esa ECOSPHERE

SYNTHESIS & INTEGRATION

Grasslands—more important for ecosystem services than you might think

J. Bengtsson,[1,2,]† J. M. Bullock,[3] B. Egoh,[4,5] C. Everson,[6] T. Everson,[7] T. O'Connor,[8] P. J. O'Farrell,[5,9] H. G. Smith,[10,11] and R. Lindborg[2,12]

[1]*Department of Ecology, Swedish University of Agricultural Sciences (SLU), Box 7044, SE-75007 Uppsala, Sweden*
[2]*Stellenbosch Institute for Advanced Study (STIAS), Wallenberg research centre at Stellenbosch University, Marais Street, Stellenbosch 7600 South Africa*
[3]*NERC Centre for Ecology & Hydrology, Benson Lane, Wallingford, Oxfordshire OX10 8BB UK*
[4]*Department of Earth System Science, University of California Irvine, Irvine, California 92697 USA*
[5]*Natural Resources and the Environment, CSIR, P.O. Box 320, Stellenbosch 7599 South Africa*
[6]*Centre for Water Resources Research, School of Agriculture, Earth and Environmental Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg 3209 South Africa*
[7]*School of Life Sciences, University of KwaZulu-Natal, Private Bag X01, Scottsville, Pietermaritzburg 3209 South Africa*
[8]*South African Environmental Observation Network, PO Box 2600, Pretoria 0001, South Africa*
[9]*Percy FitzPatrick Institute of African Ornithology, University of Cape Town, Private Baf X3, Rondebosch 7701, Cape Town, South Africa*
[10]*Department of Biology, Lund University, SE-223 62 Lund, Sweden*
[11]*Centre for Environmental and Climate research, Lund University, SE-223 62 Lund, Sweden*
[12]*Department of Physical Geography, Stockholm University, SE-106 91 Stockholm, Sweden*

Citation: 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(2):e02582. 10.1002/ecs2.2582

Abstract. Extensively managed grasslands are recognized globally for their high biodiversity and their social and cultural values. However, their capacity to deliver multiple ecosystem services (ES) as parts of agricultural systems is surprisingly understudied compared to other production systems. We undertook a comprehensive overview of ES provided by natural and semi-natural grasslands, using southern Africa (SA) and northwest Europe as case studies, respectively. We show that these grasslands can supply additional non-agricultural services, such as water supply and flow regulation, carbon storage, erosion control, climate mitigation, pollination, and cultural ES. While demand for ecosystems services seems to balance supply in natural grasslands of SA, the smaller areas of semi-natural grasslands in Europe appear to not meet the demand for many services. We identified three bundles of related ES from grasslands: water ES including fodder production, cultural ES connected to livestock production, and population-based regulating services (e.g., pollination and biological control), which also linked to biodiversity. Greenhouse gas emission mitigation seemed unrelated to the three bundles. The similarities among the bundles in SA and northwestern Europe suggest that there are generalities in ES relations among natural and semi-natural grassland areas. We assessed trade-offs and synergies among services in relation to management practices and found that although some trade-offs are inevitable, appropriate management may create synergies and avoid trade-offs among many services. We argue that ecosystem service and food security research and policy should give higher priority to how grasslands can be managed for fodder and meat production alongside other ES. By integrating grasslands into agricultural production systems and land-use decisions locally and regionally, their potential to contribute to functional landscapes and to food security and sustainable livelihoods can be greatly enhanced.

Key words: biodiversity; Europe; food security and agricultural production systems; grassland biome; semi-natural grasslands; South Africa.

Received 27 May 2018; revised 6 November 2018; accepted 12 November 2018; final version received 20 December 2018. Corresponding Editor: Debra P. C. Peters.

† **E-mail:** Jan.Bengtsson@slu.se

Introduction

Grasslands are one of the major ecosystems of the world, covering close to one-third of the Earth's terrestrial surface (Suttie et al. 2005, Lemaire et al. 2011). Extensively managed grasslands are recognized globally for their high biodiversity (Habel et al. 2013), and together with other rangelands, they often contribute to agricultural production through livestock grazing on forage that cannot be used directly by humans (Erb et al. 2016). Three major types of grasslands can be distinguished within agricultural production systems: natural, semi-natural, and improved grasslands (Bullock et al. 2011, Lemaire et al. 2011). Natural grasslands forming the grassland biomes are natural areas mainly created by processes related to climate, fire, and wildlife grazing (Parr et al. 2014), but are also used by livestock. Semi-natural grasslands are the product of human management, require livestock grazing or hay-cutting for their maintenance, and will generally be encroached by shrubs and trees if taken out of production (Queiroz et al. 2014). Improved grasslands are pastures resulting from plowing and sowing agricultural varieties or non-native grasses with high production potential. They are usually artificially fertilized and maintained by intensive management (Suttie et al. 2005, Pilgrim et al. 2010). We focus on the former two types of grasslands, because of their importance for biodiversity, their decline in area worldwide, and the fact that their full capacity to deliver ecosystem services (ES) as part of agricultural production systems is not well appreciated.

Natural and semi-natural grasslands, hereafter collectively called grasslands, have played an important role in people's livelihoods for millennia as areas producing fodder for animals (Emanuelsson 2009). Despite an increasing demand for animal products due to a growing human population and increased per capita consumption of these products, the requirement for greater meat and dairy production is not leading to an increase in grassland areas used for grazing but is being met rather by the production of fodder on cropland and improved grasslands (Naylor et al. 2005, Erb et al. 2016). Competition for land and other resources for agriculture is predicted to increase considerably by 2050 (FAO 2009, Smith et al. 2010), accentuated by ongoing climate change (Harvey and Pilgrim 2011, Röös et al. 2017). This has led to an increased focus on food production and food security in science and policy (e.g., Godfray et al. 2010, Foley et al. 2011, SCAR 2011, Poppy et al. 2014), often invoking the concept of sustainable intensification, in terms of the increase of food production on existing cropland (e.g., Godfray et al. 2010, Garnett et al. 2013). However, these discussions usually neglect the role grasslands might play for food security (but see, e.g., Kemp and Michalk 2011, O'Mara 2012).

Grasslands have declined worldwide during the last century (Egoh et al. 2016), mainly due to conversion to arable land for production of animal feed crops and, conversely, lack of management and abandonment (Queiroz et al. 2014). In southern Africa (SA), more than 20% of the grassland biome has been cultivated, 60% is irreversibly transformed to other land uses (Fairbanks et al. 2000), and most of the remainder is used as rangeland for livestock (O'Connor and Bredenkamp 1997). Over 90% of the semi-natural grasslands in northern Europe have been lost since the 1930s (Eriksson et al. 2002, Bullock et al. 2011, Pe'er et al. 2014). In North America, 80% of the central grasslands has been converted to cropland (Foley et al. 2005, Suttie et al. 2005). Similarly, more than 43 million hectares of the Eurasian steppe have been converted into cropland, and 60–80% of the grassland area in South America is degraded (Suttie et al. 2005).

Besides having a high conservation value and supporting food production, grasslands may also be important contributors of ES (Sala and Paruelo 1997, Pilgrim et al. 2010, Bullock et al. 2011, Lemaire et al. 2011, Lavorel et al. 2013, Werling et al. 2014, Burrascano et al. 2016, Modernel et al. 2016). However, grasslands have remained under-appreciated in the framework of ES

(Frélichová et al. 2014; see Appendix S1), and sometimes, grasslands have been combined with other rangelands that include shrubland, deserts and savannas (e.g., Sala et al. 2017). Similarly, grasslands have received substantially less attention in the multiple ES framework compared to other production systems, such as forest (Gamfeldt et al. 2013) and cropland (Robertson et al. 2014; Appendix S1). Grasslands have also been largely neglected in global policy discussions concerning ES (e.g., IPBES, Diaz et al. 2015, Pascual et al. 2017; see also Parr et al. 2014, Bond 2016), despite having been highlighted regionally in, for example, South Africa (Reyers et al. 2005, Turpie et al. 2008, Egoh et al. 2016) and the UK (Bullock et al. 2011). Not only do grasslands have a local importance for the maintenance of biodiversity and food production, but they also affect ecological processes at landscape (e.g., pollination), regional (e.g., water regulation, recreation), and global scales (e.g., climate regulation).

To understand the full potential for grasslands to deliver ES to society locally, regionally and globally, both ES supply (the capacity of an ecosystem to produce a service) and demand (the societal demand for a service) must be acknowledged (Lamarque et al. 2011), as well as synergies and trade-offs among ES (Bennett et al. 2009). However, most studies of ES do not distinguish between supply and demand (Burkhard et al. 2012, Yahdjian et al. 2015). Demand for an ES can change independently of its supply, and supply can change without altered demand. For example, the supply of water for irrigation can change irrespective of the demand from different stakeholders (farmers, conservation managers). The supply can come from different ecosystems (e.g., grassland ecosystems supply water for forage production while forest ecosystems supply drinking water; Yahdjian et al. 2015).

To provide a more detailed analysis of the ES, grasslands provide as parts of agricultural production systems, and how these systems vary in ES delivery depending on the existence and management of grasslands, we focus on the natural and semi-natural grasslands in two contrasting regions as case studies: (1) the natural grassland biome of SA and (2) the semi-natural grasslands in northwestern Europe (NE; Fig. 1). We provide an overview of the demand in society for multiple ES that can be supplied by grasslands in the two regions, and how grasslands contribute to their supply at local and regional scales. Specifically, we examine the following: (1) the general demand for a selected number of ES that can be supplied from grassland, and the extent to which supply from grassland may meet societal demands (Table 1), (2) synergies and trade-offs among grassland ES, (3) the role of biodiversity in generating these ES, and (4) how to use this knowledge to improve land-use planning and enhance food security in the face of ongoing global change.

