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From a conceptual framework to an operational approach for managing grassland functional diversity to obtain targeted ecosystem services: Case studies from French mountains

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Abstract

Research to understand and manage ecosystems to supply services has recently spurred a functional view of their biodiversity. In particular, approaches based on functional traits rather than species diversity are increasingly used to reflect interactions between organisms and their environment. These approaches bring a functional perspective to the study of community structure responses to disturbances and resources, and of their effects on ecosystem functioning and services. From an academic perspective, we propose a conceptual framework based on species functional traits to better infer how grassland management practices (fertilization, defoliation regime) along with abiotic factors influence plant, animal and microbial community composition and a range of services in grassland ecosystems. The core of the framework relies on combinations of plant functional traits and associated microbial features that specifically respond to environmental and management factors and influence ecosystem services. To overcome stakeholders' difficulty in applying the concept of functional traits, we propose an operational approach implying the mapping of plant communities distributed into five plant functional types (PFTs). The approach was used for fields in grassland-based livestock farms from two French grassland networks. We evaluated its ability to predict a range of services including forage provision and non-market services according to environmental and management drivers. PFT-based plant community composition predicted forage services reasonably well but responded weakly to environmental gradients. To cope with the observed limitations of current predictive approaches, we suggest including soil microbial functional types and adaptive management rather than using a prescriptive scheme.

Key words: cutting, fertility gradient, grass species, grazing, plant functional type, soil food web

Introduction

Increased energy costs, climate change, biodiversity losses, fluctuation of selling prices and greater concerns for environmentally friendly production are among the emerging factors that make agricultural competitiveness much harder to achieve and maintain. Unlike the rather stable context of the past decades, farmers and their advisors must now strive for a dynamic competitive advantage that requires rethinking land use to meet environmental and socio-economic challenges. Main challenges in this context are reducing negative externalities of agriculture (e.g., greenhouse gas emissions) without decreasing agricultural production and financial returns, and whenever possible increasing non-market services [e.g., cultural value, carbon (C) sequestration, erosion prevention, etc.]. Grasslands can provide a range of services[1]. For farmers, grasslands primarily provide feedstuffs for

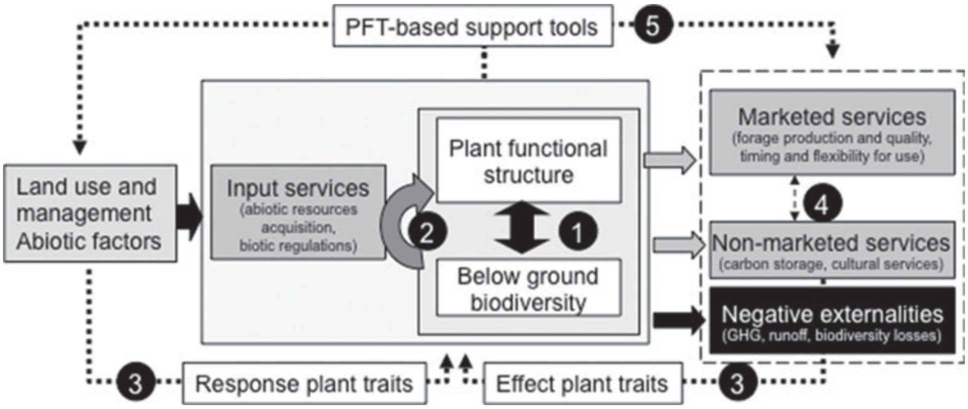

Figure 1. Ecosystem services and negative externalities potentially delivered by grasslands. Input services contribute to biological, physical and chemical processes supporting agriculture. Marketed services contribute to agricultural productivity, whereas non-marketed services do not (yet) directly contribute to agricultural income (except in specific cases such as agro-tourism farms); PFT, plant functional type; numbers (1,. . .,5) rely on key relations that are explained in the text; full arrows, biophysical relationships; dotted arrows, relationships based upon plant traits.

herds in grassland-based livestock systems and input services (e.g., maintenance of soil fertility; biological regulations) when they are introduced in crop rotations in mixed crop–livestock systems[2]. For other stakeholders such as environmental agencies and policy makers, grasslands contribute many non-marketed services. Farming, previously dedicated mainly to food production, is likely to change with an increasing recognition of grassland multifunctionality[3]. Since land use and associated land cover and management intensity influence the range of services provided by grassland biodiversity, incentives such as subsidies and regulations should promote a widening of farmers' objectives, i.e., producing forage along with delivering a range of services by managing biodiversity at different scales[4]. Two scientific challenges arise for meeting these aims. First, it is necessary to quantify the levels at which services provided by grassland agro-ecosystems are delivered and to predict them according to management and abiotic factors. Secondly, for the sake of operationality, research outputs must be translated into user-friendly tools for stakeholders, especially the farmers.

Evaluating and predicting services provided by grassland agro-ecosystems have recently progressed using an approach based on identifying the role of functional diversity. Trait distribution of the community is a consequence of environmental filters caused by either biotic or abiotic factors (e.g., land use and management) that determines ecosystem processes such as biogeochemical cycling and ecosystem productivity[5]. These processes explain the supply of services, e.g., primary production explains forage supply that can be potentially predicted by combinations of traits[6,7]. Ecosystem functioning is indeed the end result of the operation of multiple filters on a hierarchy of scales, which, by assembling individuals with appropriate responses, results in communities with varying trait compositions[8]. Ecosystem processes and services are shaped through land use and management, directly by farmers and indirectly by institutions through norms, subsidies and advice. Thus, ecosystem-based learning or decision supports based on species-trait approaches can be developed into a framework and has been recently proposed[9]. However, two main issues still need to be addressed.

First, this cascade of relations renders prediction of ecosystem services difficult. The environmental factors affecting trait distribution interact in a complex manner between management drivers such as synthetic and organic fertilizers, grassland use (date, intensity and frequency of defoliation), local climate and edaphic conditions, and legacy of previous use that can differentially act on traits related to different processes. Furthermore, relations between species functional composition and biotic and abiotic factors or ecosystem services are complex: a given trait can respond differently to several drivers, several traits may be needed to scale-up to each ecosystem process and each service may be related to a suite of processes that depend on different combinations of traits[10]. Above- and below-ground components of grassland ecosystems are also strongly linked through a variety of both direct and indirect interactions that operate across trophic levels[11–13] (Fig. 1, arrow 1). Our first objective, aiming to better understand and predict biodiversity-dependent services, was thus to propose a framework that integrates these linkages between above-ground and below-ground diversity, especially for the acquisition and retention of resources provided by functional diversity (Fig. 1, arrow 2). We aimed to build a parsimonious framework to infer grassland services based on a limited number of plant functional traits. We selected key plant traits among those responding to management and environmental factors and having major effects on processes modulating processes related to ecosystem services. For simplicity, we focused on above-ground diversity, whose role has been intensively documented during the past decade, assuming that it can be also a proxy for below-ground diversity (Fig. 1, arrow 3). Finally, we assessed whether this integrated framework can help to determine tradeoffs between services, given that optimum management is stakeholder- and scale-dependent (Fig. 1, arrow 4).

