Multiple functions of organisms and their interaction – a different approach to multifunctionality of permanent grassland

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Introduction

Since the term 'multifunctional agriculture' has been mentioned for the first time in 1993 by the European Council for Agricultural Law, it has been widely used in agricultural science and geoscience in order to understand and structure the multiple productive and non-productive outcomes on agriculturally dominated land (Zander et al., 2007; Stobbelaar, 2009). The concept of ecosystem services (ES) first came up in the late 1990s and was incorporated into the Millennium Ecosystem Assessment (MEA, 2005) which classifies them into four groups, *i.e.* provisioning, regulating, supporting and cultural services. Provisioning services are products such as food (*e.g.* meat, dairy products, herbs, raw materials, pharmacological resources) and water but also genetic material. Supporting services such as soil formation, carbon fixation, nutrient and water cycling underpin other services whereas regulating services provide stability to the natural environment *e.g.* through regulating air quality and water quality, avoiding soil erosion and water run-off. Cultural services however, allocate non-material benefits that can affect health and well-being, e.g. through recreational opportunities and aesthetic experiences (Hopkins, 2009; Petter et al, 2012).
The role and importance of permanent grassland in providing a high number of ES to all of these four groups is widely accepted (Hopkins, 2009; Lehmann, 2009; Huyghe et al., 2012). The grassland biome provides ES such as high forage quality (energy and nutrient content), it supports flora and fauna habitat and high biodiversity (Huyghe et al., 2008; Sanderson, 2010), it also serves as carbon sink (Vleeshouwers and Verhagen, 2002; Janssens et al., 2005; Gilmanov et al., 2007; Wohlfahrt et al., 2009; Petri et al., 2010), diversifies soil biota (van Eekeren, 2010; Zaller, 2012), regulates water storage (Fohrer et al., 2001) and stabilizes the soil against erosion and landslip (Cernusca et al., 1998). As grassland can only persist when it is regularly defoliated by grazers or through mowing in order to avoid reforestation, management is inherent to the persistence of the biome and its services (Mc Donald et al., 2000, Kleijn and Baldi, 2005; Scozzafava and De Sanctis, 2006). Sekercioglu (2010) has assigned several non-marketable ES to the relevant functional units and has also indicated the spatial scale of operation of the services. This scheme clearly demonstrates the specific and essential role of vegetation, plant communities and species for most of the ES provided by grassland.
Governments and the societies in European countries acknowledge that agricultural production supplies a wider range of commodities. Especially grassland farms are always considered to provide a wide range of ES and thereby achieve a higher degree of multifunctionality than arable farms, especially those that are less intensively managed, less specialized and less dependent on external resources. Although there is an ongoing debate on how to assess and approve multifunctionality, there seems to be a tendency of strongly multifunctional farms towards a higher degree of sustainability and of adaptation of intensity of production to environmental conditions (Wilson, 2009).
Understanding multifunctionality in a natural science context requires its linking to ecosystem properties, functions and services (www.fao.org) which themselves are strongly interrelated.

De Groot and co-authors (2010) have listed key questions regarding a better integration of ES into landscape planning, management and decision-making. Interestingly, they are especially asking how the relationship between landscape and ecosystem characteristics and their associated functions and services can be quantified.

Functional ecology has significantly contributed to resolving this question, but from a different perspective. While the multifunctionality debate concentrates on understanding relations between all goods and services provided mainly at agroecosystem level, functional ecologists explore serviceable relationships between organisms in their biotic and abiotic environment. In some way, the term 'function' is used in different ways. The FAO definition sees multifunctionality very broadly and concentrates on the various outcomes at larger scales in a socio-ecological context, whereas functional ecologists relate traits (*i.e.* morphological, physiological and phenological properties of organisms) and their functions to processes such as nutrient acquisition, growth rate, proliferation rate, and senescence rate. Spatial scales in functional ecology range from very small (organ) to large (biome). Thus, links exist between the ES that farming provides and the underlying mechanisms of organisms. Although both these approaches, either FAO or the scientific community of functional ecology, differ in their aims and their definition of the term 'function', they are both strongly interrelated.

