

PLANT-TRAIT-BASED MODELING ASSESSMENT OF ECOSYSTEM-SERVICE SENSITIVITY TO LAND-USE CHANGE

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Abstract. Evidence is accumulating that the continued provision of essential ecosystem services is vulnerable to land-use change. Yet, we lack a strong scientific basis for this vulnerability as the processes that drive ecosystem-service delivery often remain unclear. In this paper, we use plant traits to assess ecosystem-service sensitivity to land-use change in subalpine grasslands. We use a trait-based plant classification (plant functional types, PFTs) in a landscape modeling platform to model community dynamics under contrasting but internally consistent land-use change scenarios. We then use predictive models of relevant ecosystem attributes, based on quantitative plant traits, to make projections of ecosystem-service delivery. We show that plant traits and PFTs are effective predictors of relevant ecosystem attributes for a range of ecosystem services including provisioning (fodder), cultural (land stewardship), regulating (landslide and avalanche risk), and supporting services (plant diversity). By analyzing the relative effects of the physical environment and land use on relevant ecosystem attributes, we also show that these ecosystem services are most sensitive to changes in grassland management, supporting current agri-environmental policies aimed at maintaining mowing of subalpine grasslands in Europe.

Key words: central French Alps; climate change; ecosystem management; LAMOS (landscape modeling shell); land-use change scenarios; leaf-height-seed plant strategy scheme (LHS); subalpine grasslands.

INTRODUCTION

Evidence is accumulating that the continued provision of essential ecosystem services is vulnerable to land-use change (Foley et al. 2005, Millennium Ecosystem Assessment 2005, Tscharntke et al. 2005). In upland and mountain grasslands of Europe for instance, unpalatable and low-diversity grasslands associated with decreasing agro-pastoral use and abandonment lead to the loss of important ecosystem services such as soil fertility, slope, and snow stability as well as plant, bird, and insect diversity (Bignal and McCracken 2000, Gibon 2005). In this context, policy response for enhancing or conserving ecosystem services has focused on incentives for continued cutting of grasslands (MacDonald et al. 2000). Such ecosystem management recommendations are based on the assumption that the main drivers of ecosystem provision operate at the scale of management units. Yet, we lack a strong scientific basis for this assumption as the processes that drive ecosystem-service delivery often remain unclear (Kremen 2005, Lemaire et al. 2005, Hobbs et al. 2006). To

address this situation, Kremen (2005) has proposed the development of a research agenda centered on understanding how, and at what spatial and temporal scales, community dynamics and environmental factors influence “key ecosystem-service providers.”

We suggest using plant traits and trait-based plant classifications (plant functional types, PFTs) as “key ecosystem-service providers” (sensu Kremen 2005). Plant traits relate to universal plant functions of growth (e.g., light and nutrient acquisition, water use efficiency) and persistence (e.g., recruitment, dispersal, defense against herbivores, and other disturbances; Weiher et al. 1999). They provide a widely applicable framework for interpreting and predicting shifts in community structure in response to environmental factors (Hodgson et al. 1999, Thuiller et al. 2004, 2006, Lavorel et al. 2007). Plant traits also offer potential for linking community structure to ecosystem functions (Naeem and Wright 2003). For example, leaf traits such as leaf nitrogen content (LNC) are markers of plant nutrient economy (Wright et al. 2004) and are associated with faster nutrient cycling at the ecosystem level (i.e., higher productivity, faster litter decomposition; Garnier et al. 2004). Corresponding ecosystem efficiency is an important ecosystem attribute for services such as soil fertility or fodder production.

The ecophysiological and ecological foundation of plant traits also makes them particularly useful in

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generic process-based modeling environments (Epstein et al. 2001). These are essential tools for exploring the various spatial and temporal scales at which ecosystem-service delivery operates (Kremen 2005, Lemaire et al. 2005). Trait-based landscape succession models have been applied successfully to bridge the gap between community and landscape level processes and guide ecosystem management (e.g., Moore and Noble 1990, Pausas 1999).

Such models address key requirements to represent landscape-level processes in a way that can be related to management questions (Turner et al. 2001). This includes the representation of population dynamics (Turner et al. 1995), spatially explicit dispersal in heterogeneous habitat (With et al. 2002), and patterns of land use and natural disturbances (Dale and Pearson 1997, Dale and van Winkle 1998).

