

1 **Title**

2 Assessing ecosystem-service sensitivity to land-use change in a mountain grassland
3 landscape: A plant-trait based modeling approach.

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1 **Abstract**

2 Evidence is accumulating that the continued provision of essential ecosystem
3 services is vulnerable to land-use change. Yet, we lack a strong scientific basis for
4 this vulnerability as the processes that drive ecosystem-service delivery often remain
5 unclear. In this paper, we use plant traits to assess ecosystem-service sensitivity to
6 land-use change in sub-alpine grasslands. We use a trait-based plant classification
7 (Plant Functional Types - PFTs hereafter) in a landscape modeling platform to model
8 community dynamics under contrasting but internally consistent land-use change
9 scenarios. We then use predictive models of relevant ecosystem attributes, based on
10 quantitative plant traits, to make projections of ecosystem-service delivery. We show
11 that plant traits and PFTs are effective predictors of relevant ecosystem attributes for
12 a range of ecosystem services including provisioning (fodder), cultural (land
13 stewardship), regulating (land-slide and avalanche risk), and supporting services
14 (plant diversity). By analyzing the relative effects of the physical environment and
15 land use on relevant ecosystem attributes, we also show that these ecosystem
16 services are most sensitive to changes in grassland management, supporting current
17 agri-environmental policies aimed at maintaining mowing of sub-alpine grasslands in
18 Europe.

19 **Key-words**

20 Central French Alps, sub-alpine grasslands, ecosystem management, LAMOS,
21 (Landscape MOdeling Shell), Leaf-Height-Seed plant strategy scheme (LHS), land-
22 use change scenarios, climate change

1 Introduction

2 Evidence is accumulating that the continued provision of essential ecosystem
3 services is vulnerable to land-use change (Foley et al., 2005, Millennium Ecosystem
4 Assessment, 2005, Tscharrntke et al., 2005). In upland and mountain grasslands of
5 Europe for instance, unpalatable and low-diversity grasslands associated with
6 decreasing agro-pastoral use and abandonment lead to the loss of important
7 ecosystem services such as soil fertility, slope and snow stability as well as plant,
8 bird and insect diversity (Bignal & McCracken, 2000, Gibon, 2005). In this context,
9 policy response for enhancing or conserving ecosystem services has focused on
10 incentives for continued cutting of grasslands (MacDonald et al., 2000). Such
11 ecosystem management recommendations are based on the assumption that the
12 main drivers of ecosystem provision operate at the scale of management units. Yet,
13 we lack a strong scientific basis for this assumption as the processes that drive
14 ecosystem service delivery often remain unclear (Kremen, 2005, Lemaire et al.,
15 2005, Hobbs et al., 2006). To address this situation, Kremen (2005) has proposed
16 the development of a research agenda centered on understanding how, and at what
17 spatial and temporal scales, community dynamics and environmental factors
18 influence 'key ecosystem-service providers'.

19 We suggest using plant traits and trait-based plant classifications (Plant Functional
20 Types, PFTs hereafter) as 'key ecosystem-service providers' (*sensu* Kremen, 2005).
21 Plant traits relate to universal plant functions of growth (e.g., light & nutrient
22 acquisition, water use efficiency) and persistence (e.g., recruitment, dispersal,
23 defence against herbivores and other disturbances) (Weiher et al., 1999). They
24 provide a widely applicable framework for interpreting and predicting shifts in

1 community structure in response to environmental factors (Hodgson et al., 1999,
2 Lavorel et al., 2006, Thuiller et al., 2004, Thuiller et al. 2006). Plant traits also offer
3 potential for linking community structure to ecosystem functions (Naeem & Wright
4 2003). For example, leaf traits such as leaf nitrogen content (LNC) are markers of
5 plant nutrient economy (Wright et al., 2004) and are associated with faster nutrient
6 cycling at the ecosystem level (i.e., higher productivity, faster litter decomposition –
7 Garnier et al., 2004). Corresponding ecosystem efficiency is an important ecosystem
8 attribute for services such as soil fertility or fodder production.

9 The ecophysiological and ecological foundation of plant traits also makes them
10 particularly useful in generic process-based modeling environments (Epstein et al.,
11 2001). These are essential tools for exploring the various spatial and temporal scales
12 at which ecosystem-service delivery operates (Kremen, 2005, Lemaire et al., 2005).
13 Trait-based landscape succession models have been applied successfully to bridge
14 the gap between community and landscape level processes and guide ecosystem
15 management (e.g., Moore & Noble 1990, Pausas 1999).