The second issue to be addressed is related to the fact that a trait-based approach is rarely implemented by the intended end-users, especially farm advisors, and is not well-tailored for enhancing the learning process in a management perspective[14]. Trait-based agro-ecosystem models and indicators used to represent and understand grassland ecosystem functioning are not necessarily salient for end-users, i.e., they are often not perceived as relevant by decision makers[15]. Thus, our second objective was to propose an operational approach to infer multiple-service delivery by grasslands. It is based on broad plant groups organized into functional types defined by a suite of plant traits, which is better adapted to support learning and monitoring by farm advisors. The ability of the approach to assess grassland ecosystem services by characterizing plant communities and determining tradeoffs and synergies among services (Fig. 1, arrow 5) were evaluated. Then, considering the uncertainties of both simplifications [relying only on plant functional diversity and considering plant functional types (PFTs) instead of plant traits] and the context of environmental and management uncertainties, we suggest ways to apply and supplement this approach for guiding grassland management.

To reach these two goals, we first reviewed the literature to examine how characterizing plant growth strategies and functional traits can help understand the link between management practices and forage production or other services; we also examined to what extent above-ground biodiversity and below-ground biodiversity are linked. Next, we designed an integrated framework that summarizes the impacts of environmental and management factors on processes related to ecosystem services by characterizing plant strategies of resource use and growth. We then proposed an operational approach for building relevant support tools for end-users to infer grassland services based on a few PFTs. Finally, we evaluated this operational approach for assessing plant community responses to management and effects on services and examined how to implement this approach through support tools for assessing ecosystem services and guiding management practices.

Species-trait-based Approaches for Bridging Species Responses to Management, Environment, and Ecosystem Properties and Services: State-of-the-art

Currently, the importance of functional components of biodiversity has been described for plants[8,9]; invertebrates[16]; microorganisms[7,16]; meso- and macro-fauna[15,17]; vertebrates[18]; along with relations between these trophic levels[19]. We focused on the following main components of grasslands: plants and key species involved in the soil food web (earthworms, nematodes, bacteria and fungi).

Characterizing plant-growth strategies to link management practices to primary production and forage services

Many studies have reported that a main dimension of plant functioning and/or specialization is related to resource acquisition and use[20,21], which leads to distinguish acquisitive versus conservative plant types. This is related to a continuous variation in leaf traits, from thin, N-rich, short-lived leaves with high photosynthetic rates, to thicker, more fibrous, N-poor, longer-lived leaves with lower photosynthetic rates. Leaf traits such as specific leaf area, leaf nitrogen content and leaf dry matter content of water-saturated leaves are descriptors of these plant-growth strategies, which perform well for predicting species location on an axis of resource capture, usage and availability[22]. A second axis of specialization is usually related to plant height, which captures plant competitive ability [e.g., the leaf-height-seed (LHS) model[23]] and some aspects of plant reproductive strategy. Plant height is a key proxy to account for competition for light[23] and is positively related to root depth, another trait involved in competitive ability for water[24]. The timing of height growth is also of particular relevance to assess resource acquisition and partitioning among interacting species, leading some authors to define the second dimension of growth strategy as growth–height trajectories, in relation to flowering phenology, i.e., early versus late[25].

Species' functional-trait syndromes, i.e., suites of traits, are the outcome of their evolutionary response to selection pressures from habitat characteristics[26]. Assuming that these characteristics result from the legacy of land-use, edaphic and climate conditions, we hypothesized that plants develop similar strategies above and below ground[27–31]. Recent studies have shown correlations between morphological root traits and growth strategies defined on the basis of leaves. For example, greater specific root lengths, proportions of biomass of fine roots and root N concentration were found in fast-growing species[32]. This suggests a substantial capacity for nutrient uptake and assimilation[29], low water transport capacity[30] and fast root turnover[33]. Such trait sets may be attributable to species living in nutrient-rich habitats, allowing rapid organ turnover and growth. In contrast, high root tissue density and large diameter were characteristic of plants exhibiting a long root-lifespan[34,35] and living in nutrient-poor habitats. More recent studies[22,31] have shown correlations between leaf and root traits, revealing similar above- and below-ground plant strategies modulated by drought-tolerance capacity of species. Moreover, patterns of root traits, including decomposition rate, mirrored those of leaf traits, resulting in a similar species clustering. The highly correlated variation in root and leaf traits and potential decomposition rate also suggests that changes in functional composition of communities in response to anthropogenic changes should strongly affect biogeochemical cycles at the ecosystem level[36].

High nutrient availability favors plant species with an acquisitive strategy and/or tall stature[8], since competitive exclusion removes non-competitive species. In contrast, low nutrient availability favors conservative, stress-tolerant species, especially when facilitation exists[37]. However, significant relations are expected between plant community functional structure and other environmental gradients such as climate constraints or water stress that may involve other combinations of traits. Moreover, functional traits related to plant phenology respond to defoliation but also to resource availability[38]. Intermediate stress, however, favors the coexistence of both plant strategies for cutting as well as for grazing[39]. During the reproductive phase, canopy height before cutting or grazing best describes the effect of defoliation intensity and frequency upon plant functional composition[38].

Community functional structure is usually defined by two components: community-level weighted mean (CWM) of trait values and functional divergence (FDg) indices[8,40]. The CWM calculation is based on the 'mass-ratio' hypothesis, which assumes that the extent to which the traits of a species affect ecosystem properties depends on the abundance of the species in the community[41]. FDg describes the dissimilarity in traits among individuals (species) coexisting within a community[42]. Large values are often related to functional complementarity between species[43]. Understanding diversity effects on ecosystem functioning usually occurs by partitioning plant diversity into two processes: selection versus complementarity[44]. The former, assessed via CWM, occurs when plant species with particular traits dominate ecosystem processes [e.g., most of species having low or high leaf dry matter content (LDMC)], whereas the latter, assessed via FDg, results from better resource use due to trait differences (coexistence of species having low and high plant trait values). Such an effect is expected under intermediate levels of fertility[16,45] and disturbance. Complementarity can occur among grasses and legumes, and among grass functional types with differing traits in relation to the timing, location and rate of resource use.

Convergent results among several studies show the relevance of the plant-trait approach for successfully evaluating forage provision by permanent grasslands[46,47]. More generally, it was shown that traits such as leaf dry matter content associated with response to nutrient gradients strongly overlapped with those determining net primary production[6]. The same trends were found for tissue composition[48]: PFTs with an acquisitive strategy have a low lignin and cellulose content. Furthermore, high FDg leads to a flatter growth curve, allowing flexibility in harvest date because one can vary the harvest date without greatly changing herbage yield or its quality[48]. In addition, the balance between plant groups differing in their phenology (grass *versus* dicotyledonous species) allows the capture of more light over the growing season[49].

