Received: 30 January 2020 | Accepted: 31 March 2020
DOI: 10.1111/1365-2664.13644

Journal of Applied Ecology
BRITISH ECOLOGICAL SOCIETY

REVIEW

Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands

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Funding information
Helmholtz-Gemeinschaft

Handling Editor: Claire Wainwright

Abstract

1. Functional traits offer promising avenues to investigate how community composition and diversity define ecosystem functioning and service delivery. In recent years, many empirical studies on the importance of functional traits for ecosystem service provisioning have been undertaken, but a general understanding and synthesis of results is lacking for many ecosystems.
2. Here we focus on temperate grasslands and present a systematic literature review synthesizing how plant functional traits are interrelated with ecosystem services.
3. Based on 108 studies, we identified a core set of 40 functional traits and 11 ecosystem services. Several of these traits were only linked to one, while 75% of traits were linked to two or more ecosystem services.
4. We found that trait-specific constraints can lead to both synergies and trade-offs in the supply of multiple ecosystem services. For instance, synergies between biomass production and climate regulation can be achieved by changing morphometric root traits such as increasing root diameter, tissue density or shoot to root ratio. On the other hand, supporting fast-growing exploitative species characterized by high specific leaf area and nitrogen content typically leads to trade-offs between fodder quality and water purification.
5. *Synthesis and applications*. By applying network analysis, we found five groups of ecosystem services sharing common functional traits. Within and among these groups, we identified trade-offs among traits as well as among services and found options for synergies. These can be particularly useful in landscape planning, and when management aims focus on maintaining multifunctionality of ecosystems and maximizing corresponding ecosystem service delivery.

KEYWORDS
ecosystem services, functional traits, grasslands, multifunctionality, network analysis, plant traits, synergies, trade-offs

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1 | INTRODUCTION

Appropriate responses to the impacts of global change require an understanding of how changes in biodiversity translate into changes in the functioning of ecosystems. Such an understanding enables (a) the assessment of potential consequences for society and (b) the development of efficient and target-oriented management strategies. The concept of ecosystem services provides a framework for linking human benefits and well-being to the underlying biophysical realm of ecosystem functioning (Díaz et al., 2018; Lavorel, et al., 2017). Ecosystem services can be described from a demand perspective addressing human needs, well-being and potential valuation by stakeholders (Goodness, Andersson, Anderson, & Elmqvist, 2016; Lindemann-Matthies, Junge, & Matthies, 2010; Seppelt, Dormann, Eppink, Lautenbach, & Schmidt, 2011), or from a supply perspective emphasizing the underlying ecological functions, for example, by referring to the functional traits of species in a community (Díaz et al., 2007; Lavorel & Grigulis, 2012; Violle et al., 2015). These traits are characteristics at the individual level, including phenological, physiological or morphological features (Cornelissen et al., 2003; Violle et al., 2007). Functional traits hence depict mechanistic linkages between organisms and their environment (Lavorel & Garnier, 2002) and may serve as predictors of ecosystem service supply (Garnier & Navas, 2012).

Given the different societal demands and the necessity to manage land for different purposes (cf. concept of multifunctionality of landscapes or ecosystems; Butterfield, Camhi, Rubin, & Schwalm, 2016; Manning et al., 2018), we need to improve our understanding about which functional traits are involved in the delivery of which ecosystem services (de Bello et al., 2010). Links among individual services, driven by a shared set of ecosystem functions or corresponding functional traits, may lead to distinct groups of ecosystem services—with functions being the 'ecological processes that control the fluxes of energy, nutrients and organic matter through an environment' and services being 'the suite of benefits that ecosystems provide to humanity' (Cardinale et al., 2012, p. 60). Predicting multiple interactions within and among such groups based on functional traits can help identifying land management options that reduce trade-offs among seemingly contradicting ecosystem service demands. Moreover, this may support the identification of potential synergies among different services, that is, the possibility to support several services simultaneously by supporting plant species with traits involved in the delivery of these services. The term synergy is used here when a trait affects two or more ecosystem services in the same way such as an increase in leaf nitrogen content (LNC) that can increase both productivity and fodder quality at the same time. The term trade-off is used when a trait affects two or more ecosystem services in opposing ways. Therefore, an approach aimed at identifying functionally linked groups of ecosystem services shows several advantages over assessing services separately (de Bello et al., 2010; Spake et al., 2017).

In addition to local and landscape-scale assessments of ecosystem services, large-scale mapping efforts of groups of ecosystem services have been undertaken recently (Dittrich, Seppelt, Václavík, & Cord, 2017; Lavorel, et al., 2017). However, such approaches mostly rely on spatial surrogates that provide only non-mechanistic proxies for ecosystem services (Mouchet et al., 2014) or on co-occurrences of services defining spatially or temporally linked groups (Spake et al., 2017). Identified links between ecosystem services and functional traits can improve our ability to assess and predict the spatial and temporal distribution of services and their trade-offs considerably by already known or newly assessed relationships between environmental drivers and the respective traits.