Methods

To structure our analyses, a workshop was organized at STIAS (Stellenbosch Institute of Advanced Study) in South Africa, at which invited grassland experts (i.e., the authors) identified the major issues concerning the role of grasslands in supplying important ES. There is a wide range of typologies of ES in the literature. In our analysis, the categorization of ES was modified from the Millennium Ecosystem Assessment (MA; 2005), TEEB (2010), and the UK NEA (2011; see Table 1). For each case (NE and SA), we estimated the demand in society for ES produced in grasslands, and the supply of those ES from grasslands, on a three-level ordinal scale (low, medium, and high; Table 1). We also identified knowledge gaps based on the two regional case studies. The analysis was based on discussions and deliberations to provide a balanced and consensual judgment. Subsequently, data on these grasslands, as well as others worldwide, were obtained through a thorough survey of the scientific literature, including some of the gray literature (Sections about provisioning, regulating, and cultural services, below; Appendix S1). Since this survey focused on obtaining data on the potential of grasslands to supply the different ES, it allowed a closer scrutiny and in some cases a re-assessment of the initial results from the workshop. We did not implement a systematic review methodology because we did not have a simple set of questions. When data were available and it was relevant, we also compared ES supply from grasslands with that from other ecosystems, including forest and cropland. By combining the literature overview with expert opinion, we were able to crosscheck conclusions

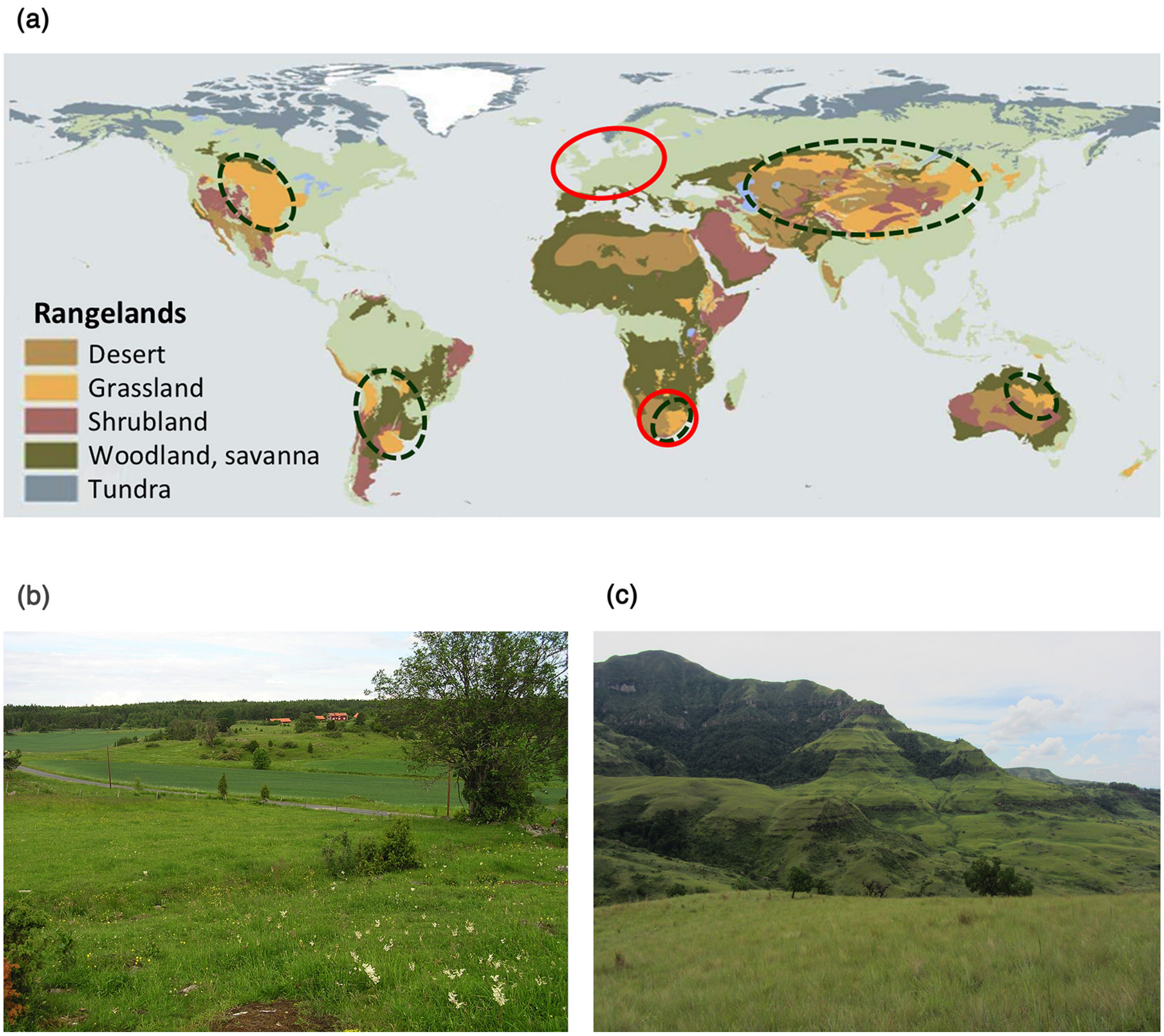

Fig. 1. (a) The global distribution of grasslands and rangelands (map modified from Wikipedia https://en.wikipedia.org/wiki/File:Rangeworld545.png; open source). The green dashed circles show the major grassland biomes, while the red circles show the two selected study regions northern Europe representing semi-natural grasslands (b) and southern Africa, representing natural grasslands (c). (b) Semi-natural grasslands in Sweden (photo R. Lindborg). (c) A natural grassland area in South Africa (photo J. Bengtsson).

from different sources to search for general trends and regularities (termed triangulation in the social sciences, e.g., O'Donoghue and Punch 2003).

We made an assessment of the discrepancy between supply and demand of ES for each case by plotting supply (x) vs. demand (y) using the three-level ordinal scale and counting the number of cases where demand was higher, similar to, or lower than supply. Whether the assessed distribution across the three categories differed between the two cases was tested by a G-test with William's correction for small sample sizes.

Ecosystem services that co-vary spatially (Raudsepp-Hearne et al. 2010) and are related either because they are based on the same ecosystem processes or are influenced by similar management or environmental drivers, are termed bundles (Bennett et al. 2009). By combining expert knowledge from the workshop and the literature, we identified potential pairwise relationships between grassland ES, and subsequently,

Table 1. Relative evaluation of supply and demand of ecosystem services from grasslands in northern Europe (NE) and southern Africa (SA).

Ecosystem service group	Ecosystem service category	Ecosystem service	Demand from society			Supply from grasslands			Other remarks
			NE	SA	Comment	NE	SA	Comment	
Water services	Provisioning	Water quantity	H	H	In general, both quality and quantity	L	H	Related to area of grasslands	
	Provisioning	Water quality	H	H		M	H		
	Regulating	Water flow regulation	H	H	In SA, both flow regulation and base flow	M	H		
Climate regulation	Regulating	C-sequestration C-storage (soil organic matter) Mitigation of greenhouse gas fluxes	M	L	In NE, payments for C-sequestration and C-trading exist, but not in SA. Therefore, M and L demand, respectively, because there is still little real political commitment to climate change mitigation that would indicate high demand from society. Political decisions are often taken that conflict with climate regulation agreements, which still are weak and ineffective in themselves	M	H		The climate regulation services were combined because they are difficult to examine separately. Several are also related to water and soil services.
Erosion prevention	Regulating		L–H	H	In NE, demand is locally high	L–H	H	In NE, potential supply varies locally	

we identified such bundles as well as possible synergies and trade-offs between ES from grasslands (Appendix S3). This was done by constructing matrices describing correlations among the ES in each of the two case studies (Appendix S3: Table S1a–b). Cluster and factor analyses were carried out on data based on the literature reviewed (Appendix S3) to explore whether our assessment of ES could identify such bundles. It was assumed that the services are to some degree produced locally in a landscape and hence to some degree spatially correlated (see Lindborg et al. 2017 for further discussion on this assumption).

(Table 1. Continued.)

Ecosystem service group	Ecosystem service category	Ecosystem service	Demand from society			Supply from grasslands			Other remarks
			NE	SA	Comment	NE	SA	Comment	
Plant biomass production	Provisioning								Fodder provides the basis for ecosystem services related to livestock production
	Provisioning	Meat production	H	H	Demand for meat in general high	L	H		
	Provisioning	Dairy	H	H	Demand for dairy is in general high, but demand explicitly from grasslands often L-M	L	M		
	Provisioning	Wool, hides	M	M		L	H		
Other products	Provisioning	Medicinal plants	L	H		0	M		
	Provisioning	Materials	L	H		0	M		
	Provisioning	Wild foods	L	L		L	L		
Agricultural crop yield	Regulating	Pollination of crop plants	H	M		M	M	Knowledge/ data on specific contribution from natural and semi-natural grasslands is insufficient	
	Regulating	Biological control of pests	H	H		M	M		
Cultural services	Cultural	Tourism and recreation	H	H		M	M		
	Cultural	Hunting	H	M		L	M		
	Cultural	Heritage Spiritual Social cohesion	M	M		H	M		
	Cultural	Cultural aspects of cattle	L	H		L	M–H		
	Cultural	Scientific	M	M		H	H		

Notes: Supply/demand as assessed by the experts on the workshop: L=low, M=medium, H=high. Ecosystem service categorization was based on the MA framework (MA, 2005), the Economics of Ecosystem and Biodiversity (TEEB, 2010), and the UK NEA (2011) typologies (see also CICES, Haines-Young and Potschin 2013). Three categories (sections) of services were used: provisioning (direct services, UK NEA), regulating (regulating and supporting, MA; indirect, UK NEA; regulation and maintenance, CICES), and cultural.