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

21 As an example, LAMOS (Landscape MOdeling Shell) is a landscape modeling
22 platform designed to account for basic vegetation dynamic processes that result from
23 the interactions between plant functional traits, habitat conditions, disturbances and
24 spatial pattern (e.g., Cousins et al. 2003, Grigulis et al. 2005). We use LAMOS and
25 plant traits to make projections of ecosystem-service provision on the basis of

1 contrasting land-use change scenarios. These scenarios provide a realistic context
2 for investigating the effects of land-use change on ecosystem services, in a dynamic
3 landscape setting. Projections will be used to rank current land-use practices
4 (mowing and fertilization), physical environmental factors (underlying altitudinal
5 gradient in fertility), and land-use legacies as drivers of ecosystem-service provision
6 at the landscape scale. Ecosystem services for which land-use drivers are most
7 important are most likely to be more sensitive to land-use change. Ecosystem
8 services for which physical environmental factors are most important are likely to be
9 more sensitive to changes in climate, for example. By enabling us to factor in
10 dispersal, LAMOS also allows us to test the importance of that essential landscape-
11 level process.

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

15 **Study site, ecosystem services and relevant ecosystem attributes**

16 *Study site*

17 The study site is set on the south facing slopes of the valley above the village of
18 Villar d'Arène in the central French Alps (45.04°N, 6.34°E). It covers 1292 hectares at
19 the headwater of the Romanche River. The climate is sub-alpine with a strong
20 continental influence due to a rain shadow effect with respect to dominant westerly
21 winds. Mean annual rainfall is 956 mm, and the mean monthly temperatures at 1650
22 m (lowest point in the study site) range between -2.6°C in January and 13°C in July.
23 At the upper limit of former arable land use (2050m), temperatures range from -4.6°C
24 in January to 11°C in July.

1 Grasslands in Villar d'Arène have a long history of agricultural and pastoral land
2 use. Former arable fields (1650 to 2000 m) have been abandoned and subsequently
3 converted to grasslands used for hay or grazing. Former (never ploughed) hay
4 meadows (1800 to 2500 m) are increasingly converted to light summer grazing by
5 sheep or cattle or no longer used for agriculture. Lavorel et al. (2004) showed that
6 grasslands on former arable land have distinct floristic composition and aggregated
7 plant trait values compared to never ploughed grasslands. This result suggests that
8 any understanding of current vegetation patterns must take into account land-use
9 legacies (Foster et al., 2003). We consider two hypotheses in explaining these land-
10 use legacies. The first one is that late-successional grasses have limited dispersal
11 ability and/or are prevented from colonizing post-arable grasslands by unknown
12 edaphic factors. The second hypothesis is that assembly history in post-arable
13 grasslands makes them resistant to later invasions by late-successional tussock
14 grasses, as suggested in Quétier et al. (submitted c).

15 *Ecosystem services provided by sub-alpine grasslands*

16 The current landscape is dominated by grassland ecosystems that are still used by
17 a small, but nevertheless active farming community based on sheep and cattle
18 rearing for lamb and steer production. The site is located in the buffer zone of the
19 Ecrins National Park and receives many thousands of visitors annually attracted by
20 opportunities for outdoor recreation, the spectacular mountain setting, and its
21 abundant and diverse fauna and flora. The contrast between the wilderness of the
22 glaciated Meije massif and the gentle grassland landscape of the opposing south-
23 facing slope is one of the main attractions to Villar d'Arène. Indeed, tourism has
24 taken over agriculture as the dominant economic activity. Former arable land has
25 given the landscape a unique distinctiveness in the form of terraced slopes extending

1 up to 2000 m above sea level. This "heritage" of the former land-use system makes
2 this cultural landscape the focus of numerous preservation efforts including subsidies
3 to the remaining farmers (Parc National des Ecrins, 2004).

4 Using 45 semi-guided interviews, we found that local people and visitors refer to a
5 variety of ecosystem services and liabilities from local grasslands (Rivoal, 2004,
6 Quétier et al., submitted a). Farming systems are heavily constrained by winter
7 fodder requirements and all machinery-accessible grasslands are cut for hay at
8 present. Relative to winter fodder stocks, available grazing area is not limiting in
9 current farming systems. Rather, shepherds recognize that selective grazing favours
10 large unpalatable tussock grasses. Grass quantity is thus an important ecosystem
11 service for hay whilst grass quality (palatability and nutritional value) is an important
12 ecosystem service for grazing. Plant diversity contributes to landscape aesthetics. It
13 also contributes to biodiversity conservation objectives of the Ecrins National Park
14 (Parc National des Ecrins, 2004). Some people worry about signs of inappropriate
15 'stewardship' that diminish cultural heritage value. All local people acknowledge that
16 poor land-use practices can increase snow gliding and associated avalanche and
17 land-slide risk.

