Plant trait-based models identify direct and indirect effects of climate change on bundles of grassland ecosystem services

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Edited by Cyrille Violle, Centre National de la Recherche Scientifique, Montpellier, France, and accepted by the Editorial Board December 2, 2013 (received for review November 14, 2012)

Land use and climate change are primary causes of changes in the supply of ecosystem services (ESs). Although the consequences of climate change on ecosystem properties and associated services are well documented, the cascading impacts of climate change on ESs through changes in land use are largely overlooked. We present a trait-based framework based on an empirical model to elucidate how climate change affects tradeoffs among ESs. Using alternative scenarios for mountain grasslands, we predicted how direct effects of climate change on ecosystems and indirect effects through farmers' adaptations are likely to affect ES bundles through changes in plant functional properties. ES supply was overall more sensitive to climate than to induced management change, and ES bundles remained stable across scenarios. These responses largely reflected the restricted extent of management change in this constrained system, which was incorporated when scaling up plot level climate and management effects on ecosystem properties to the entire landscape. The trait-based approach revealed how the combination of common driving traits and common responses to changed fertility determined interactions and tradeoffs among ESs.

plant functional traits | trade-offs | global change | mountain agriculture

Ecosystem services (ESs) are increasingly used to assess and make land and natural resource use decisions that typically involve tradeoffs between conflicting goals and, in particular, between the different bundles of services that a given ecosystem could provide. These decisions are, however, rarely grounded in a mechanistic understanding of the ecosystem properties or processes that enable provision of multiple ESs. At the same time, mechanisms leading to tradeoffs among ESs are still poorly understood (1). Effective ES-based management decisions, especially in a climate-change context, require that we go beyond the description of spatial co-occurrences of targeted ESs under current climates (e.g., refs. 2 and 3) to understand direct interactions between ESs, and the effects of common drivers of change in ESs (4).

A mechanistic approach to ES supply will be grounded in the relevant characteristics of the ecosystem components that contribute to it. Functional traits of ES providers are novel and powerful proxies (5, 6) that make it possible to scale well-understood functional tradeoffs from the organism level to ecosystem functioning and to ESs (7, 8). Their relevance to ES modeling rests on the discovery that response functional traits that determine community response (e.g., fertilization favors plants with nitrogen-rich leaves) overlap with effect functional traits that determine effects on ecosystem functioning (e.g., a majority of nitrogen-rich leaves promotes high primary productivity) (9).

Scenario-based studies have compared bundles of ESs, and associated positive and negative relationships, across scenarios (10), but few published studies have sought to tease out the respective effects of different scenario drivers. Large-scale studies have shown that land use effects were negligible after climate-change effects had been accounted for because, at such a coarse scale, land use was primarily driven by climate (see ref. 11 for an example of how climate and land use shape biodiversity patterns). At landscape scale, most scenario-based ES assessments have focused on land cover change (12, 13). They also considered impacts on one or several ESs, but not on bundles and tradeoffs among ESs, and, as far as we know, have not explicitly combined climate and land-use drivers to tease out their respective effects.

In this study, we demonstrate how trait-based approaches can unravel mechanisms influencing ES bundles and tradeoffs under different climate and land-use scenarios (Fig. 1). Using semi-mechanistic models of ecosystem properties (EPs) based on plant and microbial functional traits (8), we simulate the impacts of combined climate and land-use changes on ESs (14, 15).

Using data from a grassland-dominated landscape in the French Alps, we analyzed the responses to four plausible scenarios of a set of EPs (8) identified by stakeholders as contributing to locally important ESs such as water quality, aesthetic value, and fodder quality and quantity (16).

Considering that changes in ESs at the landscape scale result from changes in the landscape-scale patterns in management and their plot-scale effects on biodiversity and ecosystem functioning, we used an empirical model: (*i*) to predict the potential effects of climate change on the supply of individual ESs and on their bundles, both directly or indirectly through land-management adaptation; (*ii*) to quantify the relative contributions of direct and indirect climate effects on individual ESs and their bundles; and (*iii*) to identify the underpinning mechanisms involved.

Significance

The sustainable management of the supply of ecosystem services (ESs) in a context of global change is of major importance to sustain human livelihoods. Doing sustainable management requires us to understand and to quantify the effects and mechanisms of changes in driving variables on multiple ESs. However, few studies to date have analyzed ES scenarios, and even fewer have adopted a mechanistic approach. This study presents a unique approach to examine not only the direct effects of climate on multiple ESs, but also its indirect effects through its consequences for land management and for plant functional traits. The framework was tested in an alpine grassland system using ES models based on land use, plant functional traits, and soil data.

Author contributions: P.L., S.L., and M.M. designed research; P.L. and S.L. performed research; P.L. and S.L. analyzed data; and P.L., S.L., and F.Q. wrote the paper.

The authors declare no conflict of interest.

This article is a PNAS Direct Submission. C.V. is a guest editor invited by the Editorial Board.