A first study that synthesized literature on trait–service associations was provided by de Bello et al. (2010). By associating traits with ecosystem services and their underlying ecosystem processes across trophic levels and ecosystem types, the authors were able to identify globally consistent trait–service associations, allowing the assessment of biotic effects on combined ecosystem service delivery. Here we provide a systematic review of trait–service associations, building on the approach of de Bello et al. (2010), but focusing on grasslands and plant functional traits. Focusing on a specific ecosystem allowed us to particularly investigate within-system relationships rather than obtaining cross-system relationships, for example, by comparing traits of trees and herbaceous plants. Our approach is thus less dependent on the environmental context than it would be when including a range of ecosystems.

Temperate grasslands belong to the best studied ecosystems world-wide (Violle et al., 2015). They are severely threatened by agricultural expansion for food production (Erb et al., 2016), grazing pressure (Zhang et al., 2015) and climate change (Schlaepfer et al., 2017), creating a strong need for understanding and managing their ecosystem services (Hoekstra, Boucher, Ricketts, & Roberts, 2005; Thébault, Mariotte, Lortie, & MacDougall, 2014). We further focus on vascular plants since they are the best studied taxon with respect to functional traits (de Bello et al., 2010; Díaz et al., 2016) and are key to some of the most intensively utilized ecosystem services such as primary production (Costanza et al., 2014).

We identify groups of services defined by sets of shared traits. These trait–service groups are intended to support the future monitoring and management of ecosystems to achieve the delivery of multiple services and to reduce undesired trade-offs. Particularly, we focus on the following questions: (a) Which plant functional traits show positive, negative or neutral associations with one or more ecosystem services in grasslands? (b) Which trait–service groups emerge from these associations? (c) What are the trade-offs and synergies among ecosystem services, driven by specific functional traits?

2 | MATERIALS AND METHODS

2.1 | Literature search

We performed a systematic literature search using the ISI Web of Science Core Collection on 16 December 2016, taking into account all articles published since 2005 (Figure 1). The search term consisted of ‘“plant*” AND “trait*” AND “service*”’ and was selected in order to include a wide array of studies that addressed the associations between plant functional traits and ecosystem services. This search yielded 545 articles that were complemented by 56 datasets on linkages between plant functional traits and services in grasslands included in de Bello et al. (2010). We excluded duplicates and screened the resulting set by title and abstract. Articles were included if (a) they reported specific plant traits and not only functional groups, (b) they related functional traits to at least one specific ecosystem service and (c) the research was carried out in grassland ecosystems. Articles were excluded if the focus was on breeding, genetic modification, geo-engineering or invasion of alien species. In a next step, the full text of the paper was screened and all articles that only mentioned but did not explicitly test for trait–service associations were excluded. Additionally, articles that only looked at trait responses to management changes or that were erroneously incorporated in the first steps were excluded leading to a final set of 108 articles. A list of these articles is provided in the Data sources section. Extracted data encompassed ecosystem service type, plant functional traits, direction or quantified values of trait–service associations, named trade-offs or synergies and additional information on the type of study (i.e. case study, meta-analysis). We standardized trait terminology according to the *Thesaurus of Plant Characteristics* (Garnier et al., 2017). The classification of ecosystem services followed the Millennium Ecosystem Assessment (2005).

2.2 | Identification of trait–ecosystem service associations

For identifying trait–service associations, we used the following approach: (a) to limit uncertainty in trait–service associations due to low numbers of studies investigating them, only traits with ≥2 reported associations to any ecosystem service and services with overall >2 entries in our database were considered. (b) Associations of traits with multiple services were treated as independent entries. (c) If a trait was explicitly mentioned as tested in the methods section but no results were reported, no effect was assumed. This was done to account for a potential bias resulting from reporting significant effects only. (d) Regarding the direction of trait–service associations, effect sizes were extracted if possible. However, as the number of reported effect sizes was limited, a transformation to positive, negative or non-directional effects from the qualitative and quantitative information was conducted. The analysed studies reported effect direction for continuous traits mostly based on correlations between ecosystem services and respective trait values. For categorical traits, this relationship was usually based on measures of trait diversity. The overall trait–service associations were then calculated as in Equation 1 following Harrison et al. (2014), with the modification that in addition to significant positive and negative