18 *Relevant ecosystem attributes*

19 Based on the above-mentioned interviews and our agronomical and ecological
20 expertise, we made assumptions about relevant ecosystem attributes (Table 1).
21 Grass needs to be available in sufficient quantity and quality for both hay and
22 grazing. Sward height increases grazing efficiency through increased individual bite
23 mass (Parsons et al., 1994, Prache & Peyraud, 1997). Increasing leaf toughness
24 (tensile strength) decreases grazing efficiency by decreasing bite frequency, either

1 by increasing the time necessary for handling (e.g., chewing - Illius et al., 1995) or
2 selection (increasing bite interval). Quantities available for hay can be equated to
3 above-ground biomass at cutting date. Crude protein content is an indicator of its
4 nutritional value (Bruinenberg et al., 2002). Local farmers evaluate forage quality on
5 the basis of legume abundance (Rivoal, 2004). Plant species diversity can be
6 characterized using standard indices such as Simpson's inverse index. Signs of
7 inappropriate stewardship relate to grasslands being under-used. Local people use
8 accumulated litter in the spring as an indicator of under-utilization (Rivoal, 2004).
9 Snow gliding risk also increases with litter accumulation as long bladed grass mats
10 form ideal gliding surfaces (Newesely et al., 2000, Tasser et al., 2003).

11 **Methods**

12 *Trait-based modeling of relevant ecosystem attributes*

13 Using Westoby's Leaf-Height-Seed (LHS) model of plant functional types
14 (Westoby, 1998), we clustered the dominant graminoids of sub-alpine grasslands into
15 four LHS-based PFTs. By focusing on graminoids, we explored trait combinations
16 within rather than across growth forms (as suggested in Lavorel et al., 1997). We
17 used plant traits measured on 'species x land-use trajectory' combinations where
18 species were considered to have the same trait value across plots within the same
19 land-use history. We thus took into account intraspecific variability, acknowledging
20 that functional type membership is conditional (Dyer et al., 2001). All whole plant and
21 leaf trait measurements followed Cornelissen et al. (2003). LHS-based PFTs
22 obtained were named after the archetype species in each cluster: Bromus PFT,
23 Dactylis PFT, Festuca PFT & Sesleria PFT (Quétier et al., submitted c). They have
24 contrasting nutrient economies (i.e., position on the nutrient acquisition/conservation

1 trade-off indicated by high/low leaf nitrogen content respectively – see Wright et al.,
2 2004). Results also suggest that they have contrasting competitive effects (e.g., taller
3 plants intercept more incoming light) and responses (e.g., heavier seeds confer
4 better germination potential at low light) (Goldberg & Landa, 1991). We used these
5 PFTs to parameterize LAMOS.

6 LAMOS simulates the abundance of plant functional types in relation to site
7 productivity and disturbance over a landscape map. Here, we applied a configuration
8 of LAMOS using the FATE model (Functional Attributes in Terrestrial Ecosystems,
9 Moore & Noble 1990; see also Pausas 1999) to drive within-pixel successional
10 dynamics (e.g., Cousins et al. 2003, Grigulis et al. 2005). FATE is an age-structured
11 population model that determines the abundance (equated to cover) of competing
12 PFTs based on a simple set of traits relating to plant life history, tolerance to shading
13 at different life stages, disturbance response of established plants, and recruitment
14 (Noble & Gitay 1996). Each PFT's response to fertility was assumed to follow a
15 logistic function (Walker et al. 1989), whose shape is determined by the position of
16 each PFT along the spectrum of nutrient economics (Wright et al., 2004). Hence
17 PFTs with high LNC can produce significant biomass only at high levels of fertility,
18 whereas PFTs with low LNC are tolerant of low fertility (i.e., they can produce
19 biomass) but have a lower increment of biomass per unit of fertility. For each PFT the
20 fertility response curve is hence characterized by a lower nutrient threshold
21 parameter, which is also correlated with the slope of the curve. Competition for
22 nutrients is not represented directly in LAMOS-FATE, but site fertility affects density
23 at recruitment, where the population size of recruits is scaled to fertility using the
24 fertility response curve of each PFT.