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This article contains supporting information online at www.pnas.org/lookup/suppl/doi:10.1073/pnas.1216051111/-/DCSupplemental.

www.pnas.org/cgi/doi/10.1073/pnas.1216051111

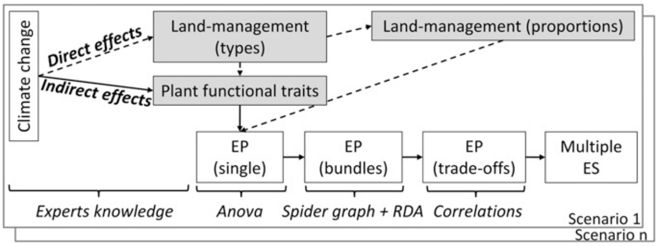

Fig. 1. Conceptual framework to develop a predictive model looking at the effects of climate and land-use change on ecosystem services (ESs). The framework distinguishes a direct pathway of climate-change effects on plant functional traits (plain arrows) from an indirect pathway through land-management adaptation resulting in change in land-management types and/or proportions in the landscape (dashed arrows). Gray boxes indicate mechanisms underlying ES delivery. Quantitative methods used at each step are indicated at the bottom of the figure.

Results

Climate Change Effects on Individual Ecosystem Properties and Their Bundles. Variations in individual EPs for the entire landscape were mostly driven by the direct climate pathway, with strong differences in EPs between each alternative and the current climate (Fig. 2, bottom left spider graph). Nitrogen mineralization (NMP), soil organic matter (SOM), and nitrate retention (RetentNO3) increased under drastic drought whereas all other EPs decreased, leading to a tradeoff in responses between these two sets of EPs. Intermittent drought only decreased plant diversity (PlantDiv) and crude protein content (CPC), and brought on earlier grass flowering onset (FloweringOnset).

EPs were much less responsive to land-management alternatives under status-quo climate (Fig. 2, top right spider graph). Only plant diversity and crude protein content and, to a smaller extent, biomass production (Gbio) were responsive to land management, increasing under the "international local" scenario and decreasing under the "drastic" and especially the "drastic local" scenarios. Combined effects of climate and land management (Fig. 2, bottom right spider graph) were dominated by climate effects (graphs mostly similar to climate only—bottom left). Additional land-use effects consisted in an enhanced loss in plant diversity under the drastic local compared with the "drastic international" scenario, and a smaller increase in CPC accompanied by a smaller decrease in litter (LitterMass) compared with current conditions under the "intermittent international" compared with the "intermittent local" scenario.

Patterns of correlation among EPs varied little across scenarios (Table S1). Of the 28 possible pairs of EPs, 11 pairs were