As an example, LAMOS (landscape modeling shell) is a landscape modeling platform designed to account for basic vegetation dynamic processes that result from the interactions between plant functional traits, habitat conditions, disturbances and spatial pattern (e.g., Cousins et al. 2003, Grigulis et al. 2005). We use LAMOS and plant traits to make projections of ecosystem-service provision on the basis of contrasting land-use change scenarios. These scenarios provide a realistic context for investigating the effects of land-use change on ecosystem services, in a dynamic landscape setting. Projections will be used to rank current land-use practices (mowing and fertilization), physical environmental factors (underlying altitudinal gradient in fertility), and land-use legacies as drivers of ecosystem-service provision at the landscape scale. Ecosystem services for which land-use drivers are most important are most likely to be more sensitive to land-use change. Ecosystem services for which physical environmental factors are most important are likely to be more sensitive to changes in climate, for example. By enabling us to factor in dispersal, LAMOS also allows us to test the importance of that essential landscape-level process.

By linking plant traits and ecosystem services, this study aims to test the usefulness of trait-based approaches in providing a stronger scientific basis for ecosystem-service management in our changing environment.

STUDY SITE, ECOSYSTEM SERVICES, AND RELEVANT ECOSYSTEM ATTRIBUTES

Study site

The study site is set on the south facing slopes of the valley above the village of Villar d'Arène in the central French Alps (45°2'24" N, 6°20'24" E). It covers 1292 ha at the headwater of the Romanche River. The climate is subalpine with a strong continental influence due to a rain shadow effect with respect to dominant westerly winds. Mean annual rainfall is 956 mm, and the mean monthly temperatures at 1650 m (lowest point in the study site) range between -2.6°C in January and 13°C in

July. At the upper limit of former arable land use (2050 m), temperatures range from -4.6°C in January to 11°C in July.

Grasslands in Villar d'Arène have a long history of agricultural and pastoral land use. Former arable fields (1650–2000 m) have been abandoned and subsequently converted to grasslands used for hay or grazing. Former (never plowed) hay meadows (1800–2500 m) are increasingly converted to light summer grazing by sheep or cattle or no longer used for agriculture. Lavorel et al. (2004) showed that grasslands on former arable land have distinct floristic composition and aggregated plant trait values compared to never ploughed grasslands. This result suggests that any understanding of current vegetation patterns must take into account land-use legacies (Foster et al. 2003). We consider two hypotheses in explaining these land-use legacies. The first one is that late-successional grasses have limited dispersal ability and/or are prevented from colonizing post-arable grasslands by unknown edaphic factors. The second hypothesis is that assembly history in post-arable grasslands makes them resistant to later invasions by late-successional tussock grasses, as suggested in F. Quétiér, P. Liancourt, A. Thébault, I. Davies, and S. Lavorel (*unpublished manuscript*).

Ecosystem services provided by subalpine grasslands

The current landscape is dominated by grassland ecosystems that are still used by a small, but nevertheless active farming community based on sheep and cattle rearing for lamb and steer production. The site is located in the buffer zone of the Ecrins National Park and receives many thousands of visitors annually attracted by opportunities for outdoor recreation, the spectacular mountain setting, and its abundant and diverse fauna and flora. The contrast between the wilderness of the glaciated Meije massif and the gentle grassland landscape of the opposing south-facing slope is one of the main attractions to Villar d'Arène. Indeed, tourism has taken over agriculture as the dominant economic activity. Former arable land has given the landscape a unique distinctiveness in the form of terraced slopes extending up to 2000 m above sea level. This "heritage" of the former land-use system makes this cultural landscape the focus of numerous preservation efforts including subsidies to the remaining farmers (Parc National des Ecrins 2004).

Using 45 semi-guided interviews, we found that local people and visitors refer to a variety of ecosystem services and liabilities from local grasslands (Rivoal 2004; F. Quétiér, F. Rivoal, P. Marty, J. de Chazal, W. Thuiller, and S. Lavorel, *unpublished manuscript*). Farming systems are heavily constrained by winter fodder requirements and all machinery-accessible grasslands are cut for hay at present. Relative to winter fodder stocks, available grazing area is not limiting in current farming systems. Rather, shepherds recognize that selective grazing favours large unpalatable tussock

TABLE 1. People, ecosystem services, and relevant ecosystem attributes in subalpine grasslands of Villar d'Arène.