1 Mowing was simulated as a uniform disturbance, removing 60% of the total
2 standing biomass annually, whatever the vegetation composition, and with maximum
3 impact (called “severity” in LAMOS). All mature PFT individuals and 90% of immature
4 *Festuca* PFT resprout following mowing, effectively keeping them immature. The
5 remaining 10% immature *Festuca* PFT are killed while immature *Bromus*, *Dactylis*
6 and *Sesleria* PFT and all propagules escape mowing unaffected (Jouglet & Dorée,
7 1991). LAMOS also makes it possible to test alternative hypotheses about dispersal
8 capacities of different PFTs, in its simplest form by restricting dispersal to the pixel
9 where seeds are produced (i.e., ‘local dispersal’).

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

17 We used nine different maps corresponding to one current and four scenario-
18 based future distributions of mowing and fertilization (Table 2), with or without a
19 dispersal constraint on the *Festuca* PFT ($4 \times 2 = 8$ maps). Land-use change
20 scenarios are based on local projections of European-wide land-use change
21 scenarios described in Rounsevell et al. (2006) and formulated on the basis of global
22 storylines (Nakicenovic et al., 2000). These proposed an understanding of trends that
23 opposed a global (type 1 scenario) and a regional (type 2 scenario) future on the one
24 hand and on the other hand a materialist (type A scenario) and an environmentally
25 and socially conscious (type B scenarios) future. Rounsevell et al. (2006) related the

1 global storylines to relevant socio-economic drivers of land-use change at the
2 European scale. We build on their results to propose four contrasting land-use
3 scenarios for Villar d'Arène. These scenarios were developed in collaboration with
4 local and regional stakeholders of farming, rural development and nature
5 conservation interests to guarantee that they are locally plausible (Daigney, 2005).

6 These consistent land-use scenarios provide us with socio-economically plausible
7 combinations of resources, disturbance and land-use legacies for modeling land-use
8 change effects on ecosystem services at the landscape scale (Tscharntke et al.,
9 2005). Each map includes an underlying fertility gradient set to reflect the site's
10 altitudinal gradient. At the high-end of the gradient, no PFTs are nutrient limited while
11 they all are at the low-end. The distribution of past-plowing is fixed and shared across
12 all nine maps. The location of fertilization and management by mowing is scenario-
13 dependent.

14 *Projecting relevant ecosystem attributes from LAMOS simulation outcomes*

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

20 Some plant traits translate directly into relevant ecosystem attributes. For instance,
21 leaf tensile strength and LNC translate into crude protein content (CP6.25 – Conklin-
22 Brittain et al., 1999) and palatability (Illius et al., 1995), respectively. Sward height
23 was measured weekly over the growing season, as the average of 10 random

1 measurements. Relative abundance of legumes and Simpson's biodiversity index
2 were calculated from point-quadrat surveys (Lavorel et al., 2004).

3 Above-ground standing biomass was harvested in early spring (around May 10th –
4 64 degree days) and full summer (around July 10th – 635 degree days) using four
5 samples of 0.25 m². Harvests were sorted into senescent and living material and
6 oven dried at 60°C for 48 hours to calculate maximum above-ground biomass in
7 mown grasslands and spring litter in un-mown grasslands. Based on previous field
8 work described in Quétier et al., submitted b), above-ground biomass in mown plots
9 was assumed to relate to ecosystem productivity and hence to LNC. Litter
10 accumulated in spring was assumed to result from either leaf tensile strength (low
11 palatability) or LNC (through decomposition rate).

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

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

18 Each map is a 70 x 100 pixel schematic representation of the study site (7000 data
19 points). To overcome the non-independence of pixels across maps, we extracted one
20 data point from each location (i.e., a 7000 points data set), each point being chosen
21 at random between the available maps. Data extraction and analysis was repeated
22 10 times.

23 We used the 10 data extractions to rank management and environmental factors
24 driving ecosystem attributes relevant for the various ecosystem services identified in

1 the study site. We used an extension of usual regression tree technique called
2 'Random Forests' (Breiman, 2001), whereby relevant ecosystem attributes (response
3 variable) are recursively separated into increasingly homogeneous groups (pixels)
4 defined by predictor variables. The resulting model defines terminal groups in terms
5 of a combination of decision rules based on threshold values for the selected
6 predictor variables. In 'Random Forests', bootstrap samples are drawn to construct
7 numerous trees (we use 1000), each one grown on a randomized subset of predictor
8 variables. The trees are grown to maximum size without pruning, and aggregation is
9 by averaging the trees. Each model is validated on an 'out-of-bag' sample that was
10 not used in the boot-strap construction of the model. The out-of-bag samples are
11 used to calculate an unbiased error rate and variable importance, eliminating the
12 need for a test set or cross-validation. Because a large number of trees are grown,
13 there is limited generalization error (that is, the true error of the population as
14 opposed to the training error only). Analyses were carried out in R package 2.2.0 (R
15 Development Core Team, 2005) using the *randomForest* library.

