CENTENARY SYMPOSIUM SPECIAL FEATURE

How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services

Sandra Lavorel[1]* and Karl Grigulis[2]

[1]*Laboratoire d'Ecologie Alpine, UMR 5553 CNRS Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France; and [2]Station Alpine Joseph Fourier, UMS 3370 CNRS Université Joseph Fourier, BP 53, 38041 Grenoble Cedex 9, France*

Summary

1. Ecosystem services (ES) lie at the core of the interactions among humans and ecosystems. Fundamental understanding of the ecological mechanisms underlying the simultaneous provision of multiple ES has been lagging behind policy and management needs and stands out as a research priority. In this paper, we focus on interactions between ES resulting from fundamental functional mechanisms.

2. Plant diversity contributes significantly to the delivery of ES. Specifically, functional composition strongly determines different ecosystem properties and services. Knowledge on associations and trade-offs among different plant traits is well established, but the consequences for ecosystem functioning and the resulting ability for ecosystems to provide multiple services have only started to be explored. We present a conceptual framework linking environmental change to changes in ecosystem functioning and to changes in ES through plant traits. We explicitly consider the leaf economics and size axes of plant functional variation, and how their responses to key environmental variables are expected to scale-up to ecosystem properties and ES.

3. The framework was tested using a structural equation modelling formalism to understand the trait-based mechanisms driving trade-offs in ES in mountain grasslands. Variations along the leaf economics spectrum (LES) towards more exploitative strategies in response to increasing fertility led to a combined increase in several ES valued by local stakeholders, including agronomic value, cultural value and soil water retention. Surprisingly, and contrary to published hypotheses, soil carbon sequestration in the studied subalpine system did not increase at lower fertility which was associated with more conservative plant strategies. Independent variation in LES and height provided alternative pathways to biomass production.

4. *Synthesis*: A trait-based framework can support the understanding and aid the management of multiple ES. We recommend testing this framework in a variety of contexts and at larger scales, using additional trait axes such as wood density or seed size.

Key-words: biodiversity effects, ecological intensification of agriculture, fertility, leaf economics spectrum, mountain grassland, multifunctionality, plant size, plant–soil (below-ground) interactions, secondary succession, structural equation model

Introduction

Ecosystem services (ES) lie at the core of the interactions among humans and ecosystems (Daily *et al.* 1997; Kareiva *et al.* 2007; Turner, Lambin & Reenberg 2007). Recent assessments including the Millennium Ecosystem Assessment and follow-up reviews have emphasized the need for ecosystem management and policy decisions to focus on multiple ES (Foley *et al.* 2005; Bennett & Balvanera 2007; Carpenter *et al.* 2009) and therefore on identifying trade-offs and synergies among services and their consequences for decisions. When based on ecological mechanisms, such trade-offs pose hard constraints to human enterprise, such as the ability for intensive production without compromising natural resources (Bennett & Balvanera 2007), while synergies offer opportunities for multiple benefits, such as pollination and conservation

*Correspondence author. E-mail: sandra.lavorel@ujf-grenoble.fr

of biodiversity of high cultural value (Hodgson *et al.* 2010). The fundamental understanding of ecological mechanisms underlying trade-offs and synergies among services is thus an outstanding priority (Bennett, Peterson & Gordon 2009; Nicholson *et al.* 2009). The existence of hard trade-offs in life has long been known to ecologists, reflecting basic principles of mass and energy conservation (e.g. Grime 1977, Chapin 1980, Southwood 1988, Niklas & Enquist 2001). Incorporating them into ecosystem service science is therefore a prerequisite for sustainable management and policy.

The number of case studies investigating patterns of provision of multiple ES has been steadily increasing (e.g. Schröter *et al.* 2005; Gimona & van der Horst 2007; Nelson *et al.* 2008; Reyers *et al.* 2009; Raudsepp-Hearne, Peterson & Bennett 2010). However, such studies have thus far mostly described spatial co-occurrence among services and in some instances between multiple ES and biodiversity. Observed trade-offs and synergies vary greatly across systems and scales. For instance, in Quebec, out of the total of 12 ES studied using the Millennium Ecosystem Assessment framework (2005), provisioning services traded-off with almost all regulating and cultural services, while all regulating services were positively correlated among each other (Raudsepp-Hearne, Peterson & Bennett 2010). In South Africa, low levels of congruence were observed between five different regulating services (surface water supply, water flow regulation, carbon storage, soil accumulation and soil retention; Egoh *et al.* 2008). Finally, relationships among ES and between ES and biodiversity (e.g. species number) differ across areas even within a region (Britain) and appear sensitive to scale (Anderson *et al.* 2009). A mechanistic understanding of such a variability of relationships is thus required.

Bennett, Peterson & Gordon (2009) suggested two possible causes for trade-offs (and synergies) among ES: different ES responding to the same driver of change or direct interactions between ES. Research on the role of biodiversity for the provision of multiple ES would be expected to address such direct interactions. However, the contribution of biodiversity to several simultaneous ecosystem functions has rarely been investigated (Reiss *et al.* 2009), and only a few recent studies have demonstrated that increasing numbers of species are required to sustain levels in increasing numbers of ecosystem functions (Hector & Bagchi 2007; Gamfeldt, Hillebrand & Jonsson 2008; Zavaleta *et al.* 2010; Isbell *et al.* 2011). In this paper, rather than focussing on the mechanisms associated with species richness effects, we take a novel approach that addresses direct interactions between ES by concentrating on well-known functional trade-offs.

Functional traits have been identified as strong candidates to quantify ecosystem service delivery given their effects on underlying ecosystem processes (Kremen 2005; De Chazal *et al.* 2008; De Bello *et al.* 2010; Díaz *et al.* 2011), and there is indeed growing evidence for their relevance (Díaz *et al.* 2007a; Suding & Goldstein 2008; Garnier & Navas 2011; Pakeman 2011 – and see below '*Ecosystem processes*'). Based on this background, Lavorel *et al.* (2011) showed that it is possible to establish models of ES delivery that explicitly incorporate trait responses to environmental and management drivers and trait

effects on ecosystem properties (i.e. ecosystem structure and processes – see Lamarque, Quétier & Lavorel 2011a) underlying ES provision. These analyses further suggested that trade-offs among single modelled ES may be related to trade-offs among plant functional traits, and conversely that independence among traits such as leaf structural and chemical traits on the one hand, and plant height on the other, allowed for independence among associated ES. Thus, we believe that combining the increasing knowledge on associations and trade-offs among plant traits as captured by plant strategy schemes (Grime 1977, Westoby 1998) and trait spectra analyses (Díaz *et al.* 2004; Wright *et al.* 2004; Chave *et al.* 2009; Freschet *et al.* 2010a) with the understanding of relationships of ES to traits through trait–ecosystem functioning relationships should strongly advance the understanding of ES synergies and trade-offs.

In this paper, we propose a conceptual framework that scales-up from relationships among plant traits to ecosystem properties and ES and which can be used to guide the understanding and the management of multiple ES. We implement this framework using the structural equation modelling formalism and illustrate it using a comprehensive data set quantifying ecosystem properties underlying key ES delivered by mountain grasslands (Lavorel *et al.* 2011).

The framework

The quantification of ES requires identifying those measurable ecosystem properties that are identified by stakeholders, including scientific experts, as contributing to each ES (Haines-Young & Potschin 2010). ES quantification thus relies on identifying and quantifying those abiotic components that determine ecosystem properties relevant to a given ES (Díaz *et al.* 2007a,b; Lamarque, Quétier & Lavorel 2011a). The conceptual framework thus proposes to build from trait relationships at the individual plant level to ecosystem properties and ES (Fig. 1). It consists of three successive steps: (i) the identification of trade-offs in plant traits, (ii) the scaling-up of these trait trade-offs to trade-offs in ecosystem properties and (iii) the translation of these functional trade-offs into hypotheses on trade-offs and synergies among ES. Below, we detail the rationale for each of these steps, based on fundamental functional ecological knowledge.

PLANT TRAITS AND PLANT FUNCTION

We assume at least two dimensions in plant function – although the framework could be extended to include more dimensions (see Westoby *et al.* 2002). These two dimensions related to the so-called leaf (Wright *et al.* 2004) or plant economics spectrum (Freschet *et al.* 2010a), and to a size axis, most commonly represented by plant height (Westoby *et al.* 2002).

The leaf economics spectrum (LES; Wright *et al.* 2004; see also Díaz *et al.* 2004) refers to the continuous variation of leaf traits from thin, nitrogen-rich, short-lived leaves with high photosynthetic rates, also referred to as the exploitative
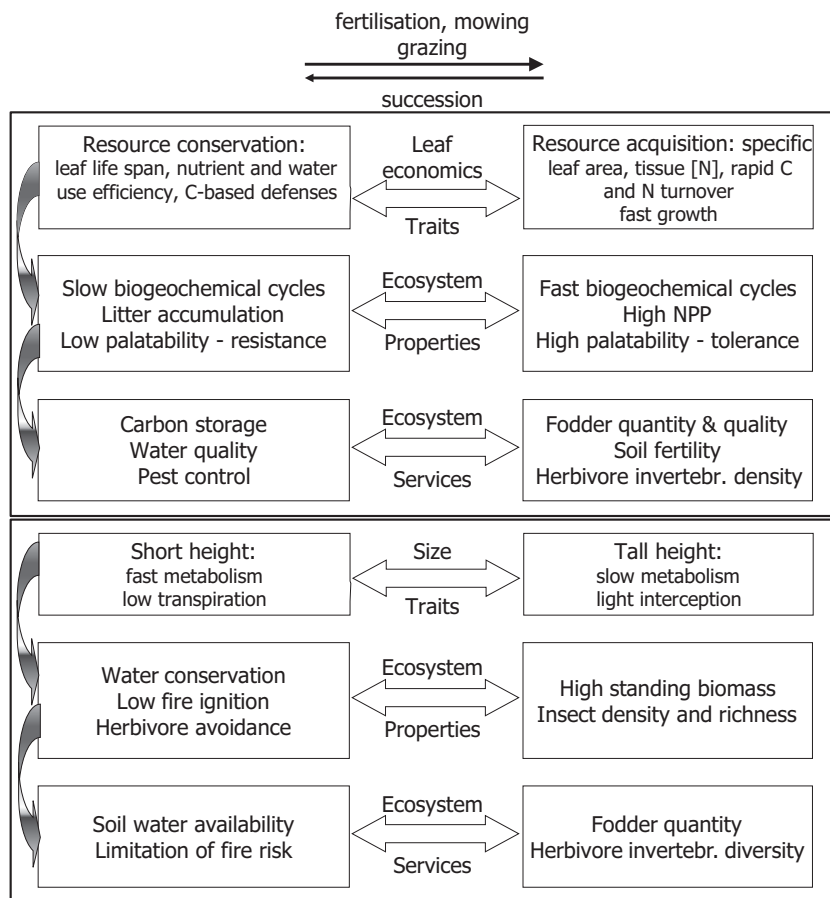
Fig. 1. Conceptual model of the scaling of trade-offs between leaf economic spectrum (upper panel) and size (lower panel) traits to ecosystem properties and ecosystem services for grasslands along gradients of management intensity (and especially fertility) or of secondary succession.

