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Ecosystem services provided by semi-natural and intensified grasslands: Synergies, trade-offs and linkages to plant traits and functional richness

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Abstract

Question: Semi-natural grasslands (SNG) are important for maintaining biodiversity and ecological processes in farmland. Current pasture-based livestock production mainly occurs on intensified grasslands (IG) that have been agronomically improved. Although it is documented that SNG and IG differ in terms of plant diversity, their ability to provide ecosystem services (ES) in farmland is less explored. Here, we review the role of SNG and IG in delivering ES, illustrate their trade-offs and synergies, and examine how ES can be assessed by using plant traits and functional richness.

Results: We found that SNG generate a wider range of ES than IG. Trade-offs exist between ES that appear more pronounced in IG between high biomass production and other ES. SNG are good in providing habitat for biodiversity, supporting pollination and cultural services. SNG also have a significantly wider range of plant functional traits and a higher functional richness, suggesting that the potential to supply ES in SNG is partly driven by higher number of species and their functional diversity.

Conclusion: Clearer trade-offs were found in IG compared with SNG, supported both by the literature and the functional richness. This suggests that functional knowledge could be a good complement to understand the mechanisms behind ES generation and could help with tailoring grassland management to sustain biodiversity, ecological functions and ES. Although both IG and SNG are likely needed for the long-term sustainability of food production, both could aim for a more balanced generation of ES, increasing biodiversity and functional redundancy at the landscape scale.

KEYWORDS
biodiversity, ecosystem function, ecosystem service supply, grassland management, multifunctionality, plant functional traits, sustainable farming

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1 | INTRODUCTION

Grasslands cover ca. 40% of the Earth's terrestrial surface and represent ca. 65% of the world's agricultural land area (Dengler et al., 2020). Two main types of grasslands can be differentiated within the European agricultural production systems: semi-natural and agro-economically intensified grasslands (Lemaire et al., 2011; Bengtsson et al., 2019). Semi-natural grasslands (SNG) are known for their high biodiversity of native species, favoured by a long history of low-intensity management through mowing (known as hay meadows) or grazing by livestock (known as pastures; Milchunas & Lauenroth, 1993; Price et al., 2022). By contrast, intensified grasslands (IG) are lower in biodiversity, use high levels of fertilization and agrochemicals, and are typically accompanied by high grazing pressure or mowing frequency (Kleijn et al., 2008). Such anthropogenic disturbance generates a significant loss of biodiversity, if management intensity is beyond carrying capacity or when grazing was not evolutionary present in the system (Milchunas & Lauenroth, 1993; Price et al., 2022).

Whereas only 100 years ago, most European livestock still grazed SNG within multifunctional pasture systems (Hartel et al., 2018), a large part of the livestock production currently occurs on technologically improved grasslands or croplands (Naylor et al., 2005). This shift in production has led to a sharp decline in European SNG area during the past century due to abandonment of less-productive land, intensification of management or the transformation of productive areas into cropland (Bardgett et al., 2021; Herzon et al., 2022). In addition, lack of management and abandonment of the remaining grasslands, pose a major threat, to not only biodiversity, but also people worldwide, especially to societies that directly rely on multiple ecosystem services (ES) from grasslands, such as food, fuel, fibres, medicinal products and cultural values (Bengtsson et al., 2019).

Compared with, for example forests, grasslands have received much less attention as an integral part of multifunctional landscapes in multiple ES assessments (Bardgett et al., 2021) or in working landscapes frameworks (Kremen & Merenlender, 2018, but see Garibaldi et al., 2021). Grasslands are important for fodder production, but extensively managed hay meadows and pastures also significantly contribute to the maintenance of high biodiversity and key ecological processes (e.g. pollination or water regulation) at local and landscape scales (Dengler et al., 2020). Diverse SNG have outstanding ecological value through harbouring soil carbon pools supporting rich biota and providing habitat for many rare and threatened species (Lindborg & Eriksson, 2004; Helm et al., 2005). In addition, SNG carry significant cultural legacy value: many of them have been similarly managed and valued by local communities for centuries. They showcase ancient European land-use systems and support the transfer of traditional ecological knowledge across generations (Plieninger et al., 2015). By contrast, intensively managed agricultural systems are designed to provide high levels of goods such as food, fodder and meat.

The contribution of biodiversity to ES provision is multi-layered and complex, and the specific links between species richness and ES provision are unclear (Mace et al., 2012; Lavorel, 2013). However, although the link between biodiversity and ecosystem functioning has been debated, positive relations have been shown in a growing number of experiments and data syntheses (Hector & Bagchi, 2007; Tilman et al., 2006a, 2006b; Lefcheck et al., 2015; Prangel et al., 2023). For example, each individual service relies on several ecosystem functions and the degree of this dependency varies significantly among services (De Bello et al., 2010; Cardinale et al., 2012). Although classical theories (Grime, 1998) have suggested that ecosystem functioning is primarily driven by the dominant species in a community, a high diversity of different species has the potential to cover a broader spectrum of different functions, potentially also increasing the provision of different services. This was confirmed by Waldén et al. (2023) who found that the supply of ES in grasslands increased with higher plant species diversity.