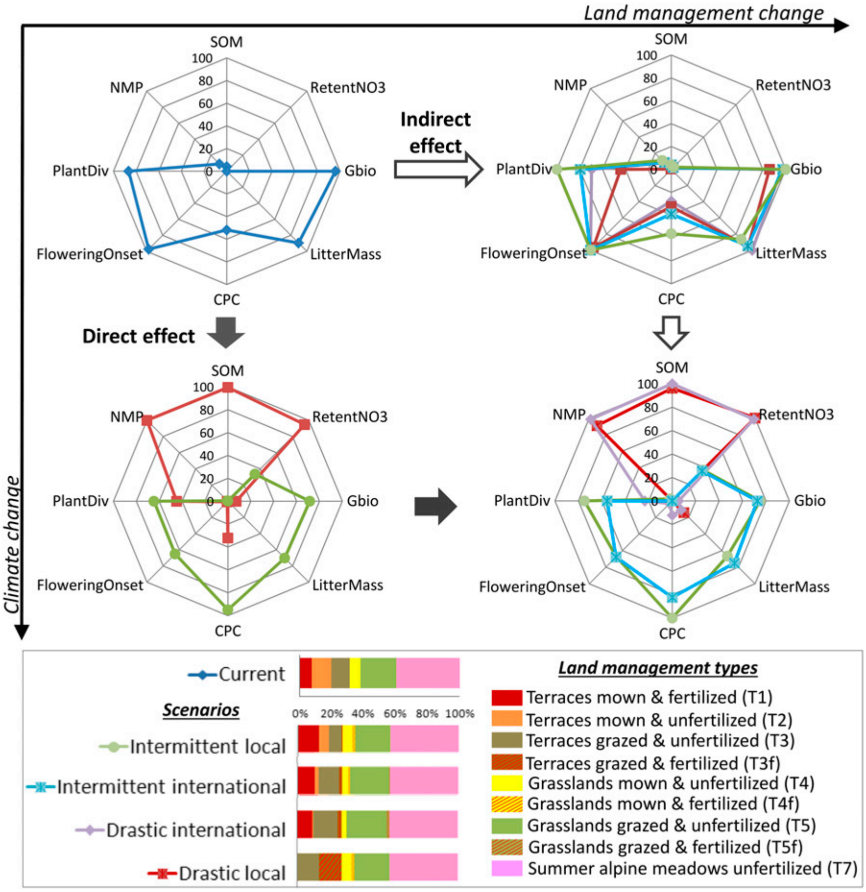

Fig. 2. Illustration of ecosystem properties (EPs) under combined land management and climate scenarios. Standardized units along each axis indicate the condition of each EP. The top left diagram represents EPs in the current context. The bottom left diagram represents the direct pathway of climate effects considering the effect of climate only under the current land-management configuration. The right side of the figure represents the indirect pathway of climate effects through land-management adaptation. The top diagram represents the effects of land management under different scenarios with current climate conditions, and the bottom diagram representing the combination of both direct and indirect effects of climate. Stack bar graphs present the percentage of each land-management type under the current situation and the four land-management scenarios. CPC, crude protein content; FloweringOnset, date of grass flowering onset; Gbio, green biomass; LitterMass, litter mass; NMP, nitrogen mineralization; PlantDiv, plant diversity; Retent NO3, nitrate retention; SOM, soil organic matter content.

Table 1. Variance partitioning by ANOVA showing the % variance accounted by direct (climate) and indirect (land management) effects for different EPs

	Climate % variance			Land management % variance		
Ecosystem properties	L	T	NT	L	T	NT
Soil organic matter	0.99	0.93	0.99	0	0.06	0.0
NO_3 retention	0.99	0.66	0.95	0	0.33	0.04
Green biomass production	0.99	0.86	0.98	0	0.13	0.01
Fodder crude protein content	0.89	0.17	0.70	0.1	0.81	0.29
Litter mass	0.98	0.68	0.96	0.02	0.28	0.04
Date of grass flowering onset	0.99	0.99	0.99	0.0	0.01	0.01
Plant diversity	0.66	0.20	0.87	0.33	0.80	0.12
Nitrogen mineralization potential	0.99	0.58	0.99	0	0.42	0.0

Results are presented for the entire landscape (L) or for terraced grasslands (T) and unterraced grasslands (NT) analyzed individually. All coefficients are significant at 0.05 level.

highly correlated (Pearson coefficient; $r \geq 0.5$), of which 7 were stable synergies across scenarios (positive correlations: Litter-Gbio, CPC-SOM, PlantDiv-SOM, PlantDiv-CPC, NMP-SOM, NMP-PlantDiv). Under current management and climate, and similarly under land-management change alone or intermittent drought, SOM, N mineralization, nitrate retention and CPC were compromised by biomass production, litter accumulation, plant diversity, and late flowering onset of grasses (Fig. 2) although only two of these negative correlations were strong (CPC-Litter, plantDiv-Litter). Drastic drought reversed the prevalence of this latter set of ESs to the benefit of the former.

Direct vs. Indirect Effects of Climate on Ecosystem Properties and Their Bundles. According to our empirical model, climate alternatives were likely to strongly influence variations in most EPs with more than 89% of variance explained by climate (ANOVAs) (Table 1) although this effect was more moderate for plant diversity. Pattern observations (Fig. 2) showed that the drastic climate alternative significantly modified all EPs. NO_3 retention, Litter, and CPC strongly responded to both land-management scenarios in comparison with current land management whereas SOM, Gbio, and NMP were significantly modified under the drastic-local scenario.

Redundancy analysis (i.e., RDA) elucidated how covariation in the set of eight EPs for the entire landscape responded to drought and land-management scenarios. The primary axis of differentiation among scenarios represented direct climate effects (Fig. 3). Simultaneous increases in nitrogen mineralization, soil organic matter, and nitrate retention were strongly and positively related to drastic droughts, at the expense of the other properties, which were favored under current climate or intermittent droughts (Fig. 3). The second axis represented contrasts across land-management scenarios. When explicitly considering area under key management types or mowing and fertilization, as explanatory variables, this second axis contrasted scenarios with a greater area under fertilization (corresponding to the drastic-local and drastic-international land-management scenarios—see also stacked bar graphs in Fig. 2, land management types T1, T3f, T4f, and T5f) from those favoring grazing against mowing (corresponding to the intermittent-local land-management scenario—see also stacked bar graphs in Fig. 2, land management types T3, T3f, T5, and T5f) (Fig. 3). Fodder crude-protein content was separated from the other EPs on this second axis, reflecting its positive response to mowing.

Mechanisms Underpinning Direct and Indirect Effects of Climate on Ecosystem Properties. The ANOVA (Table 1) for unterraced grasslands revealed the same variation of individual EPs as at the landscape scale. In contrast, on terraces, most of the variance in fodder crude protein content (81%) and in plant diversity (80%) was due to land management whereas variation of the other EPs was still mainly driven by climate (>50%). Individual RDAs for nonterraces and terraces presented the same results as for the entire landscape, with the first axis capturing variation due to climate (77% variance for nonterraces and 50% variance for terraces), and the second axis variation due to land management (7% variance for nonterraces and 29% variance for terraces).

