutrient dynamics across continental scales, similar to the Nutrient Network, which is focused on anthropogenic nutrient deposition impacts in grasslands (<http://www.nutnet.umn.edu/>) (Box 2; Knowledge gap 4).

#### REGULATING SERVICES AND DISSERVICES

Perennial grasslands provide many regulating services, including climate regulation, pollination,

disease and pest control, weed control, fresh and flood water regulation, and fire regulation. We briefly describe regulating services of both extensive and cultivated perennial grasslands and then outline potential trade-offs and synergies (Table 1).

### *Climate regulation*

Sustaining/supporting ~20% of the world's standing soil carbon stock (Ramankutty et al. 2008), grasslands are substantial regulators of atmospheric carbon. Grasslands and the grazing animals they support also contribute to significant livestock and ecosystem methane (CH<sub>4</sub>) and nitrous oxide (N<sub>2</sub>O) emissions (Rotz et al. 2013); these are atmospherically important trace gases with global warming potentials 25 and 298 times that of CO<sub>2</sub>, respectively (IPCC 2013). The balance between CO<sub>2</sub> uptake and sequestration, and CO<sub>2</sub> and trace gas (CH<sub>4</sub> and N<sub>2</sub>O) emissions ultimately drives grassland greenhouse gas reduction potential and is affected by management strategies (Soussana et al. 2010). Ruminant livestock generate methane and higher stocking rates in cultivated grasslands may contribute to greater overall methane release, compared to native grasslands. However, methane produced on an animal unit basis may actually be lower in cultivated grasslands compared to native grasslands due to improved forage digestibility (Boadi and Wittenberg 2002, Grossi et al. 2019, Sollenberger et al. 2019, Gere et al. 2021). Boadi and Wittenberg (2002) show emissions of methane per unit digestible organic matter intake were highest in cattle consuming low-quality forage that may be associated with extensively managed systems. Past studies have shown that poor forage digestibility (e.g., substantial lignin), results in greater CH<sub>4</sub> emissions through enteric fermentation (Bell et al. 2012, Sollenberger et al. 2019). Methane mitigation strategies include increasing forage quality and feed efficiency, providing feed supplements (e.g., rumen modifiers), and increasing animal production (decreasing CH<sub>4</sub> per unit of product) (Knapp et al. 2014, Beck et al. 2018). Fertilizer use in cultivated grasslands can also intensify agroecosystem N<sub>2</sub>O and CH<sub>4</sub> efflux (Mosier et al. 2004), through changes in microbial processes, although relative impacts likely vary across climatic regions. For example, grassland intensification may result in greater ecosystem methane

emissions compared to native grasslands in subtropical humid regions, but not in temperate humid regions (Paudel, Gomez-Casanovas, Boughton et al., *unpublished data*). Soil wetness is a large driver of ecosystem methane emissions in subtropical humid grasslands, regardless of intensification (Chamberlain et al. 2015, 2017). Grazing management may also affect net ecosystem greenhouse gas dynamics; in extensive grasslands, tipping the balance to a net sink when grazed, and a net source when left ungrazed (Gomez-Casanovas et al. 2018). Gomez-Casanovas et al. (2018) showed grazing removed biomass and reduced ecosystem respiration but increased soil moisture and ecosystem methane emissions. This reduction in ecosystem respiration had a relatively greater influence than the increased soil moisture and concomitant methane emissions, resulting in lower overall global warming potential in the grazed system (Gomez-Casanovas et al. 2018). Wilson et al. (2018) also showed grazing enhanced belowground carbon allocation, microbial biomass, and soil carbon in a cultivated subtropical grassland.

Perennial grasslands, both cultivated and extensive, are terrestrial sinks for carbon (Paustian et al. 1997, Conant et al. 2017). However, carbon accumulation and storage in grassland ecosystems strongly depends on grassland plant community structure, management practices, soil type, and climate (Paustian et al. 1997, Conant et al. 2001, Fornara and Tilman 2008). Grasslands can become a source of greenhouse gas emissions rather than a sink via methane emissions from saturated soils (Chamberlain et al. 2015) or N<sub>2</sub>O and CH<sub>4</sub> emissions following agrochemical inputs (Mosier et al. 2004, Soussana et al. 2010). Studies have reported cultivated grasslands in the subtropics can provide substantial carbon storage benefits compared to native grasslands (Silveira et al. 2014, Xu et al. 2018), while contrasting studies in temperate regions suggest long-term carbon storage in cultivated grasslands may not be as stable as native grasslands (Tilman et al. 2006, Fornara and Tilman 2008), potentially decreasing climate regulation services. For example, subtropical grasslands in Florida, USA, Xu et al. (2018) reported ~91–170% greater labile soil organic carbon in cultivated grasslands compared to native grasslands, likely associated with higher productivity stemming from long-term fertilizer applications and

more productive forage species. Fisher et al. (1994) similarly found a significant increase in soil carbon when native grasslands were replaced with non-native grass monocultures in South American savannahs. While cultivated pastures store a greater amount of carbon, in subtropical grasslands with a seasonally high water table they may be a greater source of methane emissions that may offset carbon storage (Chamberlain et al. 2017; Paudel et al., *unpublished data*). Additionally, high nitrogen inputs and excretion from grazing livestock with high crude protein diets may contribute to greater nitrous oxide emissions (Sollenberger et al. 2019). We have limited information and modeling (e.g., DayCent) on how agroecosystem intensification of extensively managed grasslands into cultivated grasslands influences overall greenhouse gas emissions and long-term soil carbon storage. Long-term analyses of changes in the carbon balance from conversion to intensively managed grasslands and the influences of different grassland management strategies are needed to determine climate regulation outcomes for grassland systems (Box 2; Knowledge Gap 5).

#### **Pollination regulation**

Pollination is key to maintenance of ecosystem functions and global food security. Approximately 35% of global food production depends on animal pollination (Klein et al. 2007). Although graminoids do not rely on animal pollination services, maintaining floristic diversity in native grasslands provides habitat for a wide range of bees, butterflies, hoverflies, moths, birds, and mammals that provide critical pollination services within grasslands and surrounding areas (Hoehn et al. 2008, Werling et al. 2014). Indeed, Hoehn et al. (2008) linked increased pumpkin yields in crop fields to greater functional diversity of pollinators in nearby extensive perennial grasslands. Maintaining pollination services is an important means of increasing productivity as well as supporting genetically diverse plant varieties in both perennial grasslands, crop fields, and other surrounding areas (Hooper et al. 2005). However, abundance and diversity of pollinators vary with grassland management and plant community composition (Werling et al. 2014, Sutter et al. 2017). Extensively managed grasslands with diverse flowering plants support more diverse pollinators (Sutter et al. 2017),

compared to cultivated grasslands, unless active management for legumes is included in cultivated grasslands (Sollenberger et al. 2019). Consistent with this statement, declining arthropod and bird pollinator populations were reported in cultivated old world bluestem (non-native) grassland in the Great Plains, USA (Hickman et al. 2006).

Cultivated grasslands are, in many instances, managed with herbicides to control weedy and non-native flowering forbs that may indirectly influence pollinators by reducing floral resources (Asbjornsen et al. 2014), a trade-off in terms of pollination services. Furthermore, higher stocking density and subsequent grazing can suppress the flowering of certain species in cultivated grasslands due to reduced pollinator abundance and diversity (Davidson et al. 2020). Declining pollinator abundance may lead to reproductive failure in plants and, in some conditions, can impact yields in adjacent crop fields with severe economic and human nutrition consequences (Albrecht et al. 2007, Hoehn et al. 2008). However, recent studies from humid temperate grasslands in the USA reported no difference in pollinator richness between cultivated and native grasslands (Gardiner et al. 2010, Werling et al. 2014). Although limited in number, these mixed results underscore the need for additional research to help determine pollination regulation associated with extensive and cultivated perennial grasslands (Box 2; Knowledge gap 6).