One way to assess and measure how ES are generated is to link functional traits (Violle et al., 2007) to specific ecological functions and services (Díaz et al., 2016; Cresswell et al., 2018). Because measures of functional diversity, in contrast to taxonomic diversity, are expected to predict community responses to land-use and environmental change, species traits are preferable to use rather than their identity (Jonason et al., 2016). By linking traits through function to appropriable services, it is hence possible to understand how different plant species contribute to specific ES. Because of differences in functions as a result of morphological traits, species may be limited in their capacity to contribute to a wide range of ES. For example, grassland plant species that have nectar-rich flowers and therefore contribute strongly to pollination, are often relatively small and thick-leaved, with poorly developed root architecture, making their contribution to water retention small (Waldén et al., 2023). Grasslands differ significantly in their species richness and composition depending on fertility, moisture, soil conditions, current and historical management, and other factors (Lindborg et al., 2008). Therefore, information about the species and their traits that allow comparison and evaluation of the potential delivery of ES from different types of grassland would be a major contribution to understanding the mechanisms underpinning ES generation and inform and tailor grassland management.

Here, we focus on SNG and IG, which are major contributors to European production systems and agricultural landscapes (Figure 1). Both SNG and IG can include pastures (when managed by grazing) and hay meadows (when managed for hay production) and have various historical origins and dynamics across Europe. Our overarching goal is to investigate and quantify how these grasslands with significant differences in their management intensity, differ in the provision of ES. In addition, we explore to what extent the ES supply of SNG and IG depends on their plant species richness, composition and functional traits. Specifically, we have the following objectives: (a) to examine, based on a non-quantitative literature review, the synergies and trade-offs among ES in SNG and IG for the key ES addressed in the scientific literature; and (b) to provide a mechanistic understanding of ES supply in SNG and IG by linking plant functional

FIGURE 1 Illustration of the difference between semi-natural grassland (left, Sweden) and intensified grasslands (right, Spain).

richness via functional traits to ES supply. The latter analysis is implemented using a subset of four key ES: forage production, insect pollination, carbon storage and water retention, for which we could access quantitative data in the published literature.

2 | METHODS

2.1 | Grasslands in production systems

SNG and IG are the most common grasslands in Europe. SNG are pastures or hay meadows with a long-term history of traditional low-intensity management (Dengler et al., 2020), with no seeding of commercial varieties, no or negligible agrochemical input, and without significant impacts of (recent) ploughing. Within the European Union's Common Agricultural Policy they are generally recognized as part of High Nature Value farmlands and many of them are listed as Annex I habitats in the Habitat's Directive. SNG typically require low-intensity livestock grazing or mowing as well as a certain degree of direct human management (e.g. scrub control) for their maintenance, and will generally be encroached by shrubs and trees if abandoned (Queiroz et al., 2014). Many remaining SNG are very old, with low-intensity management being present for hundreds of years (Johansson et al., 2008). IG are techno-economical improved pastures, resulting from intensified production in SNG or from establishment on former arable fields. They generally entail ploughing, sowing and re-seeding with commercial varieties or non-native grasses with high production potential, and often receive high amounts (up to hundreds of kg/ha) of agrochemicals or manure regularly (Kleijn et al., 2008). As a result, IGs typically have high production that can sustain high mowing frequency and/or high livestock density (Pilgrim et al., 2010). However, the distinction between SNG and IG can be vague, and with time an IG may become an SNG depending on applied management practices, nutrient status, humidity, availability of typical grassland species in the seed bank or in the surrounding landscape (Dengler et al., 2020).

We applied two methodological approaches to assess ES supplied by SNG and IG. First, we performed a non-quantitative review of ES supplied by SNG and IG. These results were compiled to explore the synergies and trade-offs among ES and then illustrated as a petal chart (cf. Foley et al., 2005). Second, we applied a quantitative approach to provide a mechanistic understanding of ES supply in SNG and IG by linking ES to plant functional traits.

2.2 | Qualitative analysis of synergies and trade-offs among ES generated by grasslands

Recent reviews suggest that grasslands can provide a wide diversity of ES (Milcu et al., 2013; D'Ottavio et al., 2018; Bengtsson et al., 2019; Sollenberger et al., 2019; Zhao et al., 2020). Using these reviews and the references therein as a starting point, we conducted a literature survey of the ES generated from SNG and IG, respectively. We also complemented the survey with relevant recent publications known to the authors of this research, each author being familiar with grassland ES research both at a regional and European level.

Based on the literature consulted, we extracted the 12 most relevant ES to be included in the comparison between IG and SNG service generation. The 12 ES were: (a) biomass production, (b) supply of wild foods, (c) habitat provision, (d) insect pollination, (e) biological control, (f) carbon capture, (g) carbon storage, (h) erosion control, (i) water quantity, (j) water quality, (k) tourism/recreation and (l) cultural heritage. The selection of ES was based on the following criteria: (a) to give a broad range of key examples of provisioning, regulating and cultural ES categories; (b) to capture the ES of importance for a wide range of stakeholders, including farmers; and (c) to be inclusive regarding the different regions of Europe. Supporting services are not included in this article because they are not used directly by people, being difficult to quantify and having therefore often been excluded from the majority of ES assessments (Haines-Young & Potschin, 2018). Biodiversity was not included as an ES per se, but was handled through the habitat provision for this approach, and particularly for the trait analysis approach (see below).