Stakeholder group	Ecosystem service	Stakeholder descriptions of ecosystem attributes	Modeled relevant ecosystem attributes
Local farmers	grass quantity for hay and grazing	aboveground biomass in mown grasslands, sward height, palatability for grazing	aboveground biomass in mown grasslands, sward height, palatability for grazing
Local farmers	forage quality	crude protein content, relative abundance of legumes	crude protein content, relative abundance of legumes
Visitors and locals	flowering diversity for aesthetic value	plant diversity	Simpson's biodiversity index
National Park Authority	conservation of biodiverse grasslands	plant diversity	Simpson's biodiversity index
Locals	appropriate stewardship of cultural landscape features, snow-gliding risk	large accumulations of dead grass	spring litter in unmown grasslands

grasses. Grass quantity is thus an important ecosystem service for hay whilst grass quality (palatability and nutritional value) is an important ecosystem service for grazing. Plant diversity contributes to landscape aesthetics. It also contributes to biodiversity conservation objectives of the Ecrins National Park (Parc National des Ecrins 2004). Some people worry about signs of inappropriate 'stewardship' that diminish cultural heritage value. All local people acknowledge that poor land-use practices can increase snow gliding and associated avalanche and landslide risk.

Relevant ecosystem attributes

Based on the above-mentioned interviews and our agronomical and ecological expertise, we made assumptions about relevant ecosystem attributes (Table 1). Grass needs to be available in sufficient quantity and quality for both hay and grazing. Sward height increases grazing efficiency through increased individual bite mass (Parsons et al. 1994, Prache and Peyraud 1997). Increasing leaf toughness (tensile strength) decreases grazing efficiency by decreasing bite frequency, either by increasing the time necessary for handling (e.g., chewing; Illius et al. 1995) or selection (increasing bite interval). Quantities available for hay can be equated to aboveground biomass at cutting date. Crude protein content is an indicator of its nutritional value (Bruinenberg et al. 2002). Local farmers evaluate forage quality on the basis of legume abundance (Rivoal 2004). Plant species diversity can be characterized using standard indices such as Simpson's inverse index. Signs of inappropriate stewardship relate to grasslands being under used. Local people use accumulated litter in the spring as an indicator of under-utilization (Rivoal 2004). Snow gliding risk also increases with litter accumulation as long-bladed grass mats form ideal gliding surfaces (Newesely et al. 2000, Tasser et al. 2003).

METHODS

Trait-based modeling of relevant ecosystem attributes

Using Westoby's Leaf-Height-Seed (LHS) model of plant functional types (Westoby 1998), we clustered the

dominant graminoids of subalpine grasslands into four LHS-based PFTs. By focusing on graminoids, we explored trait combinations within rather than across growth forms (as suggested in Lavorel et al. 1997). We used plant traits measured on species \times land-use trajectory combinations where species were considered to have the same trait value across plots within the same land-use history. We thus took into account intraspecific variability, acknowledging that functional type membership is conditional (Dyer et al. 2001). All whole-plant and leaf trait measurements followed Cornelissen et al. (2003). LHS-based PFTs obtained were named after the archetype species in each cluster: *Bromus* PFT, *Dactylis* PFT, *Festuca* PFT, and *Sesleria* PFT (F. Quétier, P. Liancourt, A. Thébault, I. Davies, and S. Lavorel, *unpublished manuscript*). They have contrasting nutrient economies (i.e., position on the nutrient acquisition/conservation trade-off indicated by high/low leaf nitrogen content, respectively; see Wright et al. 2004). Results also suggest that they have contrasting competitive effects (e.g., taller plants intercept more incoming light) and responses (e.g., heavier seeds confer better germination potential at low light) (Goldberg and Landa 1991). We used these PFTs to parameterize LAMOS.

LAMOS simulates the abundance of plant functional types in relation to site productivity and disturbance over a landscape map. Here, we applied a configuration of LAMOS using the FATE model (functional attributes in terrestrial ecosystems; Moore and Noble 1990; see also Pausas 1999) to drive within-pixel successional dynamics (e.g., Cousins et al. 2003, Grigulis et al. 2005). FATE is an age-structured population model that determines the abundance (equated to cover) of competing PFTs based on a simple set of traits relating to plant life history, tolerance to shading at different life stages, disturbance response of established plants, and recruitment (Noble and Gitay 1996). Each PFT's response to fertility was assumed to follow a logistic function (Walker et al. 1989), whose shape is determined by the position of each PFT along the spectrum of nutrient economics (Wright et al. 2004). Hence PFTs with high LNC can produce significant biomass only at

TABLE 2. Land-use change scenarios used to map coherent combinations of disturbance and soil resources across the simulated landscape.