Above-ground—below-ground biodiversity linkages: toward management of below-ground biodiversity

The rhizosphere is the interface between soils and plants[50], i.e., a place where biotic interactions are intense between plants and soil microorganisms. Most processes associated with above- and below-ground interactions in ecosystems occur in this relatively limited soil volume, which is directly influenced by root exudates and functioning[11]. Interactions also occur via above-ground litter inputs and decomposition and foliage-induced changes in soil microclimate. It has been shown that the diversity, abundance and/or functioning of soil microorganisms, in particular rhizospheric ones, can strongly depend on plant species or functional group[51–54]. As feedback, soil micro-organisms play a fundamental role in the biogeochemical cycling of inorganic and organic P[55] and N[56] and consequently availability of these resources to plants. Thus, they ultimately affect plant functional composition[11]. In the context of our approach, the functional characteristics of rhizospheric microbial communities can thus be viewed as 'extended functional traits' of plant species. In a recent study, it was demonstrated that plant traits can be a powerful tool for understanding the mechanisms behind plant–soil interactions and ecosystem functioning and for predicting how changes in plant–species composition associated with global change will feed back into the soil system[13]. Associated microbial functional traits can have affinity for C or N substrates or maximum substrate use rate, as demonstrated for soil nitrite oxidizers along an N gradient[57].

The multiple processes involved in plant–soil interactions largely determine the cycling of C via the forms of soil organic matter, from labile to recalcitrant, and nutrients, mainly N and P, which benefit ecosystem functioning. Accounting for soil microbial functional traits increasingly appears necessary to infer soil functioning[7] and delivery of services properly, and to adequately define appropriate management practices[13,58,59]. For instance, symbiotic and free-living biological N fixation represents a sustainable N input into N-poor agrosystems[60]. In addition, the balance between N mineralization, nitrification and denitrification determines, in relation with plants' preference for N forms, soil fertility and potential N losses from the ecosystem[61]. Thus, future agricultural practices should increasingly consider managing soil biota to enhance the delivery of a range of ecosystem services and to improve the resilience of

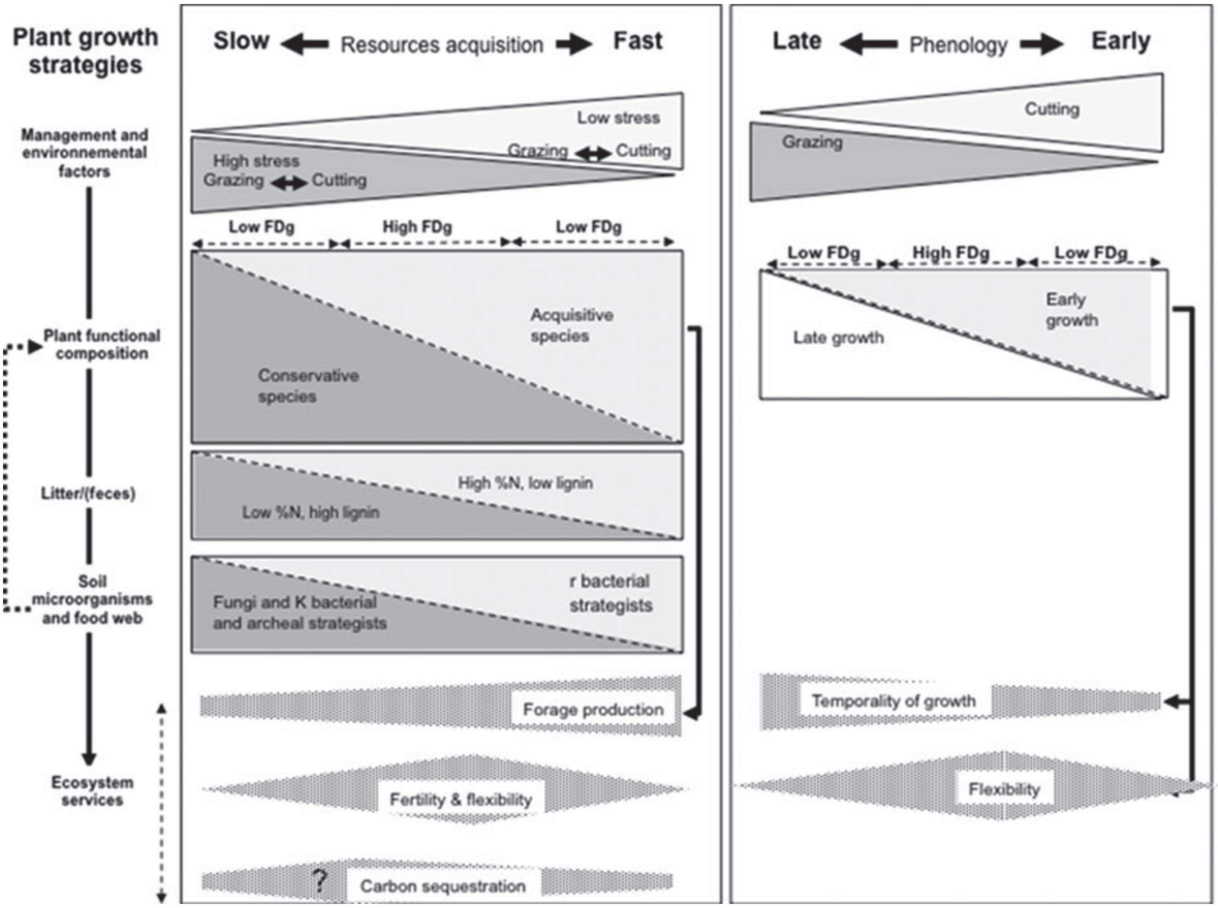

Figure 2. For two main axes of plant-growth strategies (left and right), the figure displays the relationships between (from top to bottom): management-induced stresses and disturbances; plant-community functional divergence (FDg); litter composition; soil microbial community and food web composition (from[11]); and several ecosystem services (forage production, soil fertility, flexibility for management and C sequestration); the height of the triangle or trapezium along the *X*-axis reflects the value of the criterion considered.

agricultural systems. For instance, it was demonstrated that soil arbuscular mycorrhizal fungi communities from different agricultural fields vary in their impact on plant productivity and nutrient-leaching losses[62]. Similarly, inoculation of plant-growth promoting rhizobacteria, such as *Azospirillum* strains, is currently being tested to increase crop yields[63]. This paves the way for agricultural practices that will try to directly or indirectly manage soil organisms, even microorganisms, and their functional traits in the future.