To illustrate the delivery of ES by each grassland type and the potential synergies and trade-offs between ES, we used the targeted 12 ES for visualization in a flower chart diagram, where the petal lengths quantify the relative ES provisioning (Foley et al., 2005). Based on literature from the survey, we ranked the supply of each ES for the two grassland types, SNG and IG, respectively. The ranking ranged from 0 to 1, where 0 equals no ES delivery and 1 equals full ES delivery. The ranking was finalized after discussions and deliberations among co-authors to provide a balanced and consensual judgement (cf. Bengtsson et al., 2019).

2.3 | Quantitative analysis of ES generated by plant traits and functional diversity in grasslands

To analyse plant traits and functional diversity, we selected, based on the ES overview, four services that are often included in the studies of grassland ecosystems (Zhao et al., 2020); "forage production", "insect pollination", "carbon storage" and "water retention". For each selected service, we identified relevant life-history traits based on the data from the literature (Table 1). Each service was represented by at least two traits that have been detected as a relevant indicator for particular service.

2.3.1 | Species and trait data collection

To analyse the relationship between plant traits and ES provision, we included data from SNG and IG. A literature search was conducted using the online databases Scopus and Google Scholar. The search was restricted to research conducted in Europe and under similar climatic conditions, i.e. temperate-cold with no predominant dry season (this excluded most of southern Europe). Search strings used for Scopus and Google Scholar were: (a) "intensified grassland" OR "intensive grassland" OR "improved grassland" OR "agricultural grassland" AND "species list" AND "plants"; (b) "intensified grassland" OR "intensive grassland" OR "improved grassland" OR "agricultural grassland" AND "plant" AND "abundance" OR "occurrence" OR "frequency" OR "cover"; (c) "semi-natural grassland" AND "species list" AND "plant species"; and (d) "semi-natural grassland" AND "plant species" AND "abundance" OR "occurrence" OR "frequency" OR "cover". Only articles providing full plant species lists and abundance values were included, excluding articles with no abundance values or those providing only dominant or most abundant plant species. In addition to the published species lists, we also used data available from our own previous research (Appendix S1).

A total of 23 source materials (articles and data sets) covering 40 species lists from different SNG and IG systems met our inclusion criteria. The data included species lists from 11 countries: Estonia, Sweden, Denmark, United Kingdom, Ireland, France, Germany, Austria, Belgium, Switzerland and Hungary. Of the 40 species lists, 16 originated from IG and 24 from SNG (Appendix S1). The plant species list taxonomies were unified according to The Plant List (http://www.theplantlist.org/) using the function TPL in package *Taxonstand*) in R (R Core Team, R Foundation for Statistical Computing, Vienna, AT) (R Core Team, 2021). Collective species names were not unified according to The Plant List, e.g. *Alchemilla vulgaris* agg., *Hierachium* sp., *Euphrasia officinalis* agg., *Taraxacum officinale*. Plant species that were extremely rare, i.e. were only represented once with low occurrence, were excluded or aggregated under collective species name. The included data sets had different ways of estimating species abundances (cover estimates, frequency of occurrence, etc.). To make data sets comparable, the scale of different abundance values was unified to a 0–1 scale with continuous values in between.

The traits were compiled from the TRY (Kattge et al., 2020), BiolFlor (Kühn et al., 2004), and GRoot (for root traits) (Guerrero-Ramírez et al., 2021) databases and from Tyler et al. (2021). Some missing values were filled in with the help of the WorldFlora database. After cleaning, the data set included 1,599 species across all grasslands. The few species for which we could not find any trait values or data for only one trait were excluded, leaving 1,575 species. The availability of trait data for the species varied: plant height (97% of species had available trait estimate), plant dry above-ground mass (12%), root dry mass (11%), root mass density (5%), root branching density (4%), reward index (estimated amount of pollen/nectar), (70%), flowering duration (93%) and pollination mode (100%) (Table 1). Missing values were filled by performing a trait-imputation procedure for the eight traits simultaneously using the package *missForest* (R version 1.5; R Core Team, R Foundation for Statistical Computing, Vienna, AT) (Stekhoven, 2022). Including phylogenetic information improves the performance of trait-imputation procedures (Penone et al., 2014) and we, therefore, included the first 10 phylogenetic eigenvectors in the trait matrix prior to the imputation with the *missForest* package. The phylogenetic tree was constructed with the R package *V.PhyloMaker* (Jin & Qian, 2019) using the GBOTP.extended (Zanne et al., 2014; Smith & Brown, 2018) as backbone phylogeny.

TABLE 1 Ecosystem services in semi-natural and intensified grasslands coupled to plant functional traits (trait units in parentheses) and databases from which the trait information was retrieved.