#### **Fire regulation**

Fire is a critical ecological process in maintaining grassland ecosystem health and integrity throughout the world (White et al. 2000), providing supporting, regulating, and cultural services (see, Pausas and Keeley 2019). Without fire, the maintenance of extensive grassland ecosystems is almost impossible (White et al. 2000). Donovan et al. (2017) reported increased frequency and size of large grassland wildfires in the US Great Plains in the early 21st century compared to late 20th century. Prescribed fire is a common management tool within extensive grasslands and therefore regulates intensity, severity, and fire return intervals in the landscape, helping to reduce large-scale, high-intensity fires and associated damage to humans and the environment (Depietri and Orenstein 2019) while enhancing or maintaining

several ecosystem services. In contrast, fire may be less critical in cultivated grasslands when biomass removal associated with intensive grazing reduces fuel loads (Ellis et al. 2005, McGranahan et al. 2012).

Long-term data from native perennial grasslands across the Great Plains, USA, suggest a fire return interval of ~2.59 yr (Allen and Palmer 2011), and these frequent fires are important in reducing litter and debris, invasive species, and woody encroachment (Depietri and Orenstein 2019). Noss (2012, 2018) reports even more frequent fire return intervals of 1–2 yr for southeastern US grasslands in regions of intense lightning activity. These frequent fires further reduce the probability of woody incursion and large and intense fires that are costly to physical infrastructure, human health and safety, and the environment (Depietri and Orenstein 2019, Pausas and Keeley 2019). Frequent and low-intensity fires create new open habitat with increased resources and reduced competition, allowing fire-adapted, shade intolerant, and less competitive native plant species to succeed and increase diversity across the landscape (Pausas and Keeley 2019). However, burning large contiguous areas annually reduces biodiversity (e.g., Ohwaki 2019), indicating that patch-burning may maintain more diversity across a landscape (Fuhlendorf et al. 2009). Increased plant diversity and healthy grassland conditions enhance provisioning (e.g., livestock grazing and productivity) and supporting (e.g., increase pollinator diversity and wildlife) grassland services. In Florida, USA, almost all plant communities associated with cattle grazing require natural fires or prescribed burns (Noss 2018). Prescribed fire is also utilized in cultivated pastures in Florida to improve forage nutritive value in C<sub>4</sub> grasses and remove residual standing dead biomass and weeds (Swain et al. 2013). Florida cattlemen played a significant role in maintaining a culture of prescribed burning dating back to the 1920s, until the vital role of fire was acknowledged by authorities in the 1970s onward. Now it is recognized that frequent fires help maintain or even increase water storage by reducing evapotranspiration (Pausas and Keeley 2019) and long-term carbon storage in the soil by releasing less carbon per fire event as well as facilitating accumulation of charcoal (increasing recalcitrant carbon to the soil) and rapid

regrowth of vegetation (Depietri and Orenstein 2019, Pausas and Keeley 2019). In addition, fire-adapted plants invest heavily belowground, potentially increasing carbon storage in the soil (Pausas et al. 2018) if land managers allow sufficient time for plant regrowth prior to grazing or another fire event. Frequent fire mitigates regulating disservices from infrequent, intense wildfires that may burn infrastructure, non-grassland landscapes, and release substantial carbon to the atmosphere.

Some studies, however, highlight the harmful effects of grassland fires because frequent fires have been associated with reduced growth and reproductive success of certain native C<sub>3</sub> plants (Hadley 1970) and several grassland invertebrate species (Swengel 1996, Harper et al. 2000). Swengel (1996) reported a significant decline in specialist butterflies across a large swath of grassland landscapes in the USA, and recovery of the species after fire was slow. In temperate grasslands in the US Great Plains, some of these reported disservices may be mitigated by employing patch-burn grazing to achieve structural diversity in grasslands (Fuhlendorf and Engle 2001, 2004). A landscape-scale mosaic of recently burned and intensely grazed areas along with longer time since fire areas and non-grazed areas creates a patchwork with higher overall ecosystem values (e.g., increased rangeland biodiversity) than more homogenous extensive prescribed burns (McGranahan et al. 2012). Since we have limited information on how cultivated grasslands and their management regulate fire in broader landscapes or impact various ecosystem services, future research should consider this regulating service (see Depietri and Orenstein 2019). Understanding interactions between fire and grassland management strategies is a key aspect of perennial grasslands and delivery of ecosystem services to society. Ecosystem services derived from patch-burn grazing are under experimental assessment in both grassland types in Florida, USA (E. H. Boughton, pers. comm.).

#### *Hydrology and freshwater regulation*

Clean water is crucial for environmental and human health, and perennial grasslands play an important role in providing fresh water for drinking, irrigation, esthetic, and recreational use (Asbjornsen et al. 2014). Compared to annual

cropping systems, both cultivated and extensive perennial grasslands are more effective at retaining nutrients, reducing sediment transport, and improving water infiltration and aquifer recharge, thus reducing soil erosion, flooding, and transport of nutrients into surrounding water bodies (Fargione et al. 2009, Asbjornsen et al. 2014). In a long-term research site, Fischer et al. (2019) found that grassland plant species richness influenced soil water content through effects on infiltration, shading, and water uptake. However, in contrast to extensively managed grasslands, there are clear trade-offs for freshwater services due to increased production in cultivated grasslands. For instance, Saarijärvi et al. (2007) reported 23.5 kg ha<sup>-1</sup> additional total N leached from fertilized monoculture pasture that received 220 kg N ha<sup>-1</sup> compared to unfertilized multispecies pasture in Maaninka, Finland, despite similar stocking rates as well as dung and urine N content. Increased use of agrochemicals (fertilizers) to improve provisioning services in cultivated grasslands may reduce freshwater services and endanger water quality (Tilman et al. 2001) through nutrient loading in downstream freshwater systems (Rabalais et al. 2002). Reduced freshwater quality directly harms drinking water, freshwater fish, wetlands, and associated rural economies (Vickery et al. 2001). The impacts of grassland intensification on downstream freshwater services have been examined in several watersheds (e.g., Rabalais et al. 2002, Osmond et al. 2012), but more direct comparisons of water quality in watersheds with differing proportions of extensive native and cultivated perennial grasslands are needed, including consideration of production practices (Box 2; Knowledge gap 7).

Perennial grasslands, regardless of management, have significant effects on regulating surface and groundwater quality and aquifer recharge by reducing soil erosion, sedimentation, and water runoff, increasing soil water-holding capacity, and removing impurities and nutrients without human intervention (Daily 1997). Plant community structure can affect those hydrological processes, including evaporation and runoff (Jackson et al. 2000); therefore, grassland intensification could indirectly affect water regulation through changes in plant communities and their functional traits. Some cultivated grasslands rely

on irrigation or seep irrigation under drought conditions, adding to water supply and distribution challenges. Additionally, grassland intensification may directly impact water regulation services through mechanical disturbances and chemical inputs that increase groundwater runoff and nutrient loading into surrounding water bodies (Tilman et al. 2001, Power 2010). Furthermore, use of fertilizers and herbicides in cultivated grasslands may have an enormous effect on water quality during heavy rainfall events, although impacts can potentially be mitigated by proper nutrient management or installation of innovations such as buffer strips (Hunke et al. 2015, Nash et al. 2019, Pilon et al. 2019). Water related disservices are increasing globally and have far-reaching consequences such as reduced food production, degradation of coastal and estuarine ecosystems, economic losses to freshwater fishing, shifts in species composition, and diminished biodiversity (Tilman et al. 2001, Power 2010).