Spider graphs of ecosystem properties by land-management type, reflecting changes in ecological parameters in response to climate, revealed three patterns of ecosystem properties (Fig. S1) related respectively to the three climate alternatives. Given that land management alternatives only affected the representation of different types across the landscape, and thereby the aggregate values of ecosystem properties at landscape scale, these patterns were not affected by land-management alternatives other than by the addition of new management types.

Discussion

Climate and land use are the two main drivers of change in ESs (17). Our trait-based study identifies, through a predictive model built from empirical data, direct and indirect effects of climate on EPs and attempts to tease out underlying mechanisms associated with plant functional ecology and land-use patterns at a landscape scale. Although we did not conduct a sensitivity analysis, the results discussed below give an indication of the model sensitivity under the modifications of model parameters in the two climate scenarios for the different land-management types (Table S2).

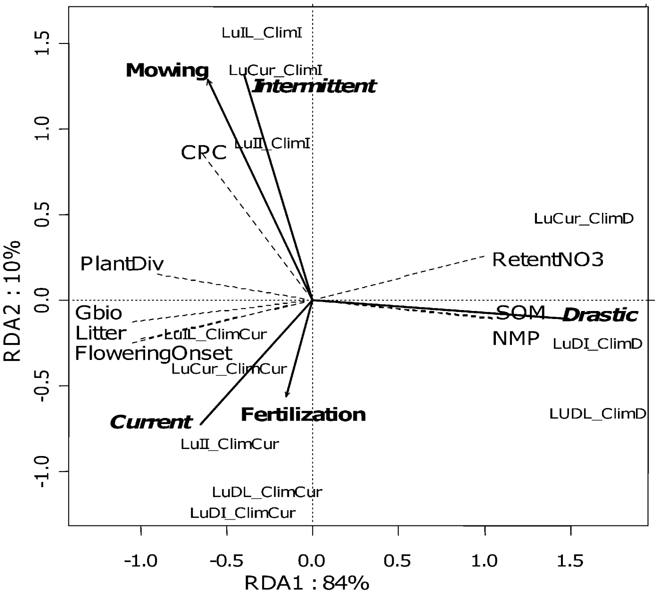

Fig. 3. Responses of EPs for all combinations of scenarios combining climate (Clim) and land-use (Lu) alternatives. Land-use alternatives were characterized by % area under mowing and % area under fertilization. Scenario combinations and their acronyms are those presented in Table S4. EPs are displayed in plain font and explanatory variables in bold. EP acronyms are presented in the Fig. 2 legend. All canonical axes were significant (Monte Carlo permutation test, $P < 0.001$), with 84% and 10% variation captured by RDA1 and RDA2, respectively.

Direct and Indirect Effects of Climate Change on EPs Underpinning ESs. Our unique approach of apportioning variance in EPs to climate and land management effects showed that, at the landscape scale, most of the EPs considered (soil organic matter, nitrogen mineralization, nitrate leaching, biomass production, litter mass, and date of grass flowering onset) responded predominantly to climate, with the strongest impacts of the drastic alternative irrespective of management. In contrast, a combined impact of climate and management was observed on a few EPs such as fodder crude protein content and plant diversity, due to marked land-management change on terraced grasslands, which most strongly contribute to variation in these EPs. Relationships between EPs did not change across scenarios.

Landscape scale effects of scenarios are an area-weighted average of effects on each of the land-management types. Thus, the relative contributions of direct and indirect climate effects were related to two main causes: (*i*) the magnitude of changes in management depending on the area under different types of management, and (*ii*) the relative magnitude of ecological effects of climate and management on EPs within each land-management type.

The small effect of land management reflected the large area of unterraced grasslands and alpine meadows (more than 70% together) that incurred, respectively, few or no changes in the different land-management scenarios (see stacked bar graphs in Fig. 2), concealing strong management effects on terraces (29% variance explained by land management change on terraces against 7% on unterraced grasslands) (*SI Text*).

The greatest impacts on EPs resulted from the conversion from mowing to grazing under the drastic-local scenario, which caused an increase of grazing on terraces from 12% to 17% of the total area (14) and a similar increase in fertilized area across the entire landscape. Such small changes in land management, even under the most severe scenario, were due to constraints specific to high-mountain environments (18), which limited options for diversification of management practices. More contrasted results may be expected in other farming systems where less productive grasslands are abandoned and where conversion from more intensive artificial and fertilized grassland or crops (e.g., maize) to grasslands is possible (19, 20), leading to stronger direct drought effects on land management.

Functional Mechanisms Underpinning Scenario Effects on EPs and Their Bundles. Because of the cold and, in some instances, dry climate, nitrogen is one of the most limiting elements for plants and soil microorganisms in subalpine grasslands, and thereby for carbon and nitrogen cycling (15, 21, 22). In our models, EPs were driven by two core sets of variables relating to fertility and plant traits, respectively (Fig. 4 and Table S3). Under the scenarios, fertility was increased by fertilization and reduced by drastic drought, and traits were modified by drastic drought and/or decreased fertility. The two climate alternatives differed in the relative strength of these two mechanisms: under intermittent drought, trait values were only modified as a result of fertilization management whereas, under drastic drought, both pathways were combined.