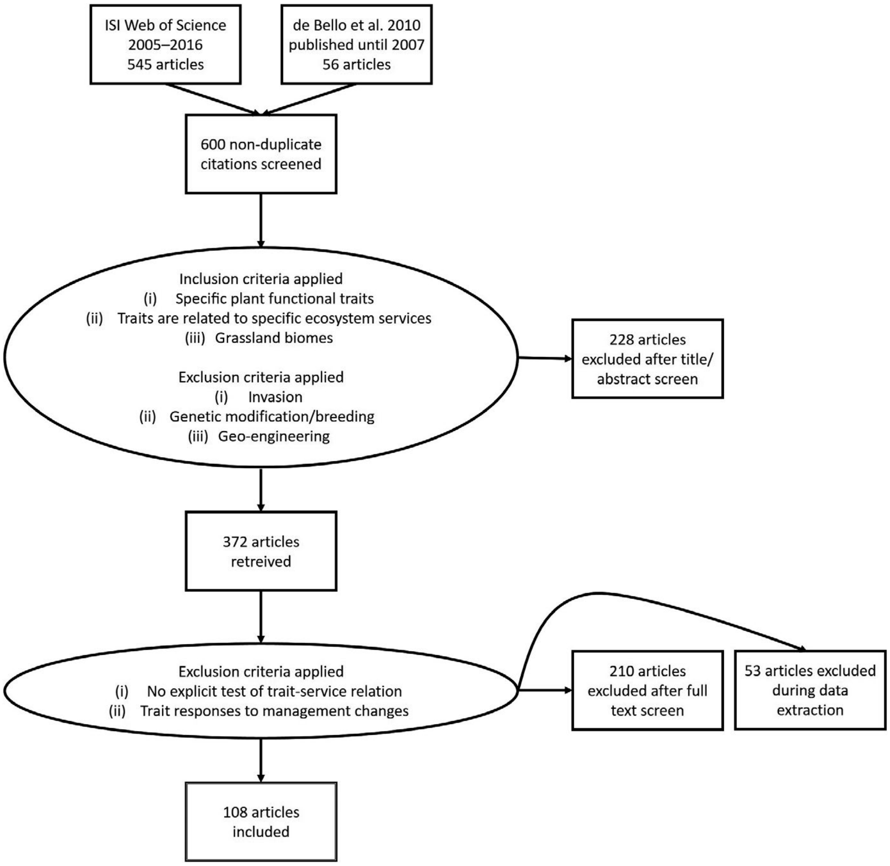

FIGURE 1 Flow diagram of literature review synthesizing how plant functional traits are interrelated with ecosystem services in temperate grasslands, following PRISMA reporting standards (Shamseer et al., 2015). Articles from de Bello et al. (2010) were not screened but directly used for data extraction

effects also non-significant associations were considered as no effect and taken into account for the calculation of the total number of associations. Values range from −1 to 1.

$$\text{Predominant direction} = \frac{\sum(\text{positive associations}) - \sum(\text{negative associations})}{\text{Total number of associations}}. \tag{1}$$

Additionally, a measure of uncertainty for trait–service associations was calculated by dividing 1 by the total number of associations reported, leading to values between 0 (lowest) and 1 (highest uncertainty). Associations reported by a number of studies will hence have lower uncertainty values than those reported only once. Moreover, if different studies reported contrasting trait–service associations (i.e. negative vs. positive), we recorded the number of such discrepancies.

2.3 | Network analysis to identify trait–service groups

A bipartite network analysis was conducted to investigate clustering within the associations of traits and services. A bipartite network is made up of two separate groups, of which linkages between members of the different groups but not within groups are possible (Dormann & Strauss, 2014). Ecological applications of this approach usually focus on trophic interactions (Schleuning et al., 2016), but network analyses have also been applied in other disciplines, for example, for investigating social or trade networks (Newman, Watts, & Strogatz, 2002; Saavedra, Stouffer, Uzzi, & Bascompte, 2011).

We identified trait–service groups based on a quantitative bipartite network of plant functional traits and ecosystem services, weighted by their calculated effects to include information about the strength of interaction. Clustering was assessed by network modularity which was analysed by allowing for the identification of nested submodules (Dormann & Strauss, 2014) using the R (R Core Team, 2018) package 'BIPARTITE' (Dormann, Fründ, Blüthgen, & Gruber, 2009). In our study, the different modules can be regarded as trait–service groups with many linkages (Dormann & Strauss, 2014). These groups were identified based on the higher prevalence of their within-interactions compared to between module interactions. To stabilize modularity computation, we re-ran the calculations 20 times using the function *metaComputeModules*. Bipartite graphs and corresponding calculations of modules were based on absolute values of trait–service associations, that is, ignoring effect direction but only considering links and their strengths, leading to groups of services impacted by the same traits but not necessarily in the same direction. However, for visualization of potential trade-offs or synergies among services and species traits, we display effect directions in the corresponding bipartite modularity diagram.

3 | RESULTS

Of the 545 articles that we screened, 52 were included in the analysis and merged with 56 articles from de Bello et al. (2010). Six per cent (7/108) of the articles were reviews, 3% (3/108) meta-analyses and 90% (98/108) were primary studies. The geographical range of studies was global, yet studies conducted in France and in whole Europe accounted for 38% and 82% of all studies respectively. Less than 29% of the studies quantified the services directly and only one publication (Lavorel & Grigulis, 2012) used a stakeholder-based approach.

3.1 | Trait–service relationships

In total, 179 plant functional traits were reported together with 16 ecosystem services. Out of these, 40 traits were included in the analysis. About 127 traits were only reported once and were therefore not considered. Twelve traits were excluded for reasons like unclear categorization and insufficient trait definition or for referring to community-level but not species-level traits. The services soil formation, contamination reduction and hazard prevention were excluded because they were reported once or twice only. Biodiversity and habitat provision were not considered because of (a) the ongoing debate if they should be perceived as ecosystem services at all (Mace, Norris, & Fitter, 2012; Silvertown, 2015) and (b) insufficient information. Of all trait–service associations, 5.6% included cultural, 5.5% provisioning, 56.1% supporting (including biomass production) and 32.6% regulating services. Uncertainty ranged from 0.05 to 1 ($M = 0.6$); 48% of the identified associations had an uncertainty of 1, meaning that they had only been reported once.