#### ***Pest regulation***

Invasive species, disease, insect, and other pest outbreaks cause enormous damage to ecosystem functions and the global economy (Pimentel et al. 2000). Perennial grasslands regulate pests and pathogens (Asbjornsen et al. 2014, Isbell et al. 2017) by increasing habitat and resource heterogeneity, housing diverse groups of arthropod predators, and supporting populations of insectivorous birds and bats (Werling et al. 2014). However, little is known about disease and pest regulation in cultivated vs. extensively managed perennial pastures. Available research suggests diverse and extensively managed pastures show reduced disease and pest infestation compared to low-diversity grasslands or cultivated pastures (Letourneau et al. 2011, Werling et al. 2014, Isbell et al. 2017, Mommer et al. 2018). For instance, continental-scale field experiments reported greater weed invasion in monoculture grasslands compared to species-rich grasslands with 29% decreased weed biomass across diverse grasslands compared to monoculture systems (Finn et al. 2013). Boughton et al. (2011) showed that non-native plant invasion dynamics differed for wetlands embedded in cultivated or extensive grasslands, with wetlands within cultivated pastures having greater non-native plant abundance and

different relationships between non-native species and abiotic conditions compared to wetlands within extensive grasslands. Mommer et al. (2018) found that 57% of pathogenic fungal units were not found in eight-species plots compared to monoculture grasslands. Therefore, we suggest there are clear trade-offs of managing cultivated perennial grasslands dominated by a single or few grass species, as grassland intensification may enable pest infestation by affecting plant community stability and self-regulation (Power 2010). Native grasslands also support abundant beneficial soil microbes that are antagonistic to many soil-borne pathogens (Latz et al. 2012). Hence, maintenance of native or relatively diverse grasslands can potentially save billions of dollars while controlling pests (Power 2010). For example, Landis et al. (2008) analyzed the economic value of biological suppression of aphids within four states of the United States, and they estimated \$239 million year<sup>-1</sup> could be saved through pest regulation associated with native grasslands. Although these few studies help provide direct comparisons of pest regulation services between extensive and cultivated grasslands, we need more direct comparisons, particularly for grasslands before and after conversion, to improve our understanding of pest regulation between perennial grassland types (Box 2; Knowledge gap 8). Also, studies are necessary to estimate the economic values of restoration or management of cultivated pastures compared to extensive grasslands because such information is valuable to underpin the basis for cost-sharing on private lands by government, non-government, and business entities (Box 2; Knowledge gap 8).

## CULTURAL SERVICES AND DISSERVICES

Characteristics and well-being of human cultures are strongly associated with the features and conditions of local ecosystems. Extensive grasslands, in particular, provide valuable cultural services such as ecotourism, recreation, hunting, and education. Extensive grasslands are home to a variety of plants and animals that people enjoy for outdoor recreation, discovery and education, natural beauty, and use for religious ceremonies (Havstad et al. 2007, Fargione et al. 2009, Asbjornsen et al. 2014, Bengtsson et al. 2019). Moreover, extensive grasslands provide habitat for

game species, creating opportunities for wildlife viewing and hunting as well as providing food and revenue for landowners and government agencies (Bengtsson et al. 2019). Guided tours (ecotourism) in extensive grasslands offer opportunities for flora and fauna viewing, local employment, and habitat protection (see, Fiedler et al. 2008). Recreational values of native grasslands also link downstream for fishing, swimming, and boating. In a recent paper, Bengtsson et al. (2019) further highlighted the values of extensive grasslands for cultural heritage, spiritual significance, and social cohesion among grassland users in Europe and Africa. These recognitions support the management and governance of grassland ecosystems. Finally, native grassland ecosystems have been the focus of outdoor classrooms and scientific research that helped develop several important ecological theories (Blair et al. 2014, Bengtsson et al. 2019).

Importantly, cultivated grasslands provide cultural services because they support the livelihoods of rural ranching communities and provide a diversified income to support a landscape mosaic and esthetic beauty. Indeed, multi-generation ranches often depend on cultivated pastures, as they support long-term economic viability. Ranching enables local communities to maintain social cohesion and family values (see Bengtsson et al. 2019). Social, cultural, and family values likely encourage effective land stewardship and investment in effective practices (Eastman et al. 2000). Social cohesion through ranching and other cultural activities also provides opportunities to teach younger generations, encouraging ranchers and their children to remain in rural areas (Lindborg et al. 2008), ensuring future food supplies. Ultimately, ecological, environmental, economic, and socio-cultural processes, including social interactions among stakeholders, support agroecosystem functions and human well-being (Bentley Brymer et al. 2020).

Despite these important cultural services, grassland management can have several cultural trade-offs. Notably, cultivated grasslands can also become a source of reduced cultural and esthetic services when cultivated grasslands lose populations of flowering herbaceous plants. Conversely, some people enjoy open monoculture pastures. In terms of wildlife habitat, cultivated grasslands reduce habitat heterogeneity

for many wildlife species and may not support similar recreational services as extensive pastures. Agrochemicals applied to cultivated grasslands can leach into downstream water systems and pollute freshwater, further decreasing recreational services in downstream aquatic ecosystems. Potential loss of recreation and tourism drives direct and indirect economic costs. For example, excessive use of fertilizer in cultivated grasslands in the 1990s in the UK led to water pollution, reducing recreation and tourism values of downstream water bodies, and increasing water treatment costs (MEA 2005).

Equally, there are also trade-offs in ecosystem services provided by extensive grasslands. Some flowering herbs in native grasslands produce abundant pollen, causing allergic responses leading to quality of life and health impacts on susceptible people (Shackleton et al. 2016). Sometimes, the presence of poisonous forbs within native grasslands can have significant negative effects on livestock production (e.g., reduced weight gain and death) (James et al. 1992, Scasta et al. 2020). As mentioned previously, fire tends to be more frequent in extensively managed perennial grasslands, with potential for seasonally poor air quality to create human health issues and social tensions between rural and urban populations. Although it is difficult to calculate cultural disservices in monetary value, these trade-offs have significant implications for sustainable agroecosystem management and human well-being, making them a critical research area. It is crucial to draw on the social sciences in conjunction with ecological research to elucidate how grassland intensification impacts human dimensions (Bentley Brymer et al. 2020; Box 2; Knowledge gap 9).

## CONCLUSION AND FUTURE DIRECTIONS

As the global demand for food, fiber, energy, and raw materials increases with a growing human population, native perennial grassland agroecosystems face continued alteration through anthropogenic land use changes (MEA 2005, Carbutt et al. 2017). Studies tracking these alterations in specific regions indicate decreased extensive grasslands and increased intensification (Hiscock et al. 2003, Toledo et al. 2014, Comer et al. 2018). Sustainable food, fiber, and energy production that maintains or enhances

multiple ecosystem services, including carbon storage and biodiversity conservation, is a major goal of food security research (Power 2010, Asbjornsen et al. 2014). Given the enormous resiliency of native grasslands to environmental and anthropogenic perturbation (Asbjornsen et al. 2014) and economic benefits of cultivated grasslands (Isselstein et al. 2005), proper management of these grasslands is vital for food production, environmental quality, and sustainable livelihoods (Bengtsson et al. 2019). However, there is relatively limited information comparing multiple ecosystem services, trade-offs, and synergies provided across a continuum from extensive to cultivated grasslands (Barral and Oscar 2012, Asbjornsen et al. 2014, Kleinman et al. 2018). There are several potential reasons for this limited information: (1) Most previous studies were short-term small-scale experiments and often focused on a single management practice as opposed to a more comprehensive approach. Consequently, although these studies provide a basis for our current scientific knowledge, they often do not provide meaningful support for multifunctionality. (2) Studies of ecosystem services from cultivated grasslands have been primarily focused on provisioning as compared to other ecosystem service interactions and synergies, (3) reduced ecosystem services or increased ecosystem disservices associated with improper management of native and cultivated grasslands have not been adequately compared, (4) the concept of ecosystem disservices has not been fully embraced due to a lack of a widely accepted definition (Shackleton et al. 2016), and (5) collaboration among researchers from multiple disciplines (e.g., ecology, soil science, microbiology, economics, wildlife biology, animal science, human sciences, and climate science) was not been widely fostered, although recently, emerging cross site research networks such as the United States Department of Agriculture (USDA) Long-Term Agroecosystem Research (LTAR) network are now facilitating continental-scale interdisciplinary research to advance sustainable intensification of agricultural production (Kleinman et al. 2018, Spiegel et al. 2018).

Existing information suggests expansion of cultivated perennial grasslands can potentially be a cause for concern due to ecological and environmental outcomes (Tilman et al. 2006).