strategy (*sensu* Grime 1977), to thicker, more fibrous, nitrogen-poor, longer-lived leaves with lower photosynthetic rates, also referred to as the conservative strategy (Fig. 1, Trait level). Overall, the LES is structured by traits associated with metabolic, carbon and nutrient turnover rates (Reich, Walters & Ellsworth 1997). The robustness of the LES has been demonstrated from local to global scales. Recently, the applicability of this spectrum to other organs has been investigated, demonstrating plant-level co-ordination in resource economics (Freschet *et al.* 2010a; Laughlin *et al.* 2010), although relationships among plant and root traits are not confirmed generically (Craine *et al.* 2005; Hummel *et al.* 2006).

The plant size axis has been recognized as a key dimension of plant strategies (Grime 1977; Westoby *et al.* 2002; Díaz *et al.* 2004; Moles *et al.* 2009). Plant height is an important component of plant life history (Moles & Leishman 2008) and affects a plants' ability to capture light (Westoby *et al.* 2002). Given the relationship with biomass, height influences metabolic rate (Enquist, Brown & West 1998), but, apart from climate, relationships between plant height and environmental factors have not been described generically (Moles *et al.* 2009). Greater height comes at a mechanical cost for maintaining stem support tissues (because of respiration), decreasing risk of breakage and lifting water to distant leaves (Westoby *et al.* 2002). Trade-offs between size and other plant traits have not

yet been established globally, but there is strong evidence for independence between the leaf (or plant) economics axis and the plant height axis (Díaz *et al.* 2004).

FROM PLANT TRAITS TO ECOSYSTEM PROPERTIES

The two plant trait axes, leaf economics and size, have been related to a series of ecosystem properties associated with biogeochemical cycling and with resource flow through food webs. We assume, based on the recent accumulation of concepts and evidence (Suding *et al.* 2008; Suding & Goldstein 2008; Garnier & Navas 2011), that ecosystem properties can be related to plant traits using semi-mechanistic models. These models are based on the premise that plant traits scale-up to ecosystem functioning through community functional structure, that is the range and relative abundances of trait values present in plant communities (Díaz & Cabido 2001). Community functional structure can be quantified using a variety of metrics. Community-weighted mean (CWM) traits represent the average trait value per unit of biomass within a community (Garnier *et al.* 2004; Violle *et al.* 2007), and the biomass ratio hypothesis (Grime 1998) implies that they should be strong predictors of vegetation effects on biogeochemical processes (see also Lavorel & Garnier 2002). Effects of community-level plant functional traits have indeed been confirmed for

above-ground net primary productivity (ANPP, Mokany, Ash & Roxburgh 2008, and specific ANPP, SANPP, Vile, Shipley & Garnier 2006), litter decomposition under field (Garnier *et al.* 2004) and controlled (Fortunel *et al.* 2009) conditions, digestibility (Pontes Da Silva *et al.* 2007), nitrification (Laughlin 2011), soil moisture (Mokany, Ash & Roxburgh 2008) and water uptake (Gross *et al.* 2008). The effects of functional divergence; the expected variance in trait values across two random samples of equal biomass within a community (Lepš *et al.* 2006), have been harder to demonstrate (Díaz *et al.* 2007a; Mokany, Ash & Roxburgh 2008; Laughlin 2011; but see Schumacher & Roscher 2009), and therefore their incorporation is not detailed in this first presentation of the framework.

Based on the evidence for effects of plant traits on ecosystem properties, we now develop predictions on how trade-offs along key axes of plant functional variation should scale-up to trade-offs in ecosystem properties.

Leaf/plant economics axis: Based on the relevance of leaf traits pertaining to the LES, which extends from the whole plant to ecosystem properties associated with biogeochemistry (Garnier & Navas 2011; see also Wardle *et al.* 2004; Orwin *et al.* 2010; Freschet *et al.* 2010b), we expect the leaf/plant economics axis to scale-up to a trade-off between ecosystem properties associated with fast turnover – productivity (and specifically SANPP), rapid litter decomposition, high N availability and turnover, high digestibility and palatability to herbivores – and ecosystem properties associated with slow turnover – litter accumulation, resistance to herbivory and soil C accumulation (Fig. 1, EP level 2). Garnier *et al.* (2004) suggested that the concomitant variations during secondary succession of shifts in plant nutrient economies (from more exploitative to more conservative) and of processes associated with carbon and nutrient turnover (decreasing SANPP and decomposition and increasing soil C pools) reflected the scaling-up from individual plant traits to key ecosystem functions. Furthermore, Bardgett & Wardle (2003) and De Deyn, Cornelissen & Bardgett (2008) have suggested that trait trade-offs along succession or other management gradients (fertility and grazing) should result in feedbacks to ecosystem functioning through plant–soil interactions. One key mechanism underlying such a systemic effect is related to the quality of organic matter, determined by leaf/plant economics traits, which determines energy and nutrient sources for soil biota (Wardle *et al.* 2004). As the quality of plant material is important to both decomposability and herbivory (Grime *et al.* 1996; Bardgett & Wardle 2003), cascading effects from plant traits to ecosystems also apply to herbivory. Based on studies of effects of specific traits on herbivory by vertebrates (Cingolani, Posse & Collantes 2005; Lloyd *et al.* 2010) and invertebrates (Pérez-Harguindeguy *et al.* 2003; Andrew & Hughes 2005), one may expect the LES to underlie the trade-off between resistance (associated with the conservative end of the LES spectrum at low resource availability) and tolerance (associated with the exploitative end of the LES spectrum at higher resource availability (Coley, Bryant & Chapin 1985; Herms & Mattson 1992)). However, the effects of traits on palatability across tro-

phic levels remain debated. While variations in palatability along secondary succession have been inferred from patterns of community-level LES (Mason *et al.* 2011), LES effects on herbivore insect density and/or diversity along succession or other management gradients have not been directly tested to our knowledge. Only one study has directly analysed trait effects on insect density (leaf toughness; Peeters, Sanson & Read 2007), and a previous study has suggested that palatability to generalist herbivores may not be relevant to actual insect diversity (Lepš, Novotný & Basset 2001). Furthermore, plant diversity manipulation experiments have identified effects on insect density and/or diversity of particular functional groups, especially legumes (Scherber *et al.* 2006), rather than of specific traits.

Size axis: The significance of the size axis for ecosystem functioning has received surprisingly less attention than the LES. The basic tenet of metabolic theory is that an organism's size is related to metabolic activity (Enquist, Brown & West 1998), and therefore, metabolism in plants can scale-up to ecosystem functions such as annual biomass production or respiration (Enquist *et al.* 2003, 2007). Under the metabolic hypothesis, we would expect relatively slower metabolism in taller plants and therefore slower biogeochemical processes and greater carbon, nutrient and water retention. Furthermore, considering that competition for light results in mixed size communities, especially in tall vegetation (Falster & Westoby 2003), we might expect the size axis to translate into a gradient of complexity in vegetation structure (Pöyry *et al.* 2006). This gradient would drive a trade-off between high total standing biomass in tall and dense communities (Falster *et al.* 2011), and short vegetation, associated with water conservation owing to low transpiration flows (Schwinning & Ehleringer 2001) and low fire ignition probability owing to fuel limitation (Lavorel & Garnier 2002). Given the influence of vegetation height and complexity on secondary consumers (Pöyry *et al.* 2006; Moles *et al.* 2009), the gradient would feed a second trade-off between high insect herbivore density and species richness in tall vegetation offering diverse niches (Scherber *et al.* 2010) and limited insect communities in short vegetation characterized by a herbivory avoidance strategy (Díaz *et al.* 2007b). However, predicting the size axis may be complicated by interactions between LES and size effects. For example, Reich (2001) suggested that plant metabolic rate is correlated with N content, rather than size. This would imply that, if the height and LES are independent, biogeochemical processes should not vary predictably along the height axis, but there is currently insufficient evidence to answer this question.

FROM ECOSYSTEM PROPERTIES TO ECOSYSTEM SERVICES

As a final step, based on the mapping of ecosystem properties to ES (Quijas, Schmid & Balvanera 2010; Lavorel *et al.* 2011), we hypothesize trade-offs will occur between bundles of ES (*sensu* Raudsepp-Hearne, Peterson & Bennett 2010) as a result of trade-offs among ecosystem properties. In the case of grass-

lands, we expect the leaf/plant resource economics axis to translate into a trade-off between one bundle consisting of fodder production (quantity and quality), maintenance of soil fertility and herbivore insect abundance, and a second bundle consisting of soil carbon storage, water quality (owing to nitrogen retention), and pest control (resistance to herbivores and pathogens; Fig. 1, ES level). In the same way, we expect the plant height axis to translate into a trade-off among a bundle consisting of fodder production and conservation of herbivore insect diversity and a second bundle consisting of soil water availability and, in regions where this is relevant, limitation of fire risk.