An Integrated Framework and Operational Approach for Managing Grasslands

A trait-based framework to infer services delivered by grasslands

For managed grasslands, plant traits include key effect traits that can be used to predict services because they integrate the effect of a large range of ecological processes, including those occurring below ground. For the resource-use dimension, fast versus slow growth plant types display differences in their ability to capture and use resources due to differences in root-system architecture[64], quality of litter[65], rhizospheric processes[66] and periods when resources are required (e.g., differing minimum-temperature thresholds for growth[58]). Low stress *vis-à-vis* resource availability (nutrients or water availability) favors acquisitive species. In this context, nutrient cycling is driven mainly by bacterial *r*-strategists with a high activity rate and a low affinity for substrates[57,67]. This supports rapid, leaky nutrient cycles and low net accumulation C in soil. These drivers and associated soil processes lead to high forage production and quality at the leafy stage. In contrast, high resource-related stress, up to a certain extent, leads to slow nutrient cycling and promotes soil C sequestration[68]. Intermediate levels of fertility allow different plant types to coexist, which allows overyielding due to complementary effects that reduce competition (input service)[69] and provides great flexibility in harvest or grazing dates[48] (Fig. 2, left side). Disturbances may reduce or amplify the effect of stress. For given climate and soil conditions, mowing promotes species with an acquisitive strategy, whereas grazing promotes species with a conservative strategy. However, the magnitude of these effects depends on grazing intensity[69]. High grazing intensity favors the return to the soil of material with a C:N ratio lower than that of litter. In contrast, low grazing intensity increases the quantity of litter with approximately twice the C:N ratio of that of green plant tissue. The level of stress and disturbance required to maximize fertility and C sequestration is not well known[70]. Nevertheless, the level of stress and disturbance that maximizes each service is likely to depend on the service considered[71]. Defoliation regime is probably the main driver of plant-community composition for the timing of herbage growth, e.g., the time at which peak herbage occurs during regrowth (Fig. 2, right side). Coexistence within a community of late and early plant strategies smoothes the herbage growth pattern[48] and may help optimize light capture.

Previous versions of this framework have been used for teaching students and training experts involved in advising farmers[14]. The current version of this framework can be extended to investigate plant traits associated with a stress factor or to identify functional groups of populations exhibiting similar responses to it (e.g., drought survival[72]). More specifically, it can be used as a first step to qualitatively design custom communities for desired ecosystem services based on hypotheses of plant functioning in species assemblages[64]. However, complementary work should be done to design an operational approach that can be used by farmer advisors.

A salient operational approach for managing grassland agro-ecosystems

From plant traits to PFTs. Although popular and successful in scientific arenas (e.g.,[73]), the plant-trait approach rarely prevails in non-scientific circles, even when delivering quantitative relations between land use, plant community composition and ecosystem processes and services. Although the approach works, stakeholder feedback shows that it is not relevant in practice because it is too time-consuming, and trait values such as LDMC and specific leaf area (SLA) are too abstract for end-users[14]. To address the approach's relevance to decision makers' needs[74], we made two changes to the characterization of grassland vegetation compared with the framework presented above. First, we classified species into functional types (i.e., groups of species sharing the same collection of attributes[75]). We adopted five grass functional types (GFTs) covering the diversity observed in species growing in the same environmental conditions in France based on six plant traits (LDMC, SLA, flowering date, leaf lifespan, leaf tensile strength, plant height)[76] (Appendix 1). These five GFTs were characterized by traits reflecting the two major growth strategies (flowering date to distinguish late versus early growth; LDMC to distinguish fast versus slow growth) (Fig. 3). We also verified that GFTs were consistently ranked according to herbage growth, i.e., slope and intercept of growth decreased (Appendix 2). Second, we focused on grass species because they have more similar plant-trait values[77] and properties[48] than dicotyledonous species coexisting in grassland communities. Consequently, we consider dicotyledonous species as a whole for estimating their overall impact on plant-community properties according to their percentage in the plant community[48]. On this basis, the response of plant-community structure to management and environmental factors and its effect upon forage provision can be analyzed via GFT assemblages to develop a generic and low-input method for farm advisors[78]. Thus, plant community structure can be characterized by:

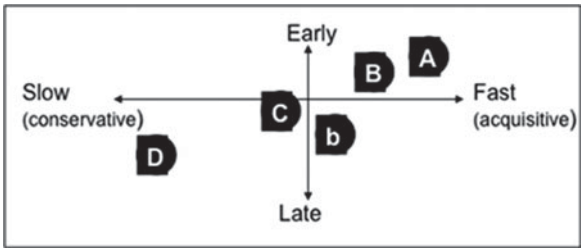

Figure 3. Mapping of five grass functional types (A, B, b, D, C) by two plant traits (leaf dry matter content, flowering date) representing two plant-growth strategies, fast versus slow, early versus late, respectively.

- the percentage of grass species in the vegetation cover (G)
- the percentage of each of the five GFTs (pi)
- a diversity index, S, characterizing the evenness of GFT percentage and richness, calculated as a Simpson index: $S = 1 - \sum_{i=1}^{n} p_i^2$; it is an indicator of plant-strategy specialization within a plant community. Based on the analysis of 1378 plant communities from a range of temperate grasslands in France, the relative abundances of the different GFTs within plant communities are unimodal[79] and can be considered as an FDg index.

Such plant community characterization via PFTs has been recently extended to perennial tropical areas, where C3 and C4 species coexist[80], and sown grasslands[64,72].

From PFTs to services. Forage production and quality can be assessed by the percentage of species having a fast growth strategy[79] because these types are composed of species with low LDMC (Table 1). Based on the framework proposed (Fig. 2), we assumed that the same was true for C sequestration. Furthermore, based on findings showing the existence of contrasted plant preferences for the different chemical forms of N (ammonium versus nitrate)[11,12], we hypothesized that, in low soil N availability conditions, the coexistence of species having different growth strategies can allow higher N uptake in comparison to plant community composed only of plants with a conservative growth strategy.

Flexibility in management allowed by the timing of herbage growth can be assessed by the proportion of GFT

Table 1. Indicators used for characterizing grassland properties and services.

Service	Component	Indicators of grassland properties	Indicators of grassland services
Forage production management	Production	GFT_{fast} (%)	Herbage yield; stocking rate
	Quality	GFT_{fast} (%)	Herbage digestibility
	Flexibility allowed by timing of herbage growth	GFT_{late} (%)	Herbage growth pattern over the growing season; date of peak herbage; spreading of harvest dates
	Flexibility allowed by diversity	S	Shape of growth curve around peak herbage
Input	Fertility permitted by coexistence of plant types having acquisitive and conservative strategies	S	N uptake/N fertilizer supplied
Non-marketed	C sequestration	GFT_{fast} (%)	Soil C content; C:N ratio soil and plant

GFT_{fast}, grass functional types having a fast growth strategy; functional diversity index.