Service	Traits	Database
Forage	Average plant height (m) Plant dry above-ground mass (g)	TRY (Kattge et al., 2020) BiolFlor (Kühn et al., 2004)
Pollination	Reward index (estimated amount of pollen/nectar, scale 0–1) Duration of flowering (months) Insect pollination (1/0)	TRY (Kattge et al., 2020) BiolFlor (Kühn et al., 2004) Tyler et al. (2021)
Carbon storage	Plant dry above-ground mass (g) Root dry mass (g)	TRY (Kattge et al., 2020)
Water retention	Root mass density (g/cm) Root branching density (branches per cm)	GRoot (Guerrero-Ramírez et al., 2021)

2.3.2 | Statistical analysis

All data analyses were performed using R statistical software (R Core Team, R Foundation for Statistical Computing, Vienna, AT) (R Core Team, 2021). To quantify the functional spaces in each of the 30 data sets, we used the Functional richness and Rao quadratic entropy (Rao Q). Functional richness measures the volume of the trait space and is determined by the species situated along the margins of the space (Jonason et al., 2016). Functional richness was computed as the volume of the convex hull (defined as the smallest convex set enclosing the points) in the *n*-dimensional trait space occupied by the species (Cornwell et al., 2006). Rao quadratic entropy considers species abundances and reflects functional divergence (Pavoine & Dolédec, 2005). We calculated functional richness and Rao Q for all traits combined and with sets of traits reflecting different ES (Table 1). The R package *fundiversity* (R version 1.0.0; R Core Team, R Foundation for Statistical Computing, Vienna, AT) (Grenié & Gruson, 2022) was used for the calculations. In addition to the functional diversity estimates, we calculated species richness and taxonomic Shannon diversity for the different data sets.

Differences in functional richness and Rao Q values between SNG and IG data sets were tested with *t*-test using the Holm method for *p*-value adjustment (Holm, 1979). Functional richness was $\log_{10}$-transformed prior to the *t*-test, to ensure uniform distribution of the data.

3 | RESULTS

3.1 | A literature overview of trade-offs and synergies among ES generated from grasslands

Very few studies directly compared SNG and IG, or conducted multiple ES assessment (cf. Bengtsson et al., 2019; Schils et al., 2022). Based on reviews and single ES studies, we found a clear difference in provision of ES between SNG and IG, in which SNG showed a greater potential to generate most of the services at relatively high levels, compared with IG (Table 2). Some ES, like water-related ES and carbon storage and sequestration, had been studied frequently, especially for IG, although not much within the ES framework (Sollenberger et al., 2019). Information about pollination and biological control was especially poor for IG. It was clear that ES generation also depends on the size of grassland, scale of analysis and the landscape context in which the grassland is located.

Clear trade-offs and synergies between ES were found for both SNG and IG (Figure 2). SNG showed a more balanced provision of a range of ES, having high supply of wild forage, habitat for biodiversity, pollination, biological control and cultural services, but relatively poor carbon capture and water quantity and quality regulation (Figure 2). In comparison, IG presented a prominent trade-off between biomass production and all the other ES. A fundamental trade-off is between biomass production and natural habitat provision (enhancing biodiversity) (Foley et al., 2005; Kok, Oostvogels, et al., 2020), yet IG also contributed less to pollination and carbon capture.

3.2 | Linking ES to functional diversity

There was a large overlap between the species found in SNG and IG, but SNG harboured considerably more species than the IG across Europe (Figure 3). Of the total 1,575 species listed in the data sets, 1,558 were found in SNG and 309 in IG. The grassland types had 292 species in common and only 17 were unique for IG.

Both taxonomic diversity estimates (species richness and Shannon diversity) and functional diversity estimates (Functional richness and Rao Q) were significantly higher in SNG data sets than in IG (Figure 3).

When analysing functional richness underpinning the selected ES, all four (forage production, carbon storage, pollination and water retention) were significantly higher in SNG than in IG (Figure 4). By contrast, when comparing the Rao Q (based on plant species abundance) characterizing functional divergence for different ES, the Rao Q was higher in SNG for all the ES, but the difference was not statistically significant after *p*-value correction (Holm, 1979; Figure 5).

4 | DISCUSSION

We found differences between the SNG and IG in all aspects we addressed: the supply of ES, species richness and functional diversity. Our assessment confirms that SNG were better at providing cultural services and biodiversity-related ES, e.g. pollination and biological control, through habitat provision, but showed a lower potential for capturing carbon and providing water. By contrast, IG clearly show a more fundamental trade-off between biomass production and natural habitat provision and biodiversity-related ES (Kok, de Olde, et al., 2020; Kok, Oostvogels, et al., 2020). Nonetheless, studies that directly compare SNG and IG for their delivery of ES and particularly for their cultural values are scarce (Schils et al., 2022). Functional richness and functional divergence (Rao Q) analyses partly confirmed the literature overview showing that SNG had a wider range of functional trait values than IG. SNG had significantly higher functional richness (Figures 3 and 4), suggesting that the potential to generate ES in SNG is higher than in IG, although high variability was noted in SNG provision of ES. This difference was underpinned by the higher species richness and higher diversity of species in SNG. Abundance-based functional divergence analysis did not show significant differences between SNG and IG (Figure 5), indicating that the few dominant species in IG are capable of providing the different ES to some extent. However, in case of any environmental perturbations (droughts, floods, etc.), SNG are likely to handle these shocks better owing their higher number of species that could buffer environmental changes because of their wide range of traits. This is congruent with theory, as species co-existing in high-diversity systems

TABLE 2 Most important ecosystem services generated from intensified (IG) and semi-natural grasslands (SNG).

