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## A methodological framework to facilitate analysis of ecosystem services provided by grassland-based livestock systems

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It remains challenging to describe ecosystem services (ES) provided by grassland diversity and their underlying drivers. Issues for characterising them are related to scale, knowledge and outcomes that are stakeholder-dependent. Forage production interests farmers, while C sequestration, species richness and the landscape mosaic interest society. To address these issues, we developed a methodological framework (MF) based on five grass functional types (GFTs) which enables usable indicators to be easily defined, such as the percentage of plants with a fast (Fast<sub>GFT</sub>) growth strategy in grasslands. The MF consists of characterising plant functional diversity at field and farm levels, analysing its response to environmental and management drivers, and its effects on ES. The MF is applied to eight farms differing in their orientation and in their management intensity. Fast<sub>GFT</sub> responds positively to the amount of fertiliser supplied and negatively to field elevation. At the field level, Fast<sub>GFT</sub> is positively correlated with herbage production and negatively with soil C content and species richness. Within-farm grassland diversity of Fast<sub>GFT</sub> allows examination of how animal feed requirements match available resources and the landscape mosaic created. Our MF addresses grassland diversity with indicators derived from GFT, which allows summarising relations between environmental and management drivers and ES, then examines trade-offs between ES.

**Keywords:** landscape; management; plant functional type; provision services; supporting services; trade-offs

### Introduction

Policy-makers at European and regional levels are keen to encourage more sustainable livestock systems, especially to reduce their environmental impacts and to enhance ecosystem services (ES). This strategy encompasses maximising provision of ES by farms (Power 2010). In a farming context, three main types of ES are distinguished (Swinton et al. 2007; Zhang et al. 2007): (i) services from agriculture, that is, provisioning services (e.g. forage or milk), (ii) non-market services, some authors distinguishing regulating services (e.g. C storage) and cultural services (e.g. attractive landscapes), and (iii) services to agriculture, that is, several supporting and regulating services called 'input services' (Le Roux et al. 2008) because they allow a decrease in chemical inputs. Better understanding of trade-offs and synergies among services relative to their beneficiaries (e.g. farmers, society) is essential for management and policy decisions (Fisher et al. 2009). Studying services provision, trade-offs and synergies in grassland-based livestock systems raises several issues. First, services are scale-dependent (Lavorel & Grigulis 2012) and are studied most at field and landscape levels (Benton et al. 2003). The farm level is under-studied even though it is the level at which land-use and management decisions are made. Previous in-depth analysis of grassland-based livestock farms shows that biodiversity can also provide a management service, enabling farmers to improve their management and working conditions (Lugnot & Martin 2013). However, this ES is not well

known, even though farmers promote it. For instance, Martin et al. (2009) show that functional plant diversity in grasslands provides flexibility in the timing of grassland use. Similarly, Nozières et al. (2011) suggest that within-farm plant diversity decreases production costs by more closely matching grassland types to animal feed requirements, thereby improving stability of the livestock system. Second, most grassland research produces results suitable for understanding effects of drivers on ES but struggles to produce results that are easily used by stakeholders (Matthews et al. 2010). Thus, particular attention should focus on building relevant and appropriate methodological frameworks (MFs) that produce salient, legitimate and credible information (Cash et al. 2003). Our objective is to evaluate strengths and weaknesses of a MF based on characterising plant functional diversity to evaluate ES and identify their main drivers, while addressing the above issues and requirements.

On grassland-based livestock farms, ecosystem properties that provide ES depend largely on plant functional diversity (the presence or abundance of particular functional groups or traits) rather than on species diversity (Hooper et al. 2005). Thereby there is growing consensus that a plant trait-based methodology may well be able to address issues such as grassland ecophysiology and help manage some of the services that grasslands deliver to humans (e.g. Diaz et al. 2007). The key hypothesis is that traits can simultaneously explain individual plant responses to biotic and abiotic factors, with ecosystem

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properties underpinning ecosystem functions (Lavorel & Garnier 2002) and associated services (Lavorel et al. 2011). Plant functional diversity in structure and composition is usually defined through two components: community-level weighted mean of trait values or functional types (i.e. groups of species sharing the same set of attributes) (Colasanti et al. 2001) and functional divergence (FD) (Lavorel et al. 2011). FD describes trait diversity among species (or functional groups) that coexist within a community (De Bello et al. 2009). It is hypothesised to operate through functional complementarity (Petchey & Gaston 2006). For example, within-community diversity in plant height is expected to improve light capture (Vojtech et al. 2008), while diversity in leaf structural and chemical traits would reflect diversity in nutrient acquisition and retention strategies (Gross et al. 2007). To characterise the relation between biodiversity and ES, it is important to define indicators of ecosystem function that indicate the extent to which an ES can be provided (Ape et al. 2012), then ensure that stakeholders can easily use them. Therefore, several researchers (e.g. Van Der Biest et al. 2014) state that there is a demand for simple MFs relying on indicators to evaluate services. These indicators can be land-use proxies (Van Der Biest et al. 2014) or can be based on grassland functional structure and composition. We explore the strength of the latter option.

Methods requiring plant trait measurements are too time-consuming and unfamiliar to stakeholders. Therefore, we developed and used a simplified MF based on grass functional types (GFTs) as indicators, in which stakeholders can easily characterise ES provided by grassland diversity in grassland-based livestock systems: forage, management, input, environmental (species richness and soil C storage) and cultural aspects (aesthetic through characterisation of within-between-grassland diversity). To evaluate its suitability for addressing the above issues and requirements, the methodology was applied to a range of management and environmental factors at different levels of organisation: field, land management unit (LMU) (i.e. parts of farms allocated to single groups of animals corresponding to single management units for production, feeding, health care, etc.) and a set of fields at farm or landscape levels. The field level is needed to characterise the response of plant functional composition to environmental factors and management practices. The LMU level is needed because averaging data at the farm level loses possible within-farm differences due to differences in the management of animal groups (e.g. cows and heifers). The level of a set of farm or landscape fields is needed to assess services related to between-grassland field diversity. To cover a large range of management factors, the MF was applied to dairy and beef farms differing in farming intensity, which influences grassland vegetation (Andrieu et al. 2007).

The paper is organised as follows. First, we describe development of the MF, especially the choice of indicators of grassland functional structure and composition, and of management and environmental drivers. Second, we

examine management and environmental factors that shape grassland functions and then analyse ES provided by grasslands at the field, LMU and farm/landscape levels. Finally, we discuss which drivers have the greatest effect on grassland functions and propose a synthetic representation of relations between management and environmental drivers, grassland functional structure and composition and ES, which allows characterisation of trade-offs and synergies between ES for different beneficiaries.

## Materials and methods

### *Development of the MF*

#### *Linking driving forces, grassland functions and ES*

We adapted a framework linking driving forces, grassland functions, ES and beneficiaries of services developed by Ape et al. (2012) (Figure 1). ES provided by grasslands were distinguished according to the level at which they were noticeable (field, farm and landscape) each of them being specific beneficiaries (Figure 1). For example, some management services are noticeable only at LMU or farm levels (emergent properties), while forage-production services are noticeable both at field and LMU levels (Table 1). When farm level is considered, it is as a whole farm (Smukler et al. 2010), while the sub-levels are key for understanding management services (Duru et al. 2013). Furthermore, we distinguished the level at which services are noticeable from the level at which data should be recorded to assess them. For forage services the levels can be similar, whereas for C storage the levels are different (Table 1). In our study, we focus on field and farm levels. Upscaling, which was not considered in this paper, requires integrating data (e.g. for C storage) or spatially explicit modelling (e.g. for landscape attractiveness). Farm orientation has only an indirect effect on grassland functions through land use and management, while environmental factors (e.g. climate, field and soil characteristics) have direct and indirect effects on grassland functions (Figure 1).

Trade-offs between services can occur for the same beneficiary (e.g. forage and management services for farmers) or between beneficiaries (e.g. forage services for farmers, C storage for society). Arbitrating between services requires developing a small number of relevant indicators of grassland functions for assessing multiple services. For this, we distinguish grassland functions (i.e. the capacity of grassland ecosystems to provide services) from ES, which contribute to human well-being (Raudsepp-Hearne et al. 2010).