In the following section, we apply this framework for scaling-up plant traits to ecosystem service trade-offs using structural equation modelling of a large data set collected in managed grasslands in the Central French Alps for a sample of ecosystem properties relevant to locally important ES (Lavorel *et al.* 2011).

Materials and methods

STUDY SITE AND FIELD DATA SET

We collected extensive data on environmental factors (topography and soil properties), vegetation composition, plant traits and ecosystem properties for a set of 63 grassland plots at the Lautaret study site (45°03′N, 6°24′E). The site is located in the Central French Alps on the south-facing slopes of Villar d'Arène and covers 13 km² with elevation ranging from 1552 to 2442 m a.s.l. (detailed site description by Quétier, Thébault & Lavorel 2007). It is managed by low- to medium-intensity livestock rearing, involving a variable combination of organic fertilization at low doses (eight tons of manure per hectare every 2–3 years), mowing and grazing at low intensity (< 2 days of livestock units per hectare per year). In total, eight land-use types were identified: three on previously cultivated terraces (currently fertilized and mown, mown but not fertilized, or unmown and grazed in spring and autumn), three on permanent grasslands with no history of cultivation and a multicentury history of mowing (currently mown, unmown and summer-grazed, and neither mown nor grazed grasslands – dominated by the large perennial grass *Festuca paniculata*), one on never mown summer grasslands (> 2000 m) and one on steep (> 30°) grazed slopes (representing only 6% of the area). The terraces, located up to 1900 m, form a gradient of sharply decreasing nitrogen and phosphorus fertility associated with decreasing plant species and functional diversity, whereas permanent grasslands

dominated by *F. paniculata*, located from 1800 to 2100 m, have intermediate nitrogen fertility, mainly as ammonium, and form a second gradient of decreasing phosphorus fertility associated with a dramatic decrease in plant species and functional diversity (Quétier, Thébault & Lavorel 2007; Robson *et al.* 2007; Robson *et al.* 2010). Summer grasslands have intermediate nitrogen and phosphorus fertility and high plant diversity. Our previous analyses of this data set demonstrated that land-use effects on plant traits and ecosystem properties were appropriately captured by a set of soil (including fertility indices and soil water–holding capacity) and topographic (especially altitude) variables, owing to the distribution of land uses through the landscape and their feedbacks to soil properties (see Lavorel *et al.* 2011).

Methods for data collection are described in detail in Lavorel *et al.* (2011). Briefly, vegetation, plant functional trait, ecosystem and environmental data (Table 1) were collected on 30 × 30 m permanent plots stratified by land use (eight categories), landscape sector (four sectors defined based on local toponymy and representing homogenous topography and distance to the village) and altitude within each of these. We used standardized protocols to determine species relative biomass (Lavorel *et al.* 2008), plant traits (Cornelissen *et al.* 2003), and abiotic and ecosystem properties (Garnier *et al.* 2007), and topography was characterized using a 10-m resolution digital elevation model. CWM trait values were calculated as the mean across species of their trait value weighted by the species relative abundance (Garnier *et al.* 2004).

STRUCTURAL EQUATION MODELLING

Ecosystems are networks made up of multiple components and of the interactions between these components. SEM analyses are a more generalized form of several types of statistical analyses, including regression and path analysis, and are well suited to the analysis of such networks. In contrast to other statistical methods, SEM can test for the significance of the overall model structure – i.e. the relationships between the components of an ecosystem – as well as of the specific parameters of the model, e.g. the strength or direction of the interactions between the components (Grace 2006). This unique statistical method enables scientists to use field data to test hypotheses about causal pathways of ecosystem functioning (Shipley 2000). It has recently been gaining considerable currency for the testing of trade-offs among plant traits (Vile, Shipley & Garnier 2006; Ordoñez *et al.* 2009) or of effects of plant traits on ecosystem functioning (Laughlin 2011; Minden & Kleyer 2011). In this study, we used SEM to assess the appropriateness of a hypothetical causal model of the ecosystem functioning of a subalpine grassland, scaling-up from plant traits to ecosystem attributes (Fig. 2). SEM models were

Table 1. List of available data by level of organization. Detailed methods for measurements of environmental parameters are presented in Garnier *et al.* (2007) and Lavorel *et al.* (2011). Field capacity was calculated based on texture and organic matter content. Nitrogen and Phosphorus Nutrition indices are indicators of nutrient availability for plant growth. Community-weighted means (CWM) were used in analyses for plant traits. Green biomass was assessed at its peak and was a proxy for annual production given that in an alpine environment initial biomass after snow melt is zero. Green biomass and standing litter were estimated using a calibrated visual method (Lavorel *et al.* 2008). Digestibility was estimated using infrared spectrometry (Pontes Da Silva *et al.* 2007)

| Environment	Plant traits (CWM)	Ecosystem properties
Altitude	Leaf dry matter content (CWM_LDMC)	Total soil C (C)
Soil P Olsen	Leaf nitrogen concentration (CWM_LNC)	Total soil N (N)
Field capacity (WHC)	Leaf phosphorus concentration (CWM_LPC)	Green biomass
Nitrogen nutrition index (NNI)	Vegetative height (CWM_VgHt)	Standing litter (litter)
Phosphorus nutrition index (PNI)		Digestibility (DIGEST)
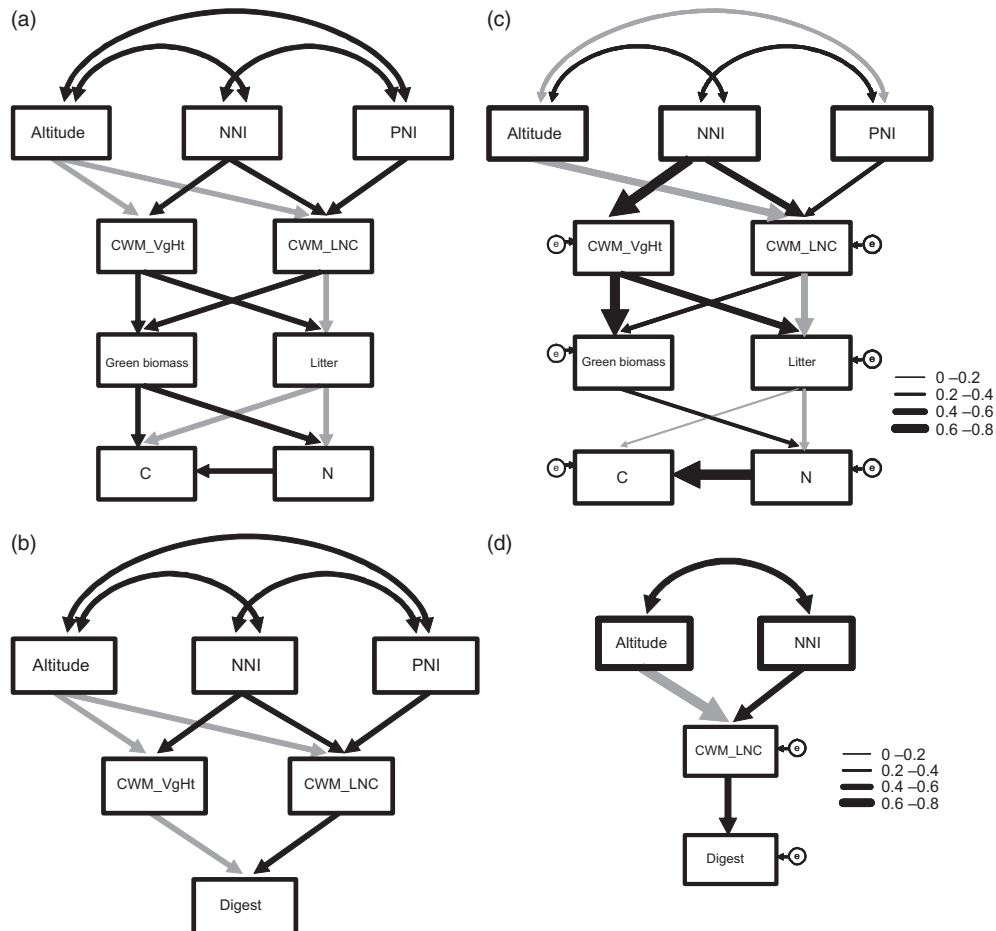
Fig. 2. Structural equation models. Initial hypothesized models for (a) ecosystem properties associated with biogeochemical cycling and (b) digestibility. Final models for (c) ecosystem properties associated with biogeochemical cycling (63 plots) and (d) digestibility (21 plots). Each of the models links successively the environmental parameter level (exogenous variables) to community-weighted mean traits and to ecosystem properties (endogenous variables). One-sided arrows represent regression weights, while two-sided arrows represent covariances or unanalysed associations. In the final models, error terms, e_i, are specified for endogenous variables, only significant regression weights between variables are shown, black regression weights indicate hypothesized and actual positive associations, while grey ones indicate hypothesized and actual negative associations, and the thickness of the regression weights represents the relative value range of the standardized regression path coefficient as indicated in the legend on the figure (exact values for these coefficients are found in Tables 2 and 3). All abbreviations are defined in Table 1.

implemented using the software Amos 16.0.1 (Amos Development Corporation, Spring House, PA, USA).

SEM is a confirmatory statistical method with *a priori* expert knowledge of the functioning of an ecosystem being used as a guide in the development of an initial conceptual model. This initial model is tested against the covariance matrix of the actual data, and the model is evaluated on the basis of whether or not the data support it. On the basis of a chi-square test of fit, a significant *P* value for the overall model indicates that the covariance structure of the data is significantly different from that of the model structure and that the model does not adequately represent the relationships in the data. A non-significant *P* value indicates that the model structure and that of the data do not differ significantly and thus, that the model is a plausible representation of the data. Other tests of the goodness-of-fit of SEM models are available, with three of these also being reported in this study [chi-square/degrees of freedom (CMIN/d.f.), comparative fit index (CFI) and the root mean square error of approximation (RMSEA)]. Models supporting the data structure have a CMIN/d.f. < 2, CFI > 0.9 and RMSEA < 0.05 (Byrne 2010). The regression path coefficients (regression weights) and correlations between the various parameters in the model are also tested using *P* statistics, with these

standardized regression path coefficients (standardized to provide a comparable metric for comparisons between all of the variables), indicating the relative strength and influence of each of the relationships in the model (interpreted as 'each one standard deviation increase in one parameter produces an *x* standard deviation change in the other parameter'). By convention, standardized regression path coefficients > 0.8 are considered as having a large degree of effect, 0.5 moderate and < 0.2 small.