We found that the number of ecosystem services that can be associated to a particular trait varies substantially, ranging from 1 to 9 (see Table 1; Figure 2; Appendix S1). We define traits showing only effects on one service as 'service-specific traits' (25% of traits) and traits showing directional effects on at least two services as 'multi-service traits' (75% of traits in our dataset). Typical examples of 'multi-service' traits were specific leaf area (SLA), LNC, vegetative plant height (VPH) or leaf dry matter content (LDMC). These were associated with services such as biomass production, soil fertility, climate regulation or aesthetic appeal amongst others. 'Service-specific' traits were for example, root nitrogen content, percentage of fine roots (both linked to erosion control) or generative plant height (linked to biomass production).

Root traits were mainly associated with erosion control, climate regulation and biomass production, floral traits with aesthetic appeal and pollination, stem and whole plant traits with biomass production. Especially for multi-service traits, inherent trade-offs for ecosystem service provisioning were evident. For example, a higher LNC positively affected biomass production, fodder quality, soil fertility and climate regulation, yet it negatively affected biocontrol, water purification and cultural heritage services. Similarly, increasing LDMC values reduced fodder quality and aesthetic appeal of the landscape while supporting climate regulation. The number of plant functional traits linked to a particular service varied considerably. For example, erosion control and soil fertility were linked to more than half of the traits, while water purification and biocontrol had

TABLE 1 Plant functional trait–ecosystem service associations identified in this literature review. All traits are ranked from top to bottom by the number of directional associations with ecosystem services. Services are sorted by decreasing number of trait–service associations from left to right. Arrows indicate the predominant direction as calculated by Equation 1, with >0.6 ↑; >0.2 < 0.6 ↗; >−0.2 < 0.2 →; >−0.6 < −0.2 ↘; <−0.6 ↓. Effect uncertainty ranged from 1 (evidence based on a single study) to values approaching 0 (with increasing numbers of studies), given by the numbers on the right, and displayed by colouring (grey = low (1 publication), light green = medium (2–4 publications), dark green = high (>4 publications)). For mean values determining the direction of arrows and for information about the number of discrepancies within trait–service associations see Appendix S1

Trait/service	Biomass production	Soil fertility	Erosion control	Climate regulation	Fodder quality	Aesthetic appeal	Water regulation	Pollination	Recreation/ heritage	Biocontrol	Water purification
Leaf nitrogen content	↗ 0.08	↗ 0.08	↘ 0.5	↗ 0.25	↗ 0.25	↘ 0.33			↓ 1	↓ 0.33	↓ 1
Plant height (VPH)	↗ 0.05	↑ 0.11	→ 1	↗ 0.5	↘ 0.5	↓ 0.25	↓ 1		↓ 1		
Specific leaf area	↗ 0.07	→ 0.06	↘ 0.5	↘ 0.25	↑ 1	↑ 1					↓ 1
Leaf dry matter content	↘ 0.07	→ 0.08	↗ 0.33	↑ 0.2	↓ 0.25	↓ 1				→ 1	
Plant C/N	→ 1	↓ 1		↑ 0.5	↑ 1			↑ 1			
Root depth	→ 1	↑ 1	↓ 1	↓ 1			↑ 1				
Leaf phosphate content	↗ 0.17	↑ 0.25		↓ 1	→ 1	↑ 1		→ 1			
Flowering duration	↑ 1	→ 0.33		↓ 1		↑ 1		↗ 0.33			
Leaf area	↗ 0.33	→ 1	↗ 0.5		↗ 0.5		↑ 0.5				
Leaf litter mass	↑ 0.5			↓ 1			↑ 1				
Plant N content (Plant N)	↓ 1	↑ 0.25		↑ 1							
Leaf tensile strength		↓ 1	→ 0.5		→ 1	↗ 0.33			↓ 1		
Leaf carbon content	↗ 0.33	↗ 0.17	→ 1	↑ 1							
Root length	↓ 1	↗ 0.25	→ 0.33	↑ 1							
Specific root length	↓ 1	→ 0.33	↗ 0.25	↓ 0.5							
Lignin/N			↓ 1			↓ 1			↓ 1		
Root diameter	↗ 0.5		↓ 0.17	↑ 1							
Leaf toughness	→ 0.5				↓ 1					↑ 1	
Root tissue density	↑ 1		→ 0.5	↑ 1							
Root/shoot	↑ 1		→ 1	↑ 1							
Stem dry matter content	↑ 0.5		↑ 0.5								

(Continues)

TABLE 1 (Continued)