Drought effects on EPs, associated mostly with microbial processes (soil organic matter, nitrogen mineralization potential, and nitrate retention) (15), resulted from the reduction in microbial activities as reduced water availability slows down litter decomposition (23) and/or microbial nitrification and denitrification activities. These effects translated to increased carbon and nitrogen sequestration (21) and thus reduced availability to plants. This feedback was reflected in the changes in plant traits toward more resource-conservative [greater leaf dry matter content (LDMC), lower leaf nitrogen concentrations (LNC)] plant strategies and decreased plant height. Effects of these plant functional changes then cascaded to EPs driven by plant traits: biomass production, standing litter, and crude protein content (7, 15).

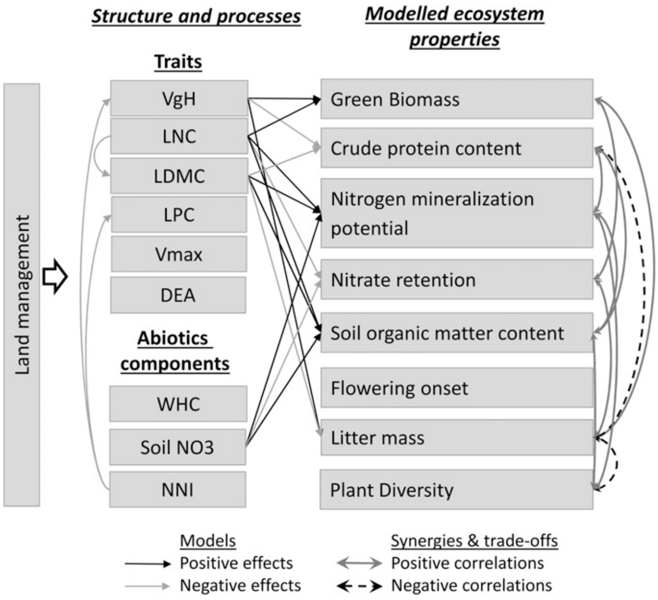

Fig. 4. Traits-based models of EPs and resulting correlations. Black and gray arrows describe positive and negative relationships, respectively, incorporated into the models (single arrows). Colored full double arrows show those correlations expected from the model structure that were verified at landscape scale. Traits: DEA, potential denitrification enzyme activity; LDMC, leaf dry matter content; LNC, leaf nitrogen concentration; LPC, leaf phosphorus concentration; VgH, vegetative height; V_{max}, maximum nitrification rate. Abiotic components: NNI, nitrogen nutrition index; SoilNO3, soil nitrate concentration; WHC, water holding capacity.

Land-management changes impacted EPs through their direct effects on nutrient availability and thereby their indirect effects on plant traits (8, 15, 22). Increased nutrient availability through manuring shifted communities from dominant resource-conservative species to a more diverse array of species with an exploitative nutrient economy (22). The main consequence of this functional shift was greater biomass production and reduced litter accumulation in terraced mown grasslands and unterraced mown grassland, but the effects were opposite in unterraced unmown grasslands (7). Conversion from mowing to extensive grazing indeed promoted dominance by species with resource-conservative leaf traits (e.g., high LDMC) and, in the case of unterraced grasslands, taller plants, especially *Festuca paniculata*, which is promoted by grazing avoidance (24).

The statistical models that we used to project EPs under the scenarios shared common or correlated driving variables across EPs and thus had direct functional consequences for the correlation structure of EPs and expected bundles (Fig. 4). Overall, observed correlations were consistent with expectations based on driving traits, such as the positive correlation between soil organic matter and nitrogen mineralization potential, both increasing with LNC and LDMC, or the negative correlation between litter mass and crude protein content, which had opposite effects from plant height. The positive correlations between nitrate retention and biomass production or standing litter were opposite to expectations from their controlling traits but could be explained by dominant fertility effects on these variables, as well as by nutrient flows (litter accumulation promoting nutrient retention and biomass production uptaking nitrates from the soil and thereby reducing leaching).

Finally, the negative relationship between standing litter and plant diversity was explained by the inhibitory effects of litter, including via light and rainfall interception, resulting in enhanced drought effects (25). Synergies between plant diversity and both SOM and NMP were likely indirect effects of fertility, which both promoted species diversity (22) and contributed to greater carbon and nutrient sequestration (Fig. 2) (15).

Thus, consistent with the framework proposed by Bennett et al. (4), the mechanisms underlying bundles of EPs and tradeoffs in response to scenarios resulted both from common responses of different EPs to fertility parameters [nitrogen nutrition indices (NNI) and NO_3], and to interactions between EPs as a result of common driving traits.

Conclusion

A methodological framework based on plant functional traits successfully unraveled effects of climate and land-use change on ES bundles at a landscape scale. In subalpine grasslands, two mechanisms underlined bundles of ESs and tradeoffs in response to scenarios: (*i*) the magnitude of change in land management across the landscape both in type and surfaces area, and (*ii*) the relative magnitude of fertility and trait-driven effects of climate and management.