Most SEM software will make suggestions for improving model fit by removing non-significant pathways and potentially adding additional ones. While care must be taken to not stray from the concept of a hypothesis confirmatory approach central to SEM and follow these suggestions blindly (possibly producing a highly significant model so well shaped to one particular data set that it is unlikely to be generally applicable), in instances where a model would fit better with the additional of a covariance between two parameters, which also makes good theoretical sense, then the modification should be made (Shipley 2000; see e.g. Ordoñez *et al.* 2009). Once a biologically plausible model has been identified, the functioning of the ecosystem can be investigated by examining the strength and direction of the modelled relationships among the variables.

The available data for the model construction were divided into three levels of organization (Table 1). A complete data set of each of these parameters was available for 63 plots, except for digestibility for which data were available for only 21 plots. A separate modelling process was carried out for this EP.

In an attempt to reduce the complexity of the eventual SEM, a correlation analysis was carried out among the parameters within each of the environment and plant trait levels of organization so as to remove any variables highly correlated with others and reduce redundancy within these explanatory variables (see Appendix S1 in Supporting Information). The parameters retained for environment were altitude, nitrogen nutrition index (NNI) and phosphorus nutrition index (PNI). The parameters retained for plant traits were CWM_LNC and CWM_VgHt, which were representative of the LES and the size axis, respectively.

SPECIFICATION OF THE INITIAL HYPOTHETICAL MODEL

Based on the trait and ecosystem properties levels of the conceptual model (Fig. 1), and using prior knowledge of the functioning to the study ecosystem and relevant variables (Lavorel *et al.* 2011), an initial hypothesized or construct model (Grace 2006) was specified as a hierarchical model with environmental parameters influencing community trait parameters, and these then regulating ecosystem properties parameters associated with biogeochemical cycling (Fig. 2a). Environmental parameters were considered as exogenous variables – not dependent on other variables in the model, while the trait and ecosystem property parameters were considered as endogenous variables, modelled as being dependent on other variables in the model. Each of the endogenous variables in an SEM model has an included error term representing the uncertainty or inaccuracy of the measurement, while correlations are included among the exogenous variables. This model specifically addressed the scaling hypothesis and did therefore not consider feedbacks among hierarchical levels (e.g. from soil carbon and nitrogen pools to fertility). The satisfactory fit of such a model would indicate that direct effects from environmental parameters to traits and onwards to ecosystem properties are relevant to the functioning of the system, though not aiming to depict a full model of biogeochemical cycling.

For the links between environmental parameters and community traits, we hypothesized that increasing altitude reduces plant height and LNC via its multiple influences on climatic and abiotic parameters (increasing climatic stress and decreasing fertility). Increasing nitrogen availability to plants (NNI, Table 1) was hypothesized to increase both plant height and LNC (i.e. exploitative leaf economics strategies) by increasing available nitrogen. Phosphorus availability to plants (PNI, Table 1) was hypothesized to increase LNC by increasing fertility. For the links between plant trait and ecosystem property parameters, increasing plant height was hypothesized to lead to increased green biomass and increased litter through the input of greater amounts of plant material. Consistent with the hypothesized scaling from the LES to biogeochemical processes, increasing LNC was also hypothesized to result in ecosystem properties reflecting faster biogeochemical cycling and thus in increased green biomass production through increased ANPP, but reduced standing litter because of more decomposable leaves (high LNC correlated with low LDMC – Fortunel *et al.* 2009; Bakker, Carreño-Rocabado & Poorter 2011). As a result, we expected increasing soil N and C with increasing green biomass (increasing inputs of organic matter via decomposition

– De Deyn, Cornelissen & Bardgett 2008: as well as potential priming effects – Fontaine *et al.* 2007). Given our prior knowledge on the highly recalcitrant nature of litter at the site, especially for *F. paniculata* given its leaf toughness (Quétier, Thébault & Lavorel 2007) and the presence of allelopathic compounds (Viard-Crétat *et al.* 2009), we also hypothesized decreasing soil N and soil C with increasing standing litter (increased immobilization) rather than increasing soil C sequestration (as hypothesized by De Deyn, Cornelissen & Bardgett 2008). Finally, a stoichiometric relationship was hypothesized to exist between soil N and soil C (soil C/N ratios), with positively correlated soil C and N pools (Cleveland & Liptzin 2007).

A separate initial model was constructed for digestibility owing to the lower number of replicate plots available for this parameter. This model followed the same logic as the biogeochemical model, with digestibility being hypothesized to increase with increasing CWM_LNC (increasing nitrogen content increasing plant digestibility), and to decrease with increasing vegetative plant height (larger plants being more fibrous and thus harder to digest; Fig. 2b).

To sum up, we expected fertility, as driven by management and altitude, to determine two trade-off axes. First, we expected a trade-off between (i) exploitative plant strategies at higher fertility or lower altitudes, resulting in faster biogeochemical cycling and hence greater green biomass production, lower litter accumulation, higher carbon and nitrogen pools and higher digestibility and (ii) conservative plant strategies at lower fertility or higher altitudes resulting in the opposite biogeochemical properties (Fig. 1, upper panel). Second, we expected a trade-off between taller plants at higher fertility or lower altitudes, resulting in greater biomass and litter accumulation by simple scaling of size and opposite properties at lower fertility or higher altitudes (Fig. 1, lower panel). Thus, we expected two alternative pathways determining greater grass production at higher fertility or lower altitudes, while the net effects for litter accumulation and hence carbon pools were uncertain owing to the coupling of positive (height) and negative (LES) effects.

TRANSLATION FROM ECOSYSTEM PROPERTIES TO ECOSYSTEM SERVICES

At the Lautaret site, several important ES and their indicators in terms of ecosystem properties were identified with local stakeholders (Quétier *et al.* 2010; Lamarque *et al.* 2011b). To summarize (see also Lavorel *et al.* 2011), given the ecosystem properties quantified here, grassland agronomic value was positively related to green biomass production and digestibility. Climate regulation was (superficially) assumed to be related to soil carbon pools. Cultural value was related negatively to litter accumulation, as well as positively to plant species diversity (see Lavorel *et al.* 2011 for details). Orthopterae diversity, measured in an ancillary study (see Appendix S2), was considered as an additional positive indicator of cultural value. These qualitative relationships were used to translate variations in ecosystem properties along the LES and size axes into expected variations in ES.

Results

BIOGEOCHEMICAL MODEL

The field data supported the hypothesized full model ($\chi^2 = 27.424$, d.f. = 19, $P = 0.095$, CMIN/d.f. = 1.443, CFI = 0.971, RMSEA = 0.085). The removal of the non-significant model pathways from altitude to vegetative height

Table 2. Biogeochemical model – standardized regression path coefficients and *P* values based on the critical ratio for regression weight (*z*) for each of the relationships in the: (a) hypothesized full model, (b) final model after deletion of non-significant regression paths

Explanatory variable	Response variable	(a) Hypothesis model		(b) Final model	
		Estimate	*P* value	Estimate	*P* value
NNI	CWM_VgHt	0.595	< 0.001	0.628	< 0.001
Altitude	CWM_LNC	−0.539	< 0.001	−0.539	< 0.001
NNI	CWM_LNC	0.493	< 0.001	0.493	< 0.001
PNI	CWM_LNC	0.231	0.017	0.231	0.017
Altitude	CWM_VgHt	0.119	0.244	–	–
CWM_VgHt	Green biomass	0.713	< 0.001	0.702	< 0.001
CWM_VgHt	Litter	0.537	< 0.001	0.546	< 0.001
CWM_LNC	Green biomass	0.307	< 0.001	0.302	< 0.001
CWM_LNC	Litter	−0.471	< 0.001	−0.479	< 0.001
Green biomass	N	0.343	0.004	0.347	0.003
Litter	N	−0.318	0.007	−0.312	0.008
Green biomass	C	−0.07	0.365	–	–
Litter	C	−0.15	0.049	−0.172	0.019
N	C	0.795	< 0.001	0.771	< 0.001

All abbreviations are defined in Table 1.

and from green biomass to soil C (Table 2a) slightly improved the fit of the model (χ^2 = 29.59, d.f. = 21, χ^2 *P* = 0.101, CMIN/d.f. = 1.409, CFI = 0.971, RMSEA = 0.081). This reduced model was adopted as the final plausible representation of the measured carbon- and nitrogen-cycling-related parameters in the Lautaret grasslands (Fig. 2c). Standardized regression path coefficients for this final model are presented in Table 2b. Community plant size (represented by CWM_VgHt) was very strongly and positively regulated by site fertility (nitrogen availability, NNI). The leaf nitrogen concentration in the community (represented by CWM_LNC) increased strongly with increasing site fertility (NNI, and to a lesser extent PNI) but was also strongly reduced with increasing altitude in response to increasing climatic severity resulting in the production of more fibrous, nitrogen-poor leaves. This increased community plant size directly and positively affected the amount of green biomass (strong effect) and litter (moderate effect). Increased leaf nitrogen concentration led to a moderate increase in the amount of green biomass present, but strongly reduced the amounts of litter present, probably due to the more easily and rapidly decom-

posable nature of high LNC, less fibrous leaves. Increased green biomass resulted in increasing pools of soil nitrogen, with cascading positive effects on soil carbon. Increased quantities of standing litter, however, only moderately decreased N pools and had weak negative effects on C pools.

DIGESTIBILITY MODEL

The field data also showed a good fit with the initial hypothesized digestibility model (χ^2 = 7.188, d.f. = 5, *P* = 0.207; CMIN/d.f. = 1.438, CFI = 0.925, RMSEA = 0.148). Table 3a shows the standardized regression path coefficients and significance for each of the model coefficients for the initial digestibility model.