Trait/service	Biomass production	Soil fertility	Erosion control	Climate regulation	Fodder quality	Aesthetic appeal	Water regulation	Pollination	Recreation/ heritage	Biocontrol	Water purification
Stem-specific density	↑ 0.33		→ 1				↓1				
Canopy structure	→ 1		↑ 0.33				↑ 1				
Beginning of flowering	↘ 0.33	→ 1			→ 1	↓ 1		→ 1			
Nitrogen fixing capacity		↗ 0.13			↑ 0.5						
Relative growth rate	↓ 1	↘ 0.5		→ 1							
Plant dry mass		↘ 0.2		↓ 0.5							
Leaf C/N	↗ 0.33	↑ 0.25									
Flower colour						↑ 0.5		↗ 0.25			
Seed number		↑ 1		↑ 1							
Growth form	→ 1	→ 0.07	↑ 0.2		→ 0.08	→ 1	→ 0.25				
Root N content (RootN)	→ 1	→ 0.5	↑ 0.33								
Root dry matter content		↓ 0.33	→ 1								
Plant height generative	↘ 0.5							→ 1			
Flower pollination syndrome		→ 1						↗ 0.5			
Root distribution evenness	↑ 0.14										
Root density			↗ 0.17								
Percentage fine roots			↑ 0.25								
Root length density			↗ 0.33								
Seed mass	→ 0.5	→ 1			→ 1	→ 1					

Abbreviation: VPH, vegetative plant height.

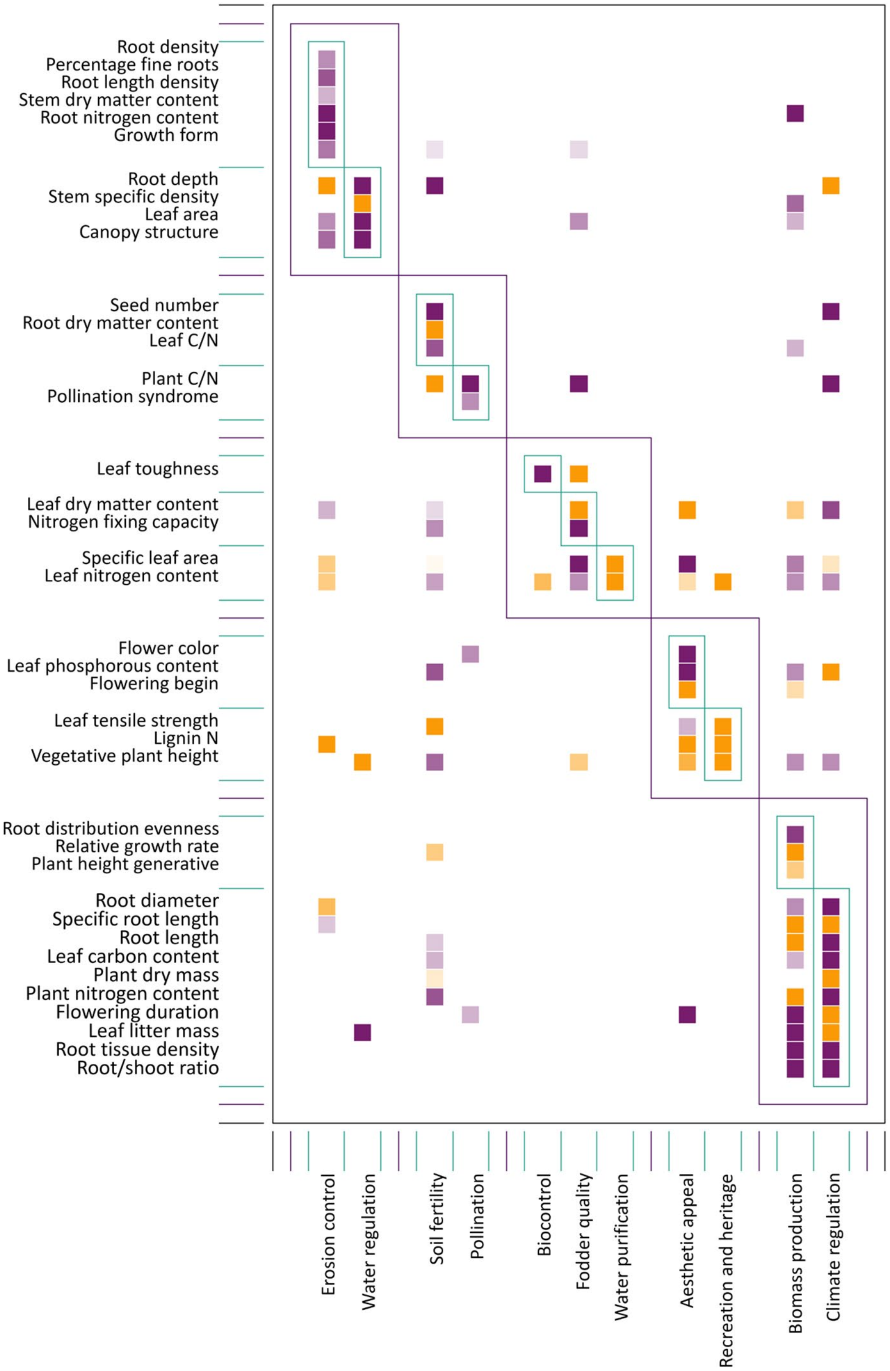

FIGURE 2 Bipartite modular web diagram illustrating associations among plant functional traits and ecosystem services in temperate grasslands. Each reported trait–service association is displayed with a square. Colours show the direction (violet, positive; yellow, negative) and colour intensity the strength of associations (light colours, weak associations; strongest colours, all associations in the same direction). Outer rectangles (violet) show modules and within rectangles (light blue) show nested modules as detected by re-running the analysis within the subset of the module. Stable results after 20 iterations; modularity = 0.28; likelihood = 0.40

only few reported linkages (cf. Creswell, Cunningham, Wilcox, & Randall, 2017).