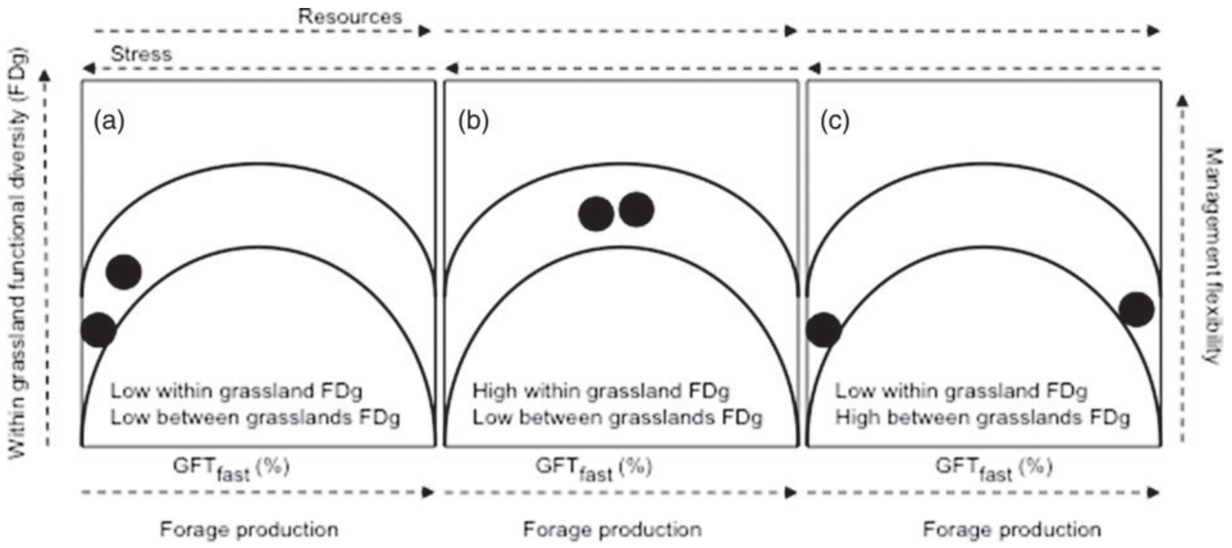

Figure 4. Relationship between functional divergence (FDg: within grassland functional diversity on *Y*-axis) and between grassland functional diversity (FDv on *X*-axis, assessed through the percentage of grass functional types having a fast growth strategy: GFT_{fast}) coupling with effects (forage production and management flexibility on *X*- and *Y*-axis, respectively) and drivers (resource availability and stress intensity on top of *X*-axis). Lines represent the enveloping curves, and circles illustrate three main patterns (a–c) considering two grasslands or sets of grasslands.

with a late growth strategy, which is related to late flowering dates (GFT_{late}). The flexibility allowed by within-plant-community diversity can be assessed by S, assuming that the more numerous these GFTs are, the flatter the growth curve around peak herbage is, as found using LDMC[48], because these communities are a mixture of GFTs with early and late flowering dates and short and long leaf lifespan.

The $GFT_{fast} \times S$ operational approach to characterize within- and between-grassland functional diversity. To propose an operational way to infer grassland responses to management and environmental drivers and their effects on ecosystem services, we considered the resource dimension of plant-growth strategy, represented by the percentage of GFT_{fast} (instead of LDMC in the trait-based framework initially presented) and the S index for GFT diversity (instead of the FDg index for LDMC) (Fig. 4). As constructed, the relation between the S index and the percentage of GFT_{fast} is parabolic, with maximum FDg expected for mean values of GFT_{fast} and minimum FDg expected for low and high values. Three main patterns are possible according to the combination of scale and level of FDg (Fig. 4). However, there is large uncertainty, because when $GFT_{fast} = 100\%$, S can theoretically vary from 0 (one GFT) to 0.5 (two GFTs with the same percentage).

Case Studies

Objectives and data

Case studies were used to evaluate the operational approach proposed, examining relations between plant

Table 2. Description of the two case studies used to test the framework.

Location	Central Pyrenees	Aubrac
Latitude/longitude	42°50N 1°17E	44°37N 2°59E
Area of sampling	about 1 × 2 km	20 × 40 km
Grass species in pasture biomass (%) (SD)	60.0 (14)	70.4 (20)
Soil pH (0–5 cm) (SD)	5.88 (0.41)	5.84 (0.41)
Annual temperature (°C) (altitude)[1]	10.8 (1000 m)	10.1 (860 m)
Annual rainfall (mm)	1014	1284
Annual potential evapotranspiration (mm)	1200	816
Range of altitude of the plots (m asl)	615–1200	800–1400
Number of farms studied	4 beef	4 beef and 4 dairy
Plant species richness (n)	239	176
Biomass or proxy	Spring growth curve (and shape): $n = 18$ spring and summer growth curve: $n = 6$	Stocking rate (8 farms 3 land-use types)
Plant analysis	C and N at herbage peak ($n = 18$)	
Soil analysis	C and N ($n = 18$)	C and N ($n = 16$)

[1] Climate data are averages over the past 10 years.
m asl, meters above sea level; SD, standard deviation.

functional composition and either environmental and management variables, or ecosystem services. Most of these relations were previously established considering a single plant trait[38,39,48,76,77]: LDMC, which reflects well on the resource-use dimension and weakly on the reproductive pattern of plant-growth strategies. We re-examined these relations to evaluate whether considering the two dimensions of plant-growth strategy performed well and whether considering pre-established PFTs instead of plant traits provided similar results.

The study was based on the data from two mountainous regions in France (Table 2) dominated by unsown species-rich grasslands used for feeding cows (grazing and hay). In these regions of sufficient precipitation, temperature is the main climate characteristic affecting plant productivity. Farm surveys were performed to record management practices, such as three defoliation regimes: cutting, grazing then cutting, and grazing only. Surveys were supplemented by calculation of Ellenberg indicator values (EIVs) for nutrients (N), soil reactivity (R) and moisture (M)[81]. EIVs reflect the relation between each species and environmental factors, and management practices. The strengths of EIVs are that they integrate species behavior over several years[82]. Plant and soil analyses were also performed to verify the consistency between expectations of the framework and observations for leaf tissue composition (e.g., cellulose) and C:N ratio.

Evaluating the approach

From PFT composition to ecosystem services. We verified that the percentage of $\mathrm{GFT}_{\mathrm{fast}}$ was a proxy for estimating forage production, herbage digestibility and several key variables of nutrient cycles. For example, it was significantly and positively correlated with spring herbage growth rate measured at the field level (network 1, Fig. 5a) as well as with stocking rate calculated for a set of fields at an annual scale (network 2, not shown, $n = 24$; $r^2 = 0.78$). $\mathrm{GFT}_{\mathrm{fast}}$ was also positively correlated with herbage growth rate measured in spring (Fig. 6a). In contrast, it was significantly and negatively correlated with plant and soil C:N ratios, the slope and intercept being greater for plants than for soil (network 1, Fig. 5b).

