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Ecosystem services in mountain pastures: A complex network of site conditions, climate and management

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ABSTRACT

Mountain pastures offer a multitude of ecosystem services (ES) such as fodder for ruminants, habitat for pollinators, climate change mitigation, aesthetic landscape for recreation, and biodiversity conservation. We aimed at analysing to which extend these ES are influenced by small-scale gradients of climate, site conditions and management – and to disentangle relationships among ES and the factors influencing them. Therefore, we quantified ES on six mountain summer farms in two contrasting regions in Switzerland: the Northern Alpine Foothills (lower elevation, higher precipitation, calcareous bedrock) and the Eastern Central Alps (higher elevation, lower precipitation, silicious bedrock). We measured six ES indicators (forage quantity, forage quality, carbon storage, colour abundance, resources for pollinators, plant diversity) and related them to explanatory factors of climate (temperature and precipitation), site conditions (soil fertility, soil acidity, terrain slope) and management (local grazing intensity, remoteness) in 66 study plots, i.e., 11 per farm. A holistic picture of the complex relationships among these factors was drawn by various statistical approaches: allometric line fitting, variance partitioning, and structural equations modelling. We found a huge heterogeneity of ES indicators and explanatory factors on each farm: the variability within farms was even higher than between regions. Variance partitioning and structural equations modelling demonstrated strongest influence of climate and site conditions and revealed trade-offs among ES indicators: High forage quantity and quality were associated with low plant diversity and grassland aesthetics, whereas diversity, aesthetics and pollinator resources were positively correlated with each other. ES indicators were explained by a range of climatic and topographic factors: High precipitation reduced plant diversity, whereas temperature increased forage quantity and quality; slope reduced soil fertility, forage quantity, forage quality and carbon storage; soil fertility in turn increased forage quantity; the farther away a pasture was from the main farm building, the lower was the forage quantity and the higher the plant diversity. Although allometric *relations* among local grazing intensity and ES indicators were strong, the *direct* influence of the management factors measured on ES was surprisingly small: Cattle preferred areas of high forage quantity and quality, and carbon storage was higher in these areas. On the other hand, places less visited by cattle offered more pollinator resources, and showed higher aesthetics and plant diversity. Trade-offs among ES prevent the realisation of all ES at the same place, but heterogeneity of mountain pastures allows to realise a broad bundle of contrasting ES on each individual summer farm.

1. Introduction

1.1. Mountain pastures: multifunctional cultural land

Mountain pastures are often simplistically perceived as peaceful, nostalgic places of recreation, grazed by emblematic cows. However, they are much more and provide a plethora of ecosystem services (ES). In Switzerland, where high-altitude grazing is conducted since millennia (Hafner and Schwörer, 2018), mountain pastures not only host 14, 000 km of hiking trails today, but cover one third of agriculturally used

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Abbreviations: CV, coefficients of variation; DM, dry matter biomass; ES, ecosystem services; GPS, global positioning system; SEM, structural equations model.

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land (Herzog and Seidl, 2018). Without transhumant mountain pasture use in summer, the nationwide stock of ruminants had to be reduced by 10 % (Stettler and Probst, 2023). This ruminant-based food production in areas where arable farming is unfeasible is an important provisioning ES. Moreover, mountain pastures offer regulating ES such as carbon storage. For instance, 75 % of all protected Swiss fens (Lauber et al., 2013), which are important areas of carbon sink, are placed in transhumant mountain pastures. Additionally, these pastures provide supporting ES such as food resources for pollinators. Finally, they host an outstanding biodiversity (Kampmann et al., 2008) and thereby contribute substantially to gene pool protection: In Switzerland, 64 % of all endangered plant species and two third of all endemic plant species are closely connected to these ecosystems (Lauber et al., 2013).