Past and current land-use	Future land-use			
	Scenario A1	Scenario A2	Scenario B1	Scenario B2
Past use: cultivated				
Fertilized and mown	NL	fertilized and mown	mown	fertilized and mown
Mown	NL	fertilized and mown	mown	fertilized and mown
Extensively grazed	NL	NL	NL	fertilized and mown
Past use: mown				
Mown	NL	NL	mown	mown
Extensively grazed	NL	NL	NL	NL

Notes: A1 is a global and materialist scenario where agro-pastoral land use is abandoned as financial support to marginal agriculture disappears and European agricultural markets open to international trade. A2 is a regional and materialist scenario in which financial support dwindles but European agricultural markets become local, giving a premium to local dairy and meat produce. B1 is a global environmentally and socially conscious scenario where subsidies for mowing-for-biodiversity increase; allowing mowing to continue. The B2 scenario is a regional environmentally and socially conscious future where agricultural subsidies promote self-reliance in local communities as a solution to environmental issues. “NL” indicates no land use.

high levels of fertility, whereas PFTs with low LNC are tolerant of low fertility (i.e., they can produce biomass) but have a lower increment of biomass per unit of fertility. For each PFT the fertility response curve is hence characterized by a lower nutrient threshold parameter, which is also correlated with the slope of the curve. Competition for nutrients is not represented directly in LAMOS-FATE, but site fertility affects density at recruitment, where the population size of recruits is scaled to fertility using the fertility response curve of each PFT.

Mowing was simulated as a uniform disturbance, removing 60% of the total standing biomass annually, whatever the vegetation composition, and with maximum impact (called “severity” in LAMOS). All mature PFT individuals and 90% of immature *Festuca* PFT resprout following mowing, effectively keeping them immature. The remaining 10% immature *Festuca* PFT are killed while immature *Bromus*, *Dactylis*, and *Sesleria* PFT and all propagules escape mowing unaffected (Jougle and Dorée 1991). LAMOS also makes it possible to test alternative hypotheses about dispersal capacities of different PFTs, in its simplest form by restricting dispersal to the pixel where seeds are produced (i.e., “local dispersal”).

In the absence of reliable information on seed shadows for common graminoid species of the study site, dispersal was simulated as unlimited, where seed rain is homogeneous across the landscape map (“bath dispersal”). Alternatively, we imposed a dispersal limitation on the *Festuca* PFT, using the “local dispersal” option. This approach should be seen as a coarse attempt to address the current lack of knowledge on the potential colonization by this PFT of former arable fields where it is currently absent after five decades of agricultural abandonment (Lavorel et al. 2004).

We used nine different maps corresponding to one current and four scenario-based future distributions of mowing and fertilization (Table 2), with or without a dispersal constraint on the *Festuca* PFT ($4 \times 2 = 8$ maps).

Land-use change scenarios

Land-use change scenarios are based on local projections of European-wide land-use change scenarios described in Rounsevell et al. (2006) and formulated on the basis of global storylines (Nakicenovic et al. 2000). These proposed an understanding of trends that opposed a global (type 1 scenario) and a regional (type 2 scenario) future on the one hand and on the other hand a materialist (type A scenario) and an environmentally and socially conscious (type B scenarios) future. Rounsevell et al. (2006) related the global storylines to relevant socio-economic drivers of land-use change at the European scale. We build on their results to propose four contrasting land-use scenarios for Villar d'Arène. These scenarios were developed in collaboration with local and regional stakeholders of farming, rural development, and nature conservation interests to guarantee that they are locally plausible (Daigney 2005).

These consistent land-use scenarios provide us with socioeconomically plausible combinations of resources, disturbance and land-use legacies for modeling land-use change effects on ecosystem services at the landscape scale (Tschardt et al. 2005). Each map includes an underlying fertility gradient set to reflect the site's altitudinal gradient. At the high-end of the gradient, no PFTs are nutrient limited while they all are at the low-end. The distribution of past plowing is fixed and shared across all nine maps. The location of fertilization and management by mowing is scenario dependent.

*Projecting relevant ecosystem attributes
from LAMOS simulation outcomes*

The aggregated trait value of each simulated pixel can be calculated by averaging the trait values of the LHS-based PFTs co-existing in the community and weighing them by each PFT's abundance (Lavorel and Garnier 2002). Traits used in the analysis are leaf nitrogen content (LNC), maximum plant height (stature), and leaf tensile strength.

Some plant traits translate directly into relevant ecosystem attributes. For instance, LNC and leaf tensile strength translate into crude protein content (CP6.25; Conklin-Brittain et al. 1999) and palatability (Illius et al. 1995), respectively. Sward height was measured weekly over the growing season, as the average of 10 random measurements. Relative abundance of legumes and Simpson's biodiversity index were calculated from point-quadrat surveys (Lavorel et al. 2004).