Given their limited impacts on ecosystem properties, in comparison with climate change, land-management changes per se only marginally affected the provision of ESs in this high-altitude, constrained grassland system. Their main impact was the decrease of plant diversity, which does not impact farmer incomes. These results confirm that managing such systems requires an understanding of tradeoffs among desired ESs.

Study Site and Methods

Study Site. The study site is located on the south-facing slopes of the Central French Alps (45°03′ N, 6°24′ E; 13 km^2 from 1,552 to 2,442 m above sea level). The area is dominated by grasslands used by extensive sheep and cattle livestock farming, which can be described as terraced or unterraced grasslands, or alpine meadows that combine past and present land management (mowing, grazing, manuring) (22), distributed along an altitudinal gradient (8). Over the last decades, several droughts have temporarily halved forage production. Farmers adapted their practices by purchasing fodder, which in turn fosters a conversion from mowing to grazing (20).

Combined Scenarios of Climate and Land-Use Change. Four coupled climate/socio-economic scenarios for the study site were developed, with a 2030 horizon, using a participatory approach involving regional experts. These scenarios were then downscaled in collaboration with local farmers to generate four land management scenarios (see ref. 14 for more details). Two climate alternatives covered the consequences of alternative drought frequencies: drastic drought—every year for four consecutive years, with up to 50% less annual forage production; or intermittent drought—every other year leading to a 15% decrease in forage production. They were combined with two socio-economic alternatives: local—local consumption and policy incentives for environmentally friendly agriculture with quality food production; or international—globalization of markets and policy incentives for preserving open landscape character. Farmers proposed two adaptations in response to the four scenarios. First, they increased the area under fertilization from 8% (current) to up to 16% [drastic-local’ and intermittent-local scenarios (Fig. 2, types T1, T3f, and T5f in the stacked bar plots for each scenario)]. Second, they favored grazing at the expense of mowing (and resorted to fodder purchases if economically possible), resulting in a reduction from 28% of the total area mown (current) to as little as 8% in the drastic-local scenario (Fig. 2, types T1, T2, and T4 in the stacked bar plots for each scenario).

Vegetation Parameters and Plant Traits. The taxonomic composition of plant communities, plant traits [vegetative height, leaf dry matter content (LDMC), leaf nitrogen concentration (LNC), and leaf phosphorus concentration (LPC)], and environmental parameters [altitude, slope, water holding capacity (WHC), nitrogen nutrition index (NNI), and phosphorus nutrition index (PNI)] were measured between 2003 and 2011 for 60 plots stratified by land-management type, landscape sector, and altitude (for more details, see ref. 8). Plant taxonomic diversity was quantified using the Simpson's index at plot level whereas plant functional diversity was estimated using community-weighted mean (CWM) and functional divergence (FD) of each functional trait separately (26).

Responses of these parameters to climate and land-management changes in each scenario (Table S2) were estimated by expert judgment. Briefly, based on a state-and-transition model, management change was assumed to switch parameter values to those associated with the new management state (22). Effects of novel fertilization were quantified using results from a pot experiment (27) and from measures at other functionally similar temperate mountain sites (28). Responses of trait and soil parameter values to drought were inferred from field and pot experiments manipulating water availability (27, 29). Nutrient immobilization under water shortage resulted in decreased plant available nutrients and in decreased fertilization responses (Table S2). Given the short time frame of scenarios (2030) compared with the slow dynamics of subalpine grasslands, we considered changes in species relative abundances, rather than species turnover. Drought did not modify species abundances directly (29) whereas organic fertilization of currently nonfertilized grasslands was assumed to result in a threefold increase in dicots and a 30% increase in legumes (22). In addition, in unterraced grassland, we assumed a shift among grasses with a 50% decrease in *Festuca nigra* and *F. paniculata* to the benefit of *Bromus erectus* (22). Under the “intermittent” alternative, we assumed that direct drought effects on plant traits were negligible (29) and that they only responded to decreasing nitrogen fertility (8). In contrast, under the “drastic” alternative, we incorporated intraspecific drought impacts, with decreased height, LNC, and LPC and increased LDMC (27) (Table S2). Projected CWMs were then calculated by combining changed composition and species trait values for each management type. Simpson diversity at the level of the species pool (i.e., gamma diversity) of each land-management type was modified according to changes in NNI (8), either for a given management type between climate scenarios, or for newly fertilized management types according to the increase in NNI resulting from fertilization. Assuming that beta diversity across plots remained constant allowed us to project alpha diversity values per plot under each scenario. Finally, based on multiannual observations, the flowering date of grasses advanced by about 21 d in the drastic alternative and 7 d in the intermittent alternative.