Tasser et al. (2020) presented a collection of 19 services of mountain ecosystems in general. As it was not possible to quantify all these ES, we selected the most relevant for mountain *pastures*: pasture and fodder production (indicated by forage quantity and quality), positive effect on the climate (indicated by carbon storage), aesthetic inspiration (colour abundance), habitats for pollinating insects (food resources for pollinators) and maintaining biodiversity (plant diversity; Table 1). As these are only indicators of ES, they come along with certain limitations. For instance, forage quantity and quality as indicators of fodder production are not directly relevant for humans, but only via grazing livestock (Richter et al., 2021). Anyway, we consider these indicators as relevant, because they are main targets of pasture management. Accordingly, there may be more precise indicators of aesthetic inspiration (Chai-allah et al., 2023; Oteros-Rozas et al., 2018) or carbon storage (Wang et al., 2023), but as outlined by Richter et al. (2023), there is a trade-off among affordability and precision of ES assessment. Thus, we aimed at quantifying the variability of the six ES indicators within and among zones with different environmental conditions.

1.2. Modifying ecosystem services by management

In many mountain regions, including the European Alps, there is an ongoing decrease in ES services, although there is high demand for ES by the human population (Grêt-Regamey and Weibel, 2020). Due to their challenging terrain, low temperature, steep slopes, and remoteness they are especially vulnerable to change in climate and land use (Hock et al., 2019). Hence, there is a broad interest in maintaining or even enhancing mountain grassland ES by management. However, in mountain pastures, agricultural options are limited: fertilisation and tillage is impossible at many sites due to rocks, shallow soils and steep slopes that hinder machine processing; pesticides and seed mixtures are hardly used because they are too expensive to economically justify their application in low-output mountain systems. Thus, the main management option at hand is to modify stocking of grazing livestock. By building fences and increasing stocking rate or density, farmers can influence the movement behaviour of cattle to a certain extent (Bailey and Brown, 2011), but the actual grazing pressure is very unevenly distributed within heterogeneous mountain pasture paddocks (Homburger et al., 2015). However, only the actual local grazing intensity is relevant for the ecosystem services provided at a certain place. Therefore, for the first time, we analyse how mountain pasture ES are related not only to overall stocking but to the actual space use of cattle recorded by high-frequency GPS tracking.

Table 1
Target variables. Terminology of ecosystem services (ES) based on Tasser et al. (2020).

Ecosystem service type	Ecosystem service	Ecosystem indicator	Measured as
Provisioning ES	Pasture and fodder production	Forage quantity	Plant biomass dry matter growing throughout the grazing season
		Forage quality	Percentage of digestible organic matter
Regulating ES	Positive effect on the climate	Carbon storage	Soil organic carbon stock
Cultural ES	Aesthetic inspiration	Colour abundance	Percentage abundance of plant species with coloured flowers
Supporting ES	Providing habitats for pollinating insects	Food resources for pollinators	Cover-weighted mean of floral reward indicator of pollen and nectar
	Maintaining biodiversity	Plant diversity	Number of vascular plant species per 25 m^2

1.3. Other explanatory factors of ecosystem services

To promote a certain ES, it is mandatory to understand to which extent an ES is influenced by management and by other factors. There are two additional factors which have the potential to modify an ES: site conditions (such as slope, soil acidity or soil fertility) and climate (such as precipitation and temperature). If, for instance, an ES was mainly driven by management factors, farm practice could be adjusted to realise the desired output. In contrast, if an ES was mainly influenced by given site conditions, it is nearly impossible to specifically modify it by management, given the limited options under mountain conditions. Finally, if an ES was driven by climatic factors, it will likely alter due to climate change. Thus, in a third step we aimed at quantifying by which driver several ES's distribution is explained to which extent, to estimate if an ES is likely to be influenced by management or by climate change.

1.4. Trade-offs among ecosystem services and their explanatory factors

Additionally, we assume that there are trade-offs among different ES in mountain pastures, as well known for lowland grasslands (Lindborg et al., 2022). Ignoring these trade-offs and promoting a single ES, may lead to undesired negative side-effects on other ES. Thus, it is all the more important to disentangle the relationships among pasture ES at multiple sites. Hence, in a last step, we aimed at quantifying trade-offs among several mountain pasture ES as well as their explanatory factors. Thereby, we put a special focus on management as the only factor that can be selectively manipulated by farmers.

To reach our four objectives of (1) quantifying the variability of ES within and among mountain pastures with contrasting environmental conditions, (2) relating them to the actual local grazing intensity, (3) disentangle the unique and joint effects of management, climate and site conditions and (4) the trade-off and synergies between them, we conducted a comprehensive survey on six running mountain summer farms.