The S index being a proxy of within-field FDg, we examined its influence on temporal dynamics of grassland forage biomass. The shape of the growth curve around peak herbage was flattened when the S index was high (Fig. 6a). Indeed, a mixture of contrasting GFTs smoothed the growth curve because they have different leaf lifespans and flowering times (see Fig. 6b for network 1). In addition, we found that for less fertilized grazed grasslands (N supplied = 24.4 ± 26 kg ha^{-1}), N uptake was significantly and positively correlated with S ($r = 0.4$; $P < 0.05$; $n = 38$; network 2). Including soil pH and moisture with EIVs increased the correlation ($r = 0.66$; $P < 0.001$). We also verified that the percentage of $\mathrm{GFT}_{\mathrm{late}}$ was a proxy for evaluating timing of herbage growth within and among growing cycles. For the first growth cycle, the higher the percentage of $\mathrm{GFT}_{\mathrm{late}}$, the later the date at which peak herbage occurred (Fig. 6b). However, the greater its percentage, the higher the herbage biomass ratio was between the second and first harvests performed in summer and in spring, respectively ($r = 0.93$; $P < 0.01$) (Table 3, network 1).

Plant-community composition response to environmental and management factors. ANOVA of $\mathrm{GFT}_{\mathrm{fast}}$ percentage was calculated to compare the three defoliation regimes and two regions, with field altitude and applied N fertilizer as covariables. We found a significant effect of region ($P < 0.01$) and defoliation regime ($P < 0.05$); $\mathrm{GFT}_{\mathrm{fast}}$ percentages were 58, 60 and 68% for cut, grazed then cut, and grazed grasslands, respectively. Effects of field altitude and applied N fertilizer were also significant ($P < 0.01$ and 0.1, respectively).

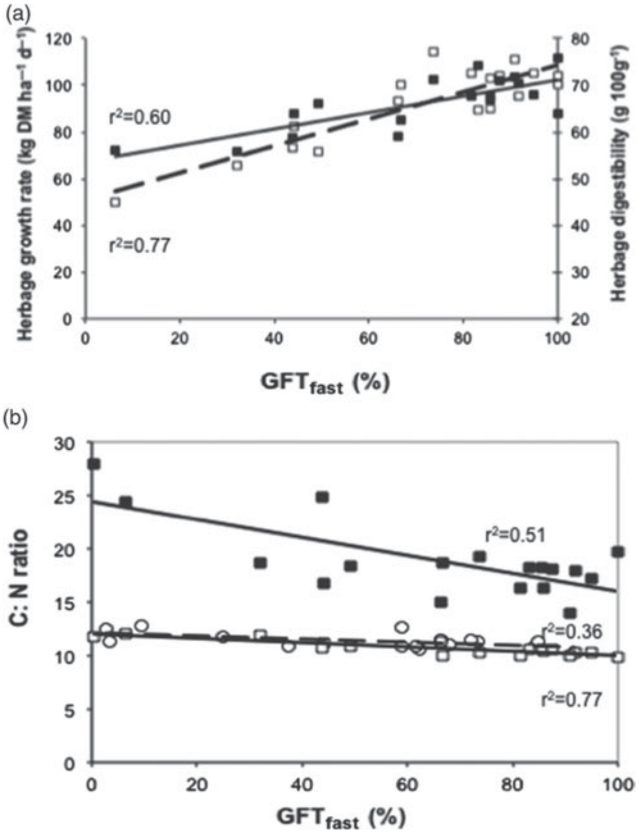

Figure 5. Relations between indicators of services (*Y*-axis) and the percentage of grass functional types having a fast growth strategy: $\mathrm{GFT}_{\mathrm{fast}}$ at the land-management-unit level. (a) Herbage growth rate (closed symbols) and plant digestibility (open symbols) for the first growing cycle (grassland network 1). (b) C:N ratios for plants (closed symbols) and soil (open symbols); squares for grassland network 1, circles for grassland network 2.

Correlations between the $\mathrm{GFT}_{\mathrm{fast}}$ percentages and raw data describing management and environmental factors were weak (Table 4). Including Ellenberg indicator values for nutrient and soil reactivity (pH) created more generic results (no effect of region) and resulted in higher correlations (Table 4). The direction of effects for temperature N (or N-EIV) and R-EIV were consistent with those expected. To test the hypothesis that FDg indices depended on levels of stress and disturbance (Fig. 4), we calculated linear regressions between each *S* and environmental (altitude, temperature and region) and management factors separately for percentage of $\mathrm{GFT}_{\mathrm{fast}} < 45\%$ or $>45\%$. For network 2, we found significant effects ($P < 0.001$): positive for N fertilization and negative for field altitude for $\mathrm{GFT}_{\mathrm{fast}} < 45\%$, and the opposite sign for both variables when $\mathrm{GFT}_{\mathrm{fast}} > 45\%$. However, this relation was not found for network 1. Therefore, this result, at least partly, validates the hypothesis that the coexistence of plants with different growth strategies captures more N.

Support tools for assessing ecosystem services from PFTs. Moving from the integrated framework to the operational approach requires shifting from the study of practices as factors for understanding agro-ecosystem functioning to mechanisms for managing multiple services in a given context, given environmental and data uncertainties. To illustrate this change, we portrayed typical grassland functional compositions using ascendant hierarchical clustering. As an example, we defined seven types of data from networks 1 and 2 (Fig. 7a). Forage services

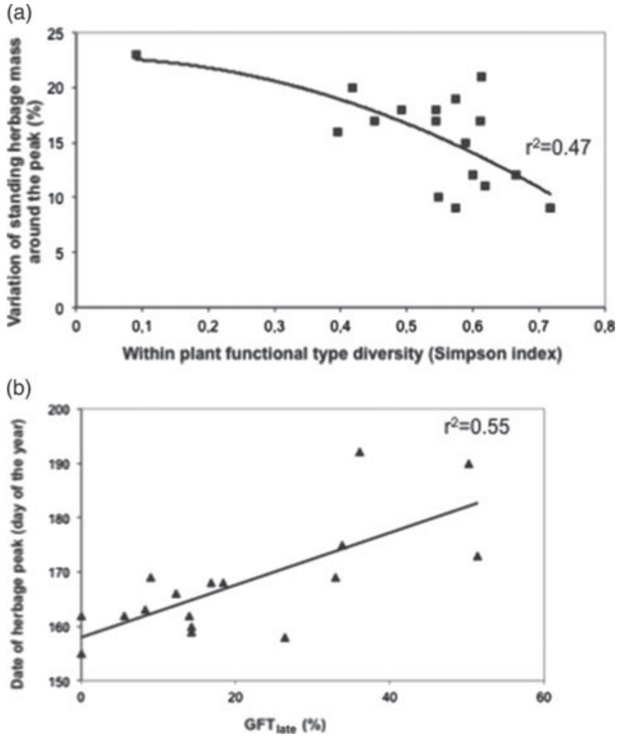

Figure 6. Herbage features related to plant functional-type composition. (a) Shape of the growth curve (±20 days around peak herbage) according to an index of grass functional-type (GFT) diversity ($P < 0.05$ when the extreme value was not considered). (b) Date (Julian days) at which peak herbage occurred according to the percentage of grass functional types having a late growth strategy: $\mathrm{GFT}_{\mathrm{late}}$. The date at which the herbage peak occurred was significantly and positively correlated with $\mathrm{GFT}_{\mathrm{late}}$.