Analysis and Overview of Results

Supply and demand of ES

The estimated demand for different ES that can be supplied from grasslands varied from high to low across the two regions (Table 1). Our analysis suggests that in NE, the estimated demand for ES that can be obtained from grasslands was often higher than the estimated supply from grasslands, while in SA, demand was usually similar to supply, with no trend toward higher or lower demand vs. supply (Fig. 2). This likely reflects the great decreases in semi-natural and natural grasslands in NE. It suggests that policies to increase the area of grasslands and manage them to enhance ES would meet a demand from society in developed regions such as NE and North America. In contrast, the finding that societal demand for ES in SA was often matched by supply from grasslands suggests that here more emphasis should be on improving management of existing grasslands and development of policies mitigating their decrease and degradation. This seems especially important given the likelihood that SA will become hotter and drier with climate change (e.g., Collier et al. 2008), and the increasing pressure on land as human populations grow (e.g., Holden and Otsuka 2014).

The demands for water supply (quantity, quality, and flow regulation), livestock products, agricultural production-related services, and recreation were generally high in both SA and NE. Demand for other services differed between regions, for example, wild food, materials, and medicinal plants being low in NE and high in SA compared to hunting and animal-mediated pollination, which were higher in NE (Schulp et al. 2012, Bommarco et al. 2013, Schulp et al. 2014; Table 1). Climate change affects humans globally. However, although payment systems for mitigating climate change and decreasing greenhouse gases have been widely discussed, for example, REDD+ and CDM for forests (Jackson et al. 2008), the efficiency of these systems in grasslands has been questioned (Parr et al. 2014). Thus, the actual political, as well as the general, demand for climate regulation from grasslands seems presently low in NE and almost nil in SA. This demand may increase if the agreements on the Paris climate meeting in 2015 are indeed translated into stricter and more effective policies for climate change mitigation by 2020 (European Commission 2018; it has, however, been questioned whether the Paris agreement will be effective in keeping climate change below +2°, e.g., Anderson 2015). Table 1 compiles estimates of the general demand for specific ES in the two regions and how they may be met by supply.

That grasslands can supply a large number of provisioning, supporting, and cultural ES was evident for both NE and SA (Table 1; see sections below for details). Most important among these are services related to water, such as water quantity and flow regulation, erosion control, and carbon storage, and in SA also meat, wool, and hide

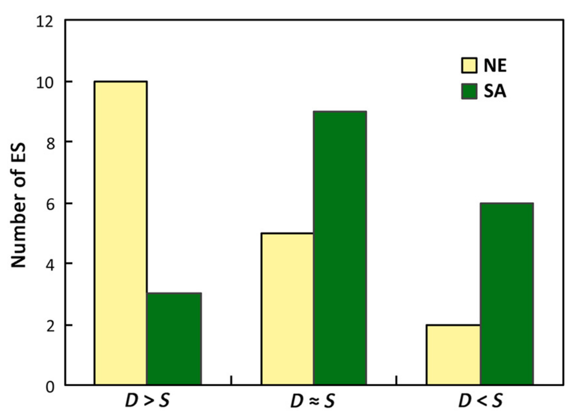

Fig. 2. The number of ecosystem services (ES) where demand (D) was assessed to be higher, similar or lower than supply (S) in northern Europe (NE; yellow) vs. southern Africa (SA; green). The figure is based on the assessments of demand and supply of ES in Table 1. The distributions differ significantly between the two areas (*G*-test, $G_{adj} = 6.78$, $P < 0.05$, df = 2), with NE having significantly more services where demand was assessed as higher than supply than expected by chance: sign tests: $P = 0.02$, SA: $P = 0.26$, excluding D≈S). Note: This tests if the assessments differ between the two areas, not whether there is a real difference.

production (Table 1). The supply of the three latter ES in NE is likely limited because of the small areas of semi-natural grasslands presently used for animal production. Cultural aspects of grasslands are of intermediate to large importance in both SA and NE. Grasslands may contribute to, for example, cultural heritage, social cohesion, and recreation (Table 1). However, in many cases the specific contribution of grasslands, rather than open landscapes in general, to cultural values has not been clarified. Similarly, there are surprisingly few studies explicitly relating grasslands to ES contributing to agricultural yield, that is, biological control or pollination, despite the large number of studies on how these ES are enhanced by semi-natural habitats in agricultural landscapes in Europe.

Biodiversity and grassland ecosystem services

Based on the literature, we find surprisingly little evidence that the high small-scale biodiversity found in natural and semi-natural grasslands is strongly related to the supply of ES (Appendix S2: Table S1). Grasslands have been playing a prominent role in biodiversity–ecosystem functioning research. However, most of this research is from synthetic grassland experiments, and apart from effects on biomass production, the importance of biodiversity, especially of high local species richness beyond 10 species, remains to be examined for most grassland ES (see Bullock et al. 2011). Water services and erosion control are mainly dependent on vegetation, where structure, complementarity in function and traits of specific plant species, is more important than species richness. This is also likely the case for the processes involved in carbon sequestration and storage. Soil processes usually depend on functional diversity of soil organisms (Setälä 2002, Wardle et al. 2011), but not species richness per se. However, the different processes involved in climate regulation are carried out by functionally different sets of species, indicating that a larger number of functional groups and thus species may be needed for multiple than for single ES (Gamfeldt et al. 2008).

Increased plant diversity often results in enhanced biomass production in experimental grasslands (e.g., Hector et al. 1999, Tilman et al. 2001, Bullock et al. 2007). In most of these cases, the species involved are common and not of high conservation value. However, Lyons et al. (2005) made a case for rare species having an effect on ecosystem functioning. There are very few studies specially examining this for grasslands, but Mouillot et al. (2013) found evidence for this among alpine grassland plants. The role of rare species and high biodiversity for ES is thus unresolved and may be more related to stability and resilience of ES delivery than to process rates (e.g., Elmqvist et al. 2003, Loreau et al. 2003) or to ecosystem multifunctionality (Soliveres et al. 2016).

Bundles of ecosystem services

Our exploratory analysis identified three bundles of ES that were similar in the two areas (Fig. 3). One bundle was dominated by water ES and also included the key grassland ES fodder production. A number of cultural ES that are connected to livestock production, for example, tourism and social coherence, formed a second bundle. This bundle encompassed more services in SA than in NE; in SA, it also included use of medicinal plants, wild food, and materials. Meat production linked to the water services bundle in SA, whereas it linked to cultural services in NE. A third bundle consisted of the regulating services pollination and biological control, which are not directly linked to fodder and livestock production. These were also linked to biodiversity. A fourth group of ES was mainly defined by the lack of relatedness to other services, both within the group and with the three bundles. In SA, this group only included mitigation of greenhouse gas (GHG) emissions. In NE, it included mitigation of GHG emissions, wild foods and materials, medicinal plants, and hunting.

The similarities among the bundles in SA and NE suggest that there are generalities in ES relations among natural and semi-natural grassland areas. Specifically, (1) water services and carbon storage, (2) cultural ES, and (3) population-based and biodiversity-related services could be identified in both areas. The ES found within each bundle are likely to be suitable to manage together. However, we emphasize that empirical data on ecosystem service relationships in grasslands are needed to confirm these findings, as done by Birkhofer et al. (2018) for arable fields.