Ecosystem services	Explanation	Confidence term SNG	Confidence term IG	Comments	Reference
Provisioning					
Plant biomass production	Fodder production	WE	WE	Generally higher production in IG than in SNG	Zisenis et al. (2011), Sollenberger et al. (2019)
Wild food and other products	Production of harvestable wild products (e.g. food, pharmaceutical, ornamental)	EI	EI	SNG are better providers than IG, mostly because of historical ecological knowledge and values	Sucholas et al. (2017), Torralba et al. (2018), Vári et al. (2020)
Regulating					
Habitat provision	Maintaining nursery population and habitats	WE	IC	Generally higher provision in SNG, but few studies are conducted in IG	Dengler et al. (2020), Wilson et al. (2012), Kok, de Olde, et al. (2020)
Pollination	Pollination of crops and wildflowers	WE	IC	SNG is important for pollination in the landscape. Few studies directly relate SNG and IG to crop production	Werling et al. (2014), Taki et al. (2010)
Biological control	Pest control for crop production	EI	EI	SNG is more important for pest control. Few studies directly relate SNG and IG to crop production	Jonsson et al. (2014), Perrot et al. (2021)
Carbon capture	Carbon sequestration through photosynthesis	IC	UR	Carbon capture is generally higher in IG, but results are inconclusive and site dependent	Dlamini et al. (2016), Sollenberger et al. (2019), Lal (2004), Soussana et al. (2010)
Carbon storage	Carbon sink in the soil	WE	WE	Carbon storage is higher in SNG than in IG	
Erosion control	Reducing run-off and stabilizing soil	IC	IC	Long-term permanent vegetation in SNG may prevent run-off and stabilize soils, in contrast to IG	Pilgrim et al. (2010), Fu et al. (2011)
Water quantity	Infiltration and storage capacity	UR	UR	SNG generally better. In IG potentially important, but site-specific and dependent on conditions	Sollenberger et al. (2019), Posthumus and Morris (2010), Guo et al. (2020)
Water quality	Cleaning water through infiltration	EI	IC	Potentially provided by SNG, likely lower in IG, but data inconclusive	Cadman et al. (2013), Sollenberger et al. (2019)
Cultural					
Tourism/recreation	Possibilities for recreation	EI	IC	Clearly linked to high levels of biodiversity and multifunctionality of SNG, but less clear with IG	Hönigova et al. (2012), Martino and Muenzel (2018)
Cultural heritage	Historical activities, legacies and biological values	WE	WE	Cultural heritage is highly related to SNG but not to IG	Fischer et al. (2008), Lindborg et al. (2008), Bullock et al. (2011)

Note: The confidence terms listed are based on the four-box model for qualitative communication according to IPBES procedure (IPBES, 2018). EI: established but incomplete; IC: inconclusive; UR: unresolved; WE: well established.

often have traits that are unequally important for various functions, hence complementing each other at the community level (Hector & Bagchi, 2007).

Overall, biomass production was found to be higher in IG than in SNG, although differences occurred depending on location (Sollenberger et al., 2019). The higher grassland productivity is an effect of increased technological innovations, such as irrigation and fertilization, and is linked to management intensity such as frequency of cuts and number of livestock units per area. By contrast, the functional richness related to forage and biomass production

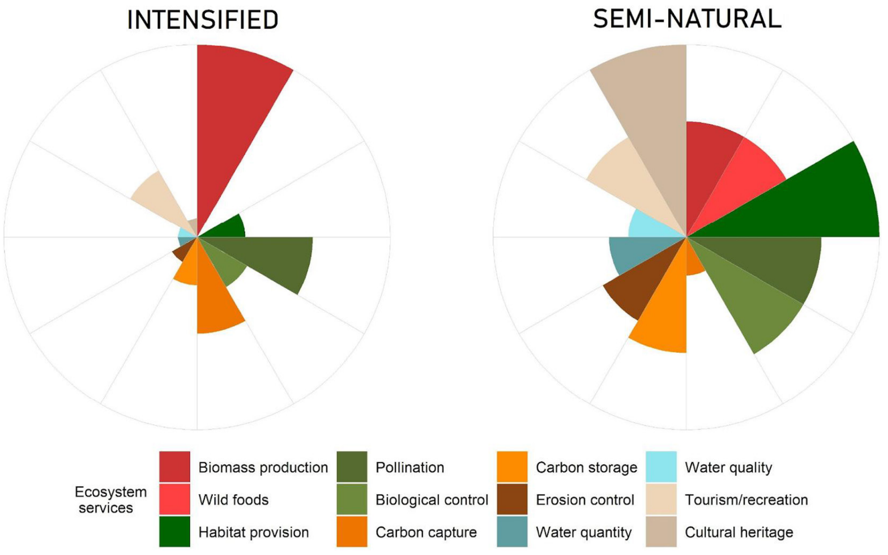

FIGURE 2 Most important ecosystem services (ES) generated from intensified grasslands and semi-natural grasslands. The ES estimates are based partly on the existing literature (Table 2) and partly on the authors' expert assessment (for those ES where the confidence term was inconclusive or unresolved; Table 2). Each estimate ranges from 0 to 1, with petal sizes close to 0 meaning that delivery of that specific ES is low in relative terms.