The non-significant pathways from PNI to CWM_LNC, from altitude to CWM_VgHt and from CWM_VgHt to digestibility were removed from the initial model, together with the resulting dead-end variables (environmental or plant trait parameters with no significant links to ecosystem-level parameters after the removal of the non-significant pathways), and this new digestibility model was re-analysed. These changes

Table 3. Digestibility model – standardized regression path coefficients and *P* values based on the critical ratio for regression weight (*z*) for each of the relationships in the: (a) hypothesized full model, (b) final model after deletion of non-significant regression paths

Explanatory variable	Response variable	(a) Hypothesis model		(b) Final model	
		Estimate	*P* value	Estimate	*P* value
NNI	CWM_LNC	0.658	0.005	0.589	0.002
PNI	CWM_LNC	−0.105	0.631	–	–
Altitude	CWM_LNC	−0.707	0.001	−0.652	< 0.001
NNI	CWM_VgHt	0.467	0.033	–	–
Altitude	CWM_VgHt	0.006	0.979	–	–
CWM_Vg Ht	DIGEST	−0.231	0.225	–	–
CWM_LNC	DIGEST	0.519	0.006	0.432	0.032

All abbreviations are defined in Table 1.

considerably improved the fit of the model ($\chi^2 = 1.981$, d.f. = 2, $P = 0.371$; CMIN/d.f. = 0.991, CFI = 1.00, RMSEA < 0.001), which was adopted as the final plausible representation of the regulation of digestibility in the Lautaret grasslands (Fig. 2d). The digestibility of vegetation was regulated primarily by CWM_LNC, with a strong positive relationship between leaf nitrogen concentration and the nutritional value of the vegetation (Table 3b). The regulation path of CWM_LNC by NNI and altitude was robust for the subset of 21 plots sampled for digestibility compared to the full set of 63 plots (comparison of regression paths and effects between Tables 2b and 3b).

Discussion

SCALING FROM PLANT TRAITS TRADE-OFFS TO TRADE-OFFS IN ECOSYSTEM PROPERTIES

We hypothesized that plant traits pertaining to the LES and size scale-up to ecosystem properties and that these relationships feed on to the variation of ecosystem properties along environmental gradients. These hypotheses were translated into a structural equation model of ecosystem properties relevant to biogeochemistry and digestibility in the Lautaret grasslands. The two final models for biogeochemistry and digestibility confirm our hypotheses that key environmental parameters (altitude and fertility) regulate the plant functional strategies in these grasslands (represented by plant vegetative height and leaf nitrogen concentration) and show how these differing plant functional strategies regulate the amounts and digestibility of green biomass, litter quantities and ultimately the pools of soil carbon and nitrogen. These results are conceptually consistent with the response-effect model, describing common plant trait responses to environmental variation and their effects on ecosystem functioning (Lavorel & Garnier 2002; Suding *et al.* 2008). Few studies have provided direct evidence for this model so far (Gross *et al.* 2008; Suding & Goldstein 2008; Fortunel *et al.* 2009; Klumpp & Soussana 2009; Pakeman 2011), and to our knowledge, only one study used a SEM formulation for a formal test of sequential effects from environmental parameters to community-level plant traits and to ecosystem properties (Minden & Kleyer 2011 – see also Laughlin 2011 for a model of nitrification and its' links to the LES axis). Finally, it is important to note that neither the response-effect model nor the SEM formulation presented here are intended as full depictions of ecosystem functioning, including important plant–soil feedbacks (Wardle *et al.* 2004; De Deyn, Cornelissen & Bardgett 2008). Instead, they provide tests of plausible representations of a set of causal relationships underlying observed patterns (Shipley 2000).

We further hypothesized that each of the LES and the plant size axis would scale to trade-offs among ecosystem properties. Trait variation in the Lautaret grasslands was driven by two correlated environmental gradients, altitude and fertility (assessed through N and P available to growth, NNI and PNI, respectively).

Based on preliminary data exploration, leaf nitrogen concentration was chosen as the trait representative of the LES, in preference to a multivariate LES axis (data not shown). Consistent with predictions, community LNC increased strongly with increasing site fertility (NNI, and to a lesser extent PNI; Garnier *et al.* 2007; Ordoñez *et al.* 2009), but decreased with increasing altitude, reflecting the increased dominance by species with more fibrous, nitrogen-poor leaves. The final SEM showed that, as expected based on the response-effect model (Lavorel & Garnier 2002), the LES scaled at the community level to a trade-off between production of more abundant, more digestible and more decomposable biomass (and hence less standing litter) in more fertile or lower altitude plots, and reduced biomass production, low digestibility but increased litter accumulation in less fertile or higher altitude plots. This scaling has been hypothesized to operate along secondary succession (Garnier *et al.* 2004) and/or fertility gradients (Bardgett & Wardle 2003), but empirical confirmation remains scarce (Vile, Shipley & Garnier 2006; Fortunel *et al.* 2009; Pakeman 2011; see also Bakker, Carreño-Rocabado & Poorter 2011; Minden & Kleyer 2011). The LES-based gradient of increasing biomass quantity and quality with increasing fertility further translated into a trade-off between greater nitrogen pools in more fertile plots (fertilized terraces, mown permanent grasslands and summer grasslands) and lower N pools in less fertile plots (unmown terraces and unmown permanent grasslands, as well as steep grazed slopes). Increased N pools with increasing biomass production under more fertile conditions likely reflected input of high-quality, nitrogen-rich organic plant material through rapid decomposition in more fertile plots (Quétier, Thébault & Lavorel 2007), as well as potentially direct fertilization effects for the terraces. As expected given the strong positive correlation between N and C pools, the same patterns were observed for carbon pools. Such responses were opposite to the prediction that carbon pools should increase with the shift to more conservative species strategies (Bardgett & Wardle 2003; Garnier *et al.* 2004; De Deyn, Cornelissen & Bardgett 2008). The decreases in C and N pools with increasing standing litter likely resulted from the retention and immobilization of C and N in recalcitrant (high C:N; presence of phenolics in the case of *F. paniculata* – Viard-Crétat *et al.* 2009), slowly decomposing standing litter, as well as from increased uptake of scarce labile N by soil microbes with high microbial C:N ratio, suggesting that fungi slowed C and N cycling (Robson *et al.* 2010).

Interestingly, the SEM revealed how community vegetative height was associated with an alternative functional path, resulting from the independence between the LES and plant height axes (Díaz *et al.* 2004; confirmed for dominant grasses at this site by Gross, Suding & Lavorel 2007). The tall and more productive communities were separated on the basis of the LES (represented by LNC) in terms of litter accumulation, which was low in fertilized and mown terraces that were dominated by species with an exploitative strategy (*Dactylis glomerata*, abundant legumes and large dicots), and high in permanent grasslands dominated by the very conservative (Gross, Suding & Lavorel 2007) poorly

decomposable, tall cespitous grass, *F. paniculata* and other abundant conservative species (Quétier, Thébault & Lavorel 2007). As a result, tall size could result in either high soil N pools in fertilized and mown terraces because of inputs of abundant good-quality material or in low N pools in *F. paniculata* grasslands because of sequestration in abundant litter (Robson *et al*. 2010). Taken together, these results also suggest that in these mountain grasslands biogeochemistry was indeed controlled by tissue N rather than by size (Reich 2001); this result is also supported by a multivariate analysis of community traits and ecosystem properties for an agricultural management gradient on the western coast of Scotland (Pakeman 2011).

TRANSLATION INTO ECOSYSTEM SERVICES TRADE-OFFS

We hypothesized that trade-offs among ecosystem properties underpinned by the LES and the plant size axis would scale to trade-offs among ES. Considering the above patterns of ecosystem properties, the response of agronomic value to altitude and fertility was complex and reflected the two alternative pathways for biomass production and their opposite consequences in terms of digestibility. Overall, the LES translated into a trade-off between high agronomic value in high-altitude summer grasslands with high-LNC species and in fertilized and mown terraces dominated by tall and exploitative species, and low agronomic value in lower unfertilized and unmown terraces dominated by short and conservative species, while agronomic value was intermediate in *F. paniculata* grasslands, which combined high productivity but low digestibility.

Contrary to recent hypotheses (De Deyn, Cornelissen & Bardgett 2008) and as discussed earlier, climate regulation through soil carbon sequestration decreased with decreasing fertility associated with more conservative strategies and poorer-quality plant material. It is important to note that those land uses considered as more fertile were relatively low to intermediate fertility as compared with intensively managed habitats, e.g. north-western European grasslands, and may thus not be considered as a representative of very fertile, high C and N turnover ecosystems with low carbon sequestration.

Litter accumulation, and as a consequence low plant species diversity (Quétier, Thébault & Lavorel 2007), underpinned decreasing cultural value with decreasing fertility and the associated dominance by conservative species. Orthopterae density and species diversity were assessed for a subset of 15 plots from terraces and permanent grasslands (Moretti *et al*. 2011). A SEM of this additional data revealed that while a satisfactory model could not be obtained for Orthopterae density, Orthopterae species richness was controlled negatively by altitude and green biomass, likely as a result of temperature effects (as greater biomass results in shadier, cooler microenvironments – see Unsicker *et al*. 2010; see Appendix S2). Given that biomass production was controlled primarily by vegetation height for this 15-plot subset (see Appendix S2), our hypothesis of increasing insect diversity along the size axis was rejected.

Finally, though data were insufficient (12 plots) for further investigation within the SEM framework, Gross *et al*. (2008) showed that, in more fertile grasslands, higher biomass production and greater community mean leaf area resulted in a slower loss of soil water through the growing season. Whereas in *F. paniculata* grasslands, where biomass production was also high, the negative effects of litter accumulation on rainfall penetration resulted in strong water deficit. This suggests that, in these grasslands, contrary to our hypothesis, soil water retention was controlled by the LES rather than by the size axis.