#### *Selection of indicators of grassland functional structure and composition*

Although credible, feedback from stakeholders shows that the trait-based methodology to characterise plant functional diversity is not relevant in practice because it is too time-consuming (Duru, Cruz & Theau 2010). To be

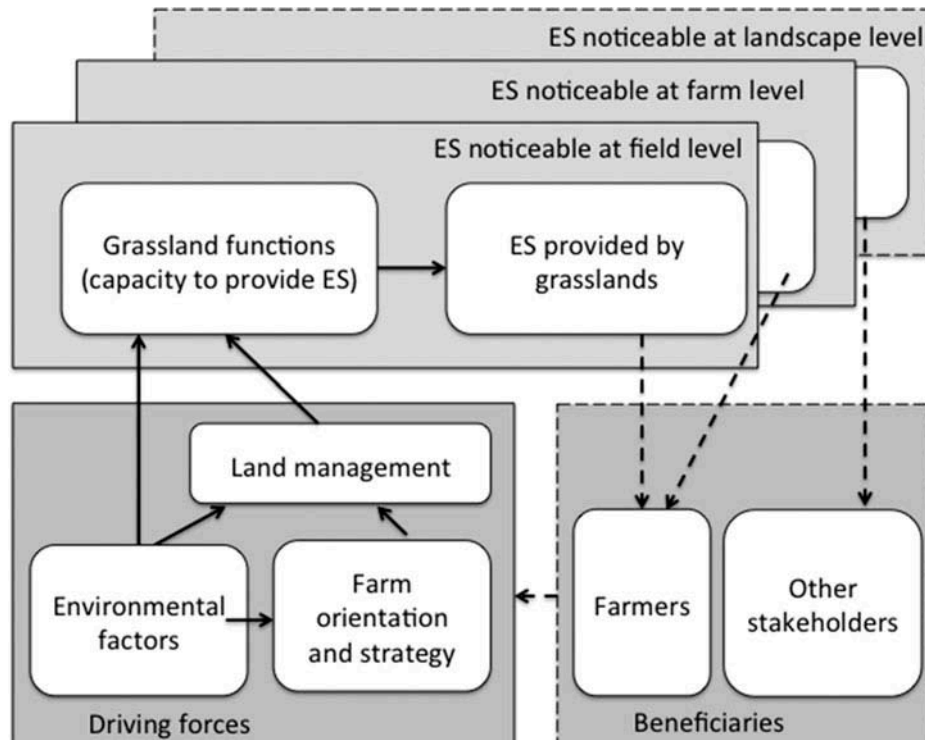


Figure 1. Relations between ES noticeable at different levels, their drivers and beneficiaries; dotted arrows indicate relations that were not studied.

Table 1. Mapping of grassland properties to grassland services.

Services		Organisational level		Indicators	
Types	component	at which services are noticeable for targeted beneficiaries	for recording data	of grassland functions (potential services)	of services provided by grassland (used services)
Forage	Production and quality	LMU, field (farmer)	Field; LMU	Fast <sub>GFT</sub> <sup>††</sup> (aggregated at LMU level)	Stocking rate <sup>‡</sup>
Management	Flexibility allowed by temporality of herbage growth	LMU, field (farmer)	LMU (field <sup>†</sup> )	Late <sub>GFT</sub> (aggregated at LMU level)	Spreading of harvest dates
	Adequacy between forage characteristics and animal feed requirements	LMU (farmer)	LMU/ farm	GFT distribution regarded to animal feed requirement and inputs (fertiliser, labour) (aggregated at LMU level)	Degree at which forage characteristics match animal feed requirements
Input	Fertility	Field (farmer)	Field	Div <sub>GFT</sub> N uptake permitted by within-field diversity (S)	Siomass production/ N supplied
Environmental	C sequestration	Landscape	Field	Fast <sub>GFT</sub>	Soil C content
	Species richness	Field -> landscape (society)	Field	Fast <sub>GFT</sub> ; Sum <sub>GFT</sub>	Number of species
Cultural	Field mosaic	Field -> landscape (society)	Set of fields, landscape	Fast <sub>GFT</sub> × Div <sub>GFT</sub> mapped at different levels	Visual within and between fields diversity

Notes: <sup>†</sup>level not considered in this study.

<sup>‡</sup>reflect the forage production and its use intensity.

<sup>††</sup>Fast<sub>GFT</sub> Late<sub>GFT</sub> are the percentage of GFTs having a fast and a late growth strategy respectively.

Sum<sub>GFT</sub> is the percentage of grass species in biomass in a grassland.

relevant to decision-makers (Cash et al. 2003), that is, for the practical use of knowledge by farmers, we previously made a major change in the methodology for

characterising grassland vegetation (Duru, Theau, et al. 2011). We classified grass species into functional types (Colasanti et al. 2001) rather than using continuous traits,

even though the latter are expected to better represent changes in the intensity of processes (Lavorel & Garnier 2002). Based on leaf and phenological plant traits, five (A, B, b, C and D) elementary GFTs were defined (Cruz et al. 2010). These GFTs were ranked by leaf dry matter content (LDMC), which increases from type A to D, and flowering date, which is latest for types b and D (Duru et al. 2013). When combined, these elementary types reflect two major growth strategies (Sun & Frelich 2011): fast (Fast<sub>GFT</sub>: A and B) vs. slow (Slow<sub>GFT</sub>: b, C and D) and early (Early<sub>GFT</sub>: A, B and C) vs. late (Late<sub>GFT</sub>: b, D), which are meaningful for farmers (Duru et al. 2013). Based on the observation that grass and dicotyledonous species that coexist in grassland communities display similar or constant differences in plant-trait values (e.g. Ansquer et al. 2009) for six plant traits and several ecosystem properties (Duru, Cruz & Theau 2010)), we focused on GFTs expressed as the percentage of grass species in the herbage mass (Sum<sub>GFT</sub>). Consequently, we consider dicotyledonous species only as a whole to estimate their overall impact on plant-community properties (Duru, Cruz & Theau 2010). FD (Div<sub>GFT</sub>) was estimated as the relative percentages of GFTs:

$$\text{Div}_{\text{GFT}} = 1 - \sum_{i=1}^n p_i^2,$$

where  $p_i$  is the percentage of each of the five GFTs;  $\sum p_i = 100$ .

#### *Selection of indicators of ES provided by grasslands*

Based on the four indicators of grassland functional composition (Fast<sub>GFT</sub>, Late<sub>GFT</sub>, Sum<sub>GFT</sub> and Div<sub>GFT</sub>), forage services were previously assessed at the plant-community level (Duru, Ansquer, et al. 2010; Duru et al. 2013). Forage production and herbage quality at the leafy stage are correlated with the percentage of Fast<sub>GFT</sub>, which have high growth rates and low lignin content. In this paper, we examine whether these indicators (or combination of them) can be used to predict a larger set of services based on the Zhang et al. (2007) classification, that is, ES from agriculture (here, forage production, regulating services and aesthetic value) and ES to agriculture (here, management and input services), paying attention to the level(s) at which their assessment is most relevant. For each service, Table 1 lists the indicator used for assessing potential services and the services used. For forage production, in addition to measurements of standing herbage mass at the leafy stage, we used the stocking rate calculated at the LMU level as a proxy.

Management services comprise two components. We assume that the percentage of Late<sub>GFT</sub> is an indicator for the timing flexibility for grassland use, because GFTs growing late in the season offer a large time window for harvesting forage. Thus, we examine the relation between Late<sub>GFT</sub> (potential service) and the range of harvest dates on farms throughout the growing season (used service).

The second management service studied depends on how the farmer organises grassland diversity to match animal feed requirements (Duru, Theau, et al. 2011). Typically, such a service can be assessed only at the LMU level. In fact, farmers combine fields allocated to different forage crops into several assemblages, with each single assemblage allocated to feed a particular herd batch. The number and nature of such assemblages are designed to meet objectives, such as to increase self-sufficiency of the system (i.e. the ratio of forage production to consumption), reduce operational costs or increase flexibility in organising work. Hence, we chose to investigate the farm as a set of such assemblages. To assess this, we ranked animal feed requirements according to the targeted herbage quality (assessed by Fast<sub>GFT</sub> averaged at the LMU level): beef cow < milk cow for grazing, hay or silage; heifer < cow (for dairy farms). Assessing this management service requires examining within-between-farm GFT distribution of animal feed requirements and inputs (e.g. fertiliser, labour) as potential service. Therefore, we first compared plant functional composition of LMUs within each farm, then examined whether there was a between-farm effect of the farm orientation or stocking density on each of the within-farm LMU effects. This can indicate whether a specialisation of plant types exists for certain land-use types, that is, grasslands fulfilling the same function in the feeding system.

For grasslands, input services are mainly related to the coexistence of plant functional types or groups with different growth strategies within a community (e.g. Div<sub>GFT</sub>). It was observed that this improves nutrient or light capture (e.g. Fornara & Tilman 2009). Focusing on fertility, we examine if plant functional type diversity should result in producing the same biomass with less fertiliser. We hypothesised that fertility services would be highest for grasslands with high within-field functional diversity. To test this, we compared N uptake of grasslands with different Div<sub>GFT</sub>.