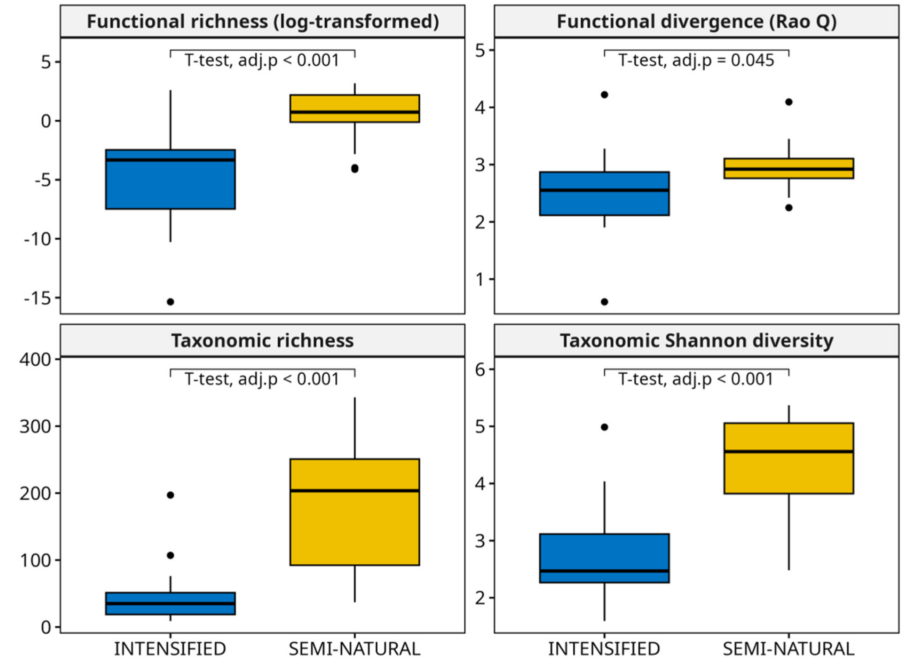

FIGURE 3 Functional and taxonomic diversity in intensified ($n=16$) and semi-natural ($n=24$) grassland data sets. (Upper) Functional richness and Rao Q based on eight traits (plant height, plant dry mass, root dry mass, root mass density, root branching density, reward index, flowering duration and insect pollination). (Lower) Taxonomic richness and Shannon diversity. Whereas functional and taxonomic richness are based on species occurrences, calculations of Rao Q and Shannon diversity include species abundance estimates.

was higher in SNG than in IG. This is a bit surprising, but suggests that the potential of high fodder production in SNG is not fully developed and has the potential to increase. However, higher nutrient levels in IG maximize the biomass production of a few dominant species, and fertilizing SNG would decrease biodiversity by shifting community composition towards taller and high-yielding species that outcompete smaller, less-competitive and more stress-tolerant species (Tillman et al., 1996). We suggest that the high functional richness of SNG indicates a stronger ability to use limited resources, i.e. fill different niches of resource acquisition. High functional richness in traits related to fodder production also suggests that SNG fodder production is more likely to withstand different climatic and environmental fluctuations compared with IG.

The ability of SNGs to act as habitat providers is well documented, although differences occur also for this service depending on local biophysical conditions (Dengler et al., 2020; Kok, de Olde, et al., 2020). SNG are found to be biodiversity "hotspots", and play key roles in the dispersal of different organisms (Wilson et al., 2012; Dengler et al., 2020). IG, having higher nutrient levels and favouring high-yielding varieties, do not reach the same high level of biodiversity across different trophic levels. The high plant richness of SNG was also confirmed in this study when comparing species lists and overlap between SNG and IG. IG have the potential to improve in habitat provision when the management is designed to support biodiversity or when soils start to lose nutrients as they become permanent (Sexton & Emery, 2020).

Insect pollination and biological control are ES that are clearly linked to habitat provision because they are generated by insects dependent on suitable and connected habitats for their survival (Lindborg et al., 2017). Several studies show a positive effect of

