Using plant functional traits to understand the landscape distribution of multiple ecosystem services

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Summary

1. Spatially explicit understanding of the delivery of multiple ecosystem services (ES) from global to local scales is currently limited. New studies analysing the simultaneous provision of multiple services at landscape scale should aid the understanding of multiple ES delivery and trade-offs to support policy, management and land planning.

2. Here, we propose a new approach for the analysis, mapping and understanding of multiple ES delivery in landscapes. Spatially explicit single ES models based on plant traits and abiotic characteristics are combined to identify 'hot' and 'cold' spots of multiple ES delivery, and the land use and biotic determinants of such distributions. We demonstrate the value of this trait-based approach as compared to a pure land-use approach for a pastoral landscape from the central French Alps, and highlight how it improves understanding of ecological constraints to, and opportunities for, the delivery of multiple services.

3. Vegetative height and leaf traits such as leaf dry matter content were response traits strongly influenced by land use and abiotic environment, with follow-on effects on several ecosystem properties, and could therefore be used as functional markers of ES.

4. Patterns of association among ES were related to the dominant traits underlying different ecosystem properties. The functional decoupling between height and leaf traits provided alternative pathways for high agronomic value, as well as determining hot and cold spots of ES. Traditional land uses such as organic fertilization and mowing or altitude summer grazing were also linked with ES hot spots, because functional characteristics supporting fodder production and quality are compatible with species and functional diversity.

5. *Synthesis.* Analyses of ES using plant functional variation across landscapes are a powerful approach to understanding the fundamental ecological mechanisms underlying ES provision, and trade-offs or synergies among services. Sustainable management of species and functionally diverse grassland could simultaneously aim at conserving biodiversity and locally important ES by taking advantage of correlations and trade-offs among different plant functional traits.

Key-words: determinants of plant community diversity and structure, ecosystem services, functional trade-offs, landscape modelling, mountain grassland management, plant functional traits

Introduction

Ecosystem services (ES) provide the link between ecosystems – their biodiversity and their functioning – and human society (Millennium Ecosystem Assessment 2005). Most ecosystems provide a diversity of services, such as food and fodder provi-

sion, regulation of climate and water quality, pollination, and aesthetic and recreational values (Millennium Ecosystem Assessment 2005). Policy, management and land planning urgently require spatial analyses of multiple ES at global (Naidoo *et al.* 2008), continental (Metzger *et al.* 2006; Kienast *et al.* 2009) and regional (Chan *et al.* 2007; Egoh *et al.* 2009; Eigenbrod *et al.* 2010) scales (Carpenter *et al.* 2009). There is also a critical need for new studies mapping the simultaneous

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provision of multiple services at landscape scale (Naidoo & Ricketts 2006; Gimona & van der Horst 2007) to advance the understanding of ES trade-offs and synergies (Bennett, Peterson & Gordon 2009). Such studies are also required to support the modelling of land-use change (Verburg *et al.* 2009) and the design of sustainable land architectures (de Groot *et al.* 2009; Turner 2010).

Ecosystem service assessments often make the assumption that ES can be mapped uniquely to land use or land cover (LULC) (Naidoo & Ricketts 2006; Verburg, *et al.* 2009; Eigenbrod *et al.* 2010), especially at large scales where LULC effects are at best corrected by a few simple modifiers, such as coarse altitude or slope classes, or landscape heterogeneity for which extensive information is available (Kienast *et al.* 2009; Eigenbrod *et al.* 2010). Yet this approach can introduce errors because it does not account for spatial variability in biophysical variables (e.g. soils, topography) or processes (Eigenbrod *et al.* 2010). For example Eigenbrod *et al.* (2010) demonstrated that mapping ES over England using either land cover or more refined proxies based on strong causal drivers for specific services resulted in a poor fit to primary data, as well as introducing errors in the identification of ES hotspots. While of some use to depict broad-scale patterns of ES delivery in the absence of better data, the use of LULC proxies is also incompatible with the analysis of mechanisms that drive ES delivery because ecosystem functioning often varies across a LULC class due to biophysical heterogeneity (e.g. topography, soil type) or management (e.g. grazing intensity, logging practices) (Quétier *et al.* 2007; Grêt-Regamey *et al.* 2008; Bennett, Peterson & Gordon 2009; Reyers *et al.* 2009; Willemen *et al.* 2010) and biotic responses to these factors.

We propose to address this limitation by a refined analysis at landscape scale of some of the ecological mechanisms that drive ES delivery. Ecosystem service delivery has been related to ecosystem biological characteristics (Kremen 2005), and more specifically to functional traits (Kremen 2005; De Chazal *et al.* 2008; De Bello *et al.* 2010). In particular, for plants there is growing evidence for the effects of community-level functional traits on ecosystem processes that underlie important ES (Suding & Goldstein 2008). Following the biomass ratio hypothesis (Grime 1998), community-weighted mean traits, which represent the average trait value for a unit of biomass within a community (Garnier *et al.* 2004; Violle *et al.* 2007), explain variation in net above-ground primary productivity (specific ANPP, Vile, Shipley & Garnier 2006; ANPP Mokany, Ash & Roxburgh 2008), litter decomposition under field (Garnier *et al.* 2004) and controlled (Cornelissen *et al.* 1999; Fortunel *et al.* 2009) conditions, digestibility (Pontes Da Silva *et al.* 2007), or soil moisture (Mokany, Ash & Roxburgh 2008) and water uptake (Gross *et al.* 2008). Effects of functional divergence, i.e. the expected variance in trait values across two random units of biomass within a community (Lepš *et al.* 2006), have also been hypothesized to operate through functional complementarity (Petchey & Gaston 2006). For example, within-community diversity in plant heights is expected to enhance light capture (Vojtech *et al.*

2008), while diversity in leaf structural and chemical traits would reflect diversity in nutrient acquisition and retention strategies (Gross *et al.* 2007), and therefore affect primary productivity (Schumacher & Roscher 2009) and decomposition (Scherer-Lorenzen 2008). However, their demonstration has so far remained more elusive for such ecosystem processes that appear to be dominated by biomass ratio effects (Diaz *et al.* 2007; Mokany, Ash & Roxburgh 2008; but see Schumacher & Roscher 2009). Functional trait data is becoming increasingly available thanks to standardized measurement methods, which have promoted their wide use (Cornelissen *et al.* 2003), and to large trait data bases (Kleyer *et al.* 2008; Kattge *et al.* 2010). Quantitative models of ES built from plant traits and environmental variables (Diaz *et al.* 2007) have been used at the ecosystem level to quantify and project ES for current management and future scenarios (Quétier *et al.* 2007). However, such applications have projected ES using unique values for trait means or divergence and of abiotic factors within a given land use (Quétier *et al.* 2009), ignoring the finer-scale biotic (e.g. plant species composition) and abiotic (e.g. topography and soils) variation within each land use that needs to be considered for a spatially explicit landscape analysis.