Aboveground standing biomass was harvested in early spring (around 10 May; 64 degree-days) and full summer (around 10 July; 635 degree-days) using four samples of 0.25 m². Harvests were sorted into senescent and living material and oven dried at 60°C for 48 hours to calculate maximum aboveground biomass in mown grasslands and spring litter in un-mown grasslands. Based on previous field work described in Quétier et al. (2007), aboveground biomass in mown plots was assumed to relate to ecosystem productivity and hence to LNC. Litter accumulated in spring was assumed to result from either leaf tensile strength (low palatability) or LNC (through decomposition rate).

Data collected on field plots representing the dominant land-use change trajectories was used to fit generalized linear models linking ecosystem attributes relevant to ecosystem-service delivery to the relative abundance of PFTs and their aggregated trait values. Statistical analysis was carried out in S-Plus (version 6.0.2, release 1; Insightful Corporation, Seattle, Washington, USA).

*Ranking management, and environmental factors
driving ecosystem-service provision*

Each map is a 70 × 100 pixel schematic representation of the study site (7000 data points). To overcome the nonindependence of pixels across maps, we extracted one data point from each location (i.e., a 7000-point data set), each point being chosen at random between the available maps. Data extraction and analysis was repeated 10 times.

We used the 10 data extractions to rank management and environmental factors driving ecosystem attributes relevant for the various ecosystem services identified in the study site. We used an extension of usual regression tree technique called "random forests" (Breiman 2001), whereby relevant ecosystem attributes (response variable) are recursively separated into increasingly homogeneous groups (pixels) defined by predictor variables. The resulting model defines terminal groups in terms of

a combination of decision rules based on threshold values for the selected predictor variables. In "random forests," bootstrap samples are drawn to construct numerous trees (we use 1000), each one grown on a randomized subset of predictor variables. The trees are grown to maximum size without pruning, and aggregation is by averaging the trees. Each model is validated on an "out-of-bag" sample that was not used in the bootstrap construction of the model. The out-of-bag samples are used to calculate an unbiased error rate and variable importance, eliminating the need for a test set or cross-validation. Because a large number of trees are grown, there is limited generalization error (that is, the true error of the population as opposed to the training error only). Analyses were carried out in R package 2.2.0 (R Development Core Team 2005) using the *randomForest* library.

We used a continuous (fertility) and five binary (management, fertilization, land-use legacies, and dispersal) predictor variables to investigate their relative importance in model construction for each relevant ecosystem attribute. Their importance was assessed as the percentage increase in error rate when the predictor variable is randomly shuffled (permutation) in the out-of-bag sample used for validation of the model. The bigger the increase, the more important the factor is in explaining the predicted variable.

RESULTS

*Land-use change scenarios used for projecting
relevant ecosystem attributes*

A1 is a global and materialist scenario where agropastoral land use is abandoned as financial support to marginal agriculture disappears and European agricultural markets open to international trade (Table 2). A2 is a regional and materialist scenario in which financial support dwindles but European agricultural markets become local, giving a premium to local dairy and meat produce. This process drives intensification of grass management on the most productive and accessible parts of the study landscape (former arable fields that are currently mown). B1 is a global environmentally and socially conscious scenario where subsidies for mowing-for-biodiversity increase; allowing mowing to continue. The B2 scenario is a regional environmentally and socially conscious future where agricultural subsidies promote self-reliance in local communities as a solution to environmental issues. This process favors sustainable stewardship of the grassland resource through fertilization and mowing. Table 2 illustrates the combined distribution of fertilization and mowing relative to past plowing for future scenarios and the current land-use patterns.

Projecting relevant ecosystem attributes from plant traits

Table 3 gives details of the generalized linear models obtained using field data on aggregated plant traits and relative abundance of LHS-based PFTs. Sward height

TABLE 3. Generalized linear models used to link relevant ecosystem attributes to plant traits and plant functional type (PFT) abundances in field plots.