For regulating services, we examined relations between Fast<sub>GFT</sub> and soil C content and species richness. Fast<sub>GFT</sub> is an indicator of weighted LDMC (Pakeman & Marriott 2010), which is correlated with soil C content. Additionally, species richness is expected to decrease with decreasing nutrient availability (Ceulemans et al. 2013), for which Fast<sub>GFT</sub> is also an indicator (Duru et al. 2013). Conversely, the likelihood of increased dicotyledonous species richness is strong when Sum<sub>GFT</sub> is low, because grasslands usually have more dicotyledonous species than grass species.

In an agricultural context, permanent grasslands have intrinsically high aesthetic value (Sanderson et al. 2013). Some vegetation features at field level such as flower diversity (Quetier et al. 2007) or vegetation-related feature (landscape heterogeneity) are attractive for humans due to their aesthetic value (Lindemann-Matthies et al. 2010). Although aesthetic preferences are highly subjective (Rodríguez-Ortega et al. 2014), we postulate that the heterogeneity of vegetation in phenology, height and colour at

different spatial levels (from within-field to a set of fields) can provide raw data for assessing landscape attractiveness. We, thus, used two of the above indicators ( $\text{Sum}_{\text{GFT}}$  and  $\text{Div}_{\text{GFT}}$ ) to assess landscape diversity, especially its aesthetic component (Frank et al. 2013), at different levels.

#### Selection of indicators of management and environmental drivers

The strength of relations between drivers and services depends on the accuracy with which driver gradients are characterised. They remain difficult to assess accurately, especially for managed grasslands, because most real situations are complex, differing in climate, soil and management (defoliation and fertilisation). These differences are reflected in the intensity of stress (mainly nutrients and temperature, even in the same biogeographic area) and disturbance (defoliation intensity, frequency and time) that grasslands experience. Choice of management indicators was based on previous studies of permanent grasslands (Duru, Ansquer, et al. 2010; Duru et al. 2013).

Plant nutrient availability and soil conditions (moisture content and pH) were assessed with the Ellenberg index (EIV, Ellenberg et al. 1992), which characterises species' nutrient (N-EIV), soil moisture (M-EIV) and soil reactivity (R-EIV) preferences on a scale from 1 to 9. N-EIV was shown to be a better indicator of fertility than one based on plant N content, which is short-term and environment-dependent (Duru et al. 2011a). Observations of species abundance allowed abundance-weighted EIVs to be calculated for the entire grassland. The advantage of EIVs is that they integrate plant species behaviour over many years (Schaffers & Sykora 2000). Furthermore, N-EIV is strongly correlated with P and K availability in the topsoil (Ersten et al. 1998; Schaffers & Sykora 2000).

To characterise defoliation regimes, sward height was measured with a sward stick (Bossuet & Duru 1992) just before the farmer used the field for cutting or grazing. Sixty measurements were collected for each grassland field. Cumulative daily temperature ( $T_{\text{sum}}$ ) for each field was calculated from 1 February up to the field's first use (Duru, Ansquer, et al. 2010).

#### Case study

##### Description

The study was performed in the Aubrac region in the southern part of the French Massif Central (44.68°N, 2.85°E). The study area occupies approximately 40 km $\times$ 20 km. Most of the area consists of unsown permanent grasslands used for dairy and beef livestock systems. To ensure a large range of management and environmental drivers (Figure 1), we chose farms with contrasting land-use types, with low or high stocking rates, and for which grassland fields range from 800 to 1400 m a.s.l. To choose farms, we performed a pre-survey with advisors and used data from the grey literature to ensure a wide range of farm diversity. We preferred analysing a small number of greatly different farms in depth rather than a larger number of representative farms in less depth. Thus, a total of eight farms, four beef (B) and four dairy (D), were chosen. For each land-use type, two types of farm were distinguished according to their stocking rate. For example, farms 1 and 2 had higher stocking rates than farms 3 and 4 (Table 2). Numbers of cows and heifers were converted into livestock units (LUs) on the basis of their live weights: a cow (650–700 kg live weight) corresponded to 1 LU, while a heifer corresponded to 0.8 LU (2–3 years old) or 0.6 LU (1–2 years old).

##### Surveys, measurements and observations

First, farms were surveyed for their main characteristics (land area and production type) and management practices. Grazing animals were categorised either as animals for production (milking cows in dairy systems, heifers, calves) or as animals for replacement or outside their production period (heifers and dry cows in dairy systems; beef suckler cows if calves are not sold at 9 months of age in beef systems, hereafter referred to as replacement animals). The feeding calendar for an average year was drawn up, and spring and early summer land use was mapped (Table 2). Then, field topology and topography (e.g. area, elevation, distance to the cowshed, ease of access for cows coming from the cowshed or a neighbouring field,

Table 2. Characterisation of farm structure and management.

Characteristics		D1	D2	D3	D4	B1	B2	B3	B4
Structure	Grassland area (ha)	54	58	77	69	105	70	115	160
	Animal units (total)	60	56	70	52	106	78	87	117
	Animal units (cow)	39	38	48	35	70	55	60	80
	Stocking density (animal unit/ha)	1.1	1.1	1	0.8	1	1.1	0.8	0.7
	Parcel area (ha)	2.5	1.8	3	2.5	3.2	2.5	5.7	6.9
Hay	Cutting area/animal unit	0.4	0.45	0.44	0.43	0.37	0.4	0.41	0.36
	Topping (%)	24	39	25	0	49	57	46	62
	N fertilisation (kg/ha)	40	31	80	120	160	73	97	69
Summer grazing	Stocking rate (animal unit/ha)	1.1	1.3	1.8	1.3	1.8	1.3	1.1	0.9
Spring grazing	Turnout (DD)	397	410	410	410	450	450	320	450
	N fertilisation (kg/ha)	14	29	46	63	15	24	0	0
	Mixed diet in spring (days)	27	20	7	15	20	7	10	25

Notes: DD: degree-days from February 1st; D: Dairy; B: Beef; 1, 2, 3, 4: farm number.

Table 3. Measurement of driving forces affecting the provision of ES.

Driving forces	Indicator	Level of analysis	Measurement
Farm orientation and strategy	Dairy vs beef	Farm	Constituting of farm sampling
	Stocking rate	Farm	Constituting of farm sampling
Environmental factors	Animal performances objectives; farmer life style		Not considered
	Topology	Field	Field distance from the cowshed
	Altitude, area		Survey
Land management	Soil moisture and reactivity	Field	Ellenberg index for moisture and reactivity
	Fertilisation (amount)	Field	Survey
	Nutrient availability	Field	Ellenberg index for nitrogen
	Cutting management (date, topping)	Field	Survey
	Cutting management (height)	Field	Field measurement
	Turnout (date)	LMU	Survey
	Stocking rate (LU per ha)	LMU	Calculation from survey data
Mixed diet in spring (days)	Group of animals	Calculation from survey data	

suitability for mechanisation) were recorded on the 169 fields of the 8 farms. Data were then mapped according to amount of fertiliser applied (organic and inorganic), nature of the first use (e.g. grazing or cutting only, early grazing that removes the apexes (topping)), date of first use and type of grazing animals. To analyse factors affecting productivity, mean amounts of mineral N fertiliser and solid or liquid manure applied to each grassland field were converted into kg, N applied per year. Data were recorded to describe farm orientation, farmer objectives, environmental factors and management practices (Table 3).

A simplified adaptation of de De DM and De Boer (1959) method was used to characterise the plant functional composition of the 169 grassland fields. One diagonally orientated transect representative of vegetation diversity was sampled between May and the beginning of June, depending on field elevation. Along the transect, 20 biomass samples were collected within 10 cm × 10 cm quadrats equidistantly distributed. Each biomass sample was exhaustively sorted and a score from 0 to 6 was assigned to each species present: (0) species present but not dominant, (1) species contributes at least one-sixth of the biomass sampled (17%), and so on, up to (6) for a species representing all the biomass sampled (100%) (Theau et al. 2010). Although about half of the species present were recorded in all grassland fields, no significant differences in plant-strategy distribution existed between this simplified method and a point quadrat method (Daget & Poissonet 1971) done on a sub-sample of 60 grassland fields (Fallour et al. 2008).

On the same subset of grassland fields ( $n = 60$ ), detailed data were recorded for herbage mass and N concentration (to calculate N uptake), soil C content and species richness. Biomass measurements were made just before the beginning of stem elongation of grass species on four 0.25 m × 0.75 m quadrats in randomly distributed each grassland community. Total N concentrations of dried and ground forage samples were determined by a CHN 2000 Analyser (LECO, St. Joseph, MI, USA). Three soil samples per grassland were taken from the 0 to 5 cm layer for measuring organic soil carbon content. This was

determined by oxidation with potassium dichromate and sulphuric acid (NF ISO 14235) (details of the normative reference in AFNOR (1994)). The original method of De DM and De Boer (1959) was used to determine the exhaustive botanical composition.