2. Material and methods

2.1. Study regions

In Switzerland, mountain summer farms (called Alp, alpage, alpe in the national languages German, French and Italian, respectively) are legally defined as transhumant agricultural units without all-year settlement, i.e., due to high elevation and a short vegetation period they can be used only during summer. Their main – and in most cases only – agricultural land use type is grazing. In the following, *farm* refers to the entirety of pastureland of a mountain summer farm, whereas *farm building* refers to the residential building for the staff during summer. The majority of these mountain summer pastures in Switzerland (Fig. 1a) are situated in two bio-geographic regions: the Northern Alpine Foothills (40.7 %) and the Eastern Central Alps (32.3 % of Swiss mountain summer pastures; calculation based on the areal statistics of Switzerland (2019) and the biogeographic regions defined by the Swiss Federal Office for the Environment (Gonseth and Sartori, 2022)). The study was therefore conducted on three mountain summer farms in each

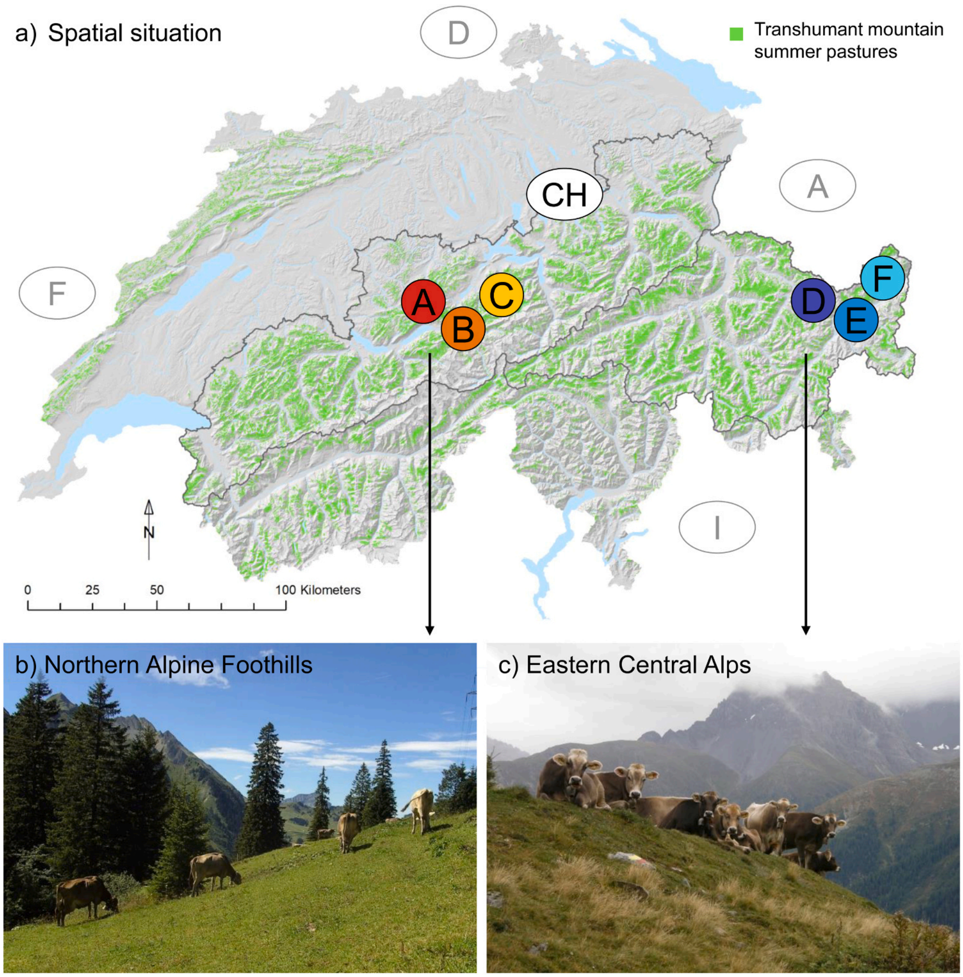


Fig. 1. Transhumant mountain summer pastures (a; green shaded) cover one third of Swiss agricultural land. The study was conducted on six representative subalpine farms in two different bio-geographic regions: the Northern Alpine Foothills (b; farm A-C) and the Eastern Central Alps (c; farm D-F).