Furthermore, existing trait-based analyses have considered ES individually rather than bundles of ES with trade-offs and synergies (Bennett, Peterson & Gordon 2009), as it is increasingly done in spatial ES assessments (Naidoo & Ricketts 2006; Egoh *et al.* 2009; Eigenbrod *et al.* 2010; Willemen *et al.* 2010). Eigenbrod *et al.* (2010) highlighted the particularly strong limitations of land use or proxy-based analyses when addressing multiple ES. We believe that using the understanding of relationships between ES and traits should strongly advance the understanding of ES synergies and trade-offs. This would be achieved by using knowledge on associations and trade-offs among traits as captured by plant strategy schemes (Grime 1977; Westoby 1998) and trait spectra analyses (Diaz *et al.* 2004; Wright *et al.* 2004; Chave *et al.* 2009).

In this study, we propose a new approach for the analysis of multiple ES delivery in landscapes. We first develop spatially explicit ES models based on plant traits and abiotic characteristics, expanding the trait-based conceptual framework (Fig. 1) (Diaz *et al.* 2007). This framework makes it possible to compare and combine land use, direct (abiotic) and indirect (trait-mediated) effects on ecosystem properties by comparing statistical models incorporating hierarchical combinations of effects. Then 'hot' and 'cold' spots of ES delivery, representing areas of high delivery for multiple vs. low delivery across services, respectively, and their determinants in terms of land use and plant traits are analysed combining multiple ecosystem properties. Using interdisciplinary data for a grassland-dominated landscape from the central French Alps, where animal husbandry and tourism are the main activities, we demonstrate how this trait-based approach improves on a pure land-use approach, and how it advances understanding of ecological constraints to, and opportunities for, the delivery of multiple services.
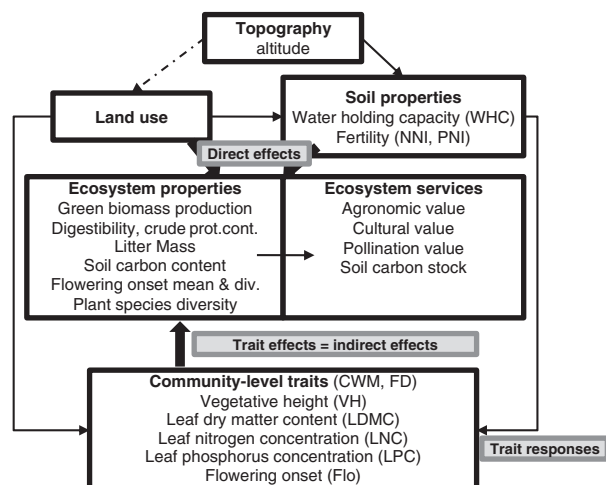
Fig. 1. Conceptual framework for the analysis of ecosystem properties underlying ecosystem services. The analysis identifies successively the direct effects of land use on ecosystem properties (*LU*); the combined direct effects of land use and abiotic variables on ecosystem properties (*LU + abiotic*); and the combination of abiotic effects with indirect effects via plant functional diversity (trait community-weighted mean and functional divergence) (*trait + abiotic*).

Materials and methods

STUDY SITE AND FIELD MEASUREMENTS

The Lautaret study site (45°03′ N, 6°24′ E) is located in the Central French Alps on the south-facing slopes of Villar d'Arène. The total area is 13 km^2 and the elevation ranges from 1552 to 2442 m a.s.l. A detailed site description can be found in (Quétier, Thébault & Lavorel 2007). Land use legacies can play a key role in determining current vegetation, soil properties and ecosystem functioning (Bruun *et al.* 2001; Fraterrigo, Turner & Pearson 2006), especially in mountain grasslands (Maurer *et al.* 2006). Therefore we considered land use

trajectories, the combinations between past and present land use mapped at site level using a combination of cadastral (1810 to present) and aerial photographic data (since 1952) (Fig. 2) (Quétier, Thébault & Lavorel 2007 – see Girel *et al.* 2010 for a detailed analysis of land use history). We analysed eight trajectories, referred to as 'land use' henceforth, three on previously cultivated terraces [currently fertilized and mown (LU1), mown (LU2), or unmown and grazed in spring and autumn (LU3)], three on never cultivated permanent grasslands with a multi-century history of mowing [currently mown (LU4), unmown and summer-grazed (LU5), and neither mown nor grazed (LU6) '*Festuca* grasslands' – dominated by the large perennial grass *Festuca paniculata*], one on never mown summer grasslands (>2000 m) (LU7) and one on steep (>30°) grazed slopes (LU8). Previous analyses have demonstrated significant differences in soils, plant species and functional composition and ecosystem properties across these land use categories, reflecting both the effects of past land use (presence or absence of cultivation) and current practices (presence or absence of mowing and of fertilization) (Quétier, Thébault & Lavorel 2007; Robson *et al.* 2007). All data were referenced in a Geographic Information System including also a 10-m Digital Elevation Model under ArcGiS 9.2, ESRI.

Vegetation, plant functional trait, ecosystem and environmental data (Fig. 1) were collected for fifty-seven 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. Vegetation composition surveys used the BOTANAL method to estimate species relative biomass (Lavorel *et al.* 2008). Plant vegetative traits [vegetative height (VH), leaf dry matter content (LDMC), leaf nitrogen and phosphorus concentrations (LNC and LPC)] assumed as relevant to ES provision (Quétier *et al.* 2007) were measured for all species making up 80% of cumulated biomass following standard protocols (Garnier *et al.* 2007). For each trait we calculated community-weighted mean (CWM; Garnier *et al.* 2004) and functional divergence (FD, using the formulation by Mason *et al.* 2003) using the F-Diversity package (Di Rienzo, Casanoves & Pla 2008). Soil texture, soil total carbon and nitrogen, and nitrogen and
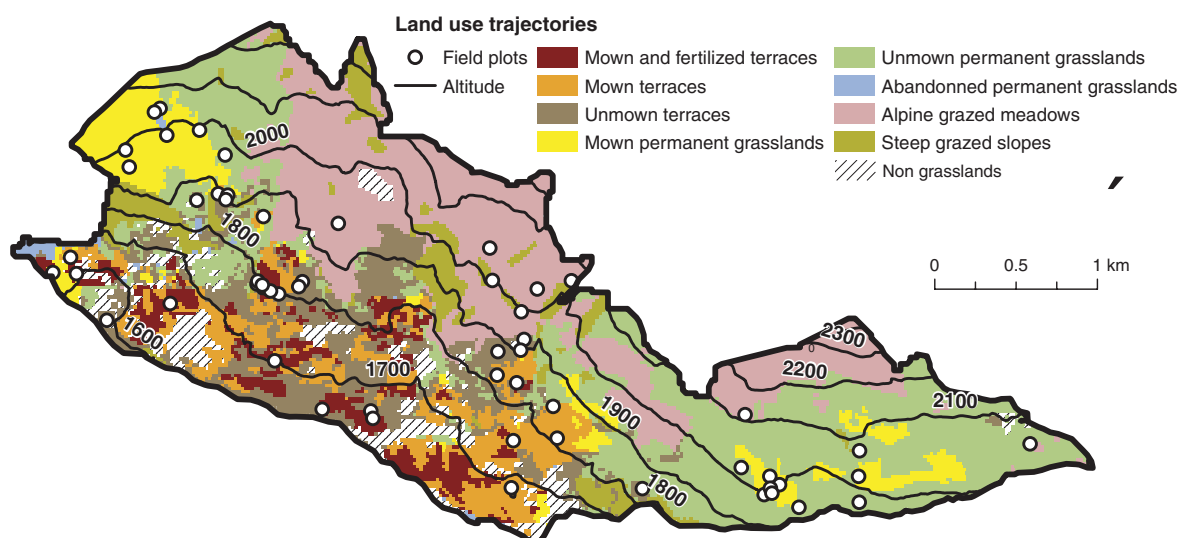