#### Statistical analysis

ANOVA was performed at the field level to examine whether there was a significant effect of fertilisation rate and main use (grazing vs. cutting) on the three components of grassland functional composition ( $Fast_{GFT}$ ,  $Late_{GFT}$  and  $Sum_{GFT}$ ). Data expressed as percentages were log-transformed to satisfy the conditions for ANOVA. Regression analyses were performed to express components of grassland functional composition according to quantitative variables of management and the environment. By design, there is a parabolic relation between  $Div_{GFT}$  and the percentage of  $Fast_{GFT}$ : maximum functional diversity is expected for moderate percentages of  $Fast_{GFT}$ , with minima at extreme percentages (Duru et al. 2011b). Thus, response of  $Div_{GFT}$  to management and environmental variables was calculated separately for  $Fast_{GFT} \geq 50\%$  and  $Fast_{GFT} < 50\%$  (Duru et al. 2013). Based on this relation, within-between-vegetation diversity for a set of fields was characterised by only two variables:  $Fast_{GFT}$  and  $Sum_{GFT}$ .

ANOVA was performed too to examine the effect of farm management strategy (i.e. stocking density) and field characteristics (i.e. distance of field from the cowshed, field elevation and area, soil pH and water availability) on field management. Land use was categorised into three classes according to level of care requirements of animals: cutting < heifer or beef cow grazing < dairy cow grazing.

Some services (forage production and inputs) were directly expressed and predicted with regression analysis according to grassland composition. For vegetation heterogeneity, only  $Fast_{GFT}$  was mapped. To assess the degree to which forage characteristics match animal feed requirements, ANOVA was used to discern whether differences



existed among LMUs within farms and whether there was an effect of farm strategy or stocking density on Fast<sub>GFT</sub>.

always significantly higher for dairy farms than for beef farms for both cut and grazed grasslands (Table 5).

**Results**

**Drivers of grassland functions**

*Relations between grassland management and field characteristics*

Grassland management (fertiliser applied and herbage used) depended significantly on topology (distance from the field to the cowshed, field area), topography (elevation) and soil characteristics (pH and depth). However, these effects varied greatly according the component of management considered (Table 4). In general, mown fields are located at a lower elevation and on deeper soils. Grazed fields for dairy cows lie closest to the cowshed, while those for heifers or beef cows are at higher elevations and furthest from the cowshed. Grasslands used for animals requiring more care (grazing by dairy cows) were located at lower elevations and had deeper soils. Fertilisation rates decreased significantly with increasing field elevation for three of the four types of grassland use (Table 4). For cut grasslands, fertilisation rates increased with increasing field area. Otherwise, they showed no clear relation with the other factors studied. Indicators of farming intensity (N fertilisation rate or N-EIV) were

*Response of plant functional composition to management and environmental factors at the field level*

There were significant effects of fertilisation and main use (cutting vs grazing) on the percentages of Fast<sub>GFT</sub> and Late<sub>GFT</sub>, and of field elevation on percentages of Sum<sub>GFT</sub> and Late<sub>GFT</sub> (Table 6). Large differences were observed in the response of Fast<sub>GFT</sub> to N fertiliser rates for both grazed and cut grasslands (not shown), which indicates that environmental factors or biodiversity control N-use efficiency. A consistent, significant response of Fast<sub>GFT</sub> to elevation and R – and M-EIV was found for both land-use types (Table 7). Based on regressions (Table 4) and the range of variation observed for the three variables (N-EIV, plant height and field elevation), nutrient availability had the greatest effect on the percentage of acquisitive species. When N-EIV changed from 3.5 to 6.5 (the minimum and maximum observed values being 3.1 and 6.9), the percentage of acquisitive grass species increased by 50%. In contrast, when canopy height increased from 20 to 80 cm or field elevation decreased by 400 m, the percentage of acquisitive grass species increased by only around 15%. Considering N-EIVs instead of N fertiliser and canopy height at harvest time to encompass both

Table 4. Anova of five field characteristics for land use and fertiliser supply (independent variables).

Variable	df	distance from the cowshed	Altitude	area	R-EIV	M-EIV	
		<i>F</i> -value ( <i>P</i> -value)	<i>F</i> -value ( <i>P</i> -value)	<i>F</i> -value ( <i>P</i> -value)	<i>F</i> -value ( <i>P</i> -value)	<i>F</i> -value ( <i>P</i> -value)	
Land use <sup>†</sup>	/	171	<b>&lt;0.0001</b>	<b>12,4 (0.001)</b>	1.7 (0.17)	1.2 (0.26)	<b>12 (0.02)</b>
Fertilisation supply	cutting	80	0.62 (0.53)	<b>11.7 &lt; 0.0001</b>	<b>3.7 (0.029)</b>	0.13 (0.78)	0.3 (0.66)
(3 classes: 0;	grazing by beef	17	0.12 (0.83)	3.5 (0.06)	1.2 (0.37)	3.4 (0.09)	1.1 (0.31)
0 < x < 75;	cows						
>75 kg/ha/year) <sup>††</sup>	grazing by heifers	39	0.60 (0.58)	0.12 (0.85)	0.99 (0.21)	<b>5.9 (0.03)</b>	0.95 (0.40)
	grazing by dairy	35	2.1 (0.25)	<b>35.1 (&lt;0.0001)</b>	1.27 (0.29)	2.1 (0.14)	0.1 (0.95)
	cows						

Notes: *P*-values <0.05 are in bold; <sup>†</sup>see column 2; <sup>††</sup>anova for fertiliser supply was done separately for each land use; R- and M-EIV: Ellenberg indicator values for soil reactivity and moisture, respectively.

Table 5. Mean values and ANOVA of N fertiliser and N-Ellenberg Indicator Value (N-EIV) for farm enterprise types (beef vs dairy) (independent variables) considering separately each of the three land-use types.

Land use	df	Farm enterprise type	Fertilisation rate (kg/ha)	N-EIV
cutting areas	81	beef farm	71	5.7
		dairy farm	100	5.9
		<i>F</i> -value ( <i>P</i> -value)	<b>8.4 (0.0048)<sup>†</sup></b>	<b>4.2 (0.04)</b>
cow grazing areas	53	beef farm	15	5.1
		dairy farm	42	5.7
		<i>F</i> -value ( <i>P</i> -value)	<b>24.8 (&lt;0.0001)</b>	<b>8.2 (0.006)</b>
heifer grazing areas	39	beef farm	17	5.4
		dairy farm	44	5.1
		<i>F</i> -value ( <i>P</i> -value)	<b>10.7 (0.002)</b>	1.9 (0.18)

Notes: *P*-values <0.05 are in bold; <sup>†</sup> see column 2.

Table 6. Mean values and ANOVA of three indicators of grassland composition (Fast<sub>GFT</sub> Late<sub>GFT</sub> Sum<sub>GFT</sub>) for fertilisation rates (independent variables) considering separately main land-use types.

Land use	Fertilisation (kg/ha)			
	(number of fields)	Fast <sub>GFT</sub>	Late <sub>GFT</sub>	Sum <sub>GFT</sub> <sup>†</sup>
Cut grasslands	149 (26)	71	26	81
	87 (19)	60	37	75
	42 (30)	62	32	75
Grazed grasslands	63 (31)	60	32	75
	33 (25)	45	26	70
	9 (38)	28	28	60
ANOVA for land use and fertilisation	Fertilisation	6.9 ( <b>0.0015</b> )	3.37 ( <b>0.037</b> )	3.6 (0.1)
	Land use	4.1 ( <b>0.007</b> )	0.51 (0.76)	8.9 ( <b>0.0002</b> )
F-value (P-value) <sup>††</sup>	Field altitude: co-variable	46.1 (< <b>0.001</b> )	14.7 ( <b>0.0002</b> )	1.1 (0.31)

Notes: <sup>†</sup>Fast<sub>GFT</sub> and Late<sub>GFT</sub> are the percentage of GFTs having a fast and a late growth strategy, respectively; Sum<sub>GFT</sub> is the percentage of grass species in biomass in a grassland; *p* values <0.05 are in bold; <sup>††</sup>df = 171.

Table 7. Regression analysis between Fast<sub>GFT</sub> (percentage of GFTs having a fast growth strategy) and some management and environmental variables.