of these regions. The three farms within each region were selected along a gradient of pasture management intensity from continuous to rotational stocking as indicated by the number of paddocks. Thereby, we covered a large range of site and management conditions, despite the limitation to six farms, which was necessary due to logistic reasons in animal GPS tracking. Site conditions of the six study farms differed between regions in terms of mean elevation (Alpine Foothills: 1400–1900 m; Central Alps: 2100–2200 m), mean annual temperature (2.7–4.8 °C; 0.2–1.4 °C), mean annual precipitation (1800–1900 mm; 1200–1300 mm) and dominating bedrock (calcareous; siliceous). Pastures in both regions consisted of semi-natural, open grasslands. All farms were regularly grazed by cattle during summer. A detailed description of livestock management is given in Homburger et al. (2015). The six farms were used as summer grazing area since centuries and there was no major change in management practice during the two decades before the study was conducted.

2.2. Plot selection

Six ecosystem service indicators (Table 1) and seven explanatory factors (Table 2) were measured in 66 plots, with 11 plots placed on each of the six farms (Fig. 1). On each farm, the positions of the plots were stratified along two gradients: slope and remoteness, i.e., the distance to the main farm building as a measure of intensity of everyday maintenance work on the pastureland. Stratification was done by calculating the range of slope and remoteness values of each farm in a 10 m grid (DTM-DOM, swisstopo, Wabern, Switzerland). For both factors, three classes were built, corresponding to the first, third and fifth quintile of all values of each farm. Combining slope and remoteness classes resulted in nine intersection classes. The largest continuous polygon of each class was identified. Within, we selected the most homogeneous part regarding vegetation structure as visible from an aerial photograph. In the field, we established a 5×5 m plot there. In four cases, the position chosen in advance was heavily disturbed, e.g. by trampling paths or marmot dens. In these cases, we set up the plot within the second largest polygon of the respective class. Finally, two additional plots were placed in the most and the least frequently grazed areas of the farm according to farmers' experience. All plots were freely accessible for the animals and marked by small pickets only.

Table 2
Explanatory factors.

Type	Factor	Indicator	Unit
Site conditions	Soil fertility	Topsoil phosphorous content	mg kg^{-1}
	Soil acidity	Topsoil pH	
	Terrain Slope	Slope	%
Climate	Temperature	Mean temperature May-Sept	°C
	Precipitation	Monthly mean precipitation May-Sept	mm
Management	Local grazing intensity	Cattle presence	LU ha^{-1} a^{-1}
	Remoteness	Distance to the farm building	m

2.3. Vegetation analysis

To measure *forage quantity* we placed a grazing exclusion cage of 1.2×1.2 m in the centre of each study plot. Vegetation was cut at a height of 4 cm twice: at the beginning and in the middle of the grazing season, after which there was no significant regrowth due to the high elevation. The harvested plant biomass was oven-dried at 60° C during 48 hours and weighted. Biomass of the two cutting dates was summed per plot. *Forage quality* was defined as the percentage of digestible organic matter in these biomass samples. Digestibility was measured in vitro using rumen extract (Tilley and Terry, 1963). For statistical analysis, digestibility values of the two vegetation development stages were averaged.

Plant diversity was determined by recording all vascular plant species in square plots of 5×5 m right before the beginning of grazing according to Lauber et al. (2001). Their percentage cover was estimated visually. The amount of *food resources offered to pollinators* (Richter et al., 2021) was quantified by extracting the "floral reward plant trait" from the BiolFlor database (Klotz et al., 2002), an indicator of the floral offer of nectar, pollen or oil on a 4-level scale. Floral reward of each plant species was weighted by its cover in the plot. *Colour abundance* as an indicator of aesthetic inspiration (Graves et al., 2017; Hoyle et al., 2018) was calculated by summing the percentage cover of all species with flowers in other colours than green and brown as indicated in the BiolFlor database.