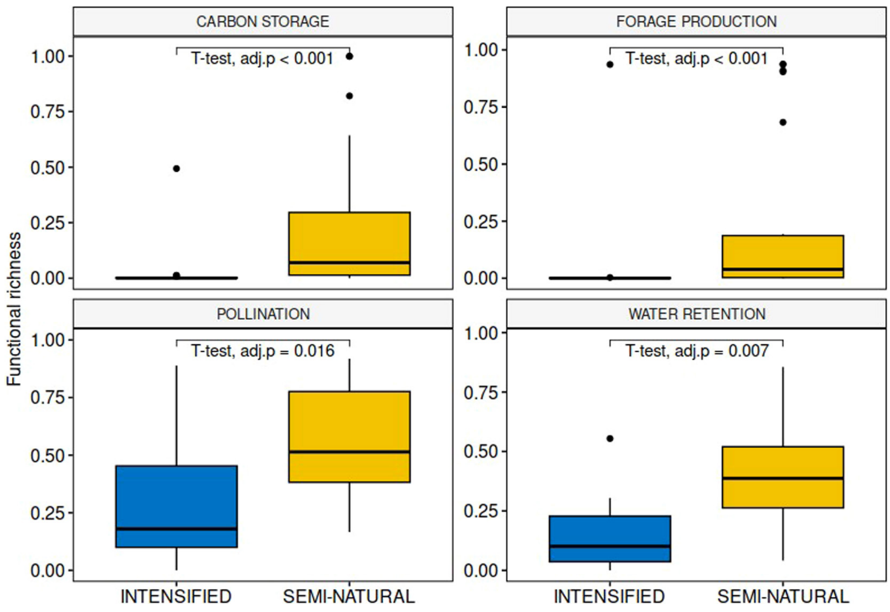

FIGURE 4 Functional richness comparison in intensified ($n = 16$) and semi-natural ($n = 24$) grassland data sets. Functional richness was calculated separately based on traits reflecting different ecosystem services: carbon storage (root dry mass, plant above-ground mass), forage production (plant height, plant above-ground mass), pollination (duration of flowering, reward index, insect pollination) and water retention (root branching density, root mass density). The *t*-test was performed on log-transformed functional richness but the values in the figure are untransformed for visualization.

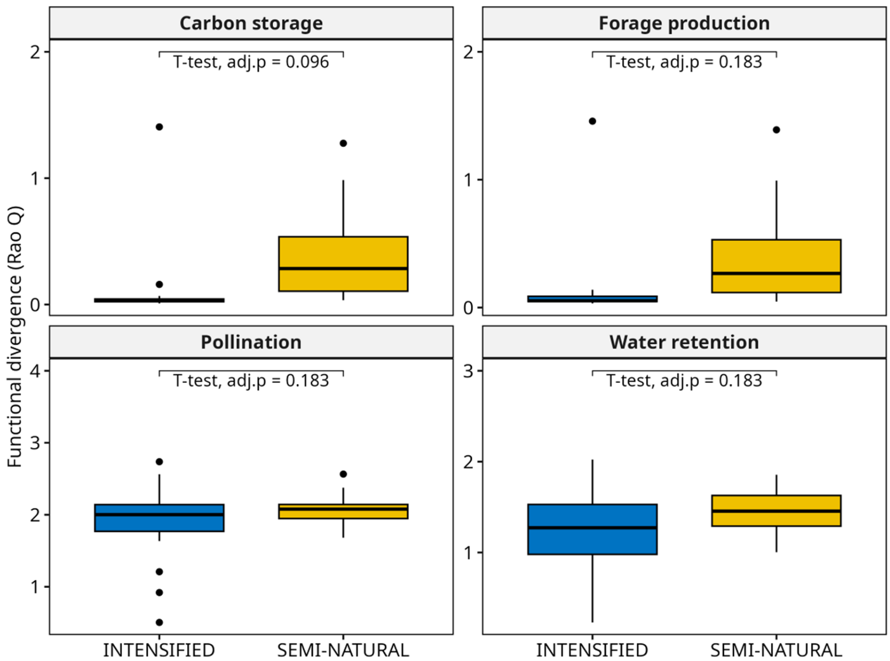

FIGURE 5 Functional divergence (Rao Q) comparison in intensified ($n = 16$) and semi-natural ($n = 24$) grassland data sets. Rao Q was calculated separately based on species abundances in different data sets and traits reflecting different ecosystem services: carbon storage (root dry mass, plant above-ground mass), forage production (plant height, plant above-ground mass), pollination (duration of flowering, reward index, insect pollination) and water retention (root branching density, root mass density).

SNG on the number of pollinators (Potts et al., 2010). Hence, SNG, may enhance these ES and additionally have a direct positive effect on agricultural pollination adjacent to these grasslands (Taki et al., 2010; Jonsson et al., 2014; Werling et al., 2014). Our functional richness analyses also indicate that plants in SNG have a wider range of pollination-related traits than IG plants. For example, insect pollination is dependent on nectar/pollen quantity and flowering time. In addition, to preserve rare pollinator species that are not major contributors to pollination, a high diversity of wildflowers is needed (Wood et al., 2013).

The role of grasslands for climate change mitigation is frequently discussed, particularly carbon storage in permanent grasslands because they may store large amounts in the soil (Lal, 2004; Smith, 2014; Bai & Cotrufo, 2022). Although, carbon sequestration increases with increased nutrient input (Sollenberger et al., 2019, but see Skinner, 2013), carbon capture and storage in grassland soils may be reduced by intensive grazing (Dlamini et al., 2016) or ploughing (Krauss et al., 2022). Carbon storage was concluded to be higher in SNG than in IG, especially with the presence of trees as in wood pastures, whereas carbon capture capacity can be higher in IG. Several management practices have been recommended to increase carbon sequestration and enhance carbon stocks in the soil, including the restoration and management of land as well as changes in management intensity and practice (Lal, 2004). The reduction of grazing pressure and mowing frequency, particularly in IG grasslands, can enhance the C stock in the soil (Eze et al., 2018) and additionally reduce other greenhouse gas emissions generated from grazing livestock (Manzan & White, 2019).