Management	management variables			environmental variables			r <sup>2</sup>	se
	N fertiliser	N-EIV	Plant height	altitude	R-EIV	M-EIV		
Grazed	+ (***)	/	/	- (***)	+ (***)	- (+)	0.55 (***)	13.0
Cut	+ (*)	/	/	- (***)	+ (***)	- (*)	0.44 (***)	12.4
Cut + grazed	/	+ (***)	+ (***)	- (***)	+ (**)	- (*)	0.63 (***)	12.2

Notes: N, R- and M-EIV: Ellenberg indicator values for nutrient, soil reactivity and moisture, respectively; number of individuals: 169.

+ or - indicated the direction of effect.

\**P* < 0.05; \*\**P* < 0.01; \*\*\**P* < 0.0001.

management types in the same model provided similar consistent results. The percentage of Late<sub>GFT</sub> was positively correlated with N-EIV (<0.001) and Tsum (*P* < 0.05), and negatively with field elevation (*P* < 0.05), but the correlation was weaker ( $R^2 = 0.22$ , *P* < 0.001).

To test the hypothesis that functional diversity depended on the levels of stress and disturbance, we established two linear regressions according to whether the percentage of Fast<sub>GFT</sub> was lesser or greater than 50%. We found significant effects (*P* < 0.001) of N fertilisation (positive) and field elevation (negative) on Fast<sub>GFT</sub> < 50%, and the opposite for both variables for Fast<sub>GFT</sub> > 50%. The same patterns were observed regardless of the percentage of grass species. For cut grasslands, Div<sub>GFT</sub> decreased as the percentage of Fast<sub>GFT</sub> increased, and the reverse was observed for grazed grasslands.

### Provision of ES by grasslands

#### Services assessed at the field level

Herbage mass just before the beginning of stem elongation significantly was correlated with the percentage of Fast<sub>GFT</sub> (Figure 2a). For the less fertilised grazed grasslands (N fertiliser = 24.4 ± 26 kg N/ha), N uptake was significantly and positively correlated with Div<sub>GFT</sub> ( $r = 0.40$ ,  $n = 38$ , *P* < 0.01). Including soil pH and moisture with EIVs increased the correlation ( $r = + 0.66$ , *P* < 0.001). This

effect was not observed for cut grasslands, which had the highest fertiliser application rates (83.2 ± 47 kg N/ha).

Both regulating services studied had a significantly negative correlation with Fast<sub>GFT</sub>. Species richness decreased significantly as Fast<sub>GFT</sub> increased (Figure 2b), and the correlation increased when considering Sum<sub>GFT</sub> ( $r = -0.75$ ; *P* < 0.001), which had a significantly negative correlation with species richness. Soil C content decreased significantly as the percentage of Fast<sub>GFT</sub> increased (Figure 2c).

#### Services assessed at LMU and landscape levels

For resource provision, a significantly positive correlation existed between stocking rate and the percentage of Fast<sub>GFT</sub> (*P* < 0.001; Figure 3a). For grazed grasslands alone, mean stocking rate and Fast<sub>GFT</sub> were highest for dairy cows and lowest for heifers. However, there were differences in stocking rate for Fast<sub>GFT</sub> > 50% for the same land use and farm strategy. Conversely, similar grassland functional composition was found for all three types of animal groups (beef cows, dairy cows and heifers). A minimum stocking rate of 0.5 animal units/ha was observed in the absence of Fast<sub>GFT</sub>. For cut areas alone, no relation was observed between stocking rate and the percentage of Fast<sub>GFT</sub>. The stocking rate depended mainly on the proportion of the cut area which was topped in early spring ( $r = +0.90$ ; *P* = 0.077). However, stocking rate

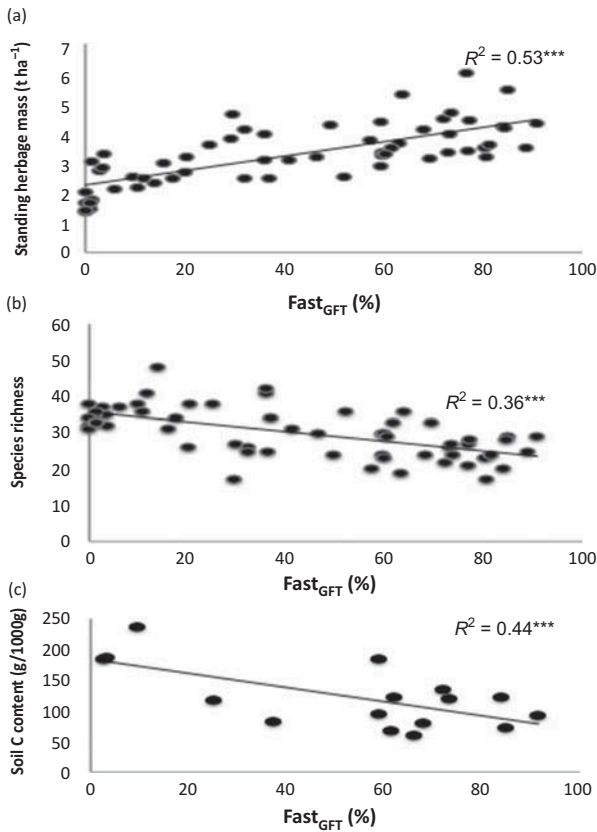


Figure 2. Relations between the percentage of GFT having an acquisitive growth strategy ( $\text{Fast}_{\text{GFT}}$ ) and (a) standing herbage mass ( $Y = -0.13X + 35.7$ ), (b) species richness ( $Y = 0.024X + 2.26$ ) and (c) soil C content in the 05 cm layer ( $Y = -1.15X + 1.84$ ).

positively correlated with N fertiliser rate and timing of the first cut ( $r = +0.82$ ;  $P < 0.05$ ).

The flexibility component of management services was represented as the mean percentage of  $\text{Late}_{\text{GFT}}$  at the LMU level. It significantly correlated with the end date of the hay harvest (Figure 3b), because fields with high GFT diversity had longer durations of harvest operations (not shown). Significant differences were observed in the percentage of  $\text{Fast}_{\text{GFT}}$  among the three LMU types (cut, grazed by cows and by heifers) for six of the eight farms (Table 8). Except for farm D3, cut LMU had the highest percentage of  $\text{Fast}_{\text{GFT}}$  (see Figure A1 for detailed description of plant composition at the farm level). This indicates that forage production and forage quality at the leafy stage ( $\text{Fast}_{\text{GFT}}$ ) were usually the highest for cut areas (except D3 and B1), followed by cow grazing areas (except for D1, B1, and B3). These data show consistent rankings of animal feed requirements and type of vegetation allocated, except for D1. There was a consistent effect of farm strategy on the percentage of  $\text{Fast}_{\text{GFT}}$  ( $P < 0.01$ ) for all LMUs (Table 8).  $\text{Fast}_{\text{GFT}}$  percentages were significantly lower for beef farms. Among dairy farms and grazing areas, there was a significant difference between  $\text{Fast}_{\text{GFT}}$ , as was the case between farms for heifers.

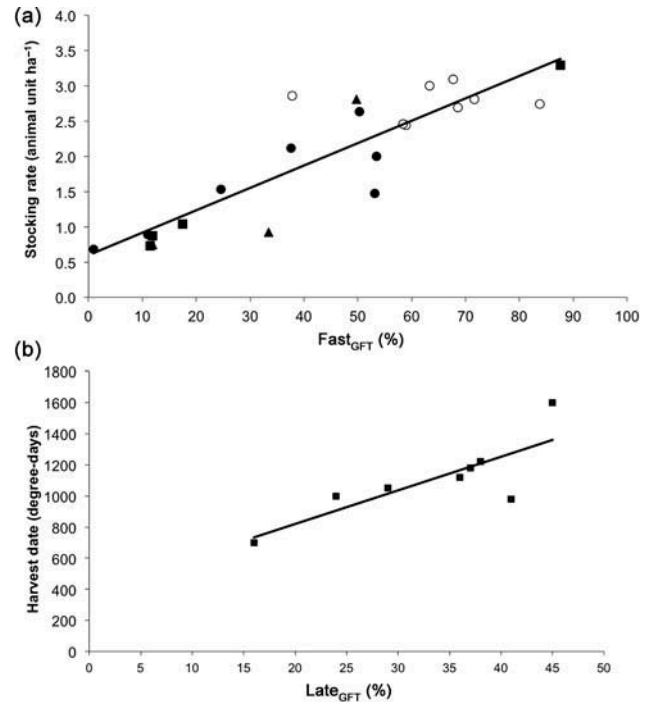


Figure 3. Relations between stocking rate and the percentage of GFT having an acquisitive growth strategy ( $\text{Fast}_{\text{GFT}}$ ), (a) ( $Y = 0.032X + 0.6$ ); end of hay harvest date and the percentage of GFTs having a late growth strategy ( $\text{Late}_{\text{GFT}}$ ), (b) ( $Y = 21.6X + 388$ ); data aggregated at the LMU level.