We have tried to illustrate the links between multiple functions and traits of grassland on the one hand and ES on the other (figure 1). The bio-physical structure of organism communities can be described as the composition and organisation of functional traits of soil, plant and animal. These traits are strongly interacting, with different directions and intensities and at different temporal and spatial scales.

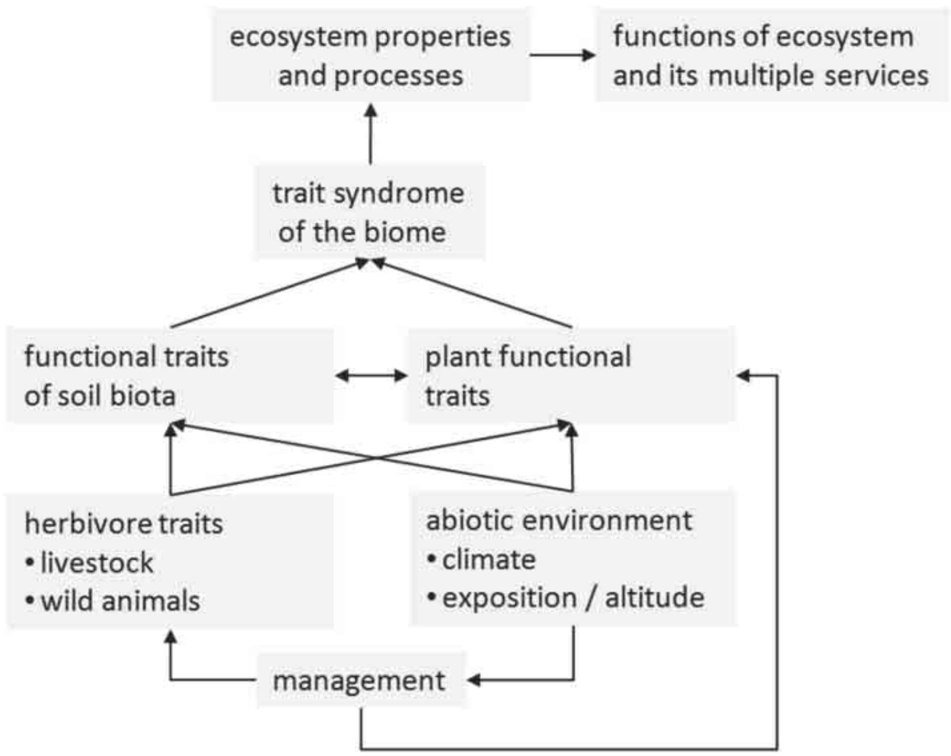

Figure 1: Linkages between functional traits of plant, soil and animal in relation to ecosystem services.

Trait relations can be linear or non-linear, and feedback regulation is common. Management is a strong driver of variation in any of these traits (Björklund et al., 1999; Gibon, 2005; van Oudenhoven, 2012), as the intensity and direction of changes in trait composition mainly depend on type and pattern of defoliation and fertilizer application (Schellberg and Pontes, 2012). In other words and within certain limits, management is the most important external driver for functional relationships on grassland. Likewise, multifunctionality of grassland (*sensu* FAO) is affected by management. Grassland is managed mainly by varying cutting frequency, grazing pressure and fertilization level. Management intensity directly influences characteristics of the grassland sward such as standing biomass, floristic composition and forage quality. Thus, it is the main driver of changes in functional traits and related provisional ES (Pötsch et al., 2005), with partly contrasting impacts. In order to better understand relationships between functional traits of grassland and related ES, we assessed ES distribution along a gradient of management intensity (figure 2). The contribution of intermediate stages of grassland vegetation to indivual ES is shown, from abandoned land across a two-cut system (*e.g. Arrhenateretum medioeuropaeum*) towards an intensively managed mowing pasture (e.g.*Lolio-Cynosuretum*).