Plant traits and functional types	Value	SE	<i>t</i>	Model explained deviance
Aboveground biomass in mown plots (Mg/ha; <i>n</i> = 9 plots)				
Intercept	−0.853375	1.49768	−0.57	60.21%
LNC	3.37	1.04	3.25	
Sward height (cm; <i>n</i> = 15 plots)				
Intercept	8.249507	16.862	0.49	56.72%
Stature (cm)	0.31	0.29	1.09	
<i>Festuca</i> PFT abundance	5.18	7.40	0.70	
<i>Dactylis</i> PFT abundance	103.31	31.48	3.28	
Legume relative abundance (<i>n</i> = 30 plots)				
Intercept	−28.14	43.14	−0.65	56.59%
<i>Sesleria</i> PFT abundance	0.90	2.58	0.35	
LNC	33.27	55.96	0.59	
LNC ²	−10.64	17.86	−0.60	
Simpson's biodiversity index (<i>n</i> = 30 plots)				
Intercept	−17.54	18.07	−0.97	55.28%
LNC	23.82	22.39	1.06	
LNC ²	−7.44	6.79	−1.10	
Spring litter in unmown plots (Mg/ha; <i>n</i> = 6 plots)				
Intercept	−1.49	0.57	−2.62	96.82%
Leaf tensile strength (g/cm)	0.0008	0.0001	11.04	

Note: "LNC" is leaf nitrogen content.

was well predicted by plant stature with a correction based on the relative abundance of *Dactylis* and *Festuca* PFTs, aboveground biomass being predicted by LNC and spring litter by leaf tensile strength. Simpson's biodiversity index showed a quadratic relationship with LNC; analogous to the hump-backed relationship linking biodiversity to productivity (Waide et al. 1999). Relative abundance of legumes was predicted by the relative abundance of the *Sesleria* PFT (which shares their small stature) and LNC (indicating soil fertility). Using results obtained across sampled field plots (Table 3), we generated landscape-scale projections of relevant ecosystem attributes using LAMOS. It is important to realize that our results should be interpreted at the landscape scale and not used for within-map comparisons.

By design, the A1 scenario had no mowing and grass for hay (aboveground biomass in mown grasslands) and is hence not represented in Fig. 1. Spring litter in unmown grasslands, grass palatability, and legume abundance were the only relevant ecosystem attributes that were noticeably different between scenario projections (Fig. 1). They mainly opposed scenarios A1, A2, and B1 on the one hand and B2 on the other (Fig. 1). The decrease in palatability and increase in spring litter was however strongest in the A1 scenario where it was associated with a slight, but significant decrease in crude protein content and sward height (Fig. 1). Increase in spring litter across A1, A2 and B1 scenarios was concentrated on post-arable grasslands (results not shown) from which the *Festuca* PFT was initially absent (Lavorel et al. 2004). When a dispersal constraint was

imposed on this PFT, scenario differences were lost (Fig. 1). Simpson's biodiversity index was projected to decrease significantly in all scenarios except B2 with no constraint on *Festuca* PFT dispersal. Its decrease was strongest in the A1 scenario (Fig. 1).

Ranking of landscape-scale drivers of ecosystem-service provision at the landscape scale

Table 4 gives the rankings of predictor variables for ecosystem attributes relevant to ecosystem provision in subalpine grasslands at the study site. By design, grassland management through mowing was the most important predictor variable for above-ground biomass and spring litter. It was also the most important variable for predicting Simpson's biodiversity index across the landscape. It was the second most important variable for predicting palatability and the abundance of legumes. Local rather than bath dispersal for the *Festuca* PFT was an important variable for spring litter in un-mown grasslands and palatability (ranking second and third, respectively; Table 4). Fertilization usually ranked last or second from last. Past plowing was the most important predictor variable for palatability and crude protein content of leaves. It was among the top three predictor variables for all relevant ecosystem attributes investigated in this study. The most important predictor variable for the abundance of legumes and sward height was soil fertility (Table 4). It was the second most important variable in predicting crude protein content of leaves and Simpson's biodiversity index. It came third for aboveground biomass in mown grasslands (Table 4).

DISCUSSION

Trait-based projections of ecosystem-service provision

Plant traits are useful to identify widely applicable, process-based relationships between vegetation response to fertility and management and associated changes in ecosystem structure and functioning (Lavorel et al. 2007). Leaf nitrogen content (LNC) for example, is a good indicator of a plant's nutrient economy, opposing nitrogen conservation (and higher N-use efficiency) under low fertility and nitrogen acquisition (and higher light-use efficiency) under high fertility (Wright et al. 2004). Community-aggregated LNC values have been demonstrated to be good predictors of primary productivity in Mediterranean old fields (Garnier et al. 2004) and in subalpine grasslands of the landscape studied here (Quétier et al. 2007). In this study, we build on this relationship to predict aboveground biomass in mown grasslands: an ecosystem attribute relevant to an important ecosystem service: forage availability (Table 3). Plant biodiversity has a hump-backed relationship with respect to primary productivity (Waide et al. 1999). Building on the process-based relationship between LNC and ecosystem productivity, we were able to build a quadratic model for predicting Simpson's biodiversity index from LNC (Table 3). Leaf tensile strength is another plant trait that provides a process-based understanding of the relationships between environmental and management changes and associated changes in ecosystem structure and functioning. Selective grazing favors unpalatable plant species with high leaf tensile strength (e.g., Illius et al. 1995; see Quétier et al. 2007 for results on subalpine grasslands studied here). High tensile strength translates into lower litter decomposition rates (e.g., Cornelissen et al. 1999, Díaz et al. 2004) slowing down biogeochemical cycles and leading to an accumulation of litter (Quétier et al. 2007). We build on this relationship to predict accumulated spring litter in un-mown grasslands (Table 4), confirming the potential of plant traits as ecosystem-service providers (sensu Kremen 2005).