Fig. 2. Field site and land use types. Land use trajectories are the combinations between past and present land use, with three land uses on previously cultivated terraces: fertilized and mown, mown, unmown and grazed in spring and autumn; three on permanent, never-cultivated permanent grasslands: mown, unmown and summer grazed, and neither mown nor grazed '*Festuca* grasslands'; never mown summer grasslands (>2000 m); steep (>30°) grazed slopes. Sampled sites are marked with white dots.

phosphorus nutrition indices (NNI and PNI, respectively) were also measured in each plot using standard protocols (Garnier *et al.* 2007). Soil water holding capacity (WHC) was calculated using texture and total carbon data (Osty 1971). Radiation was estimated within the GIS using the site's 10-m resolution Digital Elevation Model. Green and litter biomass were estimated using calibrated visual estimates (Lavorel *et al.* 2008) in 2007, 2008 and 2009, and analyses used a smoothed mean over the three years with 2008 as a reference. Crude protein content (CPC) of green biomass was estimated using near infrared spectrometry (Pontes Da Silva *et al.* 2007) for a subset of 24 plots distributed across land uses and altitudes. Flowering phenology (date of flowering onset and duration of flowering) was surveyed for all species contributing to 80% cumulated biomass in 2007 and 2008 for a subset of 39 plots distributed across land uses. Date of flowering onset was transformed to growing degree days adjusted to altitude with a $0.6\,°C\ 100\ m^{-1}$ decrease validated with two weather stations located at 1600 m and 2100 m. Functional divergence in flowering dates (FD_Flo) was calculated using a dedicated Excel© Macro (Lepš *et al.* 2006).

STATISTICAL ANALYSES

Variations across the landscape in CWM and FD for the four traits of the vegetative phase were modelled with general linear models (GLM) combining land use (one categorical variable) and abiotic variables (four continuous variables: altitude, radiation, WHC, NNI, PNI). Variation in biogeochemical ecosystem properties (EP) (green biomass production, litter mass, fodder crude protein content, soil C) was modelled using three alternative general linear models (Fig. 1): (i) land use alone (*LU*; categorical variable with eight states), (ii) land use and all abiotic variables (continuous variables) (*LU + abiotic*), and (iii) traits CWM and FD and abiotic variables (continuous variables; *trait + abiotic*) following Diaz *et al.* (2007). The land-use-alone model represents the 'default' model that would be used in the absence of ecological or terrain data, as done in studies using land use as a proxy for ES (Eigenbrod *et al.* 2010). The second model combines land use and abiotic effects and provides a purely geographic representation in the absence of ecological knowledge (e.g. Grêt-Regamey *et al.* 2008; Kienast *et al.* 2009). The comparison between these first two models identifies effects of abiotic variables that may need to be taken into account in broad-scale ES assessments. Finally, the third model combines trait and abiotic effects as proposed by Diaz *et al.* (2007). The comparison between this model and the land-use-alone model identifies the need for site-based information beyond a land use or land cover proxy, and the comparison with the *land use + abiotic* model assesses the value of additional ecological (trait) information. Given the likely priority of abiotic effects over biotic effects (Grime 1998 – see Diaz *et al.* 2007) a trait-alone model was not considered in the comparison. However, a trait-alone model was also tested in preliminary analyses for those EP (green biomass production and crude protein content) for which significant abiotic effects were retained in the combined trait and abiotic model. It produced very similar results in terms of fit and parsimony to the combined model for green biomass production, whereas for crude protein content the trait-alone model performed considerably worse than the combined model (44% vs. 62% variance explained). Therefore we present only the *trait + abiotic* model, given that for litter and soil carbon content this was actually a trait-alone model (see Table 3).

Simpson species diversity was modelled using the *LU + abiotic* model given that functional diversity should be a consequence of species diversity rather than the reverse (Lepš *et al.* 2006). Phenological ecosystem properties (CWM onset of flowering and FD_Flo, which

in fact are trait functional diversity measures) were modelled using mixed models with land use and abiotic variables as fixed effects (*LU + abiotic* model) and year as a random effect. All analyses were run using Genstat 11th Edition (VSN International, Hempstead, UK) using all subsets regression (abiotic variables, traits, biogeochemistry, species diversity) and residual estimation of maximum likelihood (REML) (phenology) with quality of prediction (adjusted R) and parsimony using the Akaike criterion as criteria for model selection within each model type (*LU + abiotic* or *trait + abiotic*).

MAPPING ECOSYSTEM PROPERTIES AND ECOSYSTEM SERVICES

Abiotic variables (WHC, NNI, PNI), and CWM and FD for each trait were modelled for each 20×20 m pixel using GLM estimated effects for each land use category and estimated regression coefficients with abiotic variables (step 1). As a second step, ecosystem properties for each pixel were calculated and mapped using model estimates for effects of land use types (*LU* and *LU + abiotic* models), and for regression coefficients on abiotic variables and traits (*LU + abiotic* and *trait + abiotic* models). For each pixel these calculations were applied to mapped estimates of abiotic variables and trait CWM and FD provided by step 1. This second step is critically novel as compared to a direct application of the model by Diaz *et al.* (2007) in that we explicitly modelled the responses of trait community-weighted means and functional divergences to environment prior to evaluating their effects on ecosystem properties. Such an approach is the key to the explicit representation of functional variation across the landscape, as opposed to the use of unique trait values within each land use (see Albert *et al.* 2010).

For each EP we thus produced one map based on pure land use effects (*LU*) and one map based on the combination of abiotic and traits effects (*trait + abiotic*). Given that the number of measured plots was insufficient for splitting into calibration and validation subsets, the two models were compared visually using mapped differences in estimates and comparisons across models of calculated total EP values per land use type.