However, there are few comparative studies of cultivated and extensive grasslands that take a holistic perspective of multiple ecosystem services and disservices, meaning many research gaps remain (Box 2). A deeper comparison of multiple ecosystem services, disservices, trade-offs, and synergies between cultivated and extensive grasslands will need to include perspectives from a broader array of practitioners (e.g., land practitioners, ranchers, and conservation practitioners) at various biogeographical and climatic scales. In particular, there are few data from tropical regions of Asia, Africa, and South America (Parr et al. 2014). Establishing long-term experiments at the ranch to the continental scale, such as currently underway with the USDA LTAR network (Kleinman et al. 2018), will enable comparison of optimized production and plant nutrient quality in cultivated and extensive grasslands. As the pressures for agricultural production drive expansion of perennial grassland intensification in areas previously managed extensively, there are numerous opportunities to support sustainable intensification. A multifunctional approach will require comparisons of trade-offs and synergies among *provisioning, supporting, regulating, and cultural services* across grassland management intensities around the world, as well as consideration of the costs:benefits of managing ecosystem disservices:services (Shackleton et al. 2016). Landscape mosaics that include a continuum from highly cultivated grasslands—likely supporting greater biomass and food production—to extensively managed grasslands—likely biodiversity hotspots as well as wildlife refuges—should be further evaluated in terms of their ability to sustain rural prosperity and reduce ecosystem disservices.

## ACKNOWLEDGMENTS

This synthesis was a contribution from the Long-Term Agroecosystem Research (LTAR) network. LTAR is supported by the United States Department of Agriculture. AC was supported by the Post-Doctoral Fellowships Program [project no. OKL03144/project accession no. 1019172], from the USDA, National Institute of Food and Agriculture (NIFA). Boughton EH was supported by NIFA grant [grant no. NIFA 2016-6709-24988] and USDA NACA [#58-0202-7-001]. SP thanks the Phipps Conservatory and Botanical

Gardens for office space and facilities. The authors declare that there is no conflict of interest.

## LITERATURE CITED

- Adler, P. R., M. A. Sanderson, P. J. Weimer, and K. P. Vogel. 2009. Plant species composition and biofuel yields of conservation grasslands. *Ecological Applications* 19:2202–2209.
- Akiyama, T., and K. Kawamura. 2007. Grassland degradation in China: methods of monitoring, management and restoration. *Grassland Science* 53:1–7.
- Albrecht, M., P. Duelli, C. Müller, D. Kleijn, and B. Schmid. 2007. The Swiss agri-environment scheme enhances pollinator diversity and plant reproductive success in nearby intensively managed farmland. *Journal of Applied Ecology* 44:813–822.
- Albrecht, M., B. Schmid, Y. Hautier, and C. B. Müller. 2012. Diverse pollinator communities enhance plant reproductive success. *Proceedings of the Royal Society B: Biological Sciences* 279:4845–4852.
- Albrecht, M., B. Schmid, M. K. Obrist, B. Schüpbach, D. Kleijn, and P. Duelli. 2010. Effects of ecological compensation meadows on arthropod diversity in adjacent intensively managed grassland. *Biological Conservation* 143:642–649.
- Alcock, D., and R. S. Hegarty. 2006. Effects of pasture improvement on productivity, gross margin and methane emissions of a grazing sheep enterprise. Pages 103–105 in C. R. Soliva, J. Takahashi, and M. Kreuzer, editors. *Greenhouse gases and animal agriculture: an update*. Elsevier International Congress Series 1293. Elsevier, Amsterdam, the Netherlands.
- Allen, M. S., and M. W. Palmer. 2011. Fire history of a prairie/forest boundary: more than 250 years of frequent fire in a North American tallgrass prairie. *Journal of Vegetation Science* 22:436–444.
- Allen, V. G., et al. 2011. An international terminology for grazing lands and grazing animals. *Grass and Forage Science* 66:2–8.
- Asbjornsen, H., V. Hernandez-Santana, M. Liebman, J. Bayala, J. Chen, M. Helmers, C. K. Ong, and L. A. Schulte. 2014. Targeting perennial vegetation in agricultural landscapes for enhancing ecosystem services. *Renewable Agriculture and Food Systems* 29:101–125.
- Auclair, A. N. 1976. Ecological factors in the development of intensive-management ecosystems in Midwestern United States. *Ecology* 57:431–444.
- Barney, J. N., and J. M. DiTomaso. 2008. Nonnative species and bioenergy: are we cultivating the next invader? *BioScience* 58:64–70.
- Barral, M. P., and M. N. Oscar. 2012. Land-use planning based on ecosystem service assessment: a case



- study in the Southeast Pampas of Argentina. *Agriculture, Ecosystems & Environment* 154:34–43.
- Beck, M. R., L. R. Thompson, J. E. White, G. D. Williams, S. E. Place, C. A. Moffet, S. A. Gunter, and R. R. Reuter. 2018. Whole cottonseed supplementation improves performance and reduces methane emission intensity of grazing beef steers. *The Professional Animal Scientist* 34:339–345.
- Beckmann, M., et al. 2019. Conventional land-use intensification reduces species richness and increases production: a global meta-analysis. *Global Change Biology* 25:1941–1956.
- Bell, M. J., R. J. Eckard, and B. R. Cullen. 2012. The effect of future climate scenarios on the balance between productivity and greenhouse gas emissions from sheep grazing systems. *Livestock Science* 147:126–138.
- Bengtsson, J., J. M. Bullock, B. Egoh, C. Everson, T. Everson, T. O'Connor, P. J. O'Farrell, H. G. Smith, and R. Lindborg. 2019. Grasslands—more important for ecosystem services than you might think. *Ecosphere* 10:e02582.
- Benizri, É., S. Piutti, M. Rue, A. Durand, J. L. Morel, and G. Echevarria. 2015. Enhanced phytoextraction of nickel from contaminated soil by hyperaccumulator plant co-cropping associated with PGPR. *In* 13th SGA Meeting Mineral Resources in a Sustainable World. Nancy, FRA, 2015/08/24–2015/08/27.
- Bennett, E. M., G. D. Peterson, and L. J. Gordon. 2009. Understanding relationships among multiple ecosystem services. *Ecology Letters* 12:1394–1404.
- Bentley Brymer, A. L., D. Toledo, S. Spiegall, F. Pierson, P. E. Clark, and J. D. Wulfhorst. 2020. Social-ecological processes and impacts affect individual and social well-being in a rural western US landscape. *Frontier in Sustainable Food Systems* 4:38.
- Blair, J., J. Nippert, and J. Briggs. 2014. Grassland Ecology. Pages 389–423 *in* R. K. Monson, editor. *Ecology and the environment, the plant sciences* 8. Springer Science+Business Media, New York, New York, USA.
- Boadi, D. A., and K. M. Wittenberg. 2002. Methane production from dairy and beef heifers fed forages differing in nutrient density using the sulphur hexafluoride (SF<sub>6</sub>) tracer gas technique. *Canadian Journal of Animal Science* 82:201–206.
- Boughton, E. H., P. F. Quintana-Ascencio, D. G. Jenkins, P. J. Bohlen, J. E. Fauth, A. Engel, S. Shukla, G. Kiker, G. Hendricks, and H. M. Swain. 2019. Trade-offs and synergies in a payment-for-ecosystem services program on ranchlands in the Everglades headwaters. *Ecosphere* 10:e02728.
- Boughton, E. H., P. F. Quintana-Ascencio, D. Nickerson, and P. J. Bohlen. 2011. Management intensity affects the relationship between non-native and native species in subtropical wetlands. *Applied Vegetation Science* 14:210–220.
- Briske, D. D., et al. 2015. Strategies to alleviate poverty and grassland degradation in Inner Mongolia: intensification vs production efficiency of livestock systems. *Journal of Environmental Management* 52:177–182.
- Capece, J. C., K. L. Campbell, P. J. Bohlen, D. A. Graetz, and K. M. Portier. 2007. Soil phosphorus, cattle stocking rates, and water quality in subtropical pastures in Florida, USA. *Rangeland Ecology & Management* 60:19–30.
- Carbutt, C., W. D. Henwood, and L. A. Gilfedder. 2017. Global plight of native temperate grasslands: going, going, gone? *Biodiversity and Conservation* 26:2911–2932.
- Chamberlain, S. D., E. H. Boughton, and J. P. Sparks. 2015. Underlying ecosystem emissions exceed cattle-emitted methane from subtropical lowland pastures. *Ecosystems* 18:933–945.
- Chamberlain, S. D., P. M. Groffman, E. H. Boughton, N. Gomez-Casanovas, E. H. DeLucia, C. J. Bernacchi, and J. P. Sparks. 2017. The impact of water management practices on subtropical pasture methane emissions and ecosystem service payments. *Ecological Applications* 27:1199–1209.
- Chen, S., et al. 2018. Plant diversity enhances productivity and soil carbon storage. *Proceedings of the National Academy of Sciences of the United States of America* 115:4027–4032.
- Chen, X., H. Y. Chen, C. Chen, Z. Ma, E. B. Searle, Z. Yu, and Z. Huang. 2020. Effects of plant diversity on soil carbon in diverse ecosystems: a global meta-analysis. *Biological Reviews* 95:167–183.
- Cleč'h, S., R. Finger, N. Buchmann, A. S. Gosal, H. Hörtnagl, O. Huguenin-Elie, P. Jeanneret, A. Lüscher, M. K. Schneider, and R. Huber. 2019. Assessment of spatial variability of multiple ecosystem services in grasslands of different intensities. *Journal of Environmental Management* 251:109372.
- Cline, L. C., S. E. Hobbie, M. D. Madritch, C. R. Buyarski, D. Tilman, and J. M. Cavender-Bares. 2018. Resource availability underlies the plant-fungal diversity relationship in a grassland ecosystem. *Ecology* 2018:204–216.
- Comer, P. J., J. C. Hak, K. Kindscher, E. Muldavin, and J. Singhurst. 2018. Continent-scale landscape conservation design for temperate grasslands of the Great Plains and Chihuahuan Desert. *Natural Areas Journal* 38:196–211.
- Conant, R. T., C. E. Cerri, B. B. Osborne, and K. Paustian. 2017. Grassland management impacts on soil carbon stocks: a new synthesis. *Ecological Applications* 27:662–668.