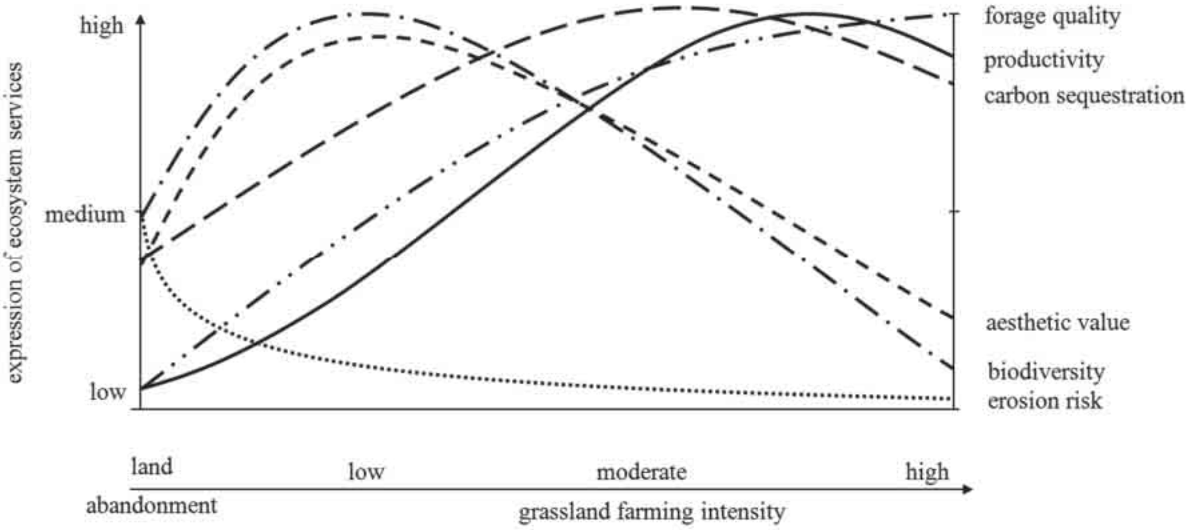

Figure 2: Relationship between farming intensity and ecosystem services on permanent grassland. Intensity is understood as a various combination of fertilization level, cutting frequency, grazing intensity, livestock density and re-seeding activity.

This graph indicates that the contribution of ES, which are provided by vegetation and soil as an inseparable system, vary with intensity. They may – at the same time – also vary with environmental conditions such as length of growing season and soil properties. Some ES occur in a synergetic way (*e.g.* aesthetic value and floristic diversity) whereas others arise diametrically (*e.g.* biodiversity and productivity).
All ES are a function of complex interactions among species and their abiotic environment, complex use and utilization patterns and various perceptions by beneficiaries (Fisher et al., 2009). However, the underlying functions on which these ES are based need further justification. Many examples exist on how human activities affect multifunctionality and how this can be assessed (Nelson et al., 2009; Renting et al., 2009). The question arises, how multifunctionality of grassland can be assessed based on the functional relationships of traits of soil and organisms. In this study we give examples of how multiple functions of organisms exhibiting certain traits explain multiple functions of the ecosystem.
When seeking to establish links between multifunctionality (*sensu* FAO) and the functional trait approach, we realized that earlier studies exist on similar topics (*e.g.* Chapin et al., 1997; Hooper et al., 2005; de Groot et al., 2010; Isbell et al, 2011). In these studies, authors have raised important questions about general relationships between ecosystem functions (EF) and functional trait composition of floral and faunal communities. However, with a stronger

focus on permanent grassland we can be more specific in our concept on trait-function. This manuscript aims at explaining multifunctionality from a different perspective, based on three examples, the production function, provisioning of forage quality and soil ES.