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

23 **Results**

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

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

15 *Projecting relevant ecosystem attributes from plant traits*

16 Table 3 gives details of the generalized linear models obtained using field data on
17 aggregated plant traits and relative abundance of LHS-based PFTs. Sward height
18 was well predicted by plant stature with a correction based on the relative abundance
19 of *Dactylis* and *Festuca* PFTs, above-ground biomass being predicted by LNC and
20 spring litter by leaf tensile strength. Simpson's biodiversity index showed a quadratic
21 relationship with LNC – analogous to the hump-backed relationship linking
22 biodiversity to productivity (Waide et al., 1999). Relative abundance of legumes was
23 predicted by the relative abundance of the *Sesleria* PFT (which shares their small
24 stature) and LNC (indicating soil fertility). Using results obtained across sampled field
25 plots (Table 3), we generated landscape-scale projections of relevant ecosystem

1 attributes using LAMOS. It is important to realize that our results should be
2 interpreted at the landscape scale and not used for within-map comparisons.

3 By design, the A1 scenario had no mowing and grass for hay (above-ground
4 biomass in mown grasslands) and is hence not represented in Figure 1. Spring litter
5 in un-mown grasslands, grass palatability and legume abundance were the only
6 relevant ecosystem attributes that were noticeably different between scenario
7 projections (Figure 1). They mainly opposed scenarios A1, A2 and B1 on the one
8 hand and B2 on the other (Figure 1). The decrease in palatability and increase in
9 spring litter was however strongest in the A1 scenario where it was associated with a
10 slight, but significant decrease in crude protein content and sward height (Figure 1).
11 Increase in spring litter across A1, A2 and B1 scenarios was concentrated on post-
12 arable grasslands (results not shown) from which the *Festuca* PFT was initially
13 absent (Lavorel et al., 2004). When a dispersal constraint was imposed on this PFT,
14 scenario differences were lost (Figure 1). Simpson's biodiversity index was projected
15 to decrease significantly in all scenarios except B2 with no constraint on *Festuca* PFT
16 dispersal. Its decrease was strongest in the A1 scenario (Figure 1).

17 *Ranking of landscape -scale drivers of ecosystem-service provision at the landscape* 18 *scale*

19 Table 4 gives the rankings of predictor variables for ecosystem attributes relevant
20 to ecosystem provision in sub-alpine grasslands at the study site. By design,
21 grassland management through mowing was the most important predictor variable
22 for above-ground biomass and spring litter. It was also the most important variable
23 for predicting Simpson's biodiversity index across the landscape. It was the second
24 most important variable for predicting palatability and the abundance of legumes.

1 Local rather than both dispersal for the *Festuca* PFT was an important variable for
2 spring litter in un-mown grasslands and palatability (ranking 2nd and 3rd respectively –
3 Table 4). Fertilization usually ranked last or second from last. Past-ploughing was the
4 most important predictor variable for palatability and crude protein content of leaves.
5 It was among the top three predictor variables for all relevant ecosystem attributes
6 investigated in this study. The most important predictor variable for the abundance of
7 legumes and sward height was soil fertility (Table 4). It was the second most
8 important variable in predicting crude protein content of leaves and Simpson's
9 biodiversity index. It came third for above-ground biomass in mown grasslands
10 (Table 4).

11 **Discussion**

12 *Trait-based projections of ecosystem-service provision*

13 Plant traits are useful to identify widely applicable, process-based relationships
14 between vegetation response to fertility and management and associated changes in
15 ecosystem structure and functioning (Lavorel et al., 2006). Leaf nitrogen content
16 (LNC) for example, is a good indicator of a plant's nutrient economy, opposing
17 nitrogen conservation (and higher N-use efficiency) under low fertility and nitrogen
18 acquisition (and higher light-use efficiency) under high fertility (Wright et al., 2004).
19 Community-aggregated LNC values have been demonstrated to be good predictors
20 of primary productivity in Mediterranean old-fields (Garnier et al., 2004) and in sub-
21 alpine grasslands of the landscape studied here (Quétier et al., submitted b). In this
22 study, we build on this relationship to predict above-ground biomass in mown
23 grasslands – an ecosystem attribute relevant to an important ecosystem service:
24 forage availability (Table 3). Plant biodiversity has a hump-backed relationship with