- Conant, R. T., K. Paustian, and E. T. Elliott. 2001. Grassland management and conversion into grassland: effects on soil carbon. *Ecological Applications* 11:343–355.
- Costanza, R., et al. 1997. The value of the world's ecosystem services and natural capital. *Nature* 387:253–260.
- Daily, G. C. 1997. *Nature's services: societal dependence on natural ecosystems*. Island Press, Washington, DC, USA.
- Davidson, K. E., M. S. Fowler, M. W. Skov, D. Forman, J. Alison, M. Botham, N. Beaumont, and J. N. Griffin. 2020. Grazing reduces bee abundance and diversity in saltmarshes by suppressing flowering of key plant species. *Agriculture, Ecosystems & Environment* 291:106760.
- Depietri, Y., and D. E. Orenstein. 2019. Fire-regulating services and disservices with an application to the Haifa-Carmel region in Israel. *Frontiers in Environmental Science* 7:107.
- Dick, M., M. A. da Silva, and H. Dewes. 2015. Life cycle assessment of beef cattle production in two typical grassland systems of southern Brazil. *Journal of Cleaner Production* 96:426–434.
- Dixon, A. P., D. Faber-Langendoen, C. Josse, J. Morrison, and C. J. Loucks. 2014. Distribution mapping of world grassland types. *Journal of Biogeography* 41:2003–2019.
- Dong, S. K., M. Y. Kang, X. J. Yun, R. J. Long, and Z. Z. Hu. 2007. Economic comparison of forage production from annual crops, perennial pasture and native grassland in the alpine region of the Qinghai-Tibetan Plateau, China. *Grass and Forage Science* 62:405–415.
- Donovan, V. M., C. L. Wonkka, and D. Twidwell. 2017. Surging wildfire activity in a grassland biome. *Geophysical Research Letters* 44:5986–5993.
- Dumont, B., et al. 2018. Associations among goods, impacts and ecosystem services provided by livestock farming. *Animal* 13:1773–1784.
- Eastman, C., C. Raish, and A. McSweeney. 2000. Small livestock operations in northern New Mexico. Pages 523–555 in R. Jemison, and R. Carol, editors. *Livestock management in the American Southwest: Ecology, Society, and Economics*. Elsevier Science, Amsterdam, the Netherlands.
- Egan, G., X. Zhou, D. Wang, Z. Jia, M. J. Crawley, and D. Fornara. 2018. Long-term effects of grassland management on soil microbial abundance: implications for soil carbon and nitrogen storage. *Biogeochemistry* 141:213–228.
- Ellis, S., P. Kanowski, and R. Whelan. 2005. National inquiry on bushfire mitigation and management. Council of Australian government's report. Commonwealth of Australia, Canberra, Australian Capital Territory, Australia.
- Fargione, J. E., T. R. Cooper, D. J. Flaspohler, J. Hill, C. Lehman, T. McCoy, S. McLeod, E. J. Nelson, K. S. Oberhauser, and D. Tilman. 2009. Bioenergy and wildlife: threats and opportunities for grassland conservation. *BioScience* 59:767–777.
- Fiedler, A. K., D. A. Landis, and S. D. Wratten. 2008. Maximizing ecosystem services from conservation biological control: the role of habitat management. *Biological Control* 45:254–271.
- Fiems, L. O., J. L. De Boever, A. De Vliegheer, D. L. De Brabander, and L. Carlier. 2002. Digestibility and intake of hay from extensively and intensively managed grassland. Pages 185–188 in I. Kyriazakis, and G. Zervas, editors. *Organic meat and milk from ruminants*. Proceedings of a joint international conference organized by the Hellenic Society of Animal Production and the British Society of Animal Science, Athens, Greece, October 4–6, 2001. EAAP publication No. 106. Academic Publishers, Wageningen, the Netherlands.
- Finn, J. A., et al. 2013. Ecosystem function enhanced by combining four functional types of plant species in intensively managed grassland mixtures: a 3-year continental-scale field experiment. *Journal of Applied Ecology* 50:365–375.
- Fischer, C., et al. 2019. Plant species richness and functional groups have different effects on soil water content in a decade-long grassland experiment. *Journal of Ecology* 107:127–141.
- Fisher, M. J., I. M. Rao, M. A. Ayarza, C. E. Lascano, J. I. Sanz, R. J. Thomas, and R. R. Vera. 1994. Carbon storage by introduced deep-rooted grasses in the South American savannas. *Nature* 371:236–238.
- Fornara, D. A., and D. Tilman. 2008. Plant functional composition influences rates of soil carbon and nitrogen accumulation. *Journal of Ecology* 96:314–322.
- Franzluebbers, A. J., and J. L. Steiner. 2016. Ecosystem services and grasslands in America. Pages 422–425 in M. Potschin, R. Haines-Young, R. Fish, and K. Turner, editors. *Routledge handbook of ecosystem services*. Routledge/Informa UK Limited, Abingdon, UK.
- Fuhlendorf, S. D., and D. M. Engle. 2001. Restoring heterogeneity on rangelands: ecosystem management based on evolutionary grazing patterns: we propose a paradigm that enhances heterogeneity instead of homogeneity to promote biological diversity and wildlife habitat on rangelands grazed by livestock. *BioScience* 51:625–632.
- Fuhlendorf, S. D., and D. M. Engle. 2004. Application of the fire-grazing interaction to restore a shifting