#### Within-between-field diversity

Vegetation heterogeneity can be assessed for sets of fields among farms or landscapes. Obviously, the more the within-field or between-field diversity, the more heterogeneous were the height and phenology (see Materials and Methods) of grasslands at both levels of organisation. For example, the GFT with an acquisitive growth strategy was mapped for two farms (Figure A2). We observed that almost 50% of the grassland area corresponds to fields with low GFT diversity ( $\text{Fast}_{\text{GFT}}$ :  $<30\%$  or  $>70\%$ ), and that most of these grasslands are close together within the landscape.

At the farm level, cutting and cow grazing areas tended to have higher percentages of  $\text{Fast}_{\text{GFT}}$  in dairy farms than in beef farms (Figure 4a). But this was not the case for heifers grazing areas. Within the range of 40–60%  $\text{Fast}_{\text{GFT}}$ , the three LMU types were observed for both types of farm. In dairy farms, the heifer LMU increased between-LMU differences due to its low percentages of  $\text{Fast}_{\text{GFT}}$ , while for beef farms the cut LMU increased between-LMU differences due to its high percentages of  $\text{Fast}_{\text{GFT}}$ . For the entire data set, we considered three components of plant diversity:  $\text{Div}_{\text{GFT}}$ ,  $\text{Fast}_{\text{GFT}}$  and  $\text{Sum}_{\text{GFT}}$  (Figure 4b). Similar patterns between  $\text{Div}_{\text{GFT}}$  and  $\text{Fast}_{\text{GFT}}$  were observed regardless of the percentage of grass species ( $\text{Sum}_{\text{GFT}}$ ), except for very low  $\text{Fast}_{\text{GFT}}$  values. Comparison of analysis at field and LMU levels (Figure 4a and b) shows that the LMU level

Table 8. Mean values and ANOVA of two indicators of grassland composition ( $\text{Fast}_{\text{GFT}}$  and  $\text{Late}_{\text{GFT}}$ ) for the three land-use types (independent variables) considering each farm separately.

Farm	Df	Land use	$\text{Fast}_{\text{GFT}}^\dagger$	$\text{Late}_{\text{GFT}}$
D1	17	cut area	71	25
		cow grazing areas	38	23
		heifer grazing areas	52	25
		<i>F</i> -value ( <i>P</i> -value)	2.3 (0.15)	0.9 (0.44)
D2	21	cut area	67	37
		cow grazing areas	50	37
		heifer grazing areas	34	53
		<i>F</i> -value ( <i>P</i> -value)	<b>7.18 (0.006)</b>	<b>3.2 (0.04)</b>
D3	19	cut area	84	10
		cow grazing areas	87	13
		heifer grazing areas	12	31
		<i>F</i> -value ( <i>P</i> -value)	<b>28.6 (0.0007)</b>	1.3 (0.24)
D4	22	cut area	58	40
		cow grazing areas	39	38
		heifer grazing areas	10	43
		<i>F</i> -value ( <i>P</i> -value)	<b>4.9 (0.02)</b>	0.6 (0.73)
B1	27	cut area	68	29
		cow grazing areas	25	30
		heifer grazing areas	53	36
		<i>F</i> -value ( <i>P</i> -value)	<b>5.55 (0.01)</b>	0.5 (0.78)
B2	25	cut area	55	35
		cow grazing areas	53	28
		heifer grazing areas	39	37
		<i>F</i> -value ( <i>P</i> -value)	2.45 (0.10)	1.2 (0.45)
B3	18	cut area	63	35
		cow grazing areas	11	36
		heifer grazing areas	19	44
		<i>F</i> -value ( <i>P</i> -value)	<b>11.8 (0.003)</b>	1.1 (0.51)
B4	20	cut area	38	44
		cow grazing areas	1	34
		heifer grazing areas	18	40
		<i>F</i> -value ( <i>P</i> -value)	<b>8 (0.0002)</b>	1 (0.55)

Notes:  $^\dagger$ percentage in biomass; significant differences among land use within a farm are indicated in bold.

$\text{Fast}_{\text{GFT}}$  and  $\text{Late}_{\text{GFT}}$  are the percentage of GFTs having a fast and a late growth strategy, respectively; D: dairy farms; B: beef farms.

greatly structures grassland diversity. In other words, grassland diversity is greater between LMUs than within them. Thus, differences in farm orientation and stocking density are required to maintain a grassland mosaic at the landscape level (Figure A2 gives an example for two farms).

## Discussion

### *A plant functional-type-based MF for linking management and ES*

Our results show that a MF based on a simplified characterisation of plant functional types allows a large set of ES at different organisational levels to be assessed, which is better than considering drivers alone. Regardless of the level considered, strong and weak correlations were found between plant functional composition and services (especially forage services) and drivers, respectively. Regression analysis has shown that  $\text{Fast}_{\text{GFT}}$  alone can predict services well (e.g. herbage production,  $R^2 = 0.69$

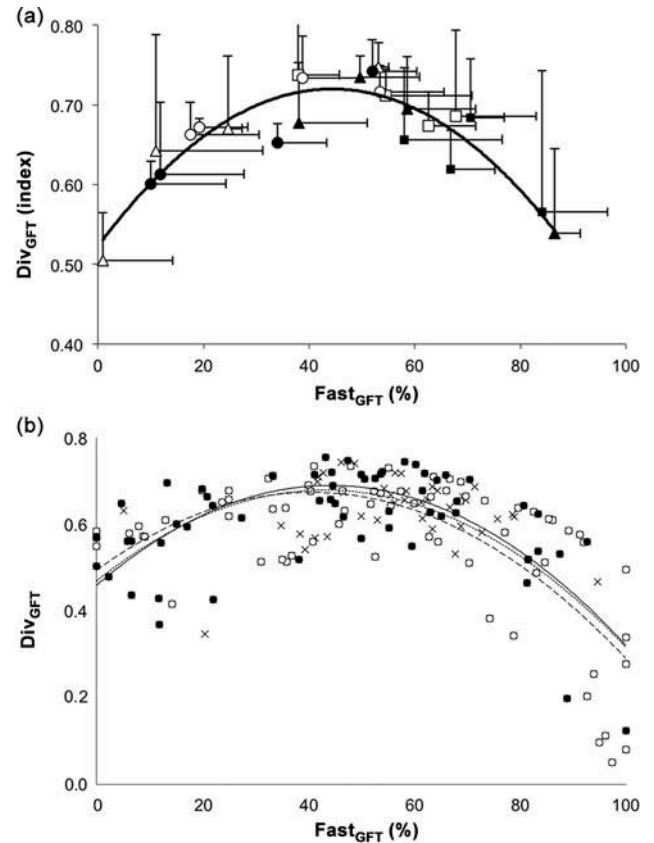


Figure 4. Relations between within-field functional diversity ( $\text{Div}_{\text{GFT}}$ ) and the percentage of GFTs having an acquisitive growth strategy ( $\text{Fast}_{\text{GFT}}$ ); a: for data aggregated at the LMU level (squares for cut grassland, circles and triangles for grassland grazed by cows and heifers, respectively, open symbols for beef farms, closed symbols for dairy farms) ( $Y = 0.0001X^2 + 0.009X + 0.52$ ); b: for all grassland fields, the percentage of grass species in herbage biomass: >80% (closed circles), 60–80% (crosses) or <60% (open circles).

in Duru, Cruz, Jouany, et al. (2010), or stocking rate,  $R^2 = 0.78$  in this paper), whereas management and environmental drivers can explain only 44% or 59% of the variance, respectively, depending on whether the explanatory variables are observed or measured. Correlations found elsewhere using plant traits instead of plant groups are no higher (e.g. Lavorel et al. 2011; Duru et al. 2012). This justifies using plant functional types as a key tool for managing grassland functional composition and predicting ES. However, the method used to characterise grassland plant functional composition is highly simplified in comparison to the measurement of plant traits. As is known, plant traits, plant functional groups or their proxies must be aggregated to assess certain ES, such as those provided by the landscape mosaic (Lavorel et al. 2011). However, aggregation does not have to reach the landscape level to be able to understand effects of management and policies on within-between-grassland diversity. Thus, we found that the LMU level performed better than the farm level for understanding in depth the degree of heterogeneity in management practices that impact ES.

The main advantage of the MF proposed is its ease of use by stakeholders. Its strength lies in not being limited to production services, as traditionally done in agronomy. The concept of plant functional types is key because it is appropriate for evaluating or predicting a wide range of ES and makes sense for farmers and other stakeholders. Farmers give positive feedback when their land is depicted through plant functional types in a bar graph (Duru et al. 2011a) or a map (Figures A1 and A2, respectively). Moreover, several agricultural consultants have adopted it, at least partly, to design grassland typologies at national (Launay et al. 2011) or regional (Carrère et al. 2012) levels. They have a great interest in the MF because of its ability to reduce a large list of species into a small number of plant functional types in an effective communication tool. It addresses four key components of forage services that fit well with farmers' expectations (Duru, Cruz, Jouany, et al. 2010).