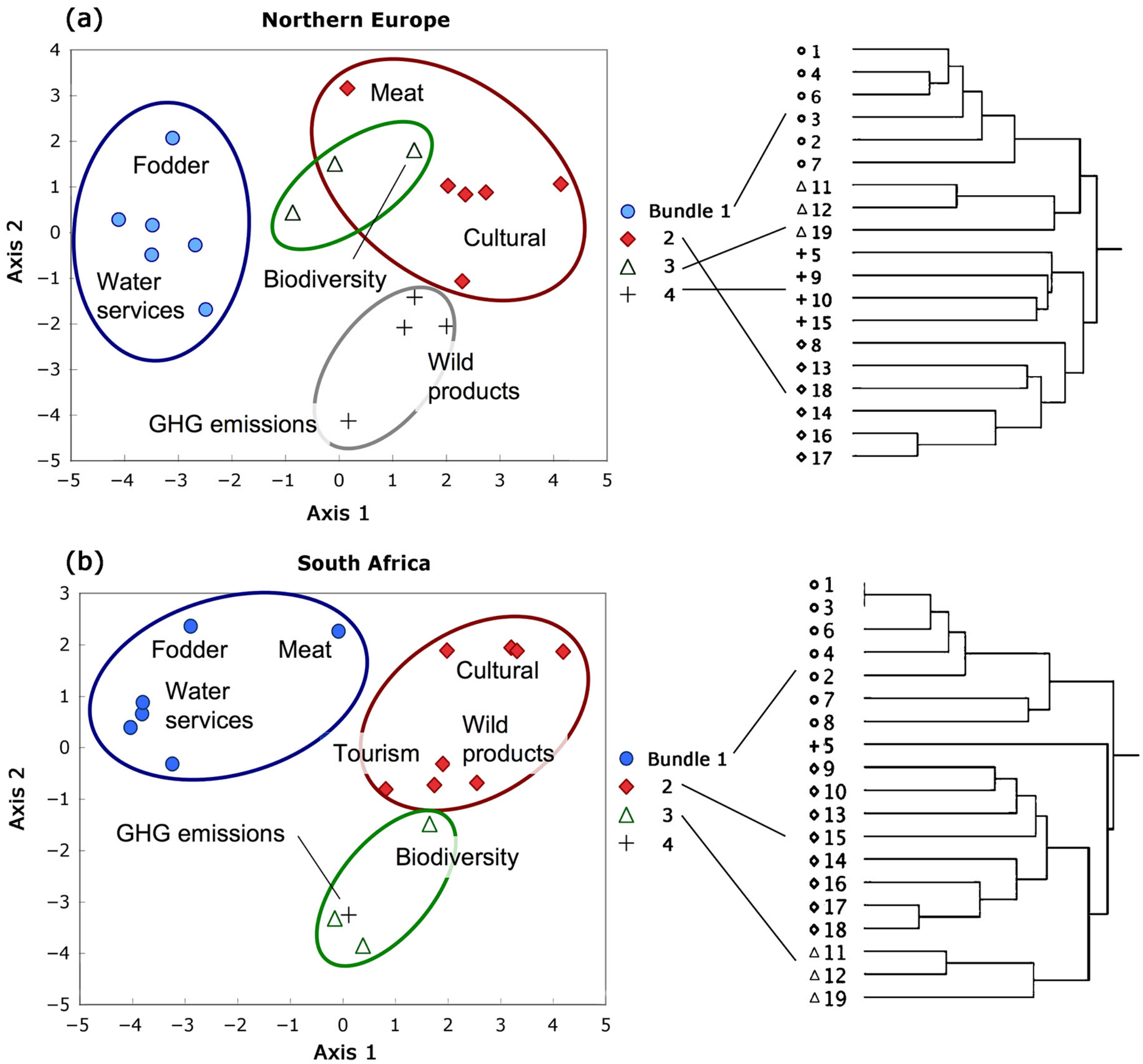

Fig. 3. Bundles of ecosystem services (ES) provided by semi-natural (a) and natural (southern Africa; b) grasslands, emerging from cluster and factor analyses of tentative correlations between ES (see Appendix S2). The numbers in the cluster diagrams (right) refer to individual services: 1, water quantity; 2, water quality; 3, water regulation; 4, carbon storage; 5, greenhouse gas (GHG) emission mitigation; 6, erosion prevention; 7, fodder production; 8, meat production; 9, wild food and materials; 10, medicinal plants; 11, pollination; 12, biological control; 13, tourism/recreation; 14, cultural heritage; 15, hunting; 16, cultural, cattle; 17, social coherence; 18, spiritual. We also included 19, Biodiversity, in the analysis in order to incorporate its importance as a policy goal (cf. Mace et al. 2012).

Provisioning and Regulating Ecosystem Services from Grasslands

Water supply

In NE, the supply of water from semi-natural grasslands is presently small because of their limited extent and smaller per unit area supply compared to, for example, forests (Weatherhead and Howden 2009). However, locally their role can be appreciated by stakeholders, both regional experts and local farmers (Lamarque et al. 2011). In SA, the supply is much greater since the inland grasslands occur in the main catchment areas of the region (Cadman et al. 2013). These natural grasslands form an effective system for water capture, high infiltration, and reduced erosion, thereby regulating stream flow in the rainy season and maintaining flows during the dry seasons (Cadman et al. 2013).

At the local scale, particular grass species may alter water supply by affecting infiltration rate and storage capacity through variation in water use efficiencies (Macleod and Ferrier 2011, Volaire et al. 2014). The water regulation capacity of grasslands (mainly timing and magnitude of stream flow) depends on season in both NE (Hönigová et al. 2012) and SA (Everson 2001). In NE, the supply is largely dependent on small-scale heterogeneity in soil texture and hillslope gradients which affect flooding and erosion (Souchere et al. 2003, Macleod and Ferrier 2011), while in SA, the processes operate at larger catchment scales. Furthermore, SA grasslands are dormant over the dry winter season and so there is no transpiration loss, compared with an evergreen vegetation cover. This maintains the perennial flow of the rivers and provision of water to downstream users during the critical low flow period. Grasslands can reduce surface runoff with 20%, or more, compared to arable land (Macleod and Ferrier 2011). Hence, grasslands presently contribute to water supply and flood regulation in SA and can also affect these ES in NE (see also below).

Climate regulation

The processes of carbon sequestration, carbon storage as soil organic matter, and fluxes of greenhouse gases in grasslands are intimately linked to each other. It is well established that carbon sequestration increases when grassland management is intensified by increased nutrient inputs, especially nitrogen (e.g., Kätterer et al. 2012, He et al. 2013). However, the climate mitigation effect of intensified management may be offset by increased emissions of greenhouse gases other than CO_2 (see below).

Permanent grasslands store large amounts of carbon in the soil (Lal 2004, Soussana et al. 2010, Bullock et al. 2011, Lemaire et al. 2011, Smith 2014), much more than croplands, and sometimes as much as forest soils (Farley et al. 2013, Burrascano et al. 2016). This carbon is rapidly decomposed and released as CO_2 if grasslands are transformed into cropland or intensified by plowing and re-sowing (Soussana et al. 2007, 2010, Kätterer et al. 2012). Hence, grasslands and their management play a role as potential sinks in the global carbon cycle (Lal 2004), both in NE and in SA. Plant species composition also influences carbon and nitrogen storage and dynamics in grasslands (e.g., Lemaire et al. 2011, Laliberté and Tylianakis 2012).

Grasslands are also sources of greenhouse gases as ruminant livestock produce methane (CH_4), although so do many wild ungulates (Du Toit et al. 2014). The water table in grasslands also affects GHG fluxes; wetter grasslands often produce methane, while drier grasslands do not (Acreman et al. 2011). In addition, nutrient application to grasslands to increase livestock production results in N_2O emissions (Soussana et al. 2010). These issues have received far less attention than carbon sequestration (exceptions are, e.g., Smith et al. 2008, Soussana et al. 2010, Bellarby et al. 2013, see also Bullock et al. 2011). How these processes balance in terms of total climate mitigation is not clear (Soussana et al. 2010) and may vary with soil properties such as carbon content (Meyer et al. 2016) or bulk density (Carolan and Fornara 2016). Bellarby et al. (2013) argued that beef and dairy production on natural grasslands and rough grazing land, as opposed to intensive grain-fed production from croplands, may reduce GHG emissions. This would require less intensive grazing systems and use of rough grazing lands, but may have other environmental benefits, such as improved biodiversity in high nature value grasslands. The carbon sequestration potential of grasslands, and whether it can balance the negative effect of livestock on GHG emissions, is debated. Many argue that the C-sequestration potential of grasslands is limited and not able to balance the livestock emissions of methane (e.g., Smith 2014, Garnett et al. 2017, Röös et al. 2017). Other authors suggest that grazed grasslands may indeed have a positive climate impact, at least in particular situations (e.g., Bellarby et al. 2013, Batalla et al. 2015, Klumpp et al. 2017).

Erosion prevention

Permanent vegetation protects against soil erosion by reducing water runoff and stabilizing the soil. Permanent grasslands can, if not overgrazed or mismanaged, contribute greatly to soil erosion prevention, both in NE (e.g., Souchère et al. 2003, Verheijen et al. 2009, Pilgrim et al. 2010) and in SA, where high energy rainfall and steep gradients result in high erosion potential (Blignaut et al. 2010, Dlamini et al. 2011; see also Fu et al. 2011 for China, and Peri et al. 2016 for Patagonia). Grasslands often show <10% of the soil erosion seen on croplands (Verheijen et al. 2009, Cerdan et al. 2010), although forested land has even lower erosion (Cerdan et al. 2010). Erosion prevention by grassland vegetation is strongly coupled to other services relating to water supply and regulation, carbon sequestration, and soil fertility (e.g., Pilgrim et al. 2010, Hou et al. 2017).

In NE, the location of grasslands in the agricultural landscape is of great importance. For example, Souchere et al. (2003) showed that in landscapes where grasslands had been converted to cropland water runoff (i.e., less infiltration), soil erosion and soil loss increased greatly, but also that a small increase in the amount of grasslands could, if well placed, contribute greatly to erosion control.

Fodder and livestock production, food quantity, and quality

Plant biomass (fodder) production provides the basis for all grassland ES related to animal production. Although fodder production varies with soil nutrients, moisture and level of grazing (Tainton 1999, Lemaire et al. 2011, UK NEA 2011, O'Mara 2012), the productivity in natural and semi-natural grasslands is lower than in improved grasslands and fodder-producing fields. Not only fodder quantity, but also quality, that is, digestibility, is important for meat and dairy production. Generally, the digestibility of natural and semi-natural grassland fodder is lower compared to that from improved grasslands, since the former contain more C4 plants generally having lower digestibility and protein content than C3 species (Poppi 2011). In addition, differences in digestibility are also attributed to fertilizer addition (ibid).

In NE, the quality of livestock products may be greater from semi-natural grasslands than from more intensive systems. Meat from animals grazing on natural grasslands contains less fat, regardless of breed (Fraser et al. 2009). Anecdotal information suggests that meat produced from natural and semi-natural grassland has a higher nutrient content and better taste, but this needs more investigation (Bullock et al. 2011). According to Coulon et al. (2004), cheese produced from livestock feeding on species-rich grasslands had better taste, aroma, and texture than cheeses from species-poor grasslands. However, meat from livestock feeding exclusively on semi-natural grasslands may not necessarily meet the quality and quantity demands from the meat industry but can be considered in alternative market chains (Bedoin and Kristensen 2013). These authors also point out that the definition of meat quality depends on which criteria different market chains consider important (ibid).