Ecosystem services were related to ecosystem properties according to indicators identified by stakeholders (Quétier *et al.* 2007, 2010) or experts (e.g. Martin *et al.* 2009) (Table 1). This approach based on social evaluation of ES rather than on a top-down scientific expert approach (e.g. Millennium Ecosystem Assessment 2005) makes it possible to quantify service provision as perceived by stakeholders (Bryan *et al.* 2010). Although necessarily site-specific (e.g. the negative perception of litter accumulation for cultural value – see Quétier *et al.* 2010 for discussion), such an approach reveals how ecosystems meet local stakeholders' expectations for services. Based on perceptions by stakeholders from the agricultural sector and Martin *et al.* (2009), grassland agronomic value was the sum of green biomass (fodder quantity), fodder quality as indicated by crude protein content, and flowering phenology (mean community onset CWM_Flo and diversity of flowering onset dates FD_Flo, each with a 0.5 weight so as to give an even weight to phenology as compared to fodder quantity and quality). The inclusion of phenology into agricultural value is important because phenology drives management strategies based on the sharp loss of fodder quality once flowering has begun, especially in grasses (Ansquer *et al.* 2009). Based on perceived indicators (Quétier *et al.* 2010) cultural value was the sum of positive effects of species diversity and flowering diversity (FD_Flo) minus litter mass. A single EP may simply be mapped onto a single ES as for soil carbon content and climate regulation. Overall, following De Chazal *et al.* (2008), we used simple rather than weighted sums of EP

Table 1. Mapping of ecosystem properties to ecosystem services based on stakeholder perception (agronomic value, cultural value; from Quétier *et al.* 2007, 2010) and expert opinion (agronomic value, pollination, soil carbon)

Ecosystem service	Ecosystem properties						
	Green biomass	Litter mass	Crude protein content	CWM flowering	FD flowering	Species diversity	Soil carbon
Agronomic	1		1	½	½		
Cultural		−1			1	1	
Pollination				1	1		
Soil carbon							1

The table presents coefficients used for the summing of individual ecosystem properties to a given ecosystem service based on stakeholders' perceptions, given positive (+1) or negative (−1) contributions. The overall positive contribution of phenology to agronomic value was divided into two variables, community mean and functional divergence of flowering dates, with a weight of ½ each (see 'Materials and methods' section).

to derive ES, because attribution of specific weights would require in-depth analyses of perception and is highly sensitive to both stakeholder sample and context (see also Quétier *et al.* 2009). Also, this method implicitly assumes linear mapping of EP to ES and an exploration of sensitivity of ES projections to their kinds of relationships to EP (Koch *et al.* 2009) is beyond the scope of this study. Ecosystem service maps produced in step 3 were simple sums of maps for relevant EP produced by step 2 (see Table 3) after scaling to a 0–100 baseline and trimming outliers to the 5–95% quantiles (Venables & Ripley 2002). Given that the entire landscape is used for agriculture production, we chose to keep continuous ES values rather than applying threshold values to assign provision (or not) of an ES to a given pixel (e.g. Chan *et al.* 2007).

ANALYSING MULTIPLE ECOSYSTEM SERVICES

The ability of different landscape locations to provide multiple ES was assessed additively across ES. A given EP could contribute to several ES, e.g. diversity of flowering onset dates (FD_Flo) contributed to agronomic, cultural and pollination services; therefore, to avoid double counts, the multiple ES map was a sum of maps for uncorrelated EP using 0–100 scaled values. To understand trade-offs and synergies underlying the provision of multiple ES, a PCA on sampled plots was used to characterize underlying patterns of correlation among EP. Coordinates on the first two axes of PCA were then calculated for each map pixel using the linear combinations of EP produced by the PCA, and the two corresponding maps represented areas of trade-offs or synergies.

Results

LANDSCAPE VARIATIONS IN VEGETATION FUNCTIONAL COMPOSITION

Community mean traits were strongly driven by land use but also influenced by altitude (Table 2; see Appendix S1 and Fig. S1 in Supporting Information). Land use determined community mean vegetative traits directly (LDMC), indirectly (LNC) or through mixed direct and indirect effects (VH and LPC), with indirect effects resulting from fertility responses. Altitude had additive direct negative effects for LNC and LPC. Mean community onset of flowering responded to land use, with additive delays due to decreased temperatures with altitude. Functional divergence within communities was variable but, with the exception of LPC and onset of flowering, had little relationship to land use or topography (Table 2).

DIRECT AND INDIRECT EFFECTS OF LAND USE AND ABIOTIC FACTORS ON ECOSYSTEM PROPERTIES

Models including abiotic factors or traits provided overall better predictions of EP than land-use-alone models, with greater nuances on the predicted effects of land use changes such as cessation of fertilization or mowing (Table 3; Appendix S1; Fig. S2). The *trait + abiotic* model was also the most parsimonious overall for green biomass and soil carbon, while both the *trait + abiotic* and *LU* models had similar empirical support (i.e. differences in AIC < 2) for litter mass, and the *LU* model was most parsimonious for crude protein content in spite of a very large increase in prediction ability (adjusted-R increasing from 43 to 62 from the *LU* to the *trait + abiotic* model).

Green biomass production, predicted by mean community traits VH and LNC and soil WHC, was highest in fertilized and mown terraces and in unmown *Festuca* grasslands, and least in unfertilized terraces and summer grasslands (Fig. 3a). Production was reduced by cessation of fertilization or of mowing in terraces that both promoted shorter and nitrogen-poorer plants, but it increased with cessation of mowing in old grasslands due to the dominance by the large grass *Festuca paniculata*. Fodder quality, predicted by mean community traits VH and LDMC and WHC, was significantly reduced by cessation of mowing, which promoted plants with denser tissues (higher LDMC), both in terraces and in *Festuca* grasslands, and improved by fertilization, which increased plant stature and decreased leaf density (LDMC) in terraces (Fig. 3b). Litter mass, predicted by VH, LPC (with CWM and FD for both) and LDMC (CWM only), was greatest following cessation of mowing in both terraces and old grasslands (Fig. 3c). For terraces especially, as well as for other grazed grasslands, litter significantly decreased with altitude, reflecting a decrease in CWM_LPC. Soil carbon stocks, predicted by mean community traits LDMC and LPC, were greatest in mown grasslands, especially in fertilized ones, and in summer grasslands (Fig. 3g). They decreased with altitude following

Table 2. Summary of statistics from General Linear Models of abiotic variables and functional diversity components, trait community-weighted mean (CWM) and functional divergence (FD)