Below, we summarise and discuss our main findings about relations between grassland functional composition, management (next section) and ES, and examine trade-offs and synergies between ES (last section).

### **Drivers of grassland functional composition and management**

At field level, the grasslands with the highest percentage of acquisitive species ( $Fast_{GFT}$ ), as well as the greatest abundance of grass species, responded significantly to management and certain environmental drivers (e.g. field elevation).  $Fast_{GFT}$  increased with increasing nutrient availability (Wilson et al. 1999) and decreased with increasing temperature (Roche et al. 2004), which was negatively correlated with field elevation (Figure 5, top). These results are consistent with studies demonstrating that the features used to distinguish GFTs (specific leaf area, LDMC) are appropriate indicators of stress, in general (Harrison et al. 2010). Stress factors for nutrient availability and mean temperature act in the same manner, favouring acquisitive species when stress is low. Our results confirm those observed for a small (Duru, Ansquer, et al. 2010) and a large (Martin et al. 2009) number of sites. Disturbances modify the effects of stress, either reducing or amplifying them. For given climatic and soil conditions, mowing promotes acquisitive species, while grazing promotes conservative species. In other words, mowing reinforces the positive effect of temperature and N on the abundance of acquisitive species (Figure 5, top). For functional diversity (here  $Div_{GFT}$ ), previous research on the intermediate stress hypothesis (Vonlanthen et al. 2006) supports the idea that maximum diversity was observed only when simultaneously considering stress and disturbance factors, as we also found. Additionally, we show that the direction of effect for stress factors depends on the current dominant plant strategy; for example, N fertiliser could decrease or increase  $Div_{GFT}$ .

Based on the farm sample studied, we found that even a single farm can contain a wide range of within-between-field functional plant diversity (Rudmann-Maure et al. 2008) and that contrasting land use within a farm can create a diversity of plant species as wide as observed at the landscape level. As observed in a different context (Beyene et al. 2006), plant functional type assemblages are the result of deliberate management choices resulting from farm enterprise type (Brodt et al. 2006) and from assets and constraints such as available facilities and field topography (Andrieu et al. 2007; Valbuena et al. 2008; Martin et al. 2009). Differences in plant functional diversity at the LMU level are the result of land use and farm enterprise type. Usually, cut grasslands have the highest percentage of acquisitive types, first because they receive more fertiliser and have consistently higher N-EIV, and second due to the direct effect of management practices on the percentage of acquisitive types (Table 7). Dairy farms have a higher percentage of acquisitive plant types for both cut and grazed areas, which is consistent with the highest digestibility of these plant types (Duru, Cruz & Theau 2010). Between-farm comparisons can show whether the potential exists to reduce the cost of feed-stuffs. For example, the dairy farm D4 has similar milk production per cow (around 5000 kg per year) even though the percentage of  $Fast_{GFT}$  differed greatly: it was highest for D3 and lowest for D4 (Table 8). Since obtaining a high percentage of  $Fast_{GFT}$  requires high fertiliser input, this indicates that production costs could be reduced if enough land were available, especially if it is grazed, so as not to increase the workload. The MF also detects discrepancies, for example, for dairy heifers on farm D3 that used high-quality herbage.

Field characteristics may explain between-farm differences in grassland functional diversity. In less-favoured areas, many farm-dependent constraints may occur (Andrieu et al. 2007; Martin et al. 2009). These include:

- (1) The proportion of grassland fields located near the cowshed, which affects the stocking rate, at least for dairy systems. In this way, D3, which has fewer pastures near the cowshed, has a higher stocking rate than D4 (3.3 vs. 2.0 animal units per ha).
- (2) The availability of summer pastures for animals with low feed requirements (dry cows, replacement heifers), because these usually unfertilised areas widen the range of GFTs encountered at the farm level. For example, dairy farms D3 and D4 can use summer pastures that usually never receive fertiliser, while this is not the case for D1 and D2.
- (3) The use of modern harvesting equipment (round-baller), which reduces dependence on the weather, shortens the harvest duration, and thus the range of vegetation types observed (Benton et al. 2003). There is little variability in functional composition between mown grasslands, except for farms B2

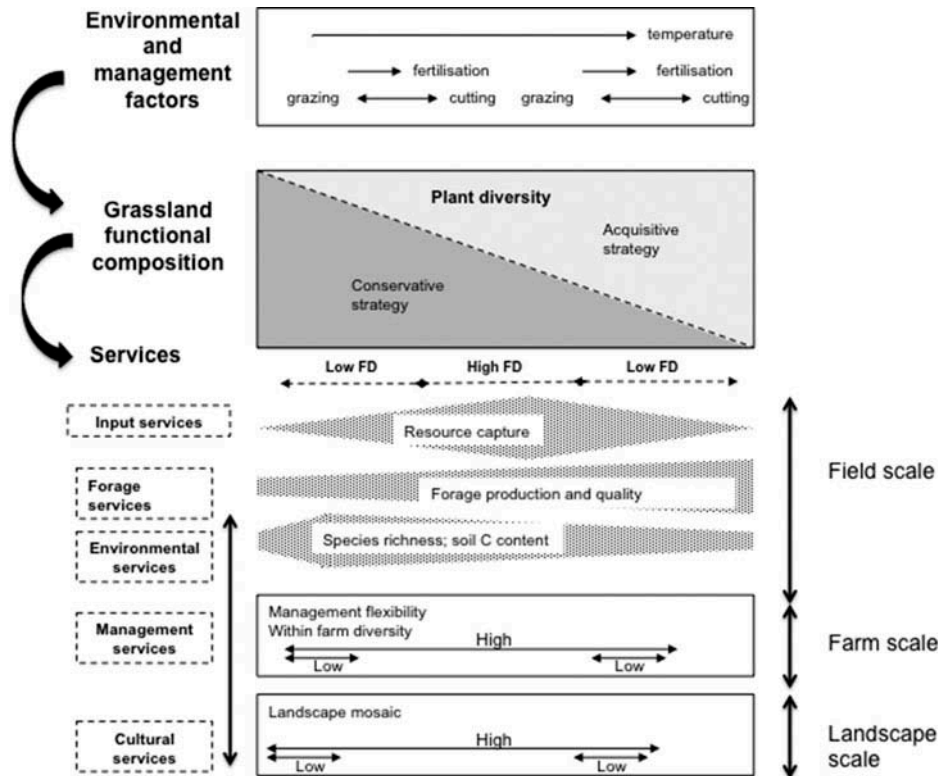


Figure 5. A framework for linking environmental and management factors to grassland functional composition and a set of ES; the shape of each triangle indicates the direction of expected effect; rectangles indicate that effects depend on stakeholder viewpoints; FD: functional diversity.

and B4, which mowed summer pastures.

The results of this study clearly show that, as White et al. (2004) suggested, there is greater uniformity in plant types within LMUs than between them. Balancing constraints and goals, there is room for different degrees of farm-level diversity of plant types. This means that some farmers choose to favour a certain range of plant types for economic (e.g. to reduce inputs) or labour reasons. Nevertheless, we did not find an effect of within-field functional diversity on stocking rate as shown at the field level (Weigelt et al. 2009). As claimed by Sanderson et al. (2004), the evidence for diversity effects is equivocal for pasturelands. However, stocking rate is probably a too coarse variable to reveal the effect of within-field functional diversity on potential complementarities between plant types.

#### Evaluation of trade-offs and synergies between ES

The MF based on GFTs allows the evaluation of a large number of ES at different organisation levels and the analysis of main trade-offs between services. We found that a set of ES can be evaluated at the field level and above (Figure 5, bottom for  $Fast_{GFT}$ ).  $Fast_{GFT}$  was a good proxy for forage production measured at the field level, thus confirming results obtained in other regions (Duru, Cruz, Jouany, et al. 2010) or assessed through the stocking

rate at the LMU level (this paper). For low N rates, we verified that the coexistence of plant functional types with different strategies for resource acquisition leads to higher input efficiency for herbage production, as suggested by Fornara and Tilman (2009) and Dybzinski et al. (2008), on the basis of species richness. For management services, we found that between-farm differences are related to the allocation of vegetation types or forage resources to different animal groups to save nutrients or feedstuff costs; for example, the capacity exists to reduce N fertiliser without affecting animal production for some land-use types, as seen above. Furthermore, our MF provides a simple method for comparing within-between-field plant functional diversity. It could help stakeholders determine the degree of grassland heterogeneity to promote (Lamarque et al. 2011).