Ecosystem Properties. We applied Generalized Linear Models (GLMs) based on field plot measurements of plant traits, microbial parameters, and abiotic variables following refs. 8 and 15 to predict variations across the landscape of various EPs (Table S3), for each 20 × 20-m pixel of the land management maps (Fig. 4 and Table S3). ESs can then be derived by combining and/or translating EPs according to rules defined through stakeholder surveys (as described in ref. 8).

To separate climate effects and land-management effects, we designed a simulation experiment by creating, in addition to the current context and the four scenario combinations of climate and land-management change, six additional artificial scenarios representing either land-management scenarios with climate status quo (four artificial scenarios) or climate scenarios with land management status quo (two artificial scenarios). Statistical models of EPs were applied to the total of eleven climate and land-use combinations, including current conditions, the four actual scenarios, and the six artificial scenarios (Table S4).

Data Analysis. There are a number of methods to describe tradeoffs and synergies among ESs (1, 3, 8, 30), but methods to directly address the causes of associations among ESs are lacking. We propose a method in three steps that moves from descriptions of bundles to the attribution of their causes to scenario drivers and ecological mechanisms.

Each of the 20 × 20-m pixels composing the landscape grid was characterized by an EP value (continuous) under each scenario, a scenario type coded using two categorical variables corresponding, respectively, to the land management and the climate alternatives (Table S4), a land management type, and mowing and fertilization as binary variables. Data were summed for the entire landscape, or alternatively for each of the three grassland types. EP values were centered and scaled to be comparable. Analyses proceeded in three steps associated with each of the three research questions.

First, we visualized changes in EPs and their bundles across scenarios for the entire landscape using spider graphs (Fig. 2). These graphs provided both a static view of positive and negative relationships between EPs for a given scenario (1), and a first dynamic view of tradeoffs in response to scenarios (30). Then, pairwise Pearson's correlation coefficients at pixel scale (Table S1) quantified interactions (positive and negative) between EPs for each scenario (3). To reduce spatial auto-correlation and increase the robustness of the model, we sampled 5,000 pixels (out of 24,531 pixels) from each dataset while keeping the proportions of land management types across the landscape.

Second, an analysis of variance (ANOVA) was performed on the sum of pixels values for each of the eleven scenarios, followed by variance partitioning to estimate the relative contribution of “climate” and “land management” (which one of the two have the strongest effect) to individual EP variation estimated by our predictive model (Table1). Consistent with the design of our simulation experiment, the combination of climate and land-use explained all the variation in the ANOVA. Post hoc Tukey honestly significant difference tests detected significant differences among levels of those explanatory variables explaining a significant amount of variation in a given EP. Then, we used a redundancy analysis (RDA) to quantify and visualize the potential relative contributions to tradeoffs among ecosystem properties across scenarios of direct climate effects vs. its indirect effects via land-management adaptation. This RDA quantified the explanatory powers of climate and land management for the matrix describing the eight ecosystem properties across the 11 scenarios. A second RDA was repeated replacing land management by the explicit percentages of mown or fertilized pixels in combination with climate as explanatory variables (Fig. 3).

Third, to identify specific mechanisms associated with scenario effects on landscape patterns, each ANOVA and RDA was run for the entire landscape (sum of pixel values of the whole landscape) and also for individual grasslands types (sum of pixel values for terraces, nonterraces, and alpine meadows, respectively). As an additional aid for interpretation, effects of individual land-management types were visualized by spider graphs describing ecosystem properties for each land-management type within each scenario (Fig. S1).

All statistical analyses were carried out with the R statistical software (version 2.14) using the ade4 and vegan packages.

ACKNOWLEDGMENTS. We thank Pierre Gos, Coline Byczek, and Emilie Crouzat for useful advice. We acknowledge the Joseph Fourier Alpine Station for logistical support. This research was conducted on the long-term research site "Zone Atelier Alpes," a member of the International Long Term Ecological Research-Europe network and the Long-Term Socio-Ecological Research networks (Zone Atelier Alpes Publication 28). This research was funded by the ERA-Net BiodivERsA, with the national funder Agence Nationale de la Rechereche, part of the 2008 BiodivERsA call for research proposals (VITAL project) and by the French Environment Ministry (Ministère de l'Ecologie, de l'Energie, du Développement Durable et de la Mer) through the GICC-2 SECALP project. M.M. and S.L. acknowledge support by European Union Project VOLANTE FP7-ENV-2010-265104.