Variable	Model	*R*	AIC	d.f.	LUT	Altitude	Radiation	WHC	NNI	PNI
Abiotic variables										
WHC	Single				< 0.001	0.009	0.024			
	Multiple	67.1	62.3	9	< 0.001	0.031	–			
NNI	Single				< 0.001	0.035	0.015	< 0.001		
	Multiple	55.8	58.6	9	< 0.001	–	–	0.045		
PNI	Single				< 0.001	0.003	0.134	0.309		
	Multiple	43.5	60.4	9	0.001	0.05	–	–		
Fertility index	Single				< 0.001	0.712	0.506	0.06		
	Multiple	59.5	56.6	8	< 0.001	–	–	–		
Traits										
CWM_VH	Single				< 0.001	0.035	0.024	0.031	< 0.001	0.749
	Multiple	79.0	67.8	9	< 0.001	–	–	–	0.004	–
CWM_LDMC	Single				0.01	0.044	0.261	0.488	0.205	0.011
	Multiple	22.4	55.6	8	0.01	–	–	–	–	–
CWM_LNC	Single				< 0.001	< 0.001	0.272	0.862	0.002	< 0.001
	Multiple	58.5	62.9	3	–	0.008	–	–	–	–
CWM_LPC	Single				< 0.001	< 0.001	0.084	0.332	0.177	< 0.001
	Multiple	80.9	59.6	10	< 0.001	0.044	–	–	*0.072*	–
CWM-Flo	Single				0.012	0.259	0.201	0.072	0.038	0.232
	Multiple	45.2	21.5	6	0.012	–	–	–	–	–
FD_VH	Single				0.007	0.023	0.417	0.713	0.369	0.024
	Multiple	24.2	64.9	8	0.007	–	–	–	–	–
FD_LDMC	Single				0.268	0.627	0.279	0.415	0.198	0.475
	Multiple	NA	NA	NA	NA	NA	NA	NA	NA	NA
FD_LNC	Single				0.072	0.465	0.2	0.64	0.021	0.233
	Multiple	12.7	65.8	8	*0.072*	–	–	–	–	–
FD_LPC	Single				< 0.001	0.018	0.263	0.517	0.173	< 0.001
	Multiple	49.9	59.9	10	< 0.001	0.004	–	0.015	–	–
FD_Flo	Single				0.937	0.001	0.957	0.271	0.24	0.161
	Multiple	35.5	31.2	1	–	0.001	–	–	–	–

For onset of flowering we used Residual Estimates Maximum-Likelihood models with year as a random effect. Single-term estimates and combined model selection were obtained using 'all subsets regression' with adjusted-*R* and Akaike information criterion (AIC) as model ranking criteria. %var, percentage variance explained; d.f., number of degrees of freedom; LUT, land-use type; WHC, water holding capacity; NNI, nitrogen nutrition index; PNI, phosphorus nutrition index; GFI, generalized fertility index; VH, vegetative height; LDCM, leaf dry matter content; MNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; Flo, date of onset of flowering; NA, model not available. Preliminary variable selection was used to choose the best descriptors of fertility for each response variable. Grey cells indicate variables that were not relevant for particular analyses. *P*-values are indicated for each response–explanatory variable combination. – indicates variables that were not retained in best multiple regression models.

CWM_LPC, especially in mown *Festuca* grasslands and summer grasslands, which were also those grasslands with lower production. Plant species diversity increased with soil nitrogen availability (NNI), which reflected mainly land use and a small effect of altitude through effects of WHC on NNI (Fig. 3f, Table 3).

LANDSCAPE PATTERNS IN ECOSYSTEM SERVICE PROVISION

Ecosystem services patterns were comparable between the pure land-use and the trait-based models, although as for EP, absolute effects of land use changes were moderated by trait-based models (Appendix S1). Agronomic value was highest for summer grasslands, which combined high fodder quality and diverse flowering phenology, but had low production due to short vegetation stature (Fig. 3i). Fertilized and mown terraces also had high agronomic value by combining high fodder quantity (green biomass) and quality resulting from tall stature and high LNC, but less diverse flowering dates. *Festuca* grasslands, especially when unmown, had a lower value in spite of their high stature and production, due to their poor fodder quality resulting from low LNC. Unmown terraces and steep slopes had the poorest value with low scores for all four EP.

Table 3. Summary of statistics from General Linear Models of ecosystem properties from abiotic variables and functional diversity components, trait community weighted mean (CWM) and functional divergence (FD)

Ecosystem properties

Variable	Model	R	AIC	d.f.	LUT	Altitude	Radiation	WHC	NNI	PNI	CWM_VH	CWM_LDMC	CWM_LNC	CWM_LPC	FD_VH	FD_LDMC	FD_LNC	FD_LPC
Green biomass	Single				<0.001	0.562	0.043	0.001	<0.001	0.024	<0.001	0.016	<0.001	<0.001	0.06	0.1	0.037	0.036
	LU	63.4	73.6	8	<0.001													
	LU+abiotic	74.2	63.0	10	<0.001			0.029	0.039									
	TRAIT+abiotic	69.9	58.6	4				0.004			<0.001	<0.001	<0.001					
Litter mass	Single				<0.001	0.002	0.09	0.023	0.091	0.036	<0.001	0.507	<0.001	<0.001	<0.001	0.157	0.163	0.009
	LU	66.0	57.4	8	<0.001	NA	NA	NA	NA	NA								
	LU+abiotic	NA	NA	NA	NA	NA	NA											
	TRAIT+abiotic	61.2	56.4	6				0.002			<0.001				<0.001			
Crude protein content	Single				0.016	0.631	0.96	0.048	0.327	0.216	0.047	0.682	0.836	0.074	0.573	0.433	0.544	0.339
	LU	42.7	23.9	7	0.016	NA	NA	NA	NA	NA								
	LU+abiotic	NA	NA	NA	NA	NA			NA	NA								
	TRAIT+abiotic	62.4	26.1	4				0.002			<0.001	0.008						
Soil carbon	Single				0.199	0.052	0.307	0.463	0.362	0.077	0.679	0.4	0.02	0.004	0.053	0.985	0.09	0.051
	LU	9.1	65.1	8	0.199													
	LU+abiotic	23.4	58.3	10	0.046	0.009		0.007										
	TRAIT+abiotic	30.7	59.0	3										<0.001				
Species diversity	Single				0.001	0.137	0.201	0.16	0.004	0.91								
	LU+abiotic	31		10					0.004					<0.001				