3.2 | Trait–service groups

The trait–service groups we identified (Table 2) based on the results of the bipartite network analysis (Figure 2) are: (a) chemical compound-related services; (b) water-related services; (c) above- and below-ground services; (d) cultural services and (e) multi-trophic level services. Within each of these groups we found synergies and trade-offs—both among species traits and among ecosystem services. Aesthetic appeal and recreation/heritage represent an example for trait-mediated synergies among ecosystem services since they are both negatively associated with lignin-to-nitrogen ratio, a trait that alters the decomposition of biomass and thereby the appearance of landscapes (Figure 2). Furthermore, in the group of water-related services, synergies between erosion control and water regulation were evident, with both being positively associated to canopy structure and leaf area that is, two plant structural traits which can affect the erosive forces of rainwater and the water cycling between plant and soil. Within the group of chemical compound-related services, a trade-off appeared between fodder and water quality. While high SLA and LNC (investment in fast-growing

TABLE 2 The five main trait–service groups that we identified, underlying ecosystem services, key traits and hypotheses for mechanisms and processes leading to this grouping with supporting references

Trait–service group	Ecosystem services	Key traits	Hypotheses	References
1. Chemical compound-related services	Fodder quality, biocontrol, water purification	Nitrogen fixing capacity, leaf dry matter content, leaf toughness, specific leaf area, leaf nitrogen content	Amount of nitrogen uptake affects water eutrophication Fast-growing versus well-protected leaf tissues affect fodder quality	Violle et al. (2015), Lamarque, Lavorel, Mouchet, and Quétier (2014)
2. Water-related services	Water regulation, erosion control	Root depth, canopy structure, leaf area, % fine roots, stem dry matter content, root nitrogen content	Roots and plant structural traits affect water cycling and erosion	Everwand, Fry, Eggers, and Manning (2014), Burylo, et al. (2012), Gould, Quinton, Weigelt, De Deyn, and Bardgett (2016)
3. Above- and below-ground services	Biomass production, climate regulation	Relative growth rate, root distribution evenness, root/shoot, root length, root tissue density, specific root length, plant nitrogen content, leaf litter mass, flowering duration	Below-ground plant investment positively affects below-ground carbon storage Root and stature traits are important for population growth performance	Abalos et al. (2014), Gos et al. (2016), Schroeder-Georgi et al. (2016)
4. Cultural services	Aesthetic appeal, recreation and heritage	Flower colour, beginning of flowering, leaf phosphorous content, lignin/N ratio, vegetative plant height	Floral traits affect landscape perception Leaf chemical traits affect decomposition which affects landscape appreciation	Lindemann-Matthies et al. (2010), Graves et al. (2017)
5. Multi-trophic level services	Soil fertility, pollination	Root dry matter content, seed number, leaf C/N, plant C/N	RDMC negatively affects nitrification rate and thereby soil fertility C/N ratios affect denitrification enzyme activity	Pommier et al. (2018), Legay et al. (2014)

highly productive tissues) promote higher fodder quality on the cost of lower water quality due to high nitrogen concentrations, low SLA and leaf nitrogen (investment in slow-growing well-protected tissues) are negatively associated with fodder quality but positively affect biocontrol and water purification.

4 | DISCUSSION

We here provide the first comprehensive overview of associations between plant functional traits and multiple services of grassland ecosystems. The geographic bias of studies included in our review (82% in Europe, especially in France) may be partly explained by the importance of grassland ecosystems in this area, representing regional hotspots of biodiversity and generating high basic and applied research interests (Gaujour, Amiaud, Mignolet, & Plantureux, 2012; Violle et al., 2015). Results have to be interpreted within these geographical limitations, and in the light of uncertainties (Table 1) and discrepancies in trait–service relationships (Appendix S1). Another limitation arises from the uneven distribution of services within the studies investigated, with especially cultural and provisioning services being underrepresented. Differences in how intensively trait–service associations have been investigated are reflected in the number of discrepancies, where commonly investigated associations show more discrepancies than those investigated once or twice only. Yet, by looking at a range of functional traits and ecosystem services, inherent trade-offs and synergies among services and traits became apparent that single studies could not identify. We also found that a large number of traits are related to multiple services. However, since our definition of these 'multi-service' traits includes both traits with the same effect direction (i.e. consistently positive or negative effects on all related ecosystem services) and traits with opposing effect directions (i.e. positive effects on one or more ecosystem services but negative effects on other services), this approach should not be confused with the concept of ecosystem multifunctionality.