2.4. Soil analysis

In each plot, 16 soil cores were taken, divided into fixed horizons of 0–10 cm and 10–30 cm soil depth, pooled per horizon, dried, sieved (<2 mm) and cleaned from roots. For samples where soil depth did not reach 30 cm, soil cores were taken down to the deepest possible horizon. *Topsoil P content* and *topsoil pH* were quantified in samples of the 0–10 cm horizon pooled per plot (pH: 2:1 in water; P: 1:10 NH_4-acetate solution). *Soil organic carbon content* was calculated by soil organic carbon concentration and bulk density (i.e., soil mass per volume) of the entire soil core. Soil organic carbon concentration was measured after combustion with an elemental analyser (Hekatech Euro EA 3000, Wegberg, Germany). To calculate bulk density, we took four additional soil cores per plot and divided each horizon's soil mass by its volume.

2.5. Management data

Local grazing intensity (Fig. 2) was measured by recording small-scale variation in cattle presence during the entire grazing period as described in Homburger et al. (2014), (2015). In brief, three to four cows per farm were GPS-tracked at 20 s recording frequency during the entire grazing season. Recorded positions were (1) discretized on a 25 m grid, (2) weighted by the number of simultaneously working logger devices to account for data gaps (Homburger et al., 2015) and (3) translated into local grazing pressure of the entire herd (livestock units per hectare per year: LU ha^{-1} a^{-1}) based on total animal numbers reported by the farmers. Local grazing intensity of each study plot was extracted from the 25 m grid by intersection with the centre of the study plots.