LU: simple land use model, *LU+abiotic*: land use and abiotic variables model, *trait+abiotic*: trait and abiotic variables model. Single-term estimates and combined model selection were obtained using 'all subsets regression' with R^2 and Akaike information criterion (AIC) as model ranking criteria. %var, percentage variance explained; d.f., number of degrees of freedom; LUT, land-use type; WHC, water holding capacity; NNI, nitrogen nutrition index; PNI, phosphorus nutrition index; VH, vegetative height; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; NA, model not available. As GFI is a linear combination of NNI and PNI, their inclusion into models is exclusive. Preliminary variable selection was used to choose the best descriptors of fertility for each response variable. Grey cells indicate variables that were not relevant for particular analyses. *P*-values are indicated for each response–explanatory variable combination. – indicates variables that were not retained in best multiple regression models.
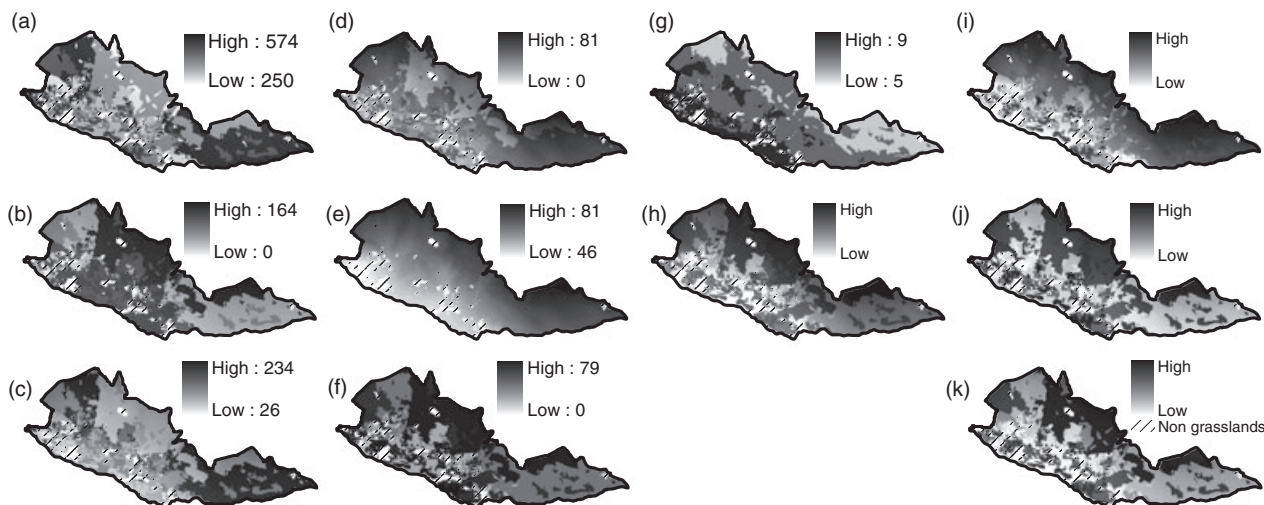
Fig. 3. Modelled distributions of ecosystem properties and ecosystem services. Ecosystem properties: (a) green biomass production (g m^{-2}), (b) fodder crude protein content (g kg^{-1}), (c) litter mass (g m^{-2}), (d) mean date of flowering onset (Julian day), (e) functional divergence of date of flowering onset (unitless), (f) species richness, (g) soil carbon concentration (%). Ecosystem services: (h) pollination value = (e) + (f), (i) agronomic value = (a) + (b) + ½(d) + ½(e), (j) cultural value = (e) + (f)–(c), (k): total ecosystem service value = (a) + (b) + (c) + (d) + (e) + (f).

Overall, agronomic value increased with altitude, which had positive effects on all four EP, especially flowering mean date and diversity. Cultural value was high for mown grasslands, especially in fertilized, and mown terraces, and for summer grasslands, which combined high species diversity, highly diverse flowering phenology and low litter mass, it was lowest for unmown grasslands, especially *Festuca* grasslands, with the opposite attributes (Fig. 3j). This was a direct land use effect for species diversity but a trait-based effect through litter accumulation associated with high LDMC and tall vegetation in unmown *Festuca* grasslands (Table 3). Climate regulation through soil C sequestration was approximated by soil carbon stocks (soil C) as described above. Pollination followed a pattern close to that of cultural value, as species diversity and diversity in flowering dates were common to these services, while species diversity was strongly negatively correlated with litter (R^2 = 0.98, P < 0.001). Total regulation value, combining soil C stocks and pollination, was highest in mown (inter alia) and summer grasslands, with maximum values for fertilized terraces (due to high C stocks and species diversity) and summer grasslands (with high values for all EP) (Fig. 3i). It

was lowest for unmown terraces, followed by unmown *Festuca* grasslands, both having low pollination value resulting from low species diversity and, for unmown terraces, particularly low C stocks due to low LNC.

PROVISION OF MULTIPLE ECOSYSTEM SERVICES

The models summing EP showed that fertilized and mown terraces offered the greatest provision and synergy among ES (Fig. 3k). Summer grasslands were also ES hot spots, despite their low production, which decreased their agronomic value. Mown but unfertilized terraces and mown permanent grasslands showed similar patterns, but with lower provision intensity for all services. In contrast, unmown *Festuca* grasslands were areas of trade-offs among services, with large production potential but low cultural and soil C stocks value. Steep slopes were also ES trade-off areas with lower agronomic value and low C stocks, but higher cultural and pollination values. Finally, unmown terraces delivered the least services, with low provision of all ES. Overall, multi-service patterns were strongly consistent between the pure land-use and the
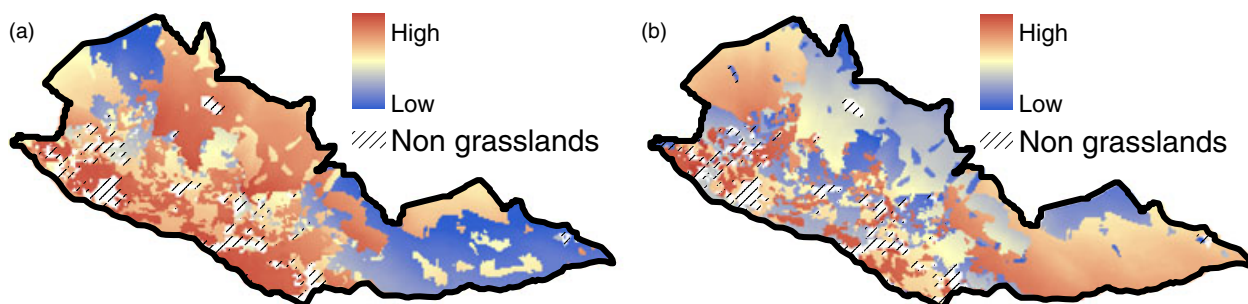

Fig. 4. Projected maps of contrasts among ecosystem properties following ordination by PCA (a) Left panel: axis 1 predominantly associated with cultural value, (b) right panel: axis 2 predominantly associated with green biomass production.

trait-based models (Appendix S1, Fig. 3g,h), although the trait-based model highlighted increased ES with altitude within land use types. The PCA of EPs elucidated these synergies and trade-offs (Fig. 4, Fig. S4). The first axis was driven by contrasts between on the one hand high plant diversity, fodder quality (CPC) and soil C in terraces and summer grasslands, and on the other hand high litter accumulation and low diversity of flowering phenology in unmown *Festuca* grasslands. This axis therefore represented contrasts in cultural value, but also potential conflicts among components of regulation services soil C stocks and pollination. The second axis was mainly driven by contrasts in green biomass production from fertilized terraces (highest production) to summer grasslands (lowest production). It also highlighted a trade-off among fodder quantity and quality contrasting high production of poor quality in unmown *Festuca* grasslands with low production of better quality in summer grasslands, although fertilized terraces had high values for both, and thereby also high agronomic value. Finally, orthogonality between cultural value (axis 1) and production (axis 2) indicated the possibility of reconciling both objectives.