The production function

From a farmers' point of view, the productivity of grassland is the most important service that it can provide. The underlying ecosystem function, the production function (de Groot et al., 2002), is that of conversion of solar energy into plant matter which can be expressed as growth rates. The environmental factors defining growth rates are mainly precipitation, temperature, soil nutrient status and soil physical and chemical properties (Craine et al., 2002). With respect to the linkage of plant functional traits to ES it is important that distinct traits exist that indicate metabolic activity leading to different growth rates (table 1). Species which exhibit high growth rates (C-types *sensu* Grime) can be characterized as producing large leaf area of low specific leaf weight, rapid stem elongation to the favor of rapid space occupation in the canopy, high leaf photosynthetic rate and high leaf N content. Species exhibiting such traits are usually dominating sites without resource limitations. At low resource levels, productivity drops to the favor of other plant types supporting other functions such as regulating and habitat functions. At resource limitations, the C-type is rather disadvantaged. Species adapted to environments of low availability of resources follow a different strategy (S-types *sensu* Grime, 1977), *i.e.* high specific leaf weight, low growth rates and large contribution of internally recycled metabolic carbon.
The productivity (as a prominent ES) that these two contrasting types of plant species can provide, can thus be explained based on the plant functional traits which have developed in response to environment-management interactions. Of course, the production function also depends on clever adaptation of cutting, grazing and fertilizer application by farmers in relation to maximum achievable growth rates.

Table 1: A selection of numerical plant functional traits relevant for plant productivity and feeding quality.

plant functional trait	measurement	reference
specific leaf area, *SLA*	leaf area meter, weighing	Diaz and Cabido, 2001
plant height, P_h		Wright, 2004
leaf stem ratio, *LSR*	weighing	Cornelissen et al., 2003
leaf dry matter content, L_{DM}	drying, weighing	Duru et al., 2009
plant C and N content, P_N, P_C	gas chromatography	
In-vitro digestibility of plant organic matter, (%dOM), *IVDOM* and energy concentration (MJ NEL kg^{-1} DM), P_{NEL}	in vitro analyses	Tilley and Terry, 1963 Menke et al., 1979
neutral detergent fibre, *NDF*, P_{NDF}	fibre analyzer	Goering and van Soest, 1970

Forage quality

High growth rates are somehow related to quality parameters of forage grasses and herbs. Although forage quality is not explicitly mentioned in the FAO documents on ES, it is essential for the provision of animal products to humans. For instance, digestibility of organic matter, NDF and protein content is since long known as the most important quality parameters in plant material harvested from grassland. As the same traits are relevant for the productivity function of the grass crop, negative as well as positive correlation with the quality parameters exist. For example, rapid growth rates are often accompanied by stem elongation leading to unfavorable leaf-stem ratios. Further, as long as the canopy is not harvested, older unproductive leaves at lower canopy layers are getting senesced, and so overall quality of the canopy declines. Management seeks to balance such positive and negative relationships between trait expression and related ES, thereby considering the temporal dynamics of production rates and quality decline. Moreover, there is another important link of plant functional traits to forage quality and ES.

Stress tolerant species (*sensu* Grime) invest more into structural biomass than into photosynthetic tissue. They also exhibit higher specific leaf weight and, associated with this, also higher tissue strength. Thereby, the rate at which microorganisms can access plant cell content in the rumen of cows is lower than with fast growing (competitive) species. In consequence, retention time of forage in the rumen increases with the proportion of species that are classified as stress tolerant due to their well adopted growth strategy.

The multifunctional role of the soil

The role of the soil in the provisioning of ES on permanent grassland is often not recognized. But, multiple interactions of soil with plants are mediated by soil organisms such as bacteria and arbuscular mycorrhiza funghi (AMF) (van der Hejden et al., 1998; Hartnett and Wilson, 2002; Johnson et al., 2004; Southworth, 2012). Further, functional ecology separates functional traits into those that indicate a response of plants to environment such as soil conditions as well as to management (so-called response traits) and those that explain the effect of plants on the soil (so-called effect), as will be explained later.

All these processes strongly act together on chemical, physical and biological traits of the soil. With respect to amount and quality of soil organic carbon, decomposition rates are important. It is well documented (de Deyn et al, 2008) that litter composition determines carbon sequestration. The accumulation of litter as well as soil carbon content is seen as an important ES provided by grassland (Conant et al., 2001; Cernusca et al., 2008). However, due to the above mentioned differences in response of species to limitations in water and nutrients, this ES may vary considerably. Further, growth rates of above ground biomass are associated with root biomass. The ratio of both depends on plant functional traits and on the availability of resources. However, the accumulation of root biomass is also associated with a series of events such as root exsudation, soil water and nutrient depletion, interaction with soil microorganisms (especially with rhizobia and AMF), and modification of soil physical properties. Some of these plant trait related events are important with respect to ES on grassland. For instance, a competitive species such as *Daucus carota* L., strongly affects soil physical structure and pore volume through its taproot and also supports carbon accumulation as well as mineral nutrient and water uptake from lower soil layers. This clearly indicates a link between functional traits and ES such as carbon sequestration. Table 2 provides a list of traits that are considered relevant for functional relationships between plant and soil.