The existence of 'single-service' traits might partly be explained by the lack of research on some, in particular hard-to-measure, traits like root traits (Burylo, Rey, Mathys, & Dutoit, 2012). However, we also found evidence for the 'service-specific' nature of some traits, in cases where studies tested a particular trait for its association with multiple ecosystem services (Table 1). For instance, growth form has been analysed in relation to biomass production, soil fertility, fodder quality, aesthetic appeal and water regulation, but was only related to erosion control (Burylo, Dutoit, & Rey, 2014). Furthermore, root traits are thought to determine particular soil services (Faucon, Houben, & Lambers, 2017), but for root nitrogen content neither an effect on soil fertility (Klumpp & Soussana, 2009; Soussana & Lemaire, 2014) nor on biomass production (Schroeder-Georgi et al., 2016) was observed. For other traits, their 'service-specific' character was more obvious. For example, flower pollination syndrome was relevant for pollination services (Fontana et al., 2014; Pakeman & Stockan, 2013). Only seed mass was not associated with any service (Table 1) and thus with any module (Figure 2).

Whether trait–service associations are due to mechanistic links among services and species traits (via ecosystem functions that result in ecosystem services and that can be indicated by species traits—cf. 'functional markers'; Garnier et al., 2004) or potentially caused by covariation among some of the services or traits remains to be further investigated for which our results provide a first basis.

4.1 | Trait–service groups

Associations among ecosystem services highlight the multifunctional character of ecosystems as they provide insights into shared drivers and ecosystem processes (Pretty et al., 2006). So far, most studies analysing such associations focused on co-occurrences of ecosystem services in time and space, usually described as ecosystem service bundles (see Spake et al., 2017 for an overview), but often without addressing underlying mechanisms. Yet, the groups of services that we found are not defined by spatial or temporal co-occurrence, but they are correlatively linked through shared functional traits leading to trait-specific synergies or trade-offs among services. Our modular web analysis identified five trait–service groups. These groups do not follow the usual classification of supporting, provisioning, regulating and cultural services but are defined by trait–service associations. One group consisted solely of cultural services, whereas two groups consisted of both regulating and provisioning services (above- and below-ground services, chemical compound-related services). Two more groups comprised regulating and supporting services (water related-services, multi-trophic level services).

Consequently, management actions focusing on improving a particular ecosystem service need to consider potential consequences for other services linked via species traits. There are only few services related to a limited number of traits, while the majority of services are linked to multiple traits. This paves the way for targeted management of trait-specific services by altering species composition according to single traits. Service-specific traits may be used to manage an ecosystem towards a maximization of single services. Examples can be found in root characteristics (root density, root length density, percentage fine roots), relevant for erosion control, or floral traits (flower colour, beginning of flowering, flowering duration) relevant for pollination or aesthetic appeal. Possible applications that could be further investigated are seed mixtures for environmental improvements like vegetation strips or cultivation and renewal of grasslands as these could be optimized to deliver a desired mix of ecosystem services (Storkey et al., 2015).

For multi-trait services, on the other hand, a range of relevant traits is available, and plant community-based management strategies can choose among these to increase synergies and avoid trade-offs among services. Examples are biomass production and erosion control that are both associated with LNC and LDMC, amongst others. Thus, slopes could be seeded with high LDMC- and low LNC-grassland species, while pastures should be seeded with low LDMC- but high LNC-species (cf. Table 1).

However, this kind of trait-based ecosystem management becomes more complicated when opposing results for the same trait–service association exist. Those discrepancies might be due to the fact that many traits are not independent from one another and due to context dependency. Even though we focused on grasslands, thus reducing context dependency, different types of grasslands with different types of use exist within different climates and landscapes. Consequently, studies investigating trait–service associations would benefit from taking environmental context into account, so in the future, this could be controlled for in meta-studies.

4.2 | The role of functional traits for ecosystem service trade-offs and synergies

In our review, we identified traits that indicate a synergy between biomass production and climate regulation (e.g. LNC, VPH, SRL, root tissue density, root/shoot). This finding contradicts the often reported trade-off between biomass production and climate regulation (Gos et al., 2016; Grigulis et al., 2013; Lavorel et al., 2011). Our results indicate that high values of LNC and VPH can promote climate regulation as well as biomass production and soil fertility—the former by means of reduced decomposition and higher inputs of organic matter into soils, the latter by increasing soil fertility in C-poor soils or lower soil layers, by reducing decomposition, plant uptake and thus supporting leaching to deeper soil layers (Grigulis et al., 2013) Yet, the often reported trade-off between biomass production and climate regulation (Gos et al., 2016; Grigulis et al., 2013; Lavorel et al., 2011) was supported by our findings as well, by traits such as root length, plant N content, LPC and LDMC. Further traits (leaf carbon content, root diameter, plant dry mass, canopy structure, VPH, lignin/N ratio) were associated with synergies among services or showed no interdependency. Hence, classifying groups of ecosystem services by their trade-offs and synergies is not as straightforward as suggested earlier (Rodríguez et al., 2006).