Other products (wild foods, plant-based raw materials)

There is no scientific documentation of high supply of wild foods from grasslands in SA or NE, although rural communities in SA often depend on food and other products from nature areas and commons for subsistence (Shackleton and Shackleton 2015, Nkambule et al. 2016). Materials such as thatch grass for houses are locally utilized in SA (Van Oudtshoorn 2012). Medicinal plants are regularly used by more than half the South African population, with an annual trade in a single province, KwaZulu-Natal, of over 4000 tonnes of plant material comprising more than 700 species and worth US $13 million (Mander 1998). More than half of the most traded species originate from grassland. However, such products are not considered important in Europe (Bullock et al. 2011, Hönigová et al. 2012).

Crop production in croplands

Historically, grasslands in NE and SA played a large role for cropland production by providing nutrients to arable fields through manure of grazing animals. This decreased greatly when crop rotations with legumes and inorganic fertilizers were introduced in the 20th century (Emanuelsson 2009). Today, the main ES from grasslands that directly affect agricultural production positively are pollination and biological control. Both were suggested to be enhanced by nearby grasslands in a US study (Werling et al.

2014). The role of semi-natural biotopes, including grasslands, for biological control has been discussed extensively (e.g., Tscharntke et al. 2007), but the specific role of grasslands is less clear, as many studies report effects of landscape structure and non-crop habitats in general. Jonsson et al. (2014) showed increasing potential for biological control with the proportion of grassland in the landscape. Pollination of insect-pollinated crops may be higher close to adjacent grasslands (Taki et al. 2010, Werling et al. 2014). However, there are surprisingly few studies explicitly relating grasslands to crop pollination, given the large attention to pollinator responses to landscape structure (e.g., Klein et al. 2007, Kennedy et al. 2013).

Cultural Ecosystem Services from Grasslands

Tourism, recreation, and hunting

Natural and semi-natural grasslands are important parts of the cultural landscape in Europe (Emanuelsson 2009). Some grasslands are protected as nature reserves or national parks and are often advertised as hotspots for local and national tourism (Everson and Morris 2006, Fischer et al. 2008) in both NE and SA. In NE, much of the semi-natural grassland is protected (Bullock et al. 2011), but only a small percentage of the SA grassland area is under protection (Rouget et al. 2004). However, since many recreational activities are related to the broader landscape, it is difficult in NE to separate the role of semi-natural grasslands from that of improved grassland (UK NEA 2011) and the overall heterogeneity of the landscape. A cultural landscape containing grasslands can also be a tourist attraction in itself (e.g., South Downs National Park in England, the Swiss Alps, the SA Drakensberg grasslands) with the landscape potentially playing a significant role in a World Heritage context (Buckley et al. 2008). Many outdoor recreation activities such as bird watching, hiking, or hunting are linked to open landscapes (Hönigová et al. 2012), although in most cases the specific contribution from grasslands has not been examined. Nkambule et al. (2016) report that local household members use SA grassland areas for recreation and cultural purposes.

Cultural heritage, spiritual, and social cohesion

The extensive use and traditional management have made grasslands in NE highly appreciated for their cultural heritage (Fischer et al. 2008, Lindborg et al. 2008). Many are parts of agri-environmental subsidy systems both for their biological and for their cultural value. Grasslands are also associated with other cultural services such as spiritual, aesthetical, and social coherence (Bullock et al. 2011, Lamarque et al. 2011, Hönigová et al. 2012). Many semi-natural grasslands in NE are located on ancient sacred places such as burial mounds and have been kept open by livestock for thousands of years (Lindborg et al. 2008). Traditional management of grasslands in terms of hay-making has played an important role as social cohesion among villagers and still does (Stenseke 2009).

Cultural aspects of livestock

Livestock keeping plays an important role in the cultural–economic history of SA (Ainslie 2013). The traditional herding system for cattle keeping is an integral part of social cohesion in rural landscapes (Salomon et al. 2013).

Scientific studies

Grassland studies is one of the scientific areas that have contributed most to development of general ecological knowledge and theory, being the testing ground for many ecological theories such as productivity–diversity relationships (Hector et al. 1999, Tilman et al. 2001), coexistence theory (Silvertown 2004), plant strategy theory (Grime 1974), and many other fields. In SA, research on grasslands has been important for, for example, succession theory (Roux 1969) and the role of fire in ecosystems (Bond and van Wilgen 1996). Research from SA catchment areas has contributed significantly to the understanding of hydrological processes (Nänni 1970*a*,*b*, Everson 2001).

Grassland Management Planning

Natural (SA) and semi-natural (NE) grasslands showed both similarities and dissimilarities in terms of ES supply and demand (Table 1). These differences, when considered in relation to synergies and trade-offs (Fig. 3), will have implications for management decisions. The demand for water-related services from grasslands is of fundamental importance in the largely semi-arid SA and in similar regions requiring large-scale management to guarantee sufficient water supply to areas of greatest water consumption in the region (Nel et al. 2013). In contrast, the supply of water-related ES from NE grasslands is less acknowledged (but see, e.g., Acreman et al. 2011). However, several studies suggest that the role of semi-natural grasslands for water supply and flow regulation can be enhanced with appropriate landscape management (see below).

The cultural use of ES is pronounced in both SA and NE. In the late 19th century, semi-natural grasslands dominated many landscapes and played a large cultural role as parts of the everyday life of rural people in western and northern Europe (Emanuelsson 2009). Increasing demand for multiple services like water and meat production, and an overall increased awareness of the ES supply potential of grasslands, could help to re-invigorate the cultural role of grasslands and strengthen the synergy between the multiple ES they supply (Stenseke 2009). The cultural role of grasslands has primarily been acknowledged when discussing the effects of intensification of agriculture globally, but the loss of cultural values is also an important negative aspect of abandonment of traditionally managed small-scale farming in NE (Queiroz et al. 2014). The negative impact, especially on cultural values and biodiversity-related services such as pollination and biological control, has been acknowledged within the European Union through subsidy systems like agri-environmental schemes (Kettunen et al. 2009).

We found some, probably inevitable, trade-offs between certain services (note that the identified bundles do not necessarily show trade-offs, as the ES in different bundles may also be independent of each other): Increasing fodder production for livestock (meat) production by management intensification through plowing and re-sowing, resulting in loss of natural and semi-natural grasslands, is likely to trade off with the mitigation of GHG emissions, carbon storage, and carbon sequestration (indicated in Fig. 3; see Soussana et al. 2010 for a balanced discussion). Biodiversity is well known to trade-off with intensified management (Stoate et al. 2009, UK NEA 2011, Burrascano et al. 2016). However, these and several other trade-offs can be modified or avoided by appropriate management practices, and these are important to identify. For example, well-managed grazing by livestock on natural or semi-natural grassland can keep GHG emissions to a minimum as opposed to intensive grain-fed animal production with higher emissions level (Peyraud 2011, Bellarby et al. 2013). Trade-offs associated with overgrazing could also be greatly reduced if grasslands are well managed. If livestock density is kept below carrying capacity, it is possible to improve water regulation (Turpie et al. 2008), carbon storage (Lal 2004, Soussana et al. 2010), erosion prevention (Fu et al. 2011), keep GHG emissions low (Soussana et al. 2010, Bellarby et al. 2013), enhance pollinator diversity (Sjödin et al. 2008), and improve cultural ES (Stenseke 2009, Hönigová et al. 2012). These benefits are not solely obtained from grazing by cattle, but also horses, sheep, goats, and combinations of grazers may contribute to good management and multiple ES from grasslands (e.g., Anderson et al. 2012).

The bundle including the regulating services pollination and biological control also included biodiversity. These two services, as well as biodiversity, are linked to the population dynamics of the service-providing species (often invertebrates). In NE, the decreasing quantity and quality of semi-natural grasslands are linked to declines in biodiversity and related ES (Stoate et al. 2009, Bommarco et al. 2012). Here, semi-natural grasslands can contribute greatly to overall landscape biodiversity despite their small area, and management should be focused on increasing their area and quality, which as we show can have positive effects on other ES. The vast areas of SA grasslands are also important for biodiversity. Although they are more intact than the current grasslands of NE, they are also becoming increasingly fragmented due to transformation to arable land, especially in more moist and fertile areas. Our results indicate that conservation of large remaining grassland areas and well-managed grazing may protect biodiversity as well as the important water-related ES in this area.

Concluding Discussion

Food security and sustainable intensification of food production have become key issues for science and policy (e.g., Godfray et al. 2010, Foley et al. 2011, SCAR 2011, Bommarco et al. 2013, Garnett et al. 2013, Poppy et al. 2014). Given the projected adverse effects of climate change on crop production, increasing food demand, and increased demand for energy and nutrient inputs, future food production most likely will need to use land areas that cannot, for various reasons, support crop production. Much of this discussion has neglected the importance of grasslands and rangelands (but see, e.g., SCAR 2011, Foley et al. 2011, O'Mara 2012). Covering twice the area suitable for crop production, the potential role of grasslands for global food security should be better recognized. Ruminant grazers are efficient converters of non-edible plant biomass such as grass into human-edible energy and nutrients (e.g., O'Mara 2012) and can do so without competing with humans for use of crops for foodstuffs. Furthermore, grassland dairy and meat production systems may not necessarily have the large climate effects attributed to intensified meat production based on cropland (Soussana et al. 2010, Peyraud 2011, Bellarby et al. 2013). Grasslands, because of their lower productivity, will probably not be able to fully substitute for cropland-based meat production to meet projected trends of increased meat demand globally (Garnett 2011, Kellermann and Salhofer 2014). However, with diet changes toward lower cropland meat consumption in developed countries and increasing concern about mitigating climate change and developing sustainable agricultural production systems, grasslands have great potential to contribute to food security, along with other important benefits related to biodiversity and a range of ES (see, e.g., Bullock et al. 2011, Garnett 2011).