2.6. Climate and topography data

Mean temperature and *monthly precipitation* were calculated during

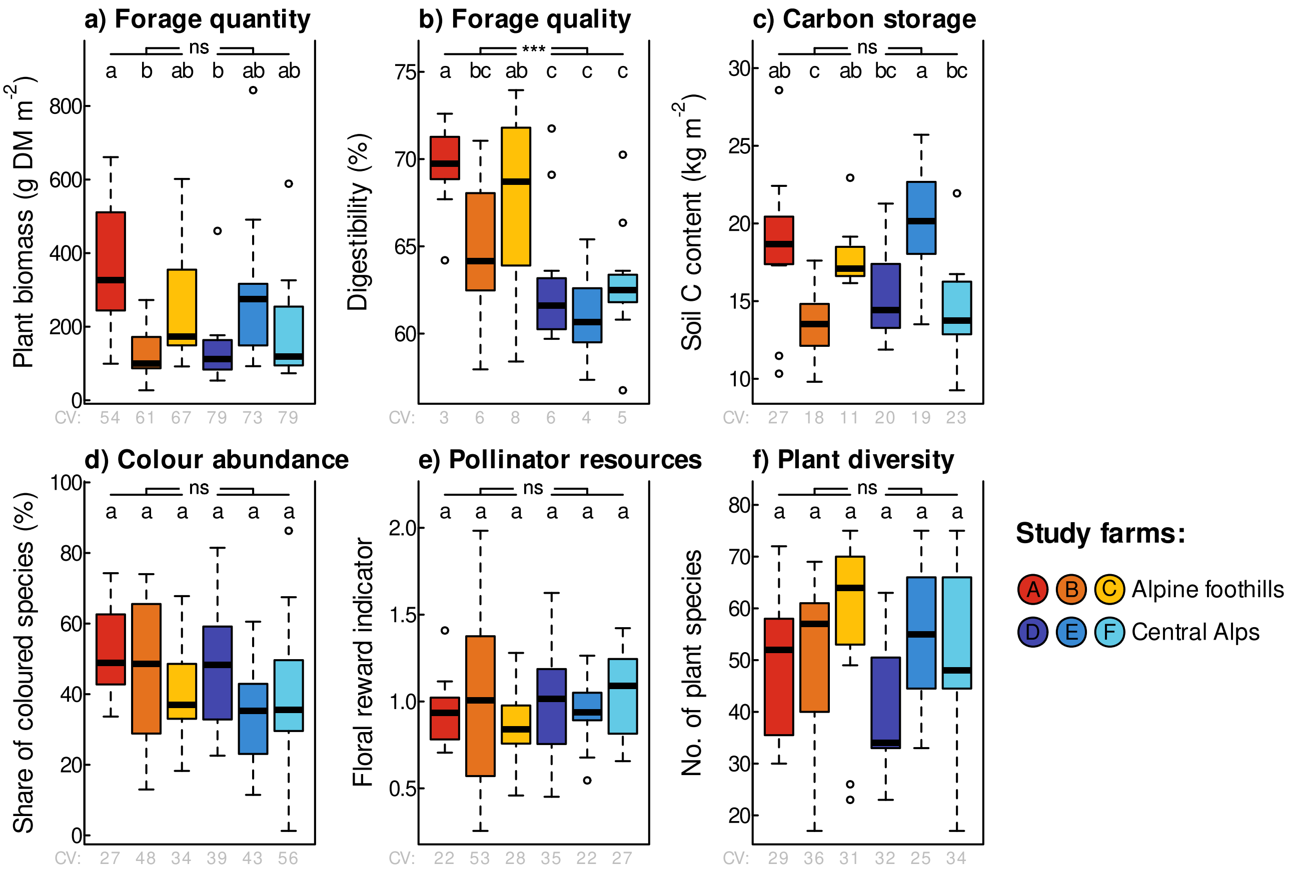


Fig. 2. Distribution of six ecosystem service indicators on six mountain summer farms: a) Forage quantity, b) forage quality, c) carbon storage, d) colour abundance, e) pollinator resources and f) plant diversity. At the upper end of each panel, the significance of the difference between regions is given (ns: not significant, *** $p<0.001$). Identical letters indicate no significant difference ($p>0.05$) among study farms, as tested by Tukey post-hoc comparisons. Grey values at the bottom show coefficients of variation (CV; standard deviation in percentage of the mean) among study plots within each farm.

the summer months of May to September, i.e. the vegetation and grazing period in the study regions. Gridded monthly means of the three decades prior to data collection (i.e., 1980–2010) derived from MeteoSwiss (Federal Office of Meteorology and Climatology) were interpolated on a 25 m grid by co-kriging with altitude using package fields in R 4.2.2 and intersected with the centre of each study plot. *Remoteness* was calculated as the Euclidian distance between a plot and the main building of each farm, i.e., the place of milking parlour and farmers' lodging. *Terrain slope* was calculated in percentage based on the SwissAlti3D digital elevation model (SwissTopo, Wabern, Switzerland) at 2 m resolution.

2.7. Statistical analyses

For each of the four objectives of the study, a specific statistical technique was used. All data analyses were carried out in R 4.3.2 (R Core Team, 2023). To quantify variation of the six ES indicators and seven explanatory factors within and among study farms (objective 1) differences were tested by Tukey post-hoc comparisons in package multcomp (Hothorn et al., 2008) and expressed by a compact letter display at a significance level of 5 %. Differences between the two regions were tested using t-test.

To evaluate non-causal relations between local grazing intensity and ES (objective 2) we applied allometric line fitting: In cases where no causal relationship is expected or where the direction of causality is unclear, a standard regression model is inappropriate because it assumes a causality of the x-variable to the y-variable. Consequently, a regression minimizes error terms for the y-variable only. To overcome this false error term attribution, we used allometric line fitting which distributes the error terms equally to both variables and applied standardized major axis estimation using package smatr (Warton et al., 2012). The relations were analysed over the whole dataset as well as within each study farm (see Pauler et al. 2020 for more detailed explanation on the interpretation).

To quantify the unique and joint effects of management, climate and site conditions on ES (objective 3), we partitioned the variation within the six ES indicators into climate (temperature and precipitation), site conditions (pH, P, slope), management (remoteness and local grazing intensity) and the study farm using package partR2 (Stoffel et al., 2021). The respective fractions explained by one or multiple explanatory factor types were displayed as Venn diagrams, for which size and positioning of the circles were determined using package Vennerable (Swinton, 2011).

Finally, the set of hypothesized effects and trade-offs between ES indicators and explanatory factors (objective 4) were investigated using piecewise structural equations modelling (SEM) using package piecewiseSEM (Lefcheck, 2016). The piecewiseSEM approach allows to take into account the grouping of data by study farms, a major advantage over traditional covariance-based SEM techniques. The resulting standardized regression coefficients were used to determine the thickness of arrows in graphical display.