- mosaic on tallgrass prairie. *Journal of Applied Ecology* 41:604–614.
- Fuhlendorf, S. D., D. M. Engle, J. A. Kerby, and R. Hamilton. 2009. Pyric herbivory: rewilding landscapes through the recoupling of fire and grazing. *Conservation Biology* 23:588–598.
- Gang, C., W. Zhao, T. Zhao, Y. Zhang, X. Gao, and Z. Wen. 2018. The impacts of land conversion and management measures on the grassland net primary productivity over the Loess Plateau, Northern China. *Science of the Total Environment* 645:827–836.
- Gardiner, M. A., J. K. Tuell, R. Isaacs, J. Gibbs, J. S. Ascher, and D. A. Landis. 2010. Implications of three biofuel crops for beneficial arthropods in agricultural landscapes. *BioEnergy Research* 3:6–19.
- Gaskin, J. F., et al. 2020. Managing invasive plants on Great Plains grasslands: a discussion of current challenges. *Rangeland Ecology & Management* 19:1–15.
- Gere, J. I., R. A. Bualó, A. L. Perini, R. D. Arias, F. M. Ortega, A. E. Wulff, and G. Berra. 2021. Methane emission factors for beef cows in Argentina: effect of diet quality. *New Zealand Journal of Agricultural Research* 64:260–268.
- Gomez-Casanovas, N., N. J. DeLucia, C. J. Bernacchi, E. H. Boughton, J. P. Sparks, S. Chamberlain, and E. H. DeLucia. 2018. Grazing alters net ecosystem C fluxes and the global warming potential of a subtropical pasture. *Ecological Applications* 28:557–572.
- Gossner, M. M., et al. 2016. Land-use intensification causes multitrophic homogenization of grassland communities. *Nature* 540:266–269.
- Griffith, A. P., F. M. Epplin, S. D. Fuhlendorf, and R. Gillen. 2011. A comparison of perennial polycultures and monocultures for producing biomass for biorefinery feedstock. *Agronomy Journal* 103:617–627.
- Grossi, G., P. Goglio, A. Vitali, and A. G. Williams. 2019. Livestock and climate change: impact of livestock on climate and mitigation strategies. *Animal Frontiers* 9:69–76.
- Hadley, E. B. 1970. Net productivity and burning responses of native eastern North Dakota prairie communities. *American Midland Naturalist* 84:121–135.
- Hahn, T., M. Heinrup, and R. Lindborg. 2018. Landscape heterogeneity correlates with recreational values: a case study from Swedish agricultural landscapes and implications for policy. *Landscape Research* 43:696–707.
- Hanisch, M., O. Schweiger, A. F. Cord, M. Volk, and S. Knapp. 2020. Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. *Journal of Applied Ecology* 57:1535–1550.
- Harper, M. G., C. H. Dietrich, R. L. Larimore, and P. A. Tessene. 2000. Effects of prescribed fire on prairie arthropods: an enclosure study. *Natural Areas Journal* 20:325–335.
- Hauck, J., C. Schleyer, K. L. Winkler, and J. Maes. 2014. Shades of greening: reviewing the impact of the new EU agricultural policy on ecosystem services. *Change and Adaptation in Socio-Ecological Systems* 1:51–62.
- Hautier, Y., et al. 2018. Local loss and spatial homogenization of plant diversity reduce ecosystem multifunctionality. *Nature Ecology & Evolution* 2:50–56.
- Havstad, K. M., D. P. Peters, R. Skaggs, J. Brown, B. Bestelmeyer, E. Fredrickson, J. Herrick, and J. Wright. 2007. Ecological services to and from rangelands of the United States. *Ecological Economics* 15:261–268.
- Hernández, F., L. A. Brennan, S. J. DeMaso, J. P. Sands, and D. B. Wester. 2013. On reversing the northern bobwhite population decline: 20 years later. *Wildlife Society Bulletin* 37:177–188.
- Hickman, K. R., G. H. Farley, R. Channell, and J. E. Steier. 2006. Effects of old world bluestem (*Bothriochloa ischaemum*) on food availability and avian community composition within the mixed-grass prairie. *The Southwestern Naturalist* 51:524–530.
- Hiscock, J. G., C. S. Thourot, and J. Zhang. 2003. Phosphorus budget—land use relationships for the northern Lake Okeechobee watershed, Florida. *Ecological Engineering* 21:63–74.
- Hoehn, P., T. Tschardt, J. M. Tylianakis, and I. Steffan-Dewenter. 2008. Functional group diversity of bee pollinators increases crop yield. *Proceedings of the Royal Society of London B: Biological Sciences* 275:2283–2291.
- Hooper, D. U., et al. 2005. Effects of biodiversity on ecosystem functioning: a consensus of current knowledge. *Ecological Monographs* 75:3–35.
- Hunke, P., E. N. Mueller, B. Schröder, and P. Zeilhofer. 2015. The Brazilian Cerrado: assessment of water and soil degradation in catchments under intensive agricultural use. *Ecohydrology* 8:1154–1180.
- IPCC [The Intergovernmental Panel on Climate Change]. 2013. *Climate change 2013: the physical science basis*. Pages 1535 in T. F. Stocker, D. Qin, G.-K. Plattner, M. M. B. Tignor, S. K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex, and P. M. Midgley, editors. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, UK.

- Isbell, F., et al. 2017. Benefits of increasing plant diversity in sustainable agroecosystems. *Journal of Ecology* 105:871–879.
- Isselstein, J., B. Jeangros, and V. Pavlu. 2005. Agronomic aspects of biodiversity targeted management of temperate grasslands in Europe—a review. *Agronomy Research* 3:139–151.
- Jackson, R. B., J. S. Sperry, and T. E. Dawson. 2000. Root water uptake and transport: using physiological processes in global predictions. *Trends in Plant Science* 5:482–488.
- James, L. F., D. B. Nielsen, and K. E. Panter. 1992. Impact of poisonous plant on the livestock industry. *Rangeland Ecology & Management* 45:3–8.
- Julian, J. P., K. M. Beurs, B. Owsley, R. J. Davies-Colley, and A. G. Ausseil. 2017. River water quality changes in New Zealand over 26 years: response to land use intensity. *Hydrology and Earth System Sciences* 21:1149–1171.
- Klein, A. M., B. E. Vaissiere, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tschamntke. 2007. Importance of pollinators in changing landscapes for world crops. *Proceedings of the Royal Society of London B: Biological Sciences* 274:303–313.
- Kleinman, P. J. A., et al. 2018. Advancing the sustainability of US agriculture through long-term research. *Journal of Environmental Quality* 47:1412–1425.
- Knapp, J. R., G. L. Laur, P. A. Vadas, W. P. Weiss, and J. M. Tricarico. 2014. Invited review: enteric methane in dairy cattle production: quantifying the opportunities and impact of reducing emissions. *Journal of Dairy Science* 97:3231–3261.
- Landis, D. A. 2017. Designing agricultural landscapes for biodiversity-based ecosystem services. *Basic and Applied Ecology* 18:1–12.
- Landis, D. A., M. M. Gardiner, W. van der Werf, and S. M. Swinton. 2008. Increasing corn for biofuel production reduces biocontrol services in agricultural landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 105:20552–20557.
- Latz, E., N. Eisenhauer, B. C. Rall, E. Allan, C. Roscher, S. Scheu, and A. Jousset. 2012. Plant diversity improves protection against soil-borne pathogens by fostering antagonistic bacterial communities. *Journal of Ecology* 100:597–604.
- Leff, J. W., et al. 2018. Predicting the structure of soil communities from plant community taxonomy, phylogeny, and traits. *ISME Journal* 12:1794–1805.
- Lemaire, G. 2012. Intensification of animal production from grassland and ecosystem services: a trade-off. *CAB Reviews* 7:1–7.
- Letourneau, D. K., et al. 2011. Does plant diversity benefit agroecosystems? A synthetic review. *Ecological Applications* 21:9–21.
- Lindborg, R., et al. 2008. A landscape perspective on conservation of semi-natural grasslands. *Agriculture, Ecosystems & Environment* 125:213–222.
- Loreau, M., N. Mouquet, and A. Gonzalez. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 100:12765–12770.
- McGranahan, D. A., D. M. Engle, S. D. Fuhlendorf, S. J. Winter, J. R. Miller, and D. M. Debinski. 2012. Spatial heterogeneity across five rangelands managed with pyric-herbivory. *Journal of Applied Ecology* 49:903–910.
- McSorley, R., and G. W. Tanner. 2007. Effects of cattle stocking rates on nematode communities in south Florida. *Rangeland Ecology & Management* 60:31–35.
- MEA [Millennium Ecosystem Assessment]. 2005. *Ecosystems and human well-being*. Island Press, Washington, DC, USA.
- Minns, A., J. Finn, A. Hector, M. Caldeira, J. Joshi, C. Palmberg, B. Schmid, M. Scherer-Lorenzen, and E. Spehn. 2001. The functioning of European grassland ecosystems: potential benefits of biodiversity to agriculture. *Outlook on Agriculture* 30:179–185.
- Mommer, L., et al. 2018. Lost in diversity: the interactions between soil-borne fungi, biodiversity and plant productivity. *New Phytologist* 218:542–553.
- Morrison, J. L., and S. R. Humphrey. 2001. Conservation value of private lands for Crested Caracaras in Florida. *Conservation Biology* 15:675–684.
- Mortimore, M., and B. Turner. 2005. Does the Sahelian smallholder's management of woodland, farm trees, rangeland support the hypothesis of human-induced desertification? *Journal of Arid Environments* 63:567–595.
- Mosier, A., R. Wassmann, L. Verchot, J. King, and C. Palm. 2004. Methane and nitrogen oxide fluxes in tropical agricultural soils: sources, sinks and mechanisms. *Environment, Development and Sustainability* 6:11–49.
- Nash, D. M., R. W. McDowell, L. M. Condrón, and M. J. McLaughlin. 2019. Direct exports of phosphorus from fertilizers applied to grazed pastures. *Journal of Environmental Quality* 48:1380–1396.
- Noss, R. F. 2012. *Forgotten grasslands of the South: natural history and conservation*. Island Press, Washington DC, USA.
- Noss, R. E. 2018. *Fire ecology of Florida and the southeastern coastal plain*. University Press of Florida, Gainesville, Florida, USA.