We have shown that natural and semi-natural grasslands, in addition to having high biodiversity, can supply additional services highly demanded from society, for example, water supply and flow regulation, carbon storage, erosion control, cultural values, pollination, and biological control of agricultural pests, and that appropriate management makes it possible to create synergies and avoid trade-offs among many of these services. The potential for grasslands to deliver these ES is likely to be substantial, and it is unlikely that conversion of grassland to forest will supply many of these services at comparable rates (Burrascano et al. 2016). Biodiversity and ES thus provide major arguments for maintaining grazed grasslands despite the large climate effects of methane-emitting livestock. We argue that the multifunctional role of semi-natural and natural grasslands is still surprisingly understudied compared to other production systems. Hence, not just biodiversity research and policy but also ecosystem service, climate, and food security research and policy should give higher priority to how grasslands and rangelands can be managed for fodder and meat production as well as for biodiversity and the other ES discussed here. By integrating grasslands into agricultural production systems and land-use decisions locally and regionally, it is possible to increase their potential to contribute to multifunctional landscapes and to biodiversity conservation as well as food security and sustainable livelihoods at the global scale.

Acknowledgments

We thank STIAS and the Wallenberg foundation hosting the initial workshop and for the funding that made this review possible. Our research on multiple ecosystem services, grasslands, and agricultural landscapes has been funded by, among others, HagmarksMistra, The Swedish Research Council FORMAS, the Research program SAPES to HGS, JB, and RL, and the UK Biodiversity and Ecosystem Services Sustainability program. Two reviewers gave valuable comments on an earlier version. The authors have no conflicts of interest to declare regarding this manuscript.

Literature Cited

Acreman, M. C., et al. 2011. Trade-off in ecosystem services of the Somerset Levels and Moors wetlands. Hydrological Sciences Journal 56:1543–1565.

Ainslie, A. 2013. The sociocultural contexts and meanings associated with livestock keeping in rural South Africa. African Journal of Range and Forage Science 30:35–38.

Anderson, K. 2015. Talks in the city of light generate more heat. Nature 528:437.

Anderson, D. M., E. L. Fredrickson, and R. E. Estell. 2012. Managing livestock using animal behaviour: mixed species stocking and flerds. Animal 6:1339–1349.

Batalla, I., M. T. Knudsen, L. Mogensen, O. del Hierro, M. Pinto, and J. E. Hermansen. 2015. Carbon footprint of milk from sheep farming systems in Northern Spain including soil carbon sequestration in grasslands. Journal of Cleaner Production 104:121–129.

Bedoin, F., and T. Kristensen. 2013. Sustainability of grassland-based beef production – Case studies of Danish suckler farms. Livestock Science 158:189–198.

Bellarby, J., R. Tirado, A. Leip, F. Weiss, J. P. Lesschen, and P. Smith. 2013. Livestock greenhouse gas emissions and mitigation potential in Europe. Global Change Biology 19:3–18.

Bennett, E. M., G. D. Peterson, and L. J. Gordon. 2009. Understanding relationships among multiple ecosystem services. Ecology Letters 12:1394–1404.

Birkhofer, K., et al. 2018. Relationships between multiple biodiversity components and ecosystem services along a landscape complexity gradient. Biological Conservation 218:247–253.

Blignaut, J. N., et al. 2010. Restoring and managing natural capital towards fostering economic development: evidence from the Drakensberg, South Africa. Ecological Economics 69:1313–1323.

Bommarco, R., D. Kleijn, and S. G. Potts. 2013. Ecological intensification: harnessing ecosystem services for food security. Trends in Ecology and Evolution 28:230–238.

Bommarco, R., O. Lundin, H. G. Smith, and M. Rundlöf. 2012. Drastic historic shifts in bumble-bee community composition in Sweden. Proceedings of the Royal Society B 279:309–315.

Bond, W. J. 2016. Ancient grasslands at risk. Science 351:120–122.

Bond, W. J., and B. W. van Wilgen. 1996. Fire and plants. Chapman and Hall, London, UK.

Buckley, R., C. Ollenburg, and L. Zhong. 2008. Cultural landscape in Mongolian tourism. Annals of Tourism Research 35:47–61.

Bullock, J. M., R. F. Pywell, and K. J. Walker. 2007. Long-term enhancement of agricultural production by restoration of biodiversity. Journal of Applied Ecology 44:6–12.

Bullock, J. M., et al. 2011. Chapter 6: Semi-natural grasslands. Pages 161–196 *in* UK NEA, The UK National Ecosystem Assessment. UNEP-WCMC, Cambridge, UK.

Burkhard, B., F. Kroll, S. Nedkov, and F. Müller. 2012. Mapping ecosystem service supply, demand and budgets. Ecological Indicators 21:17–29.

Burrascano, S., M. Chytrý, T. Kuemmerle, E. Giarrizzo, S. Luyssaert, F. M. Sabatini, and C. Blasi. 2016. Current European policies are unlikely to jointly foster carbon sequestration and protect biodiversity. Biological Conservation 201:370–376.

Cadman, M., C. deVilliers, R. Lechmere-Oertel, and D. McCulloch. 2013. Grasslands Ecosystem Guidelines: landscape interpretation for planners and managers. South African National Biodiversity Institute, Pretoria, South Africa.

Carolan, R., and D. A. Fornara. 2016. Soil carbon cycling and storage along a chronosequence of re-seeded grasslands: Do soil carbons stocks increase with grassland age? Agriculture, Ecosystems and Environment 218:126–132.

Cerdan, O., et al. 2010. Rates and spatial variations of soil erosion in Europe: a study based on erosion plot data. Geomorphology 122:167–177.

Collier, P., G. Conway, and T. Venables. 2008. Climate change and Africa. Oxford Review of Economic Policy 24:337–353.

Coulon, L. B., A. Delacroix-Buchet, B. Martin, and B. Pirisi. 2004. Relationships between ruminant management and sensory characteristics of cheeses: a review. Lait 84:221–241.

Diaz, S., et al. 2015. The IPBES Conceptual Framework – connecting nature and people. Current Opinion in Environmental Sustainability 14:1–16.

Dlamini, P., C. Orchard, G. Jewitt, S. Lorentz, L. Titshall, and V. Chaplot. 2011. Controlling factors of sheet erosion under degraded grasslands in the sloping lands of KwaZulu-Natal, South Africa. Agricultural Water Management 98:1711–1718.

Du Toit, C. J. L., H. H. Meissner, and W. A. Van Niekerk. 2014. Direct greenhouse gas emissions of the game industry in South Africa. South African Journal of Animal Science 43:376–393.

Egoh, B., J. Bengtsson, R. Lindborg, J. M. Bullock, A. P. Dixon, and M. Rouget. 2016. The importance of grasslands in providing ecosystem services: opportunities for poverty alleviation. Pages 421–441 *in* M. Potschin, R. Haines-Young, R. Fish, and R. K. Turner, editors. Routledge handbook of ecosystem services. Routledge, London and New York, New York, USA.

Elmqvist, T., C. Folke, M. Nyström, G. Peterson, J. Bengtsson, B. Walker, and J. Norberg. 2003. Response diversity and ecosystem resilience. Frontiers in Ecology and the Environment 1:488–494.

Emanuelsson, U. 2009. The rural landscapes of Europe: how man has shaped European nature. The Swedish Research Council Formas, Värnamo, Sweden.

Erb, K.-H., T. Fetzel, T. Kastner, C. Kroisleitner, C. Lauk, A. Mayer, and M. Niedertscheider. 2016. Livestock grazing, the neglected land use. Pages 295–310 *in* H. Haberl, M. Fischer-Kowalski, F. Krausmann, and V. Winiwarter, editors. Social ecology, human-environment interactions 5. Springer, New York, New York, USA.

Eriksson, O., S. A. O. Cousins, and H.-H. Bruun. 2002. Land-use history and fragmentation of traditionally managed grasslands in Scandinavia. Journal of Vegetation Science 13:743–748.

European Commission. 2018. Paris Agreement. https://ec.europa.eu/clima/policies/international/negotiations/paris_en (Downloaded 2018-12-19)

Everson, C. 2001. The water balance of a first order catchment in the montane grasslands of South Africa. Journal of Hydrology 241:110–123.

Everson, T. M., and C. D. Morris. 2006. Conservation of biodiversity in the Maloti-Drakensberg mountain range. Pages 285–291 *in* E. M. Spehn, M. Liberman, and C. Körner, editors. Land use change and mountain biodiversity. CRC Press, Boca Raton, Florida, USA.

Fairbanks, D. H. K., M. W. Thompson, D. E. Vink, T. S. Newby, H. M. van den Berg, and D. A. Everard. 2000. The South African land-cover characteristics data base: a synopsis of the landscape. South African Journal of Science 96:69–82.

FAO. 2009. The state of food and agriculture. Livestock in the balance. FAO, Rome, Italy.

Farley, K. A., L. L. Bremer, C. P. Harden, and J. Hartsig. 2013. Changes in carbon storage under alternative land uses in biodiverse Andean grasslands: implications for payment for ecosystem services. Conservation Letters 6:21–27.