3. Results

3.1. Variability of ecosystem services

Heterogeneity of ES was high – in some cases within farms (as indicated by coefficients of variation; Fig. 2), in other cases among farms (Tukey post-hoc letters; Fig. 2) or between bio-geographic regions (t-tests; Fig. 2). *Forage quantity*, for instance, varied from 27 to 843 g dry matter per square meter (g DM m^{-2}) and *forage quality* from 57 % to 74 % digestibility. The latter significantly differed between regions with higher quality in the Alpine Foothills than in the Central Alps. The other ES indicators were not influenced by region. However, c*arbon storage* differed significantly among study farms. Variability of *colour abundance*, *resources for pollinators* and *plant diversity* was high among study plots per farm, but there were no significant differences among farms or between study regions. The number of plant species per study plot showed a large range on all farms, with an overall minimum of 17 and maximum of 75 species per 25 m^2. Overall, we recorded 327 different plant species in the 66 study plots.

3.2. Variability of explanatory factors

Site conditions were highly variable among study plots within farms and differed among study farms and between regions (Fig. 3): *Soil fertility* was significantly lower and soils were significantly less *acidic* (i.e., higher pH) in the Alpine Foothills than in the Central Alps ($\text{range}_{\text{fertility}}$: 2.1–41.6 mg P kg^{-1}; range_{pH}: 4.4–7.3). It was highly variable within farms (CV: 47–95 %). *Terrain slope* was similar in both regions, but varied highly within the study farm (CV: 34–53 %) – from almost flat study plots (5 % slope) to very steep ones (87 %).

Climatic factors differed most clearly between the two regions: *Summer temperature* and *precipitation* were significantly higher in the Alpine foothills than in the Central Alps, but climatic variation within each farm was small (CV_{temp}: 4–10 %; CV_{prec}: 0–5 %).

Contrarily, management factors were not influenced by the region, but showed a highly variability within each farm: *Local grazing intensity* ranged from places never grazed throughout data collection to spots grazed most frequently (2.5 LU ha^{-1} a^{-1}) resulting in highest coefficients of variation within farm ($\text{CV}_{\text{grazing int}}$: 91–223 %; see also Fig. 4). As intended by the study design, there was a range in *remoteness* from 70 m to 1.3 km distance to the farm building. Study farms were larger in the Central Alps, resulting in a significantly higher remoteness.

3.3. (Indirect) relations of ES and local grazing intensity

Local grazing intensity was allometrically related to the ES indicators measured: Study plots which were placed in areas preferred by cattle, delivered on average other ES then plots avoided by cattle (Fig. 5; numeric output of the standardized major axis estimation is available in the appendix in Table A.1). There were significant allometric relationships between cattle presence and all ES indicators measured. Local grazing intensity was positively related to forage quantity and quality and to carbon storage, i.e., we measured significantly more biomass, higher digestibility and larger carbon storage in plots frequently grazed than in plots avoided by cattle. On the other hand, plots which were frequently visited by cattle, showed significantly lower colour abundance, offered less food resources for pollinators and hosted a lower species richness than plots where cattle grazed rarely. However, allometric relations do not indicate direct causality and can be mediated by other factors (see results of structural equations modelling).

3.4. Explanation of ES variability by climate, site conditions, management and their interactions

The high variability of ES indicators could at least partially be explained by the explanatory factors measured (Fig. 6; numeric output of the partitioning of variation calculation is available in the appendix in Table A.2). The variability in forage quality, for instance, was mainly explained by climatic factors, whereas the measured explanatory factors did not well explain the variability in carbon storage. However, farm identity explained the majority of carbon storage variation (grey frame in Fig. 6). Variability in colour abundance, pollinator resources and species richness was mainly explained by site conditions. The overall impact of management on ES was rather small. For all ES indicators, a remarkable share of variation was explained not only by a single explanatory factor, but by an interaction of two or three of them, as indicated by overlapping circles in Fig. 6.