In this study, PFTs modeled in LAMOS were parameterized using traits of their archetype species (F. Quétier, P. Liancourt, A. Thébault, I. Davies, and S. Lavorel, *unpublished manuscript*). Species-specific (idiosyncratic) effects were thus incorporated into projections of relative PFT abundance in grassland communities. Such effects are important for predicting shifts in community structure when there is little overlap between traits that respond to changes in resources and disturbance and those that affect ecosystem attributes (Lavorel and Garnier 2002). As an example, sward height could not be satisfactorily predicted from aggregated plant traits of PFTs obtained from dominant graminoids only. More specifically, stature was a poor predictor of sward height in more fertile field plots where tall leafy dicots are abundant, making graminoids less representative of the sward (Lavorel et al. 2004, Quétier

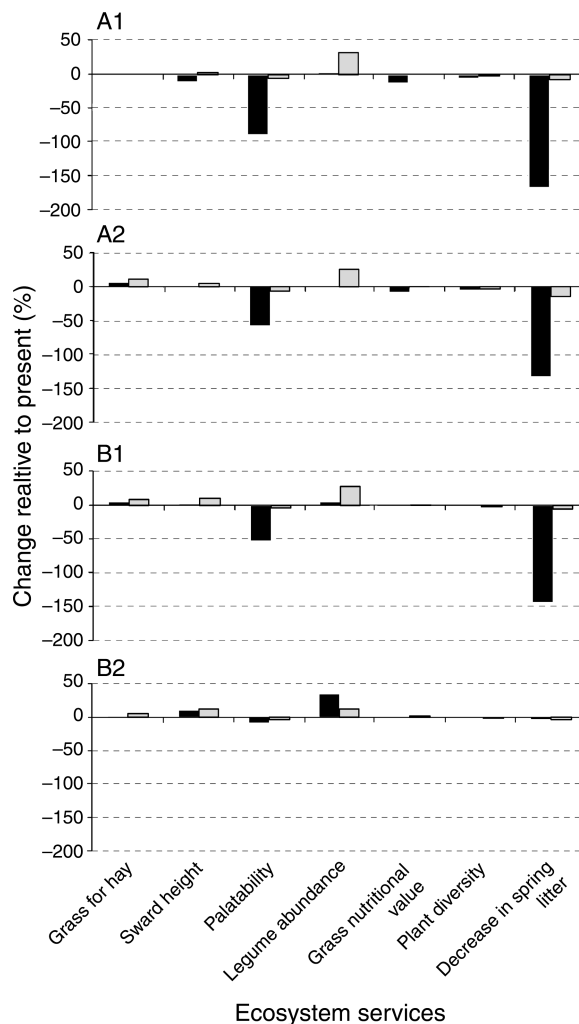


FIG. 1. Change in ecosystem attributes relevant to ecosystem services provided by subalpine grasslands to local people and visitors for the simulated land-use change scenarios (A1, A2, B1, B2) described in *Methods: Land-use change scenarios*. Black bars show results with unlimited dispersal of the *Festuca* LHS-based (leaf-height-seed) plant functional type, and gray bars show results with "local" (within-pixel) dispersal. See Table 1 for a description of ecosystem attributes.

et al. 2007). The *Dactylis* and *Festuca* PFTs are associated with higher fertility (F. Quétier, P. Liancourt, A. Thébault, I. Davies, and S. Lavorel, *unpublished manuscript*) and were used to refine our prediction of sward height (Table 3). Likewise, the slope of the increase in legume abundance with increasing aggregated LNC values (of LHS-based graminoid PFTs) differs between mown and unmown grasslands (results not shown). This results in a quadratic relationship between aggregated LNC values and legume abundance in field plots. Using the relative abundance of the *Sesleria* PFT as an additional variable, we were able to obtain an acceptable model for predicting legume abundance using a unique relationship across sampled field plots (Table 3).