Also, cultural and above- and below-ground services share positively related traits such as onset and duration of flowering, high LPC and SLA and low LDMC. Yet, management focusing on changes in VPH and LNC will lead to trade-offs between above- and below-ground services and soil fertility on the one hand and cultural services on the other hand. Also, in this case, functional traits are linked to both synergies and trade-offs among different services and thereby enable to maximize the provision of multiple services. This can for example be achieved by managing spatial and temporal patterns of different habitat types within a landscape (Verhagen, van der Zanden, Strauch, van Teeffelen, & Verburg, 2018). Yet, cultural services are influenced by appreciation and perception, with cultural appreciation being especially important in grasslands as a traditional agroecosystem in Europe (Garnier et al., 2007; Gaujour et al., 2012). High VPH and LPC associated with high litter accumulation have been related to a reduction in landscape appreciation

(Lavorel & Grigulis, 2012; Lavorel et al., 2011), where litter is attributed as an undesirable landscape feature. Graves, Pearson, and Turner (2017) found an effect of the number of flower colours on people's aesthetic preferences for wildflower communities. Still, our results indicate that empirical evidence for the effect of traits on cultural ecosystem services is scarce for services like recreation and aesthetic appeal and needs further exploration (but see Duru, Cruz, Ansquer, & Navas, 2014; Gos et al., 2016). For water purification, biocontrol and pollination only limited numbers of related traits were evident (Creswell et al., 2017). Reasons for this can be plentiful. For instance, water-related services might not be of particular interest in some grassland ecosystems, especially in those with weak water dynamics or without any water quality problems (Gaujour et al., 2012).

4.3 | Suggested future research priorities

The list of candidate traits provided in Table 1 can be highly useful for further studies as it provides a selection of traits with documented impact on ecosystem services and as it highlights uncertainties or missing information (cf. Creswell et al., 2017). Also, using standardized sets of traits can largely benefit ecosystem service research by means of increased comparability among studies (Mouchet et al., 2014). The list can be further improved if comparative studies will consistently report the relative predictive power of traits for each service (Garnier & Navas, 2012). The apparent geographical bias needs to be addressed, meaning an increased number of studies within European grasslands beyond the French Alps and even more so outside of Europe. Furthermore, research might investigate if the number of traits needed to study trait–service associations can be limited, yet still covering the full complexity of synergies and trade-offs in ecosystem service delivery. Additionally, to improve applicability, future work should directly quantify services and engage stakeholders, along with the actual needs of planning and managing ecosystems and landscapes (Cardinale et al., 2012; Cord et al., 2017). Taking mechanistic trait–service associations into account can improve management and avoid undesired outcomes of ecosystem service-related policy incentives (Bennett et al., 2015).

Moreover, below-ground plant traits are still underrepresented in the literature (Laliberté, 2017) as are stem and seed traits, although in our study, the latter had at least explanatory power. Similarly, water regulation, pollination, recreation and heritage value, biocontrol and water purification could be further investigated with trait-based approaches (Blowers, Cunningham, Wilcox, & Randall, 2017).

5 | CONCLUSIONS

We here provide an overview of trait–service groups and their inherent trade-offs and synergies among the services of grassland ecosystems that are not based on simple co-occurrences in space and time, but rather indicate mechanistic linkages via shared functional species traits. Interestingly, provisioning and regulating or cultural services not only showed trade-offs, but also synergies, mainly based on service-specific traits. The presented list of candidate traits is useful for the evaluation of service delivery at local and landscape levels. It provides an overview about trait–service associations helpful for designing experiments (Dias et al., 2013) and for supporting regional land-use management. It can hence prove valuable for policy- and decision-making (Jax et al., 2018). However, it needs to be highlighted that in real-world situations not all ecosystem services can be improved simultaneously (Turkelboom et al., 2018). If trade-offs at small scales cannot be avoided, possibilities for meeting multiple demands still exist at larger scales by changing landscape composition. Operationalization of the diverse outcomes of ecosystem service studies remains a major research need (Lautenbach et al., 2019).

ACKNOWLEDGEMENTS

The Helmholtz Association provided funding within its programme-oriented research period III (2014–2020). We thank Francesco de Bello for providing us with data from de Bello et al. (2010).

AUTHORS' CONTRIBUTIONS

S.K. conceived the idea; M.H., S.K. and O.S. designed methodology; M.H. collected data, analysed data and wrote the manuscript. All authors substantially contributed to data interpretation, critically revised the manuscript and gave final approval for publication.

DATA AVAILABILITY STATEMENT

This review was completed using data from published sources, all of which are cited in the 'Data Sources' section of this article.

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DATA SOURCES

The following list contains 108 articles included in our analysis of functional plant trait–ecosystem service relationships, synergies and trade-offs in temperate grassland ecosystems. Data are divided into (a) those that we found and accepted in the systematic literature review, and (b) those provided by de Bello et al. (2010).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Hanisch M, Schweiger O, Cord AF, Volk M, Knapp S. Plant functional traits shape multiple ecosystem services, their trade-offs and synergies in grasslands. *J Appl Ecol*. 2020;57:1535–1550. https://doi.org/10.1111/1365-2664.13644