Table 3. Late grass growth strategy (type b in percentage) and herbage yield ($\mathrm{t\,ha^{-1}}$) at first and second harvests for six grasslands of network 1.

Grassland	$\mathrm{GFT}_{\mathrm{late}}$ (%)	Harvest 1 (H1)	Harvest 2 (H2)	Ratio (H2: H1)
1	5	4.7	4.0	0.85
2	22	3.6	3.5	0.97
3	7	3.1	3.2	1.03
4	20	2.1	2.6	1.24
5	52	2.1	4.1	1.95
6	23	2.8	4.0	1.43

$\mathrm{GFT}_{\mathrm{late}}$, grass functional types having a late growth strategy.

Table 4. Regression analyses between the percentage of grass functional types having a fast growth strategy and environmental and management variables [e.g., Ellenberg indicator variables (EIV), R = soil reactivity, N = nutrients] considering raw variables or proxies of processes describing them.

		Environmental factors				Management factors			
Management		Region	Altitude	Temperature	R-EIV	N applied	N-EIV	r^2	SE[2]
Cutting	With raw variables	− 17.5***[1]	− 0.05**	/	/	0.07*		0.36***	17
(+ grazed)	With proxy of processes	/	/	8.4***	6.5***	/	9.4***	0.57***	14
Grazing	With raw variables	− 13.2*	ns			Ns	/	0.046*	21
	With proxy of processes	/	/	4.4**	8.4**	/	16.2***	0.44***	15

Regressions were calculated separately for cut and grazed grasslands considering the two grassland networks together. **$P < 0.01$; *** $P < 0.001$.

[1] Regression coefficient for each variable.

[2] Standard error.

/: means not considered in the regression analysis.

Table 5. Characterization of the seven grassland vegetation types for four features.

Grassland vegetation type	Herbage growth index (maximum = 1)	Flowering date (degree-days)	Plant digestibility at leafy stage (g kg^{-1})	Diversity index (maximum = 0.8)
1	0.93	831	831	0.32
2	0.87	856	823	0.60
3	0.78	921	810	0.67
4	0.75	890	808	0.70
5	0.69	942	804	0.73
6	0.65	848	791	0.48
7	0.50	1027	766	0.48

for each vegetation type can be assessed using previously established relations[83]. Vegetation types 1 and 7 have high and low herbage growth and digestibility as well as early and late flowering time, respectively; however, they have low functional diversity (Table 5). Vegetation types 3, 4 and 5 have the highest plant functional diversities but intermediate values for herbage growth and digestibility. Flowering time for vegetation type 6 is early, whereas herbage growth and digestibility are low. Other services can be assessed qualitatively using the framework (Fig. 4). Stakeholders may use these results confidently because species plant traits [leaf live span (LLS), tissue composition] used for defining functional types are ranked in the same order, regardless of the growing conditions[84]. Furthermore, plant community functional composition correlates well with services, at least herbage production and digestibility ($r^2 > 0.6$). Applying the $\mathrm{GFT}_{\mathrm{fast}} \times S$ framework (Fig. 4) to field data (Fig. 7b) portrays grassland at different scales (field, farm, region, etc.) by calculating the percentage of each vegetation type.

As found elsewhere (e.g.,[85]), relations between grassland functional composition and management or environmental factors are usually weak. Fundamentally, PFT provides 'average effects' that fail to provide managers with the information they need to address site-specific conditions, as found for other issues[86]. Thus, relations for predicting effects of plant composition on some components of the soil food web, such as decomposer communities, are context-dependent[11]. In addition, replacing plant traits by PFT decreases the accuracy of estimates of the relation between plant functional composition and management and environmental factors.

Toward a trial-and-error method to cope with uncertainty. Uncertainty complicates management of grasslands to obtain specific ecosystem services. The main issues are (i) which management practices are relevant for changing a given service (as seen in the case study) and (ii) which PFTs should be associated in sown grasslands when considering the services desired. The integrated framework (Fig. 2) provides an overview of combined effects of climate and management practices. Modeling relations between plant functional composition and management practices in case studies provides only weak indications (Table 4 and Fig. 4). Therefore, to cope with these uncertainties, we suggest that farm advisors use an adaptive-management approach supported by research outcomes, such as that presented in this paper. Once plant-community composition is portrayed (e.g., by the $\mathrm{GFT}_{\mathrm{fast}} \times S$ framework) and effects of environmental and management variables are roughly predicted to frame the action (e.g., using statistical models developed between plant community structure and management factors), it consists of a trial-and-error process based on monitoring plant functional structure to adjust management according to local soil and climate characteristics. Management practices can be viewed as 'experimental treatments' that