Fischer, M., K. Rudmann-Maurer, A. Weyand, and J. Stöcklin. 2008. Agricultural land use and biodiversity in the Alps - How cultural tradition and socioeconomically motivated changes are shaping grassland biodiversity in the Swiss Alps. Mountain Research and Development 28:148–155.

Foley, J., et al. 2005. Global consequences of land use. Science 309:570–574.

Foley, J., et al. 2011. Solutions for a cultivated planet. Nature 478:337–342.

Fraser, M. D., D. A. Davies, J. E. Vale, G. R. Nute, K. G. Hallett, R. I. Richardson, and I. A. Wright. 2009. Performance and meat quality of native and continental cross steers grazing improved upland pasture or semi-natural rough grazing. Livestock Science 123:70–82.

Frélichová, J., D. Vackár, A. Pártl, B. Loucková, Z. V. Harmácková, and E. Lorencová. 2014. Integrated assessment of ecosystem services in the Czech Republic. Ecosystem Services 8:110–117.

Fu, B., Y. Liu, Y. Lü, C. He, Y. Zeng, and B. Wu. 2011. Assessing the soil erosion control service of ecosystems change in the Loess Plateau of China. Ecological Complexity 8:284–293.

Gamfeldt, L., H. Hillebrand, and P. Jonsson. 2008. Multiple functions increase the importance of biodiversity for overall ecosystem functioning. Ecology 89:1223–1231.

Gamfeldt, L., et al. 2013. Higher levels of multiple ecosystem services are found in forests with more tree species. Nature Communications 4:1340.

Garnett, T. 2011. Where are the best opportunities for reducing greenhouse gas emissions in the food system (including the food chain)? Food Policy 36: S23–S32.

Garnett, T., et al. 2013. Sustainable intensification in agriculture: premises and policies. Science 341:33–34.

Garnett, T., et al. 2017. Grazed and Confused? Ruminating on cattle, grazing systems, methane, nitrous oxide, the soil carbon sequestration question – and what it all means for greenhouse gas emissions. FCRN, University of Oxford, UK. (downloaded 2017-11-17 from http://www.fcrn.org.uk/sites/default/files/project-files/fcrn_gnc_report.pdf)

Godfray, H. C. J., et al. 2010. The future of the global food system. Philosophical Transactions of the Royal Society B 365:2769–2777.

Grime, J. P. 1974. Vegetation classification by reference to strategies. Nature 250:26–31.

Habel, J. C., J. Dengler, M. Janišová, P. Török, C. Wellstein, and M. Wiezik. 2013. European grassland ecosystems: threatened hotspots of biodiversity. Biodiversity and Conservation 22:2131–2138.

Haines-Young, R., and M. Potschin. 2013. Common International Classification of Ecosystem Services (CICES): consultation on Version 4, August-December 2012. EEA Framework Contract No EEA/IEA/09/003 (Download available at www.cices.eu).

Harvey, M., and S. Pilgrim. 2011. The new competition for land: food, energy, and climate change. Food Policy 36:S40–S51.

He, N., Q. Yu, R. Wang, Y. Zhang, Y. Gao, and G. Yu. 2013. Enhancement of Carbon sequestration in soil in the temperature grasslands of Northern China by addition of Nitrogen and Phosphorus. PLoS ONE 8:e77241.

Hector, A., et al. 1999. Plant diversity and productivity experiments in European grasslands. Science 286:1123–1127.

Holden, S. T., and K. Otsuka. 2014. The roles of land tenure reforms and land markets in the context of population growth and land use intensification in Africa. Food Policy 48:88–97.

Hönigová, I., et al. 2012. Survey on grassland ecosystem services. Report to the EEA – European Topic Centre on Biological Diversity. Nature Conservation Agency of the Czech Republic, Prague, Czech Republic.

Hou, R., R. Yu, and J. Wu. 2017. Relationship between paired ecosystem services in the grassland and agro-pastoral transitional zone of China using the constraint line method. Agriculture, Ecosystems and Environment 240:171–181.

Jackson, R. B., et al. 2008. Protecting climate with forests. Environmental Research Letters 3:044006.

Jonsson, M., et al. 2014. Ecological production functions for biological control services in agricultural landscapes. Methods in Ecology and Evolution 5:243–252.

Kätterer, T., M. A. Bolinder, K. Berglund, and H. Kirchmann. 2012. Strategies for carbon sequestration in agricultural soils in northern Europe. Acta Agriculturae Scandinavica, Section A - Animal Science 62:181–198.

Kellermann, M., and K. Salhofer. 2014. Dairy farming on permanent grassland: Can it keep up? Journal of Dairy Science 97:6196–6210.

Kemp, D. R., and D. L. Michalk. 2011. Livestock production styles and managing grassland ecosystems. Pages 53–64 *in* G. Lemaire, J. Hodgson, and A. Chaddi, editors. Grassland productivity and ecosystem services. CABI, Wallingford, UK.

Kennedy, C. M., et al. 2013. A global quantitative synthesis of local and landscape effects on wild bee pollinators in agroecosystems. Ecology Letters 16:584–599.

Kettunen, M., D. Bladock, C. Adelle, T. Cooper, M. Farmer, K. Hart, and P. Torkler. 2009. Biodiversity and the EU budget: making the case for conserving biodiversity in the context of the EU budget review. WWF, Brussels, Belgium.

Klein, A.-M., B. E. Vaissière, J. H. Cane, I. Steffan-Dewenter, S. A. Cunningham, C. Kremen, and T. Tscharntke. 2007. Importance of pollinators in changing landscapes for world crops. Proceedings of the Royal Society B 274:303–313.

Klumpp, K., A. Chabbi, F. Gastal, N. Senapati, X. Charrier, O. Darsonville, and A. Creme. 2017. Carbon sink activity of managed grasslands. Geophysical Research Abstracts 19:EGU2017–EGU13783.

Lal, R. 2004. Soil carbon sequestration impacts on global climate change and food security. Science 304:1623–1627.

Laliberté, E., and J. M. Tylianakis. 2012. Cascading effects of long-term land-use changes on plant traits and ecosystem functioning. Ecology 93:145–155.

Lamarque, P., et al. 2011. Stakeholder perceptions of grassland ecosystem services in relation to knowledge on soil fertility and biodiversity. Regional Environmental Change 11:791–804.

Lavorel, S., et al. 2013. A novel framework for linking functional diversity of plants with other trophic levels for the quantification of ecosystem services. Journal of Vegetation Science 24:942–947.

Lemaire, G., J. Hodgson, and A. Chabbi, editors. 2011. Grassland productivity and ecosystem services. CABI, Wallingford, UK.

Lindborg, R., et al. 2008. A landscape perspective on conservation of semi-natural grasslands. Agriculture, Ecosystems and Environment 125:213–222.

Lindborg, R., et al. 2017. How spatial scale shapes the generation and management of multiple ecosystem services. Ecosphere 8:e01741.

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.

Lyons, K. G., C. A. Brigham, B. H. Traut, and M. W. Schwartz. 2005. Rare species and ecosystem functioning. Conservation Biology 19:1019–1024.

Mace, G. M., K. Norris, and A. H. Fitter. 2012. Biodiversity and ecosystem services: a multilayered relationship. Trends in Ecology and Evolution 27:19–26.

Macleod, C. J. A., and R. C. Ferrier. 2011. Temperate grasslands in catchment systems: the role of scale, connectivity and thresholds in the provision and regulation of water quality and quantity. Pages 229–238 *in* G. Lemaire, J. Hodgson, and A. Chaddi, editors. Grassland productivity and ecosystem services. CABI, Wallingford, UK.

Mander, M. 1998. Marketing of indigenous medicinal plants in South Africa. A case study in KwaZulu-Natal. FAO, Rome, Italy.

Meyer, R., B. R. Cullen, and R. J. Eckard. 2016. Modelling the influence of soil carbon on net greenhouse gas emissions from grazed pastures. Animal Production Science 56:585–593.

Millennium Ecosystem Assessment (MA). 2005. Ecosystems and human well-being. Synthesis. World Resources Institute, Washington, D.C., USA. http://www.millenniumassessment

Modernel, P., W. A. H. Rossing, M. Corbeels, S. Dogliotti, V. Picasso, and P. Tittonell. 2016. Land use change and ecosystem service provision in Pampas and Campos grasslands of southern South America. Environmental Research Letters 11:113 002.

Mouillot, D., et al. 2013. Rare species support vulnerable functions in high-diversity ecosystems. PLoS Biology 11:e1001569.

Nänni, U. W. 1970*a*. The effect of afforestation on stream-flow at Cathedral Peak. South African Forestry Journal 74:6–12.

Nänni, U. W. 1970*b*. Trees, water and perspective. South African Forestry Journal 75:9–17.

Naylor, R., et al. 2005. Losing the links between livestock and land. Science 310:1621–1622.

Nel, J., C. Colvin, D. Le Maitre, and J. Smith. 2013. Strategic water source areas. Report No. CSIR/NRE/ECOS/ER/2013/0031/A, Natural Resources and the Environment, CSIR, Stellenbosch.

Nkambule, S. S., H. Z. Buthelezi, and S. Munien. 2016. Opportunities and constraints for community-based conservation: the case of the KwaZulu-Natal Sandstone Sourveld grassland, South Africa. Bothalia 46:a2120.

O'Connor, T. G., and G. J. Bredenkamp. 1997. Grassland. Pages 215–257 *in* R. M. Cowling, D. M. Richardson, and S. M. Pierce, editors. Vegetation of Southern Africa. Cambridge University Press, Cambridge, UK.