This analysis highlights that, in the Lautaret grasslands, the LES underpins a shift from high agronomic and high cultural values, higher carbon sequestration and soil water retention at higher fertility to low values for all these services at lower fertility.

For the set of ES examined in this study, the size axis was mainly relevant for providing alternative pathways to high biomass production through its independence in variation from the LES. However, because the LES strongly dominated ecosystem properties and combined with biomass to determine final ES levels, such as digestibility for agronomic value or litter accumulation for soil carbon sequestration, soil water retention and cultural value, and because taller size was associated with a highly conservative strategy in *F. paniculata*, the size axis did not provide any opportunity for the ES identified as important to local stakeholders. This conclusion may be moderated considering that stakeholders may value different components of the aggregate ES (agronomic and cultural value) differently depending on their objectives. For instance, in the face of increasing risk of drought, farmers may choose to emphasize fodder quantity rather than quality. Urban visitors may not consider litter accumulation as strongly as local stakeholders in their assessment of cultural value. Finally, services not considered in our current data set such as soil protection from erosion (Tasser & Tappeiner 2005) or resistance to woody encroachment (Albert *et al*. 2008) may be enhanced by large, tough-leaved, litter accumulating grasses such as *F. paniculata*.

FINAL REMARKS AND CONCLUSION

While there is unanimous recognition that ES assessments and management strategies should consider trade-offs and synergies among ES, insights into underlying mechanisms remain remarkably scarce. We proposed a novel framework that builds on extensive knowledge in key axes of variation of plant traits and on their consequences for ecosystem functioning to provide hypotheses on mechanisms underpinning or constraining the ability of ecosystems to provide multiple services. Such a framework, which scales-up from plant-level trade-offs, to trade-offs in ecosystem properties and ecosystem functioning, and trade-offs among ES can be implemented, among other possible methods, using a structural equation modelling formalism for testing with empirical data (see Minden & Kleyer 2011).

Using an extensive data set for subalpine grasslands from the Central French Alps, we demonstrated how such a

framework and methodology can be applied to yield insights into controls of ES trade-offs as a result of trade-offs and independence among plant traits. In our case study, the leaf⁄plant economics spectrum and its response to decreasing fertility underpinned a combined decrease in several ES valued by local stakeholders in agricultural terraces. At the same time in permanent grasslands dominated by *F. paniculata*, ES were determined through the alternative functional pathway of plant height, whereby decreased fertility after cessation of mowing resulted in intermediate agronomic value caused by high biomass production but low cultural value because of litter accumulation.

Trade-offs among ES may change depending on the scale of the assessment, including the effects on the breadth of ecological gradients and vegetation types considered, e.g. we did not consider shrublands or forests. Larger, regional-scale studies have highlighted strong trade-offs among production and regulation of cultural ES (e.g. Chan *et al.* 2006; Raudsepp-Hearne, Peterson & Bennett 2010), as well as synergies among a variety of regulation services (Egoh *et al.* 2008; Raudsepp-Hearne, Peterson & Bennett 2010). The analysis of such trade-offs needs to be refined with a trait-based approach like the one proposed here. For this purpose, the detailed framework would need to be expanded to consider other functional axes of variation, e.g. the wood density axis (Chave *et al.* 2009) for forests, or the seed size axis (Moles *et al.* 2007) for processes relevant to regeneration and associated ES such as stability in the face of disturbance (see Lavorel & Garnier 2002 for a discussion on fire), as well as little explored axes in root trait variation (Craine *et al.* 2005; Hummel *et al.* 2006). The plant size axis also requires further elucidation because on the one hand, it may reflect both a cause and a consequence of environmental variation, as in the case of light availability, and on the other hand, individual plant size is strongly determined by community interactions (Westoby *et al.* 2002; Falster & Westoby 2003). Finally, ES trade-off analyses based on an in-depth understanding of plant functional traits, their environmental responses and follow-on effects on ecosystem properties are required to support new thinking about multifunctional management (Zavaleta *et al.* 2010) and ecological intensification of agriculture (Doré *et al.* 2011).

Acknowledgements

References

Albert, C.H., Thuiller, W., Lavorel, S., Davies, I.D. & Garbolino, E. (2008) Land use change and sub-alpine tree dynamics: colonisation of Larix decidua in French sub-alpine grasslands. *Journal of Applied Ecology*, **45**, 659–669.

Anderson, B.J., Armsworth, P.R., Eigenbrod, F., Thomas, C.D., Gillings, S., Heinemeyer, A., Roy, D.B. & Gaston, K.J. (2009) Spatial covariance between biodiversity and other ecosystem service priorities. *Journal of Applied Ecology*, **46**, 888–896.

Andrew, N.R. & Hughes, L. (2005) Herbivore damage along a latitudinal gradient: relative impacts of different feeding guilds. *Oikos*, **108**, 176–182.

Bakker, M.A., Carreño-Rocabado, G. & Poorter, L. (2011) Leaf economics traits predict litter decomposition of tropical plants and differ among land use types. *Functional Ecology*, **25**, 473–483.

Bardgett, R.D. & Wardle, D.A. (2003) Herbivore-mediated linkages between aboveground and belowground communities. *Ecology*, **84**, 2258–2268.

Bennett, E.M. & Balvanera, P. (2007) The future of production systems in a globalized world. *Frontiers in Ecology and the Environment*, **5**, 191–198.

Bennett, E.M., Peterson, G.D. & Gordon, L.J. (2009) Understanding relationships among multiple ecosystem services. *Ecology Letters*, **12**, 1394–1404.

Byrne, B.M. (2010) *Structural Equation Modeling with AMOS: Basic Concepts, Applications, and Programming*, 2nd Edn. Routledge, New York.

Carpenter, S.R., Mooney, H.A., Agard, J., Capistrano, D., De Fries, R.S., Díaz, S. *et al.* (2009) Science for managing ecosystem services: beyond the Millennium Ecosystem Assessment. *Proceedings of the National Academy of Sciences*, **106**, 1305–1312.

Chan, K.M.A., Shaw, M.R., Cameron, D.R., Underwood, E.C. & Daily, G.C. (2006) Conservation planning for ecosystem services. *PLoS Biology*, **4**, e379.

Chapin, F.S., III (1980) The mineral nutrition of wild plants. *Annual Review of Ecology and Systematics*, **11**, 233–260.

Chave, J., Coomes, D., Jansen, S., Lewis, S.L., Swenson, N.G. & Zanne, A.E. (2009) Towards a worldwide wood economics spectrum. *Ecology Letters*, **12**, 351–366.

Cingolani, A.M., Posse, G. & Collantes, M.B. (2005) Plant functional traits, herbivore selectivity and response to sheep grazing in Patagonian steppe grasslands. *Journal of Applied Ecology*, **42**, 50–59.

Cleveland, C. & Liptzin, D. (2007) C:N:P stoichiometry in soil: is there a "Redfield ratio" for the microbial biomass? *Biogeochemistry*, **85**, 235–252.

Coley, P.D., Bryant, J.P. & Chapin III, S. (1985) Resource availability and plant antiherbivore defense. *Science*, **230**, 895–899.

Cornelissen, J.H.C., Lavorel, S., Garnier, E., Díaz, S., Buchmann, N., Gurvich, D.E., Reich, P.B., ter Steege, H., Morgan, H.D., van der Heijden, M.G.A., Pausas, J.G. & Poorter, H. (2003) Handbook of protocols for standardised and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, **51**, 335–380.

Craine, J.M., Lee, W.G., Bond, W.J., Williams, R.J. & Johnson, L.C. (2005) Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology*, **86**, 12–19.

Daily, G.C., Alexander, S., Ehrlich, P.R., Goulder, L., Lubchenco, J., Matson, P.A., Mooney, H.A., Postel, S., Schneider, S.H., Tilman, D. & Woodwell, G.M. (1997) Ecosystem services: benefits supplied to human societies by natural ecosystems. *Issues in Ecology*, **2**, 1–16.

De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Bardgett, R., Berg, M. *et al.* (2010) Functional traits underlie the delivery of ecosystem services across different trophic levels. *Biodiversity and Conservation*, **143**, 2873–2893.

De Chazal, J., Quétier, F., Lavorel, S., Van Doorn, A. & Castro, H. (2008) Including multiple differing stakeholder values into vulnerability assessments of socio-ecological systems. *Global Environmental Change*, **18**, 508–520.

De Deyn, G.B., Cornelissen, J.H.C. & Bardgett, R.D. (2008) Plant functional traits and soil carbon sequestration in contrasting biomes. *Ecology Letters*, **11**, 516–531.

Díaz, S. & Cabido, M. (2001) Vive la différence: plant functional diversity matters to ecosystem processes. *Trends in Ecology and Evolution*, **16**, 646–655.

Díaz, S., Hodgson, J.G., Thompson, K., Cabido, M., Cornelissen, J.H.C., Jalili, A. *et al.* (2004) The plant traits that drive ecosystems: evidence from three continents. *Journal of Vegetation Science*, **15**, 295–304.

Díaz, S., Lavorel, S., De Bello, F., Quétier, F., Grigulis, K. & Robson, T.M. (2007a) Incorporating plant functional diversity effects in ecosystem service assessments. *Proceedings of the National Academy of Sciences*, **104**, 20684–20689.

Díaz, S., Lavorel, S., McIntyre, S., Falczuk, V., Casanoves, F., Milchunas, D. *et al.* (2007b) Grazing and plant traits – a global synthesis. *Global Change Biology*, **13**, 313–341.

Díaz, S., Quétier, F., Cáceres, D.M., Trainor, S.F., Pérez-Harguindeguy, N., Bret-Harte, M.S., Finegan, B., Peña-Claros, M. & Poorter, L. (2011) Linking functional diversity and social actor strategies in a framework for interdisciplinary analysis of nature's benefits to society. *Proceedings of the National Academy of Sciences*, **108**, 895–902.

Doré, T., Makowski, D., Malézieux, E., Munier-Jolain, N., Tchamitchian, M. & Tittonell, P. (2011) Facing up to the paradigm of ecological intensification in agronomy: revisiting methods, concepts and knowledge. *European Journal of Agronomy*, **34**, 197–210.