- O'Connor, T. G. 2005. Influence of land use on plant community composition and diversity in Highland Sourveld grassland in the southern Drakensberg, South Africa. *Journal of Applied Ecology* 42:975–988.
- Oenema, O., C. de Klein, and M. Alfaro. 2014. Intensification of grassland and forage use: driving forces and constraints. *Crop and Pasture Science* 65:524–537.
- Ohwaki, A. 2019. Entire-area spring burning versus abandonment in grasslands: butterfly responses associated with hibernating traits. *Journal of Insect Conservation* 23:857–871.
- O'Mara, F. P. 2012. The role of grasslands in food security and climate change. *Annals of Botany* 110:1263–1270.
- Osmond, D., D. Meals, D. Hoag, M. Arabi, A. Luloff, G. Jennings, M. McFarland, J. Spooner, A. Sharpley, and D. Line. 2012. Improving conservation practices programming to protect water quality in agricultural watersheds: lessons learned from the National Institute of Food and Agriculture-Conservation Effects Assessment Project. *Journal of Soil and Water Conservation* 67:122A–712A.
- Owens, L. B., W. M. Edwards, and R. W. Van Keuren. 1994. Groundwater nitrate levels under fertilized grass and grass-legume pastures. *Journal of Environmental Quality* 23:752–758.
- Paredes, S. S., N. P. Stritzler, A. Bono, and R. A. Distel. 2018. Perennial warm-season grass monocultures and mixtures: biomass production and soil improvement in semiarid and shallow soil conditions. *Journal of Arid Environments* 154:82–88.
- Parr, C. L., C. E. Lehmann, W. J. Bond, W. A. Hoffmann, and A. N. Andersen. 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. *Trends in Ecology & Evolution* 29:205–213.
- Pausas, J. G., and J. E. Keeley. 2019. Wildfires as an ecosystem service. *Frontiers in Ecology and the Environment* 17:289–295.
- Pausas, J. G., B. B. Lamont, S. Paula, B. Appezzato-da-Glória, and A. Fidelis. 2018. Unearthing below-ground bud banks in fire-prone ecosystems. *New Phytologist* 217:1435–1448.
- Paustian, K., O. Andrén, H. H. Janzen, R. Lal, P. Smith, G. Tian, H. Tiessen, M. Van Noordwijk, and P. L. Woomer. 1997. Agricultural soils as a sink to mitigate CO<sub>2</sub> emissions. *Soil Use and Management* 13:230–244.
- Pejchar, L., Y. Clough, J. Ekroos, K. A. Nicholas, O. Olsson, D. Ram, M. Tschumi, and H. G. Smith. 2018. Net effects of birds in agroecosystems. *BioScience* 68:896–904.
- Pilon, C., P. A. Moore Jr., D. H. Pote, J. W. Martin, P. R. Owens, A. J. Ashworth, D. M. Miller, and P. B. DeLaune. 2019. Grazing management and buffer strip impact on nitrogen runoff from pastures fertilized with poultry litter. *Journal of Environmental Quality* 48:297–304.
- Pimentel, D., L. Lach, R. Zuniga, and D. Morrison. 2000. Environmental and economic costs of nonindigenous species in the United States. *BioScience* 50:53–65.
- Plantureux, S., A. Peeters, and D. McCracken. 2005. Biodiversity in intensive grasslands: effect of management, improvement and challenges. *Agronomy Research* 3:153–164.
- Poeplau, C., D. Zopf, B. Greiner, R. Geerts, H. Korvaar, U. Thumm, A. Don, A. Heidkamp, and H. Flessa. 2018. Why does mineral fertilization increase soil carbon stocks in temperate grasslands? *Agriculture, Ecosystems & Environment* 265:144–155.
- Power, A. G. 2010. Ecosystem services and agriculture: tradeoffs and synergies. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 365:2959–2971.
- Rabalais, N. N., R. E. Turner, and W. J. Wiseman Jr. 2002. Gulf of Mexico hypoxia, aka “The dead zone”. *Annual Review of Ecology and Systematics* 33:235–263.
- Ramankutty, N., A. T. Evan, C. Monfreda, and J. A. Foley. 2008. Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. *Global Biogeochemical Cycles* 22:GB002952.
- Raudsepp-Hearne, C., G. D. Peterson, and E. M. Bennett. 2010. Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 107:5242–5247.
- Rotz, C. A., B. J. Isenberg, K. R. Stackhouse-Lawson, and E. J. Pollak. 2013. A simulation-based approach for evaluating and comparing the environmental footprints of beef production systems. *Journal of Animal Science* 91:5427–5437.
- Ryder, M. L. 1983. *Sheep and man*. Duckworth, London, UK.
- Saarijärvi, K., P. Virkajärvi, and H. Heinonen-Tanski. 2007. Nitrogen leaching and herbage production on intensively managed grass and grass-clover pastures on sandy soil in Finland. *European Journal of Soil Science* 58:1382–1392.
- Sanderson, M. A., R. H. Skinner, D. J. Barker, G. R. Edwards, B. F. Tracy, and D. A. Wedin. 2004. Plant species diversity and management of temperate forage and grazing land ecosystems. *Crop Science* 44:1132–1144.
- Sankaran, M., and D. J. Augustine. 2004. Large herbivores suppress decomposer abundance in a semi-arid grazing ecosystem. *Ecology* 85:1052–1061.