We have tried to summarize the relationships between two most important management factors, fertilizer application and cutting frequency, on the one hand and plant functional traits and related processes in soil on the other (figure 3). Many of these soil traits have not been investigated with respect to their importance in providing ES, with some exceptions (*e.g.* N_2 fixation), and especially not to how these ES can be explained on plant-soil functional relationships. We hypothesize that the responses and effects of plant functional traits at different fertilizer levels is mediated by soil traits. We therefore believe that a better understanding of ES requires more investigations on functional relationships between soil and plant traits. The different responses and effects among plant and soil are also dependent on time. For instance, we can expect a short term response of soil nitrogen content on fertilizer application, however, the related increase of soil organic matter content due to increased biomass production, root growth and dry matter decay may last many years. Long-term experiments are an excellent source of data and the only environment where undisturbed plant-soil functional relationships can be thoroughly investigated. Further, one may suggest equilibrium of soil properties after decades of constant management, however, the time from onset of the experiment until steady state of soil properties is usually not known.

Table 2: A selection of numerical soil functional traits (chemical and physical only) relevant for plant - soil functional relations.

soil functional traits	measurement	reference
soil chemical traits		
pH, S_{pH}	CaCl	Blume et al., 2011
particulate organic matter, S_{POM}	selected samples only	Kemper and Chepil, 1968; Jastrow, 1996
organic C, S_{OC}	by combustion (auto-analyser) minus carbonate C	Blume et al., 2011
organic N, S_N	by combustion (auto-analyzer)	Blume et al., 2011
available P S_{Pav}	calcium –ammonium lactate	Blume et al., 2011
sequential P extraction S_{Pfrac}		Hedley et al., 1982; Tiessen and Moir, 2008
soil physical traits		
particle fractions, S_{Pf}	pipette analysis after dispersion	Blume et al., 2011
bulk density, S_{BD}	soil cores	Blume et al. 2011
penetration resistance, S_{PR}	penetrometer	Sun et al., 2012
macropore density, S_{md}		Gaiser et al., 2012

The assessment of functional relationships between plant functional traits and soil biological traits is difficult and not well established in grassland agriculture. However, several studies indicate that management has an impact on soil fauna (Bardgett and Cook, 1998; Batary et al., 2012). Bardgett and Cook (1998) report that intensively managed systems tend to promote low diversity while lower input systems conserve diversity. They further report (Bardgett and Cook, 1998): “It is also evident that high input systems favour bacterial-pathways of decomposition, dominated by labile substrates and opportunistic, bacterial-feeding fauna. In contrast, low-input systems favour fungal-pathways with a more heterogeneous habitat and resource leading to domination by more persistent fungal- feeding fauna”.