Egoh, B., Reyers, B., Rouget, M., Richardson, D.M., Le Maitre, D. & van Jaarsfeld, A.S. (2008) Mapping ecosystem services for planning and management. *Agriculture, Ecosystems & Environment*, **127**, 135–140.

Enquist, B.J., Brown, J.H. & West, G.B. (1998) Allometric scaling of plant energetics and population density. *Nature*, **395**, 163–165.

Enquist, B.J., Economo, E.P., Huxman, T.E., Allen, A.P., Ignace, D.D. & Gillooly, J.F. (2003) Scaling metabolism from organisms to ecosystems. *Nature*, **423**, 639–642.

Enquist, B.J., Kerkhoff, A.J., Stark, S.C., Swenson, N.G., McCarthy, M.C. & Price, C.A. (2007) A general integrative model for scaling plant growth, carbon flux, and functional trait spectra. *Nature*, **449**, 218.

Falster, D.S. & Westoby, M. (2003) Plant height and evolutionary games. *Trends in Ecology & Evolution*, **18**, 337–343.

Falster, D.S., Brännström, Å., Dieckmann, U. & Westoby, M. (2011) Influence of four major plant traits on average height, leaf-area cover, net primary productivity, and biomass density in single-species forests: a theoretical investigation. *Journal of Ecology*, **99**, 148–164.

Foley, J.A., Defries, R.S., Asner, G.P., Barford, C., Bonan, G., Carpenter, S.R. *et al.* (2005) Global consequences of land use. *Science*, **309**, 570–574.

Fontaine, S., Barot, S., Barre, P., Bdioui, N., Mary, B. & Rumpel, C. (2007) Stability of organic carbon in deep soil layers controlled by fresh carbon supply. *Nature*, **450**, 277.

Fortunel, C., Garnier, E., Joffre, R., Kazakou, E., Quested, H., Grigulis, K., Lavorel, S. & consortium, V. (2009) Plant functional traits capture the effects of land use change and climate on litter decomposability of herbaceous communities in Europe and Israel. *Ecology*, **90**, 598–611.

Freschet, G.T., Cornelissen, J.H.C., Van Logtestijn, R.S.P. & Aerts, R. (2010a) Evidence of the 'plant economics spectrum' in a subarctic flora. *Journal of Ecology*, **98**, 362–373.

Freschet, G.T., Cornelissen, J.H.C., Van Logtestijn, R.S.P. & Aerts, R. (2010b) Substantial nutrient resorption from leaves, stems and roots in a subarctic flora: what is the link with other resource economics traits? *New Phytologist*, **186**, 879–889.

Gamfeldt, L., Hillebrand, H. & Jonsson, P.R. (2008) Multiple functions increase the importance of biodiversity for overall ecosystem functioning. *Ecology*, **89**, 1223–1231.

Garnier, E. & Navas, M.-L. (2011) A trait-based approach to comparative functional plant ecology: concepts, methods and applications for agroecology. A review. *Agronomy for Sustainable Development*, doi: 10.1007/s13593-011-0036-y.

Garnier, E., Cortez, J., Billès, G., Navas, M.-L., Roumet, C., Debussche, M., Laurent, G., Blanchard, A., Aubry, D., Bellmann, A., Neill, C. & Toussaint, J.-P. (2004) Plant functional markers capture ecosystem properties during secondary succession. *Ecology*, **85**, 2630–2637.

Garnier, E., Lavorel, S., Ansquer, P., Castro, H., Cruz, P., Dolezal, J. *et al.* (2007) A standardized methodology to assess the effects of land use change on plant traits, communities and ecosystem functioning in grasslands. *Annals of Botany*, **99**, 967–985.

Gimona, A. & van der Horst, D. (2007) Mapping hotspots of multiple landscape functions: a case study on farmland afforestation in Scotland. *Landscape Ecology*, **22**, 1255–1264.

Grace, J.B. (2006) *Structural Equation Modeling and Natural Systems.* Cambridge University Press, New York.

Grime, J.P. (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *The American Naturalist*, **111**, 1169–1194.

Grime, J.P. (1998) Benefits of plant diversity to ecosystems: immediate, filter and founder effects. *Journal of Ecology*, **86**, 902–906.

Grime, J.P., Cornelissen, H.J.C., Thompson, K. & Hodgson, J.G. (1996) Evidence of a causal connection between anti-herbivore defence and the decomposition rate of leaves. *Oikos*, **77**, 489–494.

Gross, N., Suding, K.N. & Lavorel, S. (2007) Leaf dry matter content and lateral spread predict response to land-use change factors for six dominant species in subalpine grasslands. *Journal of Vegetation Science*, **18**, 289–300.

Gross, N., Robson, T.M., Lavorel, S., Albert, C., Le Bagousse-Pinguet, Y. & Guillemin, R. (2008) Plant response traits mediate the effects of subalpine grasslands on soil moisture. *New Phytologist*, **180**, 652–662.

Haines-Young, R. & Potschin, M. (2010) The links between biodiversity, ecosystem services and human well-being. *Ecosystem ecology: A New Synthesis* (eds D. Raffaelli & C. Frid), pp. 110–139. Cambridge University Press, Cambridge.

Hector, A. & Bagchi, R. (2007) Biodiversity and ecosystem multifunctionality. *Nature*, **448**, 188–191.

Herms, D.A. & Mattson, W.J. (1992) The dilemma of plants: to grow or defend. *Quarterly Review of Biology*, **67**, 283–335.

Hodgson, J.A., Kunin, W.E., Thomas, C.D., Benton, T.G. & Gabriel, D. (2010) Comparing organic farming and land sparing: optimizing yield and butterfly populations at a landscape scale. *Ecology Letters*, **13**, 1358–1367.

Hummel, I., Vile, D., Violle, C., Devaux, J., Ricci, B., Blanchard, A., Garnier, E. & Roumet, C. (2006) Relating root structure and anatomy to whole-plant functioning in 14 herbaceous Mediterranean species. *New Phytologist*, **173**, 313–321.

Isbell, F., Calcagno, V., Hector, A., Connolly, J., Harpole, W.S., Reich, P.B. *et al.* (2011) High plant diversity is needed to maintain ecosystem services. *Nature*, **477**, 199–202.

Kareiva, P., Watts, S., McDonald, R. & Boucher, T. (2007) Domesticated nature: shaping landscapes and ecosystems for human welfare. *Science*, **316**, 1866–1869.

Klumpp, K. & Soussana, J.F. (2009) Using functional traits to predict grassland ecosystem change: a mathematical test of the response-and-effect trait approach. *Global Change Biology*, **15**, 2921–2934.

Kremen, C. (2005) Managing ecosystem services: what do we need to know about their ecology? *Ecology Letters*, **8**, 468–479.

Lamarque, P., Quétier, F. & Lavorel, S. (2011a) The diversity of the ecosystem services concept: implications for quantifying the value of biodiversity to society. *Compte-Rendus de l'Académie des Sciences, Biologie*, **334**, 441–449.

Lamarque, P., Tappeiner, U., Turner, C., Bardgett, R.D., Szukics, U., Schermer, M. & Lavorel, S. (2011b) Stakeholders understanding of soil fertility and biodiversity and representations of grassland ecosystem services. *Regional Environmental Change*, in press.

Laughlin, D.C. (2011) Nitrification is linked to dominant leaf traits rather than functional diversity. *Journal of Ecology*, **99**, 1091–1099.

Laughlin, D.C., Leppert, J.J., Moore, M.M. & Sieg, C.H. (2010) A multi-trait test of the leaf-height-seed plant strategy scheme with 133 species from a pine forest flora. *Functional Ecology*, **24**, 493–501.

Lavorel, S. & Garnier, E. (2002) Predicting the effects of environmental changes on plant community composition and ecosystem functioning: revisiting the Holy Grail. *Functional Ecology*, **16**, 545–556.

Lavorel, S., Grigulis, K., McIntyre, S., Garden, D., Williams, N., Dorrough, J., Berman, S., Quétier, F., Thébault, A. & Bonis, A. (2008) Assessing functional diversity in the field – methodology matters! *Functional Ecology*, **22**, 134–147.

Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Douzet, R. & Pellet, G. (2011) Using plant functional traits to understand the landscape-scale distribution of multiple ecosystem services. *Journal of Ecology*, **99**, 135–147.

Lepš, J., Novotný, V. & Basset, Y. (2001) Habitat and successional status of plants in relation to the communities of their leaf-chewing herbivores in Papua New Guinea. *Journal of Ecology*, **89**, 186–199.

Lepš, J., De Bello, F., Lavorel, S. & Berman, S. (2006) Quantifying and interpreting functional diversity of natural communities: practical considerations matter. *Preslia*, **78**, 481–501.

Lloyd, K.M., Pollock, M.L., Mason, N.W.H. & Lee, W.G. (2010) Leaf trait–palatability relationships differ between ungulate species: evidence from cafeteria experiments using native tussock grasses. *New Zealand Journal of Ecology*, **34**, 219–226.

Mason, N.W.H., Carswell, F.E., Richardson, S.J. & Burrows, L.E. (2011) Leaf palatability and decomposability increase during a 200-year-old post-cultural woody succession in New Zealand. *Journal of Vegetation Science*, **22**, 6–17.

Millennium Ecosystem Assessment (2005) *Ecosystems and Human Well-being: Synthesis.* Island Press, Washington.

Minden, V. & Kleyer, M. (2011) Testing the effect-response framework: key response and effect traits determining above-ground biomass of salt marshes. *Journal of Vegetation Science*, **22**, 387–401.

Mokany, K., Ash, J. & Roxburgh, S. (2008) Functional identity is more important than diversity in influencing ecosystem processes in a temperate native grassland. *Journal of Ecology*, **96**, 884–893.

Moles, A.T. & Leishman, M.R. (2008) The seedling as part of a plant's life history strategy. *Seedling ecology and evolution* (eds M. Leck, V. T. Parker & R. Simpson), pp. 217–238. Cambridge University Press, Cambridge.