Discussion

INDIRECT LAND USE EFFECTS ON ECOSYSTEM SERVICES THROUGH PLANT FUNCTIONAL TRAITS

Land use or land cover is a practical but imperfect surrogate for ES assessment (Eigenbrod *et al.* 2010). This is the first study identifying direct and indirect effects of land use and associated abiotic environmental variables on ES using alternative models for ecosystem properties at a landscape scale (Fig. 1). All modelled EP showed a direct land use signal. Adding abiotic variables describing topography (altitude) and soil quality (fertility and water holding capacity, themselves related to land use) (*LU + abiotic* model), or representing indirect effects through plant functional traits (*trait + abiotic* model) improved models by often similar levels. With the exception of soil carbon, which was also poorly modelled by land use alone (*LU* model), all EP were remarkably well explained by the statistical models, especially trait-based (*trait + abiotic*) or full abiotic (*LU + abiotic*) models, which afforded better prediction and, in all but the case of litter, equal or better parsimony than the pure land use model (*LU*). Overall, the best *trait + abiotic* models afforded prediction of 60–70% of the variance in EP, with usually two traits and often soil properties (WHC in most cases, nitrogen fertility for the *LU + abiotic* model of green biomass production) and altitude (in the *LU + abiotic* model).

Such a continuous quantification of land use effects within a single land cover type (permanent grasslands) goes one step further than categorical modifiers based on land condition (Naidoo & Ricketts 2006; Reyers *et al.* 2009); but see (Grêt-Regamey *et al.* 2008; Willemen *et al.* 2010). Detailed models including abiotic and/or trait effects captured abiotic heterogeneity within land use types, e.g. a 25% variation in green biomass production, litter accumulation or soil C. Green bio-

mass production measurements for an additional set of 34 independent points in 2010, covering a slightly greater altitudinal range for summer grasslands (100 m higher), validated the representativity of our core sample and predictions by the *trait + abiotic* model (significant regression between observed and predicted green biomass, $P = 0.005$). Detailed models also showed that simple land use models overestimated management change impacts by neglecting increases in predicted EP with altitude within land use types, with marked effects especially for summer grasslands and steep slopes. Altitude effects were detected for all EP either directly in abiotic models (*LU + abiotic*) or indirectly in trait-based models (*trait + abiotic*) through the influence of altitude on community traits (CWM) and field capacity (WHC), and were additive to land use, which is also determined by topography at this site as in other mountain systems (Mottet *et al.* 2006; Gellrich & Zimmermann 2007). These results confirm that for ES assessments in mountainous topography, and especially altitude and its effects on bioclimate, must be taken into account in addition to land cover (Grêt-Regamey *et al.* 2008; Kienast *et al.* 2009). Moreover, the prominent role of WHC in our models emphasizes important effects of current, and especially past, land use on soils. These include fine soil loss and increased stoniness resulting from past cropping on terraces (Bakker *et al.* 2008), long-term effects of organic fertilization on terraces (Robson *et al.* 2007), as well as continued export of organic matter through mowing, which has over the course of history concerned the entire landscape except summer grasslands and steep slopes.

Trait-based models are data-intensive, especially when considering intraspecific trait variation in relation to land use (Garnier *et al.* 2007), but data collection over entire landscapes can be facilitated by standardized and rapid methods (Cornelissen *et al.* 2003; Lavorel *et al.* 2008). For applications such as mapping of ecosystem properties and ES, trait measurements for randomly sampled individuals (Gaucherand & Lavorel 2007; Baraloto *et al.* 2009) or for entire swards or canopies (Stewart, Bourn & Thomas 2001) offer an interesting alternative to the tedious collection of species-level trait data. Landscape- and especially regional-scale applications can also now strongly benefit from the availability of plant functional trait data bases (Kleyer *et al.* 2008; Kattge *et al.* 2010), although caution is warranted with respect to trait variability in response to especially fertility (Lavorel *et al.* 2009). Such data bases will make it possible to assess ES provision at regional scale by coupling trait and vegetation data bases. Finally, remotely sensed trait surrogates such as spectral signatures of leaf chemistry (Ustin & Gamon 2010) also offer great promise for the application of such trait-based models over large scales.

ECOLOGICAL MECHANISMS UNDERLYING ECOSYSTEM SERVICE RESPONSES TO LAND USE

Trait-based assessments of global change effects on ecosystems and ES can reduce uncertainty in projections of land futures (Diaz *et al.* 2007). Prediction of ES change through traits hinges on overlaps of response and effect traits, where

traits that determine response to abiotic and land use changes are equal or correlated to traits determining effects on ecosystem functioning (Lavorel & Garnier 2002). Here all vegetative traits responded strongly to land use, except LNC, which had an indirect response through fertility effects. These same traits underpinned relevant EP, thereby providing a link from land use to EP. There is increasing evidence for such overlaps in response and effect traits (Suding & Goldstein 2008), of which this is the first landscape-scale demonstration. In addition, we were able to integrate abiotic (topography and soils) and land use effects with a parsimonious set of traits, namely plant height and key leaf traits associated with plant resource economy (Diaz *et al.* 2004). These traits have demonstrated links to biomass production, litter decomposition, fodder quality or soil water retention from species (Kazakou *et al.* 2006; Pontes Da Silva *et al.* 2007) to community level (Garnier *et al.* 2004, 2007; Gross *et al.* 2008; Fortunel *et al.* 2009). Vegetative height and LDMC were strong response traits with effects on several EP, and could therefore be used as functional markers of ES change (Garnier *et al.* 2004). Considering landscape distribution of EP in response to land use and abiotic factors requires working at community level, where trait responses and effects are indicated by community-weighted means and functional diversity (Diaz *et al.* 2007; Garnier *et al.* 2007). Analyses of this landscape-wide data set confirmed the greater relevance of CWM traits than of functional divergence identified for a subset of 15 plots with similar altitudes (Diaz *et al.* 2007). Only for litter accumulation did the inclusion of FDs for vegetative height and leaf phosphorus concentration markedly improve the prediction from models using CWM traits (61% vs. 44% variance explained). Negative effects of FD on litter accumulation suggested improved decomposition of more diverse mixes of litter types (Gartner & Cardon 2004; Scherer-Lorenzen 2008).