The synthetic representation of relations between grassland functional composition and ES allows stakeholders to examine the main trade-offs they must consider (Figure 5, bottom). For farmers, among forage and management services, an opposite trend occurred between measured herbage production and recorded production timing ( $r = -0.51$ ,  $n = 24$ ,  $P < 0.01$ ), with  $Fast_{GFT}$  and  $Late_{GFT}$  as proxies, respectively (from data used for Figure 3a and b). However, at the field level, a nonlinear relation between herbage production and yield flexibility was observed. At the LMU level, such trade-offs were not usually a problem for farmers because the priority services

depended mainly on the animal group (cow vs. heifer) or the land management (grazing vs. cutting) considered. Thus, the diversity of animal groups on a farm and of farm enterprises in a region lead to a diversity of vegetation types in a landscape which is enhanced by environmental factors such as field aspect and elevation. This explains why this kind of diversity in agriculture creates a mosaic of vegetation types within and between farms that directly contributes to landscape attractiveness, which is important for tourism (Junge et al. 2011) and indirectly and more broadly to multiple ES (Smukler et al. 2010) (Figure 5).

### Conclusion

In less-favoured areas such as mountains, farms have high grassland diversity due to diversity in abiotic factors (elevation), farm orientation (beef, dairy), enterprise (cows, heifers) and management (grazing, cutting). To describe ES provided by grassland diversity and their underlying drivers, we have developed a MF based on GFTs. Due to its ease of use and credibility, this MF should help agricultural experts and farm advisors understand implications of different management choices on grassland diversity and on a large set of ES noticeable by farmers, tourists and other members of society. The field level may be sufficient for assessing their impact on plant diversity, while the land-use type and farm levels are still needed to understand the drivers of management practices. Our MF can also help local policy-makers who intend to support biodiversity with subsidies based on stocking-rate thresholds calculated for a set of fields or the entire farm. Our results clearly show that field and farm levels are too small and too large, respectively. The LMU level seems to be the right level for gathering data for management and/or vegetation, then engaging discussion between beneficiaries of ES to identify trade-offs and synergies.

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No potential conflict of interest was reported by the authors.

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Appendix

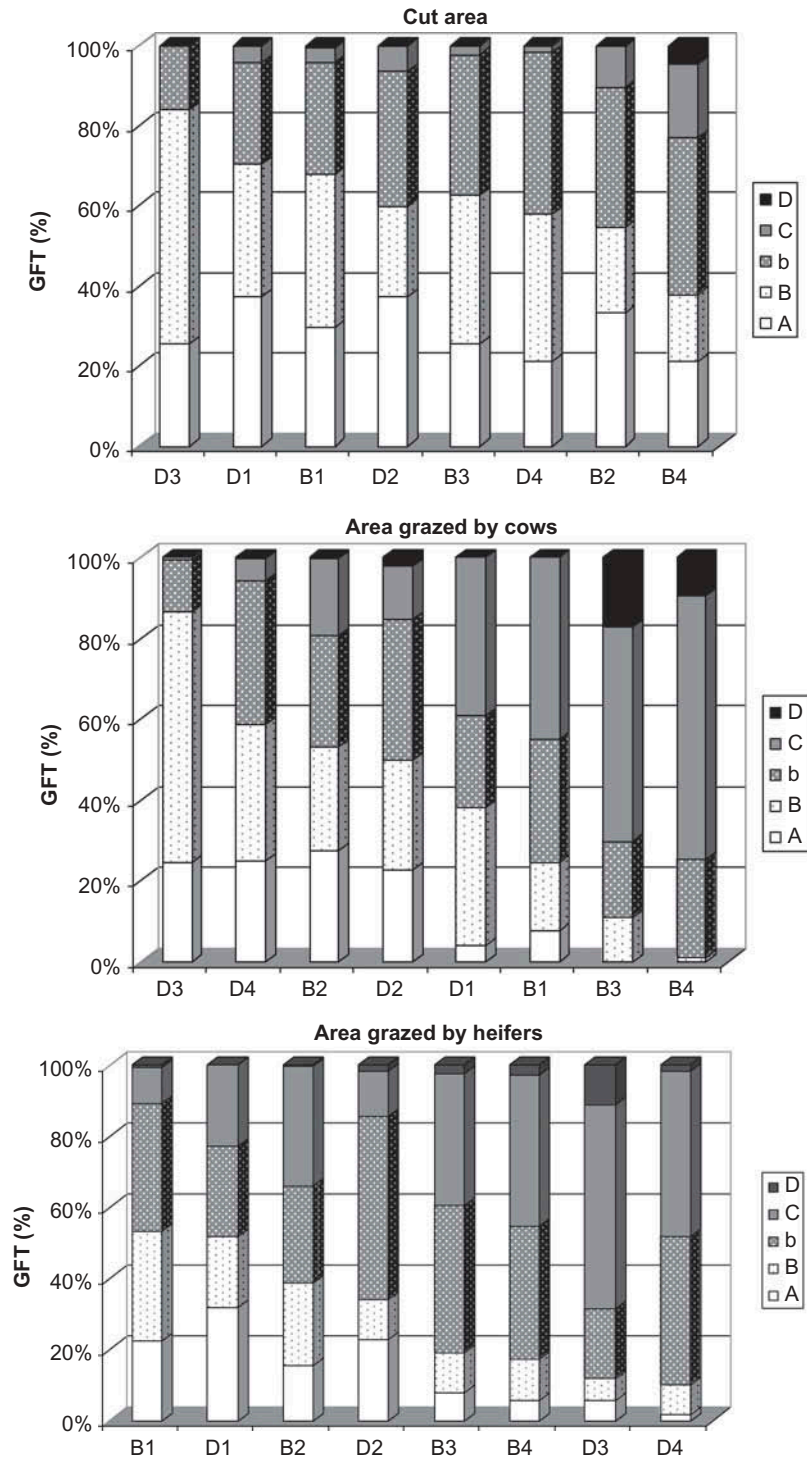


Figure A1. Bar graphs for five GFTs ranked from fast growth strategy (A) to low growth strategy (D) for the dairy (Di) and beef (Bi) farms. Data were averaged for the whole grassland fields having the same use: cutting, grazing by cows and heifers.

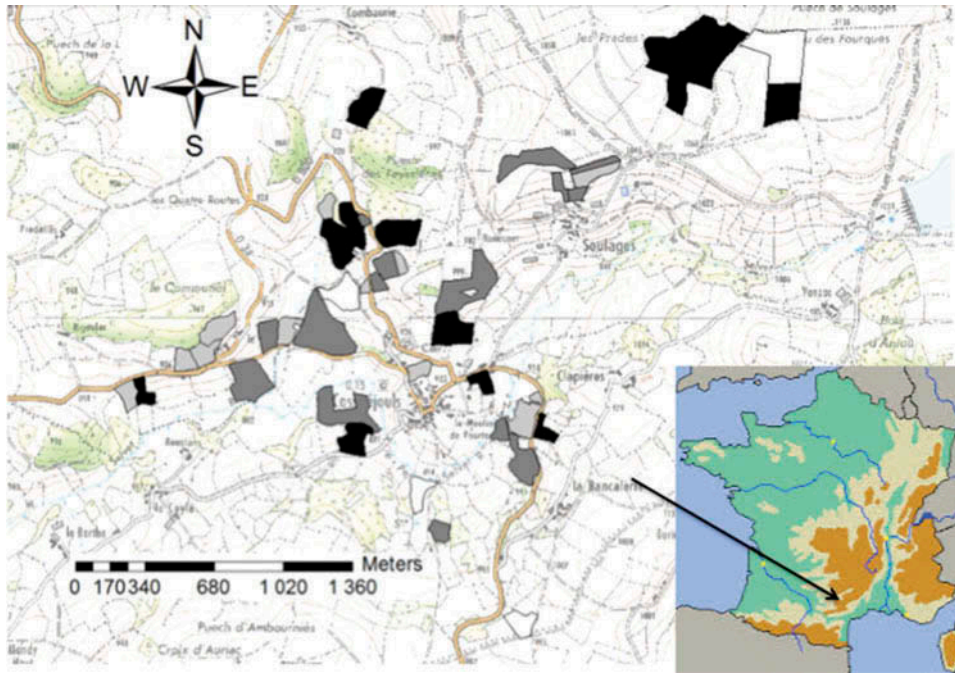


Figure A2. Maps of vegetation diversity for two farms located in the same district. The four colours correspond to different percentages of GFT having an acquisitive growth strategy: w30% (white), 30–50 (light grey), 50–70 (dark grey), >70% (black); the small map shows the location of the studied area within France.