Moles, A.T., Ackerly, D.D., Tweedle, J.C., Dickie, J.B., Smith, R., Leishman, M.R., Mayfield, M.M., Pitman, A., Wood, J.T. & Westoby, M. (2007) Global patterns in seed size. *Global Ecology & Biogeography*, **16**, 109–116.

Moles, A.T., Warton, D.I., Warman, L., Swenson, N.G., Laffan, S.W., Zanne, A.E., Pitman, A., Hemmings, F.A. & Leishman, M.R. (2009) Global patterns in plant height. *Journal of Ecology*, **97**, 923–932.

Moretti, M., Ibanez, S., De Bello, F., Rixen, C. & Lavorel, S. (2011) Toward an understanding of trophic relationships between plants and herbivore invertebrates. Proceedings of the 54th Symposium of the International Association for Vegetation Science. Lyon, France.

Nelson, E., Polasky, S., Lewis, D.J., Plantiga, L.J., Lonsdorf, E.V., White, D., Bael, D. & Lawler, J.J. (2008) Efficiency of incentives to jointly increase carbon sequestration and species conservation on a landscape. *Proceedings of the National Academy of Sciences*, **105**, 9471–9476.

Nicholson, E., Mace, G.M., Armsworth, P.R., Atkinson, G., Buckle, S., Clements, T. *et al.* (2009) Priority research areas for ecosystem services in a changing world. *Journal of Applied Ecology*, **46**, 1139–1144.

Niklas, K.J. & Enquist, B.J. (2001) Invariant scaling relationships for interspecific plant biomass production rates and body size. *Proceedings of the National Academy of Sciences, USA*, **98**, 2922–2997.

Ordoñez, J.C., Van Bodegom, P.M., Witte, J.-P.M., Wright, I.J., Reich, P.B. & Aerts, R. (2009) A global study of relationships between leaf traits, climate and soil measures of nutrient fertility. *Global Ecology and Biogeography*, **18**, 137–149.

Orwin, K.H., Buckland, S.M., Johnson, D., Turner, B.L., Smart, S., Oakley, S. & Bardgett, R.D. (2010) Linkages of plant traits to soil properties and the functioning of temperate grassland. *Journal of Ecology*, **98**, 1074–1083.

Pakeman, R.J. (2011) Multivariate identification of plant functional response and effect traits in an agricultural landscape. *Ecology*, **92**, 1353–1365.

Peeters, P.J., Sanson, G. & Read, J. (2007) Leaf biomechanical properties and the densities of herbivorous insect guilds. *Functional Ecology*, **21**, 246–255.

Pérez-Harguindeguy, N., Díaz, S., Vendramini, F., Cornelissen, J.H.C., Gurvich, D.E. & Cabido, M. (2003) Leaf traits and herbivore selection in the field and in cafeteria experiments. *Austral Ecology*, **28**, 642–650.

Pontes Da Silva, L., Soussana, J.F., Louault, F., Andueza, D. & Carrère, P. (2007) Leaf traits affect the above-ground productivity and quality of grasses. *Functional Ecology*, **21**, 844–853.

Pöyry, J., Luoto, M., Paukkunen, J., Pykälä, J., Raatikainen, K. & Kuussaari, M. (2006) Different responses of plants and herbivore insects to a gradient of vegetation height: an indicator of the vertebrate grazing intensity and successional age. *Oikos*, **115**, 401–412.

Quétier, F., Thébault, A. & Lavorel, S. (2007) Linking vegetation and ecosystem response to complex past and present land use changes using plant traits and a multiple stable state framework. *Ecological Monographs*, **77**, 33–52.

Quétier, F., Rivoal, F., Marty, P., De Chazal, J. & Lavorel, S. (2010) Social representations of an alpine grassland landscape and socio-political discourses on rural development. *Regional Environmental Change*, **10**, 119–130.

Quijas, S., Schmid, B. & Balvanera, P. (2010) Plant diversity enhances provision of ecosystem services: a new synthesis. *Basic and Applied Ecology*, **11**, 582–593.

Raudsepp-Hearne, C., Peterson, G.D. & Bennett, E.M. (2010) Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proceedings of the National Academy of Sciences*, **107**, 5242–5247.

Reich, P.B. (2001) Body size, geometry, longevity and metabolism: do plant leaves behave like animal bodies? *Trends in Ecology and Evolution*, **16**, 674–680.

Reich, P.B., Walters, M.B. & Ellsworth, D.S. (1997) From tropics to tundra: a global convergence in plant functioning. *Proceedings of the National Academy of Sciences, USA*, **94**, 13730–13734.

Reiss, J., Bridle, J.R., Montoya, J.M. & Woodward, G. (2009) Emerging horizons in biodiversity and ecosystem functioning research. *Trends in Ecology & Evolution*, **24**, 505–514.

Reyers, B., O'Farrell, P.J., Cowling, R.M., Egoh, B.N., Maitre, D.C.L. & Vlok, J.H.J. (2009) Ecosystem services, land-cover change, and stakeholders: finding a sustainable foothold for a semiarid biodiversity hotspot. *Ecology and Society*, **14**, 38. [online].

Robson, T.M., Baptist, F., Clément, J.C. & Lavorel, S. (2010) Land use in subalpine grasslands affect N cycling via changes in plant community and soil microbial uptake dynamics. *Journal of Ecology*, **98**, 62–73.

Robson, T.M., Lavorel, S., Clément, J.C. & Le Roux, X. (2007) Neglect of mowing and manuring leads to slower nitrogen cycling in subalpine grasslands. *Soil Biology and Biogeochemistry*, **39**, 930–941.

Scherber, C., Mwangi, P.N., Temperton, V.M., Roscher, C., Schumacher, J., Schmid, B. & Weisser, W.W. (2006) Effects of plant diversity on invertebrate herbivory in experimental grassland. *Oecologia*, **147**, 489–500.

Scherber, C., Eisenhauer, N., Weisser, W.W., Schmid, B., Voigt, W., Fischer, M. *et al.* (2010) Bottom-up effects of plant diversity on multitrophic interactions in a biodiversity experiment. *Nature*, **468**, 553–556.

Schröter, D., Cramer, W., Leemans, R., Prentice, I.C., Araújo, M.B., Arnell, N.W. *et al.* (2005) Ecosystem service supply and vulnerability to global change in Europe. *Science*, **310**, 1333–1337.

Schumacher, J. & Roscher, C. (2009) Differential effects of functional traits on aboveground biomass in semi-natural grasslands. *Oikos*, **118**, 1659–1668.

Schwinning, S. & Ehleringer, J.R. (2001) Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems. *Journal of Ecology*, **89**, 464–480.

Shipley, B. (2000) *Cause and Correlation in Ecology – A User's Guide to Path Analysis, Structural Equations and Causal Inference*. Cambridge University Press, Cambridge.

Southwood, T.R.E. (1988) Tactics, strategies and templets. *Oikos*, **52**, 3–18.

Suding, K.N. & Goldstein, L.J. (2008) Testing the Holy Grail framework: using functional traits to predict ecosystem change. *New Phytologist*, **180**, 559–562.

Suding, K.N., Lavorel, S., Chapin III, F.S., Díaz, S., Garnier, E., Goldberg, D., Hooper, D.U., Jackson, S.T. & Navas, M.L. (2008) Scaling environmental change from traits to communities to ecosystems: the challenge of intermediate-level complexity. *Global Change Biology*, **14**, 1125–1140.

Tasser, E. & Tappeiner, U. (2005) New model to predict rooting in diverse plant community compositions. *Ecological Modelling*, **185**, 195–211.

Turner, B.L., Lambin, E.F. & Reenberg, A. (2007) The emergence of land change science for global environmental change and sustainability. *Proceedings of the National Academy of Sciences*, **104**, 20666–20671.

Unsicker, S.B., Franzke, A., Specht, J., Köhler, G., Linz, J., Renker, C., Stein, C. & Weisser, W.W. (2010) Plant species richness in montane grasslands affects the fitness of a generalist grasshopper species. *Ecology*, **91**, 1083–1091.

Viard-Crétat, F., Lefèbvre, M., Gallet, C. & Lavorel, S. (2009) A leachate a day keeps the seedlings away: mowing and the inhibitory effects of *Festuca paniculata* in subalpine grasslands. *Annals of Botany*, **103**, 1271–1278.

Vile, D., Shipley, B. & Garnier, E. (2006) A structural equation model to integrate changes in functional strategies during old-field succession. *Ecology*, **87**, 504–517.

Violle, C., Navas, M.L., Vile, D., Kazakou, E., Fortunel, C., Hummel, I. & Garnier, E. (2007) Let the concept of trait be functional! *Oikos*, **116**, 882–892.

Wardle, D.A., Bardgett, R.D., Klironomos, J.N., Setälä, H., Van der Putten, W.H. & Wall, D.H. (2004) Ecological linkages between aboveground and belowground biota. *Science*, **304**, 1629–1633.

Westoby, M. (1998) A leaf-height-seed (LHS) plant ecology strategy scheme. *Plant and Soil*, **199**, 213–227.

Westoby, M., Falster, D.S., Moles, A.T., Vesk, P.A. & Wright, I.J. (2002) Plant ecological strategies: some leading dimensions of variation between species. *Annual Review of Ecology and Systematics*, **33**, 125–159.

Wright, I.J., Reich, P.B., Westoby, M., Ackerly, D.D., Baruch, Z., Bongers, F. *et al.* (2004) The worldwide leaf economics spectrum. *Nature*, **428**, 821–827.

Zavaleta, E.S., Pasari, J.R., Hulvey, K.B. & Tilman, G.D. (2010) Sustaining multiple ecosystem functions in grassland communities requires higher biodiversity. *Proceedings of the National Academy of Sciences*, **107**, 1443–1446.

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Variable selection for the Lautaret data set.

Appendix S2. Structural equation model for Orthopterae species richness.

As a service to our authors and readers, this journal provides supporting information supplied by the authors. Such materials may be re-organized for online delivery, but are not copy-edited or typeset. Technical support issues arising from supporting information (other than missing files) should be addressed to the authors.