O'Donoghue, T., and K. Punch. 2003. Qualitative educational research in action: doing and reflecting. Routledge, Abingdon, UK.

O'Mara, F. P. 2012. The role of grasslands in food security and climate change. Annals of Botany 110:1263–1270.

Parr, C. L., C. E. R. Lehmann, W. J. Bond, W. A. Hoffmann, and A. N. Andersen. 2014. Tropical grassy biomes: misunderstood, neglected, and under threat. Trends in Ecology and Evolution 29:205–213.

Pascual, U., et al. 2017. Valuing nature's contributions to people: the IPBES approach. Current Opinion in Environmental Sustainability 26:7–16.

Pe'er, G., et al. 2014. EU agricultural reform fails on biodiversity. Science 344:1090–1092.

Peri, P. L., M. V. Lencinas, J. Bousson, R. Lasagno, R. Soler, H. Bahamonde, and G. M. Pastur. 2016. Biodiversity and ecological long-term plots in Southern Patagonia to support sustainable land management: the case of PEBANPA network. Journal of Nature Conservation 34:51–64.

Peyraud, J. L. 2011. The role of grasslands in intensive animal production in North-west Europe: conditions for a more sustainable farming system. Pages 179–187 *in* G. Lemaire, J. Hodgson, and A. Chaddi, editors. Grassland productivity and ecosystem services. CABI, Wallingford, UK.

Pilgrim, E. S., et al. 2010. Interactions among agricultural production and other ecosystem services delivered from European temperate grasslands. Advances in Agronomy 109:117–154.

Poppi, D. P. 2011. Nutritional constraints for grazing animals and the importance of selective grazing behaviour. Pages 19–26 *in* G. Lemaire, J. Hodgson, and A. Chaddi, editors. Grassland productivity and ecosystem services. CABI, Wallingford, UK.

Poppy, G. M., et al. 2014. Food security in a perfect storm: using the ecosystem services framework to increase understanding. Philosophical Transactions of the Royal Society B 369:20120288.

Queiroz, C., R. Beilin, C. Folke, and R. Lindborg. 2014. Farmland abandonment: Threat or opportunity for biodiversity conservation? Frontiers in Ecology and the Environment 12:288–296.

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.

Reyers, B., J. Nel, B. Egoh, Z. Jonas, and M. Rouget. 2005. National Grasslands Biodiversity Program: grassland Biodiversity Profile and Spatial Biodiversity Priority Assessment. CSIR Report Number: ENV-S-C 2005–102.

Robertson, G. P., K. L. Gross, S. K. Hamilton, D. A. Landis, T. M. Schmidt, S. S. Snapp, and S. M. Swinton. 2014. Farming for ecosystem services: an ecological approach to production agriculture. BioScience 64:404–415.

Röös, E., B. Bajželj, P. Smith, M. Patel, D. Little, and T. Garnett. 2017. Greedy or needy? Land use and climate impacts of food in 2050 under different livestock futures. Global Environmental Change 47:1–12.

Rouget, M., et al. 2004. South African National Spatial Biodiversity Assessment 2004: technical Report. Volume 1: terrestrial Component. South African National Biodiversity Institute, Pretoria, South Africa.

Roux, E. R. 1969. Grass. A Story of Frankenwald. Oxford University Press, Cape Town, South Africa.

Sala, O., and J. Paruelo. 1997. Ecosystem services in grasslands. In Nature's services: societal dependence on natural ecosystems. Pages 237–251 *in* G. C. Daily, editor. Nature's services: Societal dependence on natural ecosystems. Island Press, Washington, D.C., USA.

Sala, O. E., L. Yahdjian, K. Havstad, and M. R. Aguiar. 2017. Rangeland ecosystem services: nature's supply and humans' demand. Pages 467–489 *in* D. D. Briske, editor. Rangeland systems. Springer series on environmental management. Springer, Cham, Switzerland.

Salomon, M., C. Cupido, and I. Samuels. 2013. The good shepherd: remedying the fencing syndrome. African Journal of Range and Forage Science 30:71–75.

SCAR. 2011. Sustainable food consumption and production in a resource-constrained world. The 3rd SCAR Foresight Exercise. European Commission – Standing Committee on Agricultural Research (SCAR). Report. http://www.scar.org

Schulp, C. J., R. Alkemade, K. Klein Goldewijk, and K. Petz. 2012. Mapping ecosystem functions and services in Eastern Europe using global-scale data sets. International Journal of Biodiversity Science, Ecosystem Services and Management 8:156–168.

Schulp, C. J., S. Lautenbach, and P. H. Verburg. 2014. Quantifying and mapping ecosystem services: demand and supply of pollination in the European Union. Ecological Indicators 36:131–141.

Setälä, H. 2002. Sensitivity of ecosystem functioning to changes in trophic structure, functional group composition and species diversity in below-ground food webs. Ecological Research 17:207–215.

Shackleton, S., and C. Shackleton. 2015. Not just farming: natural resources and livelihoods in land and agrarian reform. Pages 191–205 *in* B. Cousins and C. Walker, editors. Land divided, land restored: land reform in South Africa for the 21st century. PLAAS – Institute for Poverty, Land and Agrarian Studies, Cape Town, South Africa.

Silvertown, J. 2004. Plant coexistence and the niche. Trends in Ecology and Evolution 19:605–611.

Sjödin, E., J. Bengtsson, and B. Ekbom. 2008. The influence of grazing intensity and landscape composition on pollinator diversity. Journal of Applied Ecology 45:763–772.

Smith, P. 2014. Do grasslands act as a perpetual sink for carbon? Global Change Biology 20:2708–2711.

Smith, P., et al. 2008. Greenhouse gas mitigation in agriculture. Philosophical Transactions of the Royal Society B 363:789–813.

Smith, P., et al. 2010. Competition for land. Philosophical Transactions of the Royal Society B 365:2941–2957.

Soliveres, S., et al. 2016. Locally rare species influence grassland ecosystem multifunctionality. Philosophical Transactions of the Royal Society B 371:20150269.

Souchère, V., C. King, N. Dubreuil, V. Lecomte-Morel, Y. Le Bissonnais, and M. Chalat. 2003. Grassland and crop trends: role of the European Union Common Agricultural Policy and consequences for runoff and soil erosion. Environmental Science and Policy 6:7–16.

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.

Soussana, J. F., et al. 2007. Full accounting of the greenhouse gas (CO_2, N_2O, CH_4) budget of nine European grassland sites. Agriculture, Ecosystems and Environment 121:121–134.

Stenseke, M. 2009. Local participation in cultural landscape maintenance: lessons from Sweden. Land Use Policy 26:214–223.

Stoate, C., et al. 2009. Ecological impacts of early 21st century agricultural change in Europe – A review. Journal of Environmental Management 91:22–46.

Suttie, J. M., S. G. Reynolds, and C. Batello. 2005. Grasslands of the world. FAO, Rome, Italy.

Tainton, N. 1999. Veld management in South Africa. University of Natal Press, Pietermaritzburg, South Africa.

Taki, H., K. Okabe, Y. Yamaura, T. Matsuura, M. Sueyoshi, S. Makino, and K. Maetoe. 2010. Effects of landscape metrics on Apis and non-Apis pollinators and seed set in common buckwheat. Basic and Applied Ecology 11:594–602.

TEEB. 2010. The economics of ecosystems and biodiversity: ecological and economic foundations. P. Kumar, editor. Earthscan, Washington, D.C., USA. http://www.teebweb.org/our-publications/teeb-study-reports/ecological-and-economic-foundations

Tilman, D., P. B. Reich, J. Knops, D. Wedin, T. Mielke, and C. Lehman. 2001. Diversity and productivity in a long-term grassland experiment. Science 294:843–845.

Tscharntke, T., et al. 2007. Conservation biological control and enemy diversity on a landscape scale. Biological Control 43:294–309.

Turpie, J. K., C. Marais, and J. N. Blignaut. 2008. The working for water programme: evolution of payments for ecosystem services mechanism that addresses both poverty and ecosystem service delivery in South Africa. Ecological Economics 65:788–798.

UK NEA. 2011. The UK National Ecosystem Assessment: synthesis of the Key Findings. UNEP-WCMC, Cambridge, UK.

Van Oudtshoorn, F. 2012. Guide to grasses of Southern Africa. Briza Publications, Pretoria, South Africa.

Verheijen, F. G. A., R. J. A. Jones, R. J. Rickson, and C. J. Smith. 2009. Tolerable versus actual soil erosion rates in Europe. Earth Science Reviews 94:23–38.

Volaire, F., K. Barkaoui, and M. Norton. 2014. Designing resilient and sustainable grasslands for a drier future: adaptive strategies, functional traits and biotic interactions. European Journal of Agronomy 52:81–89.

Wardle, D. A., R. D. Bardgett, R. M. Callaway, and W. H. Van der Putten. 2011. Terrestrial ecosystem responses to species gains and losses. Science 332:1273–1277.

Weatherhead, E. K., and N. J. K. Howden. 2009. The relationship between land use and surface water resources in the UK. Land Use Policy 26:S243–S250.

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.

Yahdjian, L., O. E. Sala, and K. M. Havstad. 2015. Rangeland ecosystem services: shifting focus from supply to reconciling supply and demand. Frontiers in Ecology and Environment 13:44–51.

Supporting Information

Additional Supporting Information may be found online at: http://onlinelibrary.wiley.com/doi/10.1002/ecs2.2582/full