Plants are crucial for carbon sequestration and storage through the creation of biomass both above-ground and particularly below-ground (roots) (Bai & Cotrufo, 2022). Biomass creation below-ground can be up to five times higher than that above-ground (Yang et al., 2019). When comparing these traits in the functional richness analysis, results indicated that plant communities in SNG can be significantly more effective in soil carbon storage than plant communities in IG. According to Bai and Cotrufo (2022) and Yang et al. (2019), plant diversity is key driver for carbon sequestration and storage in the soil as well as for promoting soil health. This study, along with the existing literature, suggests that species-rich plant communities can enhance carbon storage in the soil, which is likely explained by some form of interspecific interaction or complementarity effect (Yang et al., 2019). However, soil carbon storage and sequestration is driven by both biotic and abiotic factors (Bai & Cotrufo, 2022), particularly temperature and precipitation (De Deyn et al., 2008). Although above- and below-ground (root) biomass are crucial traits for capturing and storing carbon, local abiotic factors and the eventual grassland management, will determine soil carbon storage and residence time (De Deyn et al., 2008).

The water-related ES supplied from European grasslands are currently relatively little discussed, although they are relevant in specific contexts (Faccioni et al., 2019) and have a potential to become prominent (Lemaire et al., 2011). In general, water quality is negatively affected by fertilizers (increased N and P) and high stocking rates increasing the nutrient load in run-off (Sollenberger et al., 2019). Although no specific publications directly compare SNG and IG, the trend is well documented when comparing permanent grasslands and croplands (Schils et al., 2022). This suggests that IG, with large amounts of nutrients in the soil and high stocking rates, will have a negative impact on water quality. At the local scale, particular plant species may alter the water supply by affecting infiltration rate and storage capacity through differences in functional traits leading to variation in water-use efficiencies (Lemaire et al., 2011; Volaire et al., 2014). Root mass, branching density and root system are important traits regulating water in grasslands. Similar to the literature survey, our trait analysis showed that water retention capacity is higher in SNG than in IG. This may also have implications for coping with drought. Experiments show that plant species with less biomass and less-sophisticated root systems, e.g. annuals, are more sensitive to drought (Tillman et al., 1996).

4.1 | Managing for ES provision in farmland

ES provision from grasslands depends strongly on their management (Milcu et al., 2013). IG are "designed" to maximize food production, which usually happens at the expense of other ES that have not been traditionally considered in high-intensity management systems. Conversely, SNG are characterized by more balanced provision of different ES. When managing for ES, synergies and trade-offs also need to be accounted for (Nowak-Olejnik et al., 2020). In our study, there were clear differences between SNG and IG, where significant trade-offs emerged between biomass production and provision of other services in IG, but were more nuanced in SNG. Similarly, plant functional richness in SNG was higher for forage production, carbon storage and water retention. The relationship between plant functional traits and the delivery of ES also suggests that particular ES can be promoted when targeting particular plant communities and traits, enhancing synergies and mitigating trade-offs. Understanding that several species are contributing to the same function through higher trait diversity can also inform management. In SNG, for example, some species can compensate for the potential loss of other species (functional redundancy), which may counteract perturbations, like drought, hence increasing the resilience of the grassland (Craine et al., 2012).

Trade-offs and synergies may vary with spatial scale, because the provision of ES is highly dependent on the underpinning ecological functions which operate at different spatial scales (Lindborg et al., 2017). Population-based ES, like insect pollination, as well as water regulation, are dependent on the surrounding landscape, whereas fodder production and carbon storage are more affected by the local environment (water and nutrient availability). Hence, both local conditions and the wider landscape context are important to consider to avoid trade-offs and promote synergies among services. Both IG and SNG are likely needed for long-term sustainability of food production, as they partly complement each other. However, significantly more effort must be put into landscape-scale spatial configuration of farming systems to ensure more balanced provision of ES. In addition, perceptions and values around cultural ES are very context dependent (Milcu et al., 2013; Bernués et al., 2019) and can vary across stakeholders and sociodemographic factors (Bernués & Rodríguez-Ortega, 2016; Nowak-Olejnik et al., 2020). Hence, accounting for a plurality of perspectives on what is desirable, as well as coordinated interventions at different scales (from field, to farm to region or to global context) is needed (Pereira et al., 2020). This study shows the importance of SNG in securing a range of ES. In addition, IG management should be steered towards a more balanced provision of ES. For example, trade-offs related to high livestock intensity could be reduced if the density is kept below carrying capacity, resulting in increased biodiversity, enhanced pollinator diversity, improved water quality, maintained carbon storage and improved cultural ES.

AUTHOR CONTRIBUTIONS

RL initiated the idea, conducted the literature survey and led the writing. TR conducted most of the analysis with contribution from EP. All authors contributed to the writing of the manuscript and gave final approval for publication.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from: https://figshare.com/articles/dataset/_/22492396.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Appendix S1. List of datasets used in the study.

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