1 respect to primary productivity (Waide et al., 1999). Building on the process-based
2 relationship between LNC and ecosystem productivity, we were able to build a
3 quadratic model for predicting Simpson's biodiversity index from LNC (Table 3). Leaf
4 tensile strength is another plant trait that provides a process-based understanding of
5 the relationships between environmental and management changes and associated
6 changes in ecosystem structure and functioning. Selective grazing favors unpalatable
7 plant species with high leaf tensile strength (e.g., Illius et al., 1995 – see Quétier et
8 al., submitted b for results on sub-alpine grasslands studied here). High tensile
9 strength translates into lower litter decomposition rates (e.g., Cornelissen et al.,
10 1999, Diaz et al., 2004) slowing down biogeochemical cycles and leading to an
11 accumulation of litter (Quétier et al., submitted b). We build on this relationship to
12 predict accumulated spring litter in un-mown grasslands (Table 4), confirming the
13 potential of plant traits as ecosystem-service providers (*sensu* Kremen, 2005).

14 In this study, PFTs modelled in LAMOS were parameterized using traits of their
15 archetype species (Quétier et al., submitted c). Species-specific (idiosyncratic)
16 effects were thus incorporated into projections of relative PFT abundance in
17 grassland communities. Such effects are important for predicting shifts in community
18 structure when there is little overlap between traits that respond to changes in
19 resources and disturbance and those that affect ecosystem attributes (Lavorel &
20 Garnier, 2002). As an example, sward height could not be satisfactorily predicted
21 from aggregated plant traits of PFTs obtained from dominant graminoids only. More
22 specifically, stature was a poor predictor of sward height in more fertile field plots
23 where tall leafy dicots are abundant, making graminoids less representative of the
24 sward (Lavorel et al., 2004, Quétier et al., submitted b). The *Dactylis* and *Festuca*
25 PFTs are associated with higher fertility (Quétier et al., submitted c) and were used to

1 refine our prediction of sward height (Table 3). Likewise, the slope of the increase in
2 legume abundance with increasing aggregated LNC values (of LHS-based graminoid
3 PFTs) differs between mown and un-mown grasslands (results not shown). This
4 results in a quadratic relationship between aggregated LNC values and legume
5 abundance in field plots. Using the relative abundance of the *Sesleria* PFT as an
6 additional variable, we were able to obtain an acceptable model for predicting legume
7 abundance using a unique relationship across sampled field plots (Table 3).

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

9 We used plant traits and trait-based PFTs to make projections of changes in
10 relevant ecosystem attributes in subalpine grassland landscape. We show that
11 grassland management is the most important factor affecting plant diversity at the
12 spatial scale considered here. This result suggests that the aesthetic and
13 conservation value of sub-alpine grasslands at the study site is most sensitive to
14 land-use change. By design, grassland management through grazing is also the
15 most important factor driving grass availability for hay-cutting and spring litter -
16 making the cultural heritage value of the study landscape sensitive to land-use
17 change (as recognized by local people – Rivoal, 2004). Considering that past-
18 plowing will not change in the future, grass palatability - and thus grass availability for
19 grazing - is also most sensitive to changes in grassland management through
20 mowing. Our results also suggest that changing the underlying fertility gradient
21 through fertilization would have little impact at the landscape scale. The landscape's
22 value for hay production and grazing as well as its cultural and natural heritage value
23 are most sensitive to land-use change. These results support current agri-
24 environmental schemes aimed at maintaining grassland management in marginal

1 agricultural areas such as sub-alpine grasslands (e.g., Stampfli & Zeiter, 1999
2 MacDonald et al., 2000, but see Kleijn et al., 2006).

3 Land-use change is the main threat to slope stability through increasing snow-
4 gliding associated with spring litter in un-mown plots. However, on the basis of field-
5 level data, we also hypothesized that dispersal of the *Festuca* PFT could have a
6 strong effect on ecosystem-service delivery in the study landscape (Quétier et al.,
7 submitted b & c). Our results support these predictions: at the landscape scale
8 differences in *Festuca* PFT dispersal have a considerable effect on spring litter
9 accumulation and palatability (Figure 1). This effect reflects the *Festuca* PFT's strong
10 leaf tensile strength (Quétier et al., submitted b). Ecosystem attributes are not the
11 only drivers of snow-gliding risk, and climate changes affecting snow fall and
12 accumulation will certainly play a major role in shaping such processes (Newesely et
13 al., 2000, Tasser et al., 2003). In fact, our results suggest that sward height, legume
14 abundance and crude protein content of leaves are most sensitive to changes in the
15 site's bioclimatic altitudinal gradient. Climate change, by increasing or decreasing the
16 length and intensity of the growing season, could lead to important shifts in the
17 fertility gradient of the study site thereby modifying nutrient limitations to PFT growth
18 (Körner, 2003). It can thus be hypothesized that the landscape's value for grazing is
19 more sensitive to climate change than to land-use change. A more explicit integration
20 of climatic envelop models (e.g., BIOMOD - Thuiller, 2003) with landscape-scale
21 succession models such as LAMOS would represent progress in assessing
22 ecosystem sensitivity to interacting climate and land-use change (Guisan & Thuiller,
23 2005, Midgley & Thuiller, 2005).