ASSESSING MULTIPLE ECOSYSTEM SERVICES

Ecosystem services were even-weight sums of relevant EP, and likewise for the assessment of multiple services (De Chazal *et al.* 2008). Alternative methods may use weights elicited from stakeholders (Gimona & van der Horst 2007) (for example, farmers at this site rank fodder quantity, phenology and quality differently depending on field functions in their farming system) or different weights across stakeholder groups (see De Chazal *et al.* 2008), or across alternative future scenarios (Quétier *et al.* 2009). The following discussion focuses on the benefits of plant functional trait information to understand the mechanisms underlying ES provision. Through its component EP, agronomic value was influenced evenly by vegetative height and leaf traits (LNC and LDMC being negatively correlated), with soil WHC and altitude as modifiers. These traits, as well as WHC, propagated a strong land use signal and a fairly strong altitude signal (Table 3). The negative correlation between green biomass production (fodder quantity) and Crude Protein Content (fodder quality) (PCA axis 2) reflects opposite effects of plant height on these two EP and captures effects of *Festuca paniculata* and other tall grasses with poor

nutritive quality, especially after flowering, in contrast with smaller species of high value such as legumes (e.g. *Astragalus danicus*, *Oxytropus campestris*) and some dicots (e.g. *Helianthemum grandiflorum*, *Potentilla aurea*) found in summer grasslands. Having species with tall stature and/or high LNC (e.g. *Dactylis glomerata*, *Heracleum sphondylum*, *Onobrychis montana*), fertilized terraces scored high for both quantity and quality. Height and leaf traits such as LNC have indeed been shown to be independent axes of functional variation over continents (Diaz *et al.* 2004) and for this site (Gross, Suding & Lavorel 2007). Diversity of flowering dates (PCA axis 1) added a dimension of variation in agronomic value by being independent from these vegetative traits. Such a combination of independent EP based on independent traits supported the overall value of summer grasslands in spite of their low production, or of fertilized terraces in spite of less diverse flowering dates. Cultural and regulation values shared similar patterns through common EP species diversity and flowering diversity, and the negative correlation ($R^2 = 0.89$, $P < 0.001$) between litter (negative component of cultural value) and soil C (positive component of regulation value). Cultural value was strongly influenced by the well-known negative correlation between litter and species diversity (PCA axis 1; $R^2 = 0.97$, $P < 0.001$), with an additional positive altitude effect through flowering diversity. High cultural value could be attained alternatively with short height (summer grasslands) or with high LPC (fertilized terraces). The regulation value was influenced by two leaf traits LDMC and LNC, with an additional positive altitude effect through flowering diversity. The negative correlation among these leaf traits afforded alternative pathways to increased soil C in fertilized terraces (high LNC), in lower unfertilized terraces and unmown *Festuca* grasslands (high LDMC), and in the lower part of summer grasslands (higher LDMC and LNC). Lower unfertilized and mown terraces and unmown *Festuca* grasslands had higher regulation than cultural value due to this higher soil C.

Consistent with other recent studies, there was a landscape-scale diversity of associations among different types of ES (Chan *et al.* 2007; Naidoo *et al.* 2008; Egoh *et al.* 2009). Service hotspots, with synergy among nearly all services, were fertilized terraces and summer grasslands, which currently represent 5% and 23% of the landscape, respectively. Conversely, unmown *Festuca* grasslands, which represent 28% of the landscape, appeared as areas of trade-offs among services. Unmown terraces (11% of the total area) were services cold spots with low provision for all services, yet our analysis did not consider their agronomic function in terms of spatial complementarity during the annual cycle (Andrieu, Josien & Duru 2007). Ecosystem services hot spots coincided with higher species and functional diversity (Fig. 3, Fig. S1), while areas of ES trade-offs and cold spots were least diverse, suggesting that, unlike in other regions and especially with more intensive agriculture (Chan *et al.* 2007), sustainable management could simultaneously conserve biodiversity and locally important ES. The synergy among multiple ES was facilitated by both the independence of components of agronomic (green biomass production) vs. cultural and regulation services (litter and spe-

cies diversity) (orthogonal ordination in the PCA), and the common and/or positively correlated EP contributing to cultural and regulation services (plant diversity, soil C), providing the mechanisms for how at multi-functionality hot spots different ES enhance one another (Bennett, Peterson & Gordon 2009; Willemen *et al.* 2010). These patterns of independence or conversely correlation were in part related to dominant traits underlying each service. Vegetative height, which determined green biomass production and fodder quality, was a key driver of agronomic value whereas leaf traits played a stronger role for components of regulation and cultural values (soil C, litter). The functional decoupling between these two sets of traits thus contributes not only to agronomic value but also to high multiple ES delivery by fertilized and mown terraces–and conversely to the low score for unmown terraces, with the other land use types scoring high for one but not another service. Consequently, production can be enhanced by moderate organic fertilization without degrading other ES and the biodiversity that underlies them, as long as appropriate leaf traits are promoted. The future vulnerability of ES hotspots will also be directly linked to land use and possible climate change effects on plant traits (Quétier *et al.* 2007).

Conclusion

Models of ES using abiotic variables and plant traits rather than land use alone afford refined representation of relevant ecosystem properties. They also unravel mechanisms controlling ES delivery, and trade-offs or synergies in provision of multiple ES. Trait-based approaches may be generalized to services provided by other organisms than plants (e.g. pollination, pest control) (De Bello *et al.* 2010). Alternative methods to simple statistical models include structural equation models (Grace 2006) and process models (Nelson *et al.* 2009) and more complex approaches could be considered for aggregation of ecosystem properties and of ES to address multi-functionality. In a subalpine grassland landscape traditional land uses such as organic fertilization and mowing or altitude summer grazing supported ES hot spots because functional characteristics supporting production and fodder quality are compatible with species and functional diversity. Conversely, key vulnerabilities are expected from land change that decreases biodiversity and promotes plant types associated with ES cold spots and/or strong trade-offs among services. The relevance of this model to broader and more diverse landscapes needs to be tested to explore more extreme scenarios including agricultural abandonment and woody encroachment.

Acknowledgements

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Supporting Information

Figure S1. Modelled maps of abiotic environmental variables and plant functional diversity.

Figure S2. Comparison of modelled ecosystem properties using a land-use-only model (M1) vs. the full model including direct abiotic effects and indirect effects through plant functional diversity (M3).

Figure S3. Modelled ecosystem services using a land-use-only model vs. the full model including direct abiotic effects and indirect effects through plant functional diversity.

Figure S4. Results from the Principal Components Analysis on Ecosystem Properties.

Appendix S1. Comparison of models of ecosystem properties and ecosystem services.

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