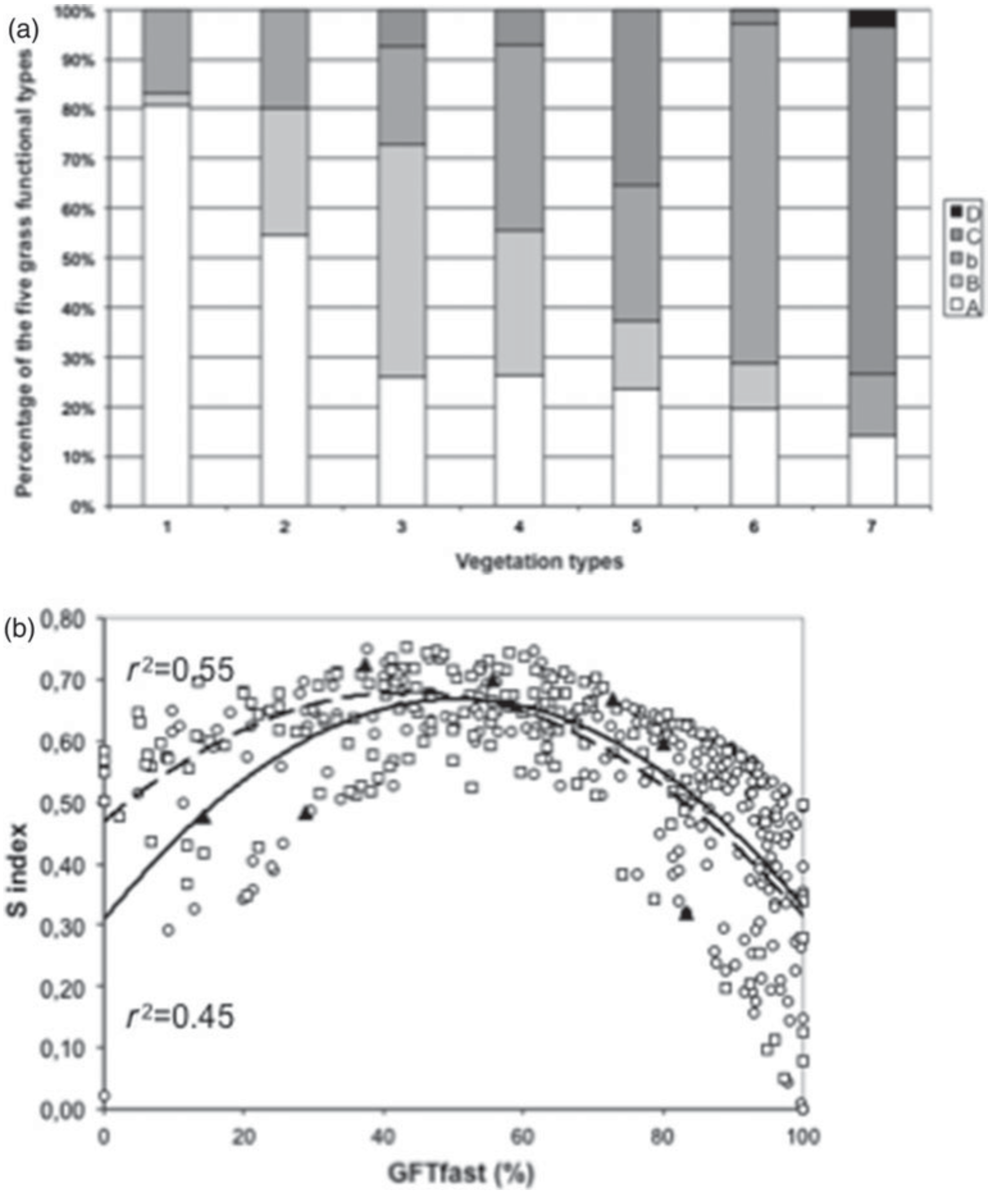

Figure 7. Support of relations between services and management and environmental factors; example based on 415 fields located in two regions. (a) Percentage of the five grassland functional types (GFTs) of seven assemblage types, ranked according to decreasing percentage of grass functional types having a fast growth strategy (GFT_{fast}) established from cluster analysis. (b) Observed distribution of mean functional divergence (*S* index) as a function of percentages of GFT_{fast} for Aubrac (squares) and Ercé (circles); triangles are for mean percentages of the seven assemblage types.

are implemented according to the management design. Learning could occur by monitoring plant functional structure, even though changes in soil biota functional structure can require several years to occur, as shown after changes in grassland management[87] and in conservation agriculture[88].

Conclusion

Based on the analysis of plant-growth strategies influenced by resources and phenology, coupled with a review of above-ground–below-ground biodiversity linkages, we have shown that plant traits and associated soil microbial community and food web composition can be aggregated into an integrated framework. It shows how plant traits shape a large set of services provided by grassland agro-ecosystems (forage and management services, fertility, and magnitude of C sequestration) and how they respond to land use and management practices. To put this framework into practice, we developed an operational approach based on PFTs and showed how support tools can be built from it. We have shown that restricting grassland characterization to above-ground plant traits for simplicity and choosing PFTs in a management perspective lead to uncertainty in predicting

Table A1. ANOVA of the five grass functional types for LDMC and flowering time.

Grass functional types	LDMC		Flowering time		
	Significance	**Growth strategy**	**Significance**	**Growth strategy**	**Example of species**
A	a	Fast	a	Early	*Holcus lanatus* L.; *Lolium perenne* L.
B	ab	Fast	b	Early	*Arrhenatherum elatius* L., *Dactylis glomerata* L.
b	bc	Slow	c	Late	*Agrostis capillaris* L., *Phleum pratense* L.
C	c	Slow	b	Early	*Briza media* L., *Festuca rubra* L.
D	d	Slow	c	Late	*Deschampsia cespitosa* L., *Molinia coerulea* L.

Data having a different letter in the same column were significantly different at the 5% level.

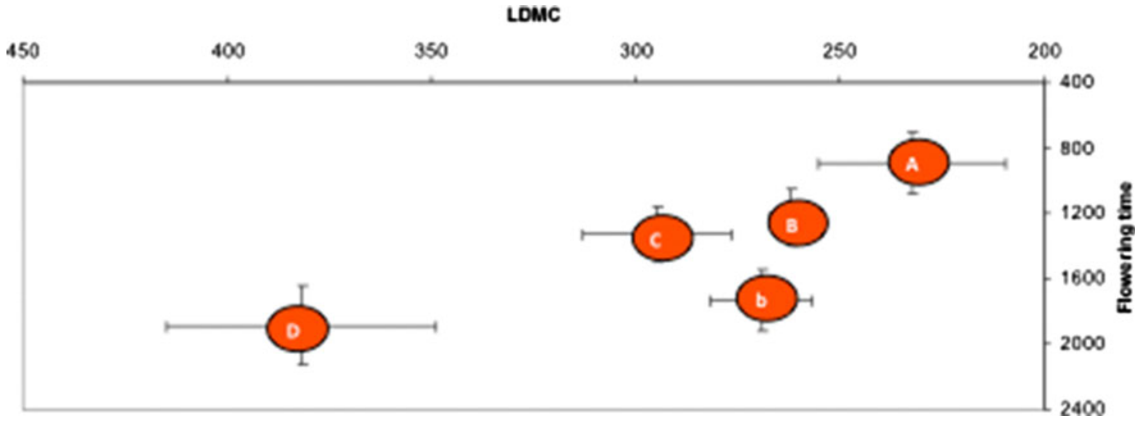

Figure A1. Ranking grass functional type according to decreasing LDMC (leaf dry matter content in mg g^{-1}) and flowering time in degree-days (°C) values; bars on the figure are standard deviations.

services from management practices and environmental factors alone. To cope with this uncertainty, we suggested a trial-and-error approach.

To generalize the approach, relations between drivers and ecosystem services should be established across scales[89], e.g., exploiting within- and among-site environmental heterogeneity of soil, climate and management. Additional sound relations between these drivers and ecosystem services can be expected. On the other hand, the applicability of the integrated framework and operational approach to sown grasslands must be evaluated in more depth. They can be used to define which species should be associated in mixtures according to the services targeted (e.g., to increase grazing season length or soil fertility) and to monitor plant-community composition to adjust defoliation management across seasons or years.

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Table A2. Comparison of slope and intercept of the relationship between W and day of year for the five GFTs.

Source	df	*F*	*P*
Day of year	1	309.77	0.0000
Intercept	4	7.37	0.0001
Slope	4	2.68	0.0438

Table A3. Regression coefficients.

GFT	Intercept	Slope
A	−1088	16.2
B	−763	11.8
b	−692	11.4
C	−652	10.5
D	−451	7.7

Appendix 1

Characterization of five pre-established grass functional types (GFT: A, B, b, C, D) for leaf dry matter content and flowering time (Table A1, Figure A1); analysis was done for the 30 most currently observed perennial grass species in France[79] among the 38 studied by Cruz[76].

Appendix 2

Analysis of spring growth of grass species ($n = 15$) growing in a pure stand (Tables A2 and A3); for each species;

sward was cut at two, three or four times at different places for measuring standing herbage mass (W), (number of data = 55); after[90].

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