1 **Conclusion**

2 Our results suggest that the ability of sub-alpine grasslands to provide for grazing
3 (through palatability) and the preservation of their plant diversity and cultural heritage
4 (signs of appropriate stewardship) is sensitive to land-use change. In this study we
5 only addressed the sensitivity of ecosystem services directly related to grassland
6 ecosystem attributes, hence not addressing the full range of benefits and/or liabilities
7 that people derive from these ecosystems. We nevertheless show that plant traits
8 and the relative abundance of PFTs can be used as simple predictor variables for
9 ecosystem attributes relevant to a wide range of ecosystem services provided by
10 mountain grasslands. Because plant traits are a generic tool for linking environmental
11 and management change to ecosystem structure and functioning, we suggest their
12 use as 'ecosystem-service providers' in exploring the effects of environmental and
13 management changes on ecosystem-service provision by vegetation such as
14 grasslands (Kremen, 2005).

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1 **Tables**

Stakeholder	Ecosystem Service	Stakeholder Descriptions of Ecosystem Attributes	Modelled Relevant Ecosystem Attributes
Local farmers	Grass quantity for hay & grazing	Above-ground biomass in mown grasslands	
		Sward height	
		Palatability for grazing	
	Forage quality	Crude protein content	
		Relative abundance of legumes	
National Park Authority	Flowering diversity for aesthetic value	Plant diversity	Simpson's biodiversity index
Visitors and locals	Conservation of biodiverse grasslands		
Locals	Appropriate stewardship of cultural landscape features	Large accumulations of dead grass	Spring litter in un-mown grasslands
	Snow-gliding risk		

2

3 Table 1: People, ecosystem services and relevant ecosystem attributes in sub-alpine
 4 grasslands of Villar d'Arène.

5

Past land-use	Current land-use	Future land-use			
		Scenario A1	Scenario A2	Scenario B1	Scenario B2
Cultivated	Fertilized and mown	-	Fertilized and mown	Mown	Fertilized and mown
	Mown	-	Fertilized and mown	Mown	Fertilized and mown
	Extensively grazed	-	-	-	Fertilized and mown
Mown	Mown	-	-	Mown	Mown
	Extensively grazed	-	-	-	-

1

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

4

Generalized Linear Models used to link relevant ecosystem attributes to plant traits and trait-based PFT abundances in field plots		Value	Standard Error	t value	Explained deviance
Above-ground biomass in mown plots (T/ha) (n=9)	Intercept	-0.8533753	1.497684	-0.57	60.21%
	LNC	3.37	1.04	3.25	
Sward Height (cm) (n=15)	Intercept	8.249507	16.86201	0.49	56.72%
	Stature (cm)	0.31	0.29	1.09	
	Festuca PFT abundance	5.18	7.40	0.70	
	Dactylis PFT abundance	103.31	31.48	3.28	
Legume relative abundance (n = 30)	Intercept	-28.14	43.14	-0.65	56.59%
	Sesleria 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 (n = 30)	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 un-mown plots (T/ha) (n=6)	Intercept	-1.49	0.57	-2.62	96.82%
	Leaf tensile strength (g/cm)	0.0008	0.0001	11.04	

5

6 Table 3: Generalized Linear Models used to link relevant ecosystem attributes to
7 plant traits and plant functional type abundances in field plots

8

1

Ranking of predictor variables contributing or relevant ecosystem attributes at the landscape scale		Grass for hay	Grass for grazing		Grass nutritional quality		Plant diversity	Spring litter in un-mown grasslands
		Above-ground biomass in mown grasslands	Sward height	Palatability	Abundance of legumes	Crude protein content	Simpson's biodiversity index	
Land-use change drivers	Mowing	1 (<i>by design</i>)	3	2	2	3	1	1 (<i>by design</i>)
	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-ploughing	2	2	1	3	1	3	3
	Festuca dispersal	5	5	3	4	5	4	2