TABLE 4. Mean ranking of environmental and management predictor variable importance in “random forest” models of relevant ecosystem attributes (at the landscape scale).

Predictor variable	Grass for hay	Grass for grazing		Grass nutritional quality		Plant diversity	Spring litter in un-mown grasslands
	Aboveground biomass in mown grasslands	Sward height	Palatability	Abundance of legumes	Crude protein content	Simpson's biodiversity index	Simpson's biodiversity index
Land-use change drivers							
Mowing	1 (by design)†	3	2	2	3	1	1 (by design)†
Fertilization	4	4	4	5	2	5	5
Environmental change drivers							
Soil fertility gradient	3	1	5	1	4	2	4
Land-use legacies							
Past plowing	2	2	1	3	1	3	3
<i>Festuca</i> dispersal	5	5	3	4	5	4	2

Note: Means were calculated from 10 model runs, using 10 different data sets extracted from the nine simulated maps.

† By design, mowing is the most important predictor variable (rank 1) for “grass for hay” and “spring litter in un-mown grasslands” as these ecosystem services are only provided by mown grasslands.

Ecosystem-service sensitivity to changes in land-use at the landscape scale

We used plant traits and trait-based PFTs to make projections of changes in relevant ecosystem attributes in subalpine grassland landscape. We show that grassland management is the most important factor affecting plant diversity at the spatial scale considered here. This result suggests that the aesthetic and conservation value of subalpine grasslands at the study site is most sensitive to land-use change. By design, grassland management through grazing is also the most important factor driving grass availability for hay cutting and spring litter, making the cultural heritage value of the study landscape sensitive to land-use change (as recognized by local people [Rivoal 2004]). Considering that past plowing will not change in the future, grass palatability—and thus grass availability for grazing—is also most sensitive to changes in grassland management through mowing. Our results also suggest that changing the underlying fertility gradient through fertilization would have little impact at the landscape scale. The landscape's value for hay production and grazing as well as its cultural and natural heritage value are most sensitive to land-use change. These results support current agri-environmental schemes aimed at maintaining grassland management in marginal agricultural areas such as subalpine grasslands (e.g., Stampfli and Zeiter 1999, MacDonald et al. 2000; but see Kleijn et al. 2006).

Land-use change is the main threat to slope stability through increasing snow-gliding associated with spring litter in unmown plots. However, on the basis of field-level data, we also hypothesized that dispersal of the *Festuca* PFT could have a strong effect on ecosystem-service delivery in the study landscape (Quétiér et al. 2007). Our results support these predictions: at the landscape scale differences in *Festuca* PFT dispersal have a considerable effect on spring litter accumulation

and palatability (Fig. 1). This effect reflects the *Festuca* PFT's strong leaf tensile strength (Quétiér et al. 2007). Ecosystem attributes are not the only drivers of snow-gliding risk, and climate changes affecting snow fall and accumulation will certainly play a major role in shaping such processes (Newesely et al. 2000, Tasser et al. 2003). In fact, our results suggest that sward height, legume abundance and crude protein content of leaves are most sensitive to changes in the site's bioclimatic altitudinal gradient. Climate change, by increasing or decreasing the length and intensity of the growing season, could lead to important shifts in the fertility gradient of the study site thereby modifying nutrient limitations to PFT growth (Körner 2003). It can thus be hypothesized that the landscape's value for grazing is more sensitive to climate change than to land-use change. A more explicit integration of climatic envelop models (e.g., BIOMOD [Thuiller 2003]) with landscape-scale succession models such as LAMOS would represent progress in assessing ecosystem sensitivity to interacting climate and land-use change (Guisan and Thuiller 2005, Midgley and Thuiller 2005).

CONCLUSION

Our results suggest that the ability of subalpine grasslands to provide for grazing (through palatability) and the preservation of their plant diversity and cultural heritage (signs of appropriate stewardship) is sensitive to land-use change. In this study we only addressed the sensitivity of ecosystem services directly related to grassland ecosystem attributes, hence not addressing the full range of benefits and/or liabilities that people derive from these ecosystems. We nevertheless show that plant traits and the relative abundance of PFTs can be used as simple predictor variables for ecosystem attributes relevant to a wide range of ecosystem services provided by mountain grasslands. Because plant traits are a generic tool for linking environmental and

management change to ecosystem structure and functioning, we suggest their use as “ecosystem-service providers” in exploring the effects of environmental and management changes on ecosystem-service provision by vegetation such as grasslands (Kremen 2005).

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