- Saul, G., G. Kearney, and D. Borg. 2011. Pasture systems to improve productivity of sheep in south-western Victoria 2. Animal production from ewes and lambs. *Animal Production Science* 51:982–989.
- Scasta, J. D., T. Jorns, J. D. Derner, B. Stam, M. McClaren, C. Calkins, and W. Stewart. 2020. Toxic plants in sheep diets grazing extensive landscapes: insights from Fecal DNA metabarcoding. *Livestock Science* 236:104002.
- Searchinger, T., R. Heimlich, R. A. Houghton, F. Dong, A. Elobeid, J. Fabiosa, S. Tokgoz, D. Hayes, and T. H. Yu. 2008. Use of US croplands for biofuels increases greenhouse gases through emissions from land-use change. *Science* 319:1238–1240.
- Shackleton, C. M., S. Ruwanza, G. S. Sanni, S. Bennett, P. De Lacy, R. Modipa, N. Mtati, M. Sachikonye, and G. Thondhlana. 2016. Unpacking Pandora's box: understanding and categorising ecosystem disservices for environmental management and human wellbeing. *Ecosystems* 19:587–600.
- Silveira, M. L., S. Xu, J. Adewopo, A. J. Franzluebbbers, and G. Buonadio. 2014. Grazing land intensification effects on soil C dynamics in aggregate size fractions of a Spodosol. *Geoderma* 230:185–193.
- Sollenberger, L. E., M. M. Kohmann, J. C. Dubeux, and M. L. Silveira. 2019. Grassland management affects delivery of regulating and supporting ecosystem services. *Crop Science* 59:441–459.
- Soussana, J. F., T. Tallec, and V. Blanfort. 2010. Mitigating the greenhouse gas balance of ruminant production systems through carbon sequestration in grasslands. *Animal* 4:334–350.
- Spiegel, S., et al. 2018. Evaluating strategies for sustainable intensification of US agriculture through the Long-Term Agroecosystem Research network. *Environmental Research Letters* 13:034031.
- Steiner, J. L., A. J. Franzluebbbers, and C. L. Neely. 2009. Expanding horizons of farming with grass. Pages 216–234 in A. J. Franzluebbbers, editor. *Farming with grass: achieving sustainable mixed agricultural landscapes*. Soil Water Conservation Society, Ankeny, Iowa, USA.
- Steiner, J. L., A. J. Franzluebbbers, C. Neely, T. Ellis, and E. Aynekulu. 2014. Enhancing soil and landscape quality in smallholder grazing systems. Pages 63–104 in R. Lal, and B. A. Stewart, editors. *Soil management of smallholder agriculture*. Advances in Soil Science Series. CRC Press, Boca Raton, Florida, USA.
- Sutter, L., P. Jeanneret, A. M. Bartual, G. Bocci, and M. Albrecht. 2017. Enhancing plant diversity in agricultural landscapes promotes both rare bees and dominant crop-pollinating bees through complementary increase in key floral resources. *Journal of Applied Ecology* 54:1856–1864.
- Suttie, J. M., S. G. Reynolds, and C. Batello. 2005. *Grasslands of the world*. Food & Agriculture Organization of the United Nations, Rome, Italy.
- Swain, H. M., E. H. Boughton, P. J. Bohlen, and L. L. O'Gene. 2013. Trade-offs among ecosystem services and disservices on a Florida ranch. *Rangelands* 35:75–87.
- Swengel, A. B. 1996. Effects of fire and hay management on abundance of prairie butterflies. *Biological Conservation* 76:73–85.
- Tilman, D., K. G. Cassman, P. A. Matson, R. Naylor, and S. Polasky. 2002. Agricultural sustainability and intensive production practices. *Nature* 418:671–677.
- Tilman, D., J. Fargione, B. Wolff, C. D'Antonio, A. Dobson, R. Howarth, D. Schindler, W. H. Schlesinger, D. Simberloff, and D. Swackhamer. 2001. Forecasting agriculturally driven global environmental change. *Science* 292:281–284.
- Tilman, D., J. Hill, and C. Lehman. 2006. Carbon-negative biofuels from low-input high-diversity grassland biomass. *Science* 314:1598–1600.
- Toledo, D., M. Sanderson, K. Spaeth, J. Hendrickson, and J. Printz. 2014. Extent of Kentucky bluegrass and its effect on native plant species diversity and ecosystem services in the Northern Great Plains of the United States. *Invasive Plant Science and Management* 7:543–552.
- Tscharntke, T., A. M. Klein, A. Kruess, I. Steffan-Dewenter, and C. Thies. 2005. Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecology Letters* 8:857–874.
- van der Heijden, M. G., J. N. Klironomos, M. Ursic, P. Moutoglou, R. Streitwolf-Engel, T. Boller, A. Wiemken, and I. R. Sanders. 1998. Mycorrhizal fungal diversity determines plant biodiversity ecosystem variability and productivity. *Nature* 396:69–72.
- Van Vooren, L., B. Reubens, S. Broekx, D. Reheul, and K. Verheyen. 2018. Assessing the impact of grassland management extensification in temperate areas on multiple ecosystem services and biodiversity. *Agriculture, Ecosystems and Environment* 267:201–212.
- Vickery, J. A., J. R. Tallwin, R. E. Feber, E. J. Asteraki, P. W. Atkinson, R. J. Fuller, and V. K. Brown. 2001. The management of lowland neutral grasslands in Britain: effects of agricultural practices on birds and their food resources. *Journal of Applied Ecology* 38:647–664.
- Wagg, C., M. J. O'Brien, A. Vogel, M. Scherer-Lorenzen, N. Eisenhauer, B. Schmid, and A. Weigelt. 2017. Plant diversity maintains long-term ecosystem productivity under frequent drought by increasing short-term variation. *Ecology* 98:2952–2961.

- Wagg, C., K. Schlaeppli, S. Banerjee, E. F. Kuramae, and M. G. A. van der Heijden. 2019. Fungal-bacterial diversity and microbiome complexity predict ecosystem functioning. *Nature Communications* 10:4841.
- Wang, C., D. Liu, and E. Bai. 2018. Decreasing soil microbial diversity is associated with decreasing microbial biomass under nitrogen addition. *Soil Biology and Biochemistry* 120:126–133.
- Wang, K. H., R. McSorley, P. Bohlen, and S. M. Gathumbi. 2006. Cattle grazing increases microbial biomass and alters soil nematode communities in subtropical pastures. *Soil Biology and Biochemistry* 38:1956–1965.
- Werling, B. P., et al. 2014. Perennial grasslands enhance biodiversity and multiple ecosystem services in bioenergy landscapes. *Proceedings of the National Academy of Sciences of the United States of America* 111:1652–1657.
- White, R. P., S. Murray, and M. Rohweder. 2000. Grassland ecosystems pilot analysis of global ecosystems. World Resources Institute, Washington, DC, USA.
- Williams, D. G., and Z. Baruch. 2000. African grass invasion in the Americas: ecosystem consequences and the role of ecophysiology. *Biological Invasions* 2:123–140.
- Wilson, C. H., M. S. Strickland, J. A. Hutchings, T. S. Bianchi, and S. L. Flory. 2018. Grazing enhances belowground carbon allocation, microbial biomass, and soil carbon in a subtropical grassland. *Global Change Biology* 24:2997–3009.
- Wilson, G. W. T., C. W. Rice, M. C. Rillig, A. Springer, and D. C. Hartnett. 2009. Soil aggregation and carbon sequestration are tightly correlated with the abundance of arbuscular mycorrhizal fungi: results from long-term field experiments. *Ecology Letters* 12:452–461.
- Xu, S., M. L. Silveira, L. E. Sollenberger, P. Viegas, J. J. Lacerda, and M. V. Azenha. 2018. Conversion of native rangelands into cultivated pasturelands in subtropical ecosystems: impacts on aggregate-associated carbon and nitrogen. *Journal of Soil & Water Conservation* 73:156–163.
- Yang, Y., D. Tilman, G. Furey, and C. Lehman. 2019. Soil carbon sequestration accelerated by restoration of grassland biodiversity. *Nature Communications* 10:1–7.
- Zhang, W., T. H. Ricketts, C. Kremen, K. Carney, and S. M. Swinton. 2007. Ecosystem services and dis-services to agriculture. *Ecological Economics* 64:253–260.
- Zhou, J., G. W. T. Wilson, A. B. Cobb, G. Yang, and Y. Zhang. 2019a. Phosphorus and mowing improve native alfalfa establishment, facilitating restoration of grassland productivity and diversity. *Land Degradation & Development* 30:647–657.
- Zhou, J., F. Zhang, Y. Huo, G. W. Wilson, A. B. Cobb, X. Xu, X. Xiong, L. Liu, and Y. Zhang. 2019b. Following legume establishment, microbial and chemical associations facilitate improved productivity in degraded grasslands. *Plant and Soil* 443:273–292.
- Zografou, K., M. T. Swartz, V. P. Tilden, E. N. McKinney, J. A. Eckenrode, and B. J. Sewall. 2020. Stable generalist species anchor a dynamic pollination network. *Ecosphere* 11:e03225.

## SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3837/full>