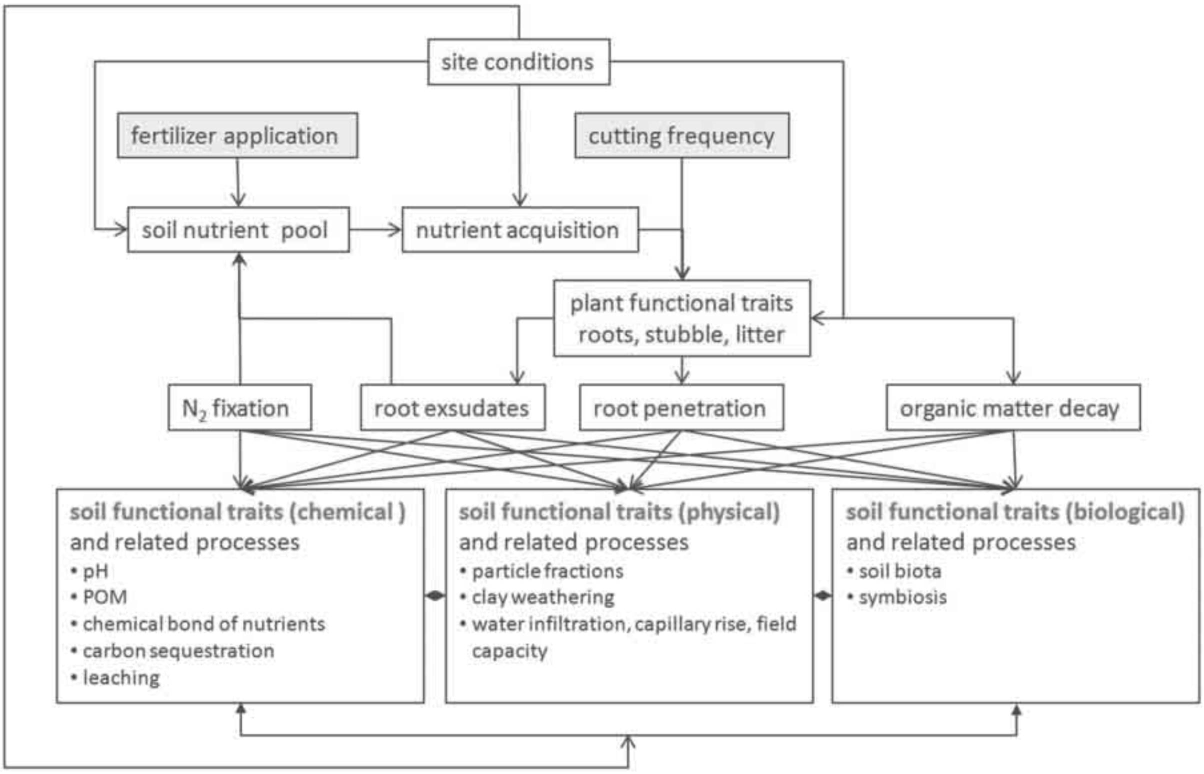

Figure 3: Relationships between functional traits and processes in soil as affected by cutting frequency and fertilization. The following processes are considered as most relevant, (i) the release of exsudates from roots influencing soil pH and availability of nutrients (mainly P), (ii) root penetration into the soil modifying pore volume, macropore and bulk density as well as water infiltration and surface runoff, (iii) decomposition of soil organic matter strongly determining soil biota and nutrient turnover, (iv) symbiotic fixation of atmospheric N_2.

Conclusions

In this presentation we tried to highlight some functional relationships between organisms and biotic and abiotic environmental conditions on grassland with respect to the ES provided. Since the “functional approach” has developed in ecology, grassland science in agriculture has rarely considered the theory and also not often conducted respective experiments. However, it is clear that plant functions ever have been in the centre of agronomic science, but the link to properties, processes, functions and services *sensu* MEA are still less developed. We therefore vote for a strong interdisciplinary research, where all disciplines that can contribute to a better understanding of functions in the entire system, get more involved. It is interesting to see how far such interdisciplinary research has already developed elsewhere. For instance, ecologists and soil scientists worked out research approaches for studies where remote sensing and geographic information systems are used to detect properties of plant communities and soil, allowing the identification of traits that are linked to processes and ES (Barrios, 2007; Wenzel, 2013). From decades long remote sensing research it becomes clear, that such links can only be provided if functionalities are understood that explain the role of organisms in a mechanistic rather than in an empirical way.
Moreover, a transition of the functional trait approach to soil and animal science requires more attention. The term ‘soil functional trait’ is rarely used although many soil-plant interactions can precisely be addressed. Nearly no attention has the term “animal traits” received in relation to functional ecology and grassland science. This is surprising as the grazing animal is an inherent part of the grassland system. We can, for instance, imagine that different func-

tional traits of mouth and hoof of grazers on the one hand as well as grazing preferences and sward damage on the other are interrelated. The key question is if we can be successful in predicting organisms' interaction and performance in the very complex environment of grassland based on an approach that follows functional ecology.

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