1. Raudsepp-Hearne C, Peterson GD, Bennett EM (2010) Ecosystem service bundles for analyzing tradeoffs in diverse landscapes. *Proc Natl Acad Sci USA* 107(11):5242–5247.
2. Nelson E, et al. (2009) Modeling multiple ecosystem services,biodiversity conservation, commodity production, and tradeoffs at landscape scales. *Front Ecol Environ* 7(1): 4–11.
3. Chan KMA, Shaw MR, Cameron DR, Underwood EC, Daily GC (2006) Conservation planning for ecosystem services. *PLoS Biol* 4(11):e379.
4. Bennett EM, Peterson GD, Gordon LJ (2009) Understanding relationships among multiple ecosystem services. *Ecol Lett* 12(12):1394–1404.
5. de Bello F, et al. (2010) Towards an assessment of multiple ecosystem processes and services via functional traits. *Biodivers Conserv* 19(10):2873–2893.
6. Kremen C (2005) Managing ecosystem services: What do we need to know about their ecology? *Ecol Lett* 8(5):468–479.
7. Lavorel S, Grigulis K (2012) How fundamental plant functional trait relationships scale-up to trade-offs and synergies in ecosystem services. *J Ecol* 100(1):128–140.
8. Lavorel S, et al. (2011) Using plant functional traits to understand the landscape distribution of multiple ecosystem services. *J Ecol* 99(1):135–147.
9. Lavorel S, Garnier E (2002) Predicting changes in community composition and ecosystem functionning from plant traits: Revisiting the Holy Grail. *Funct Ecol* 16: 545–556.
10. Bohensky EL, Reyers B, Van Jaarsveld AS (2006) Future ecosystem services in a Southern African river basin: A scenario planning approach to uncertainty. *Conserv Biol* 20(4):1051–1061.
11. Thuiller W, Araujo MB, Lavorel S (2004) Do we need land-use to model species distributions in Europe? *J Biogeogr* 31:353–361.
12. Grêt-Regamey A, Bebi P, Bishop ID, Schmid WA (2008) Linking GIS-based models to value ecosystem services in an Alpine region. *J Environ Manage* 89(3):197–208.
13. Gascoigne WR, et al. (2011) Valuing ecosystem and economic services across land-use scenarios in the Prairie Pothole Region of the Dakotas, USA. *Ecol Econ* 70(10): 1715–1725.
14. Lamarque P, et al. (2013) Taking into account farmers' decision making to map fine-scale land management adaptation to climate and socio-economic scenarios. *Landsc Urban Plan* 119(2013):147–157.
15. Grigulis K, et al. (2013) Relative contributions of plant traits and soil microbial properties to mountain grassland ecosystem services. *J Ecol* 101(1):47–57.
16. Lamarque P, Quétier F, Lavorel S (2011) The diversity of the ecosystem services concept and its implications for their assessment and management. *C R Biol* 334(5-6): 441–449.
17. Carpenter SR, et al. (2009) Science for managing ecosystem services: Beyond the Millennium Ecosystem Assessment. *Proc Natl Acad Sci USA* 106(5):1305–1312.
18. Mottet A, Ladet S, Coque N, Gibon A (2006) Agricultural land-use change and its drivers in mountain landscapes: A case study in the Pyrenees. *Agric Ecosyst Environ* 114(24):296–310.
19. Martin G, Felten B, Duru M (2011) Forage rummy: A game to support the participatory design of adapted livestock systems. *Environ Model Softw* 26(12):1442–1453.
20. Nettier B, Dobremez L, Coussy JL, Romagny T (2010) Attitudes of livestock farmers and sensitivity of livestock farming systems to drought conditions in the French Alps. *J Alp Res* 98(1):383–400.
21. Robson TM, Baptist F, Clement JC, Lavorel S (2010) Land use in subalpine grasslands affects nitrogen cycling via changes in plant community and soil microbial uptake dynamics. *J Ecol* 98(1):62–73.
22. Quétier F, Thebault A, Lavorel S (2007) Plant traits in a state and transition framework as markers of ecosystem response to land-use change. *Ecol Monogr* 77(1):33–52.
23. Coûteaux MM, Bottner P, Berg B (1995) Litter decomposition, climate and liter quality. *Trends Ecol Evol* 10(2):63–66.
24. Quétier F, Liancourt P, Thébault A, Davies ID, Lavorel S (2011) Assessing long-term land-use legacies in subalpine grasslands by using a plant trait-based generic modelling framework. *Plant Ecol Divers* 4(4):391–402.
25. Gross N, Liancourt P, Choler P, Suding KN, Lavorel S (2010) Strain and vegetation effect on local limiting resources explain the outcome of biotic interactions. *Perspect Plant Ecol Evol Syst* 12:9–19.
26. Díaz S, et al. (2007) Incorporating plant functional diversity effects in ecosystem service assessments. *Proc Natl Acad Sci USA* 104(52):20684–20689.
27. Grassein F (2009) Mécanismes de variation des traits fonctionnels dans les prairies des Alpes. PhD thesis (Université Jospeh Fourier, Grenoble, France).
28. Ansquer P (2006) Caractérisation agroécologique des végétations prairiales naturelles en réponse aux pratiques agricoles: Apports pour la construction d'outils de diagnostic. PhD thesis (Institut National Polytechnique de Toulouse, Toulouse, France).
29. Benot M-L, et al. (2013) How extreme summer weather may limit control of Festuca paniculata by mowing in subalpine grasslands. *Plant Ecol Divers* 6(3-4):393–404.
30. Rodríguez JP, et al. (2006) Trade-offs across space, time, and ecosystem services. *Ecol Soc* 11(1):28.