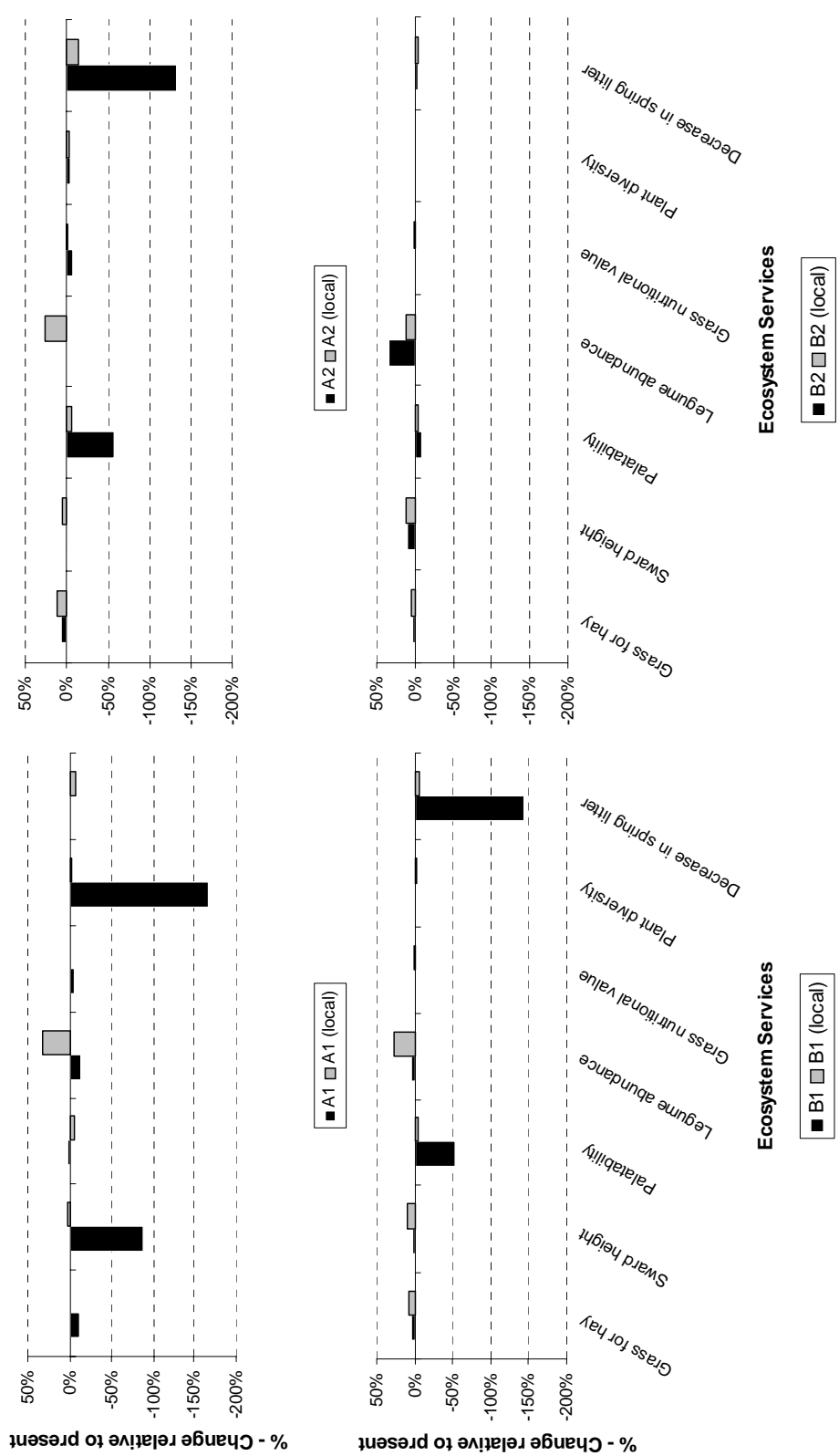
2

3 Table 4: Average ranking of environmental and management predictor variable
 4 importance in 'random forest' models of relevant ecosystem attributes. Averages
 5 were calculated from 10 model runs, using 10 different data-sets extracted from the
 6 nine simulated maps.

7 **Figure legends**

8 Figure 1: Percent-change in ecosystem attributes relevant to ecosystem services
 9 provided by sub-alpine grasslands to local people and visitors for 8 simulated land-
 10 use change scenarios which are described in the main text. On the left hand-side,
 11 dispersal of the Festuca LHS-based Plant Functional Type is unlimited ('bath') whilst
 12 on the right hand side only 'local' (within-pixel) dispersal is permitted. See Table 1 for
 13 a description of ecosystem attributes.

1 Figures



2

3 Figure 1