3.5. Trade-offs and synergies among ES and explanatory factors

The SEM disentangled complex relationships among ES and explanatory factors within mountain pastures (Fig. 7; numeric output of

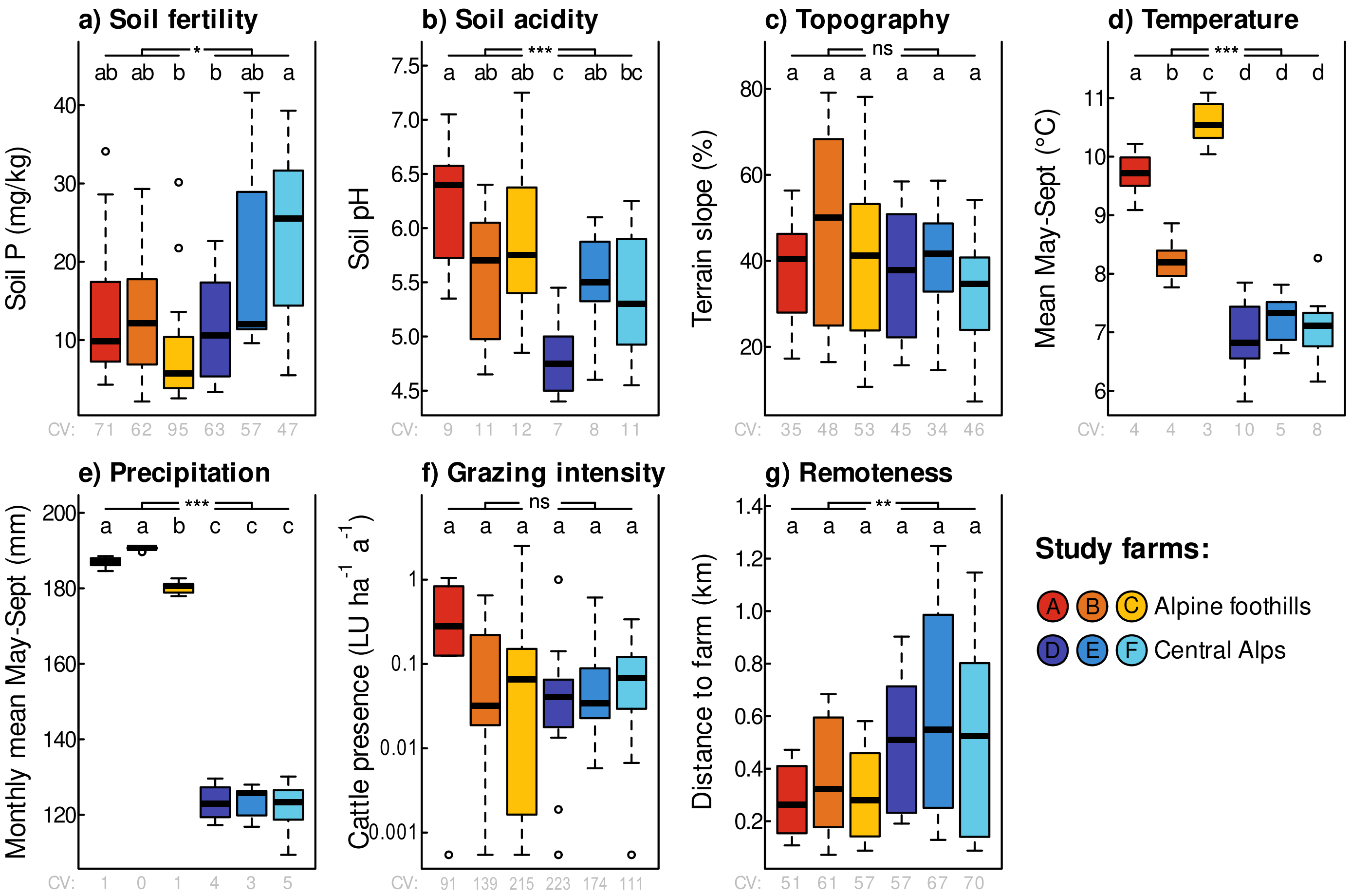


Fig. 3. Characteristics of seven explanatory factors on six mountain summer farms: site conditions measured as a) topsoil phosphorous content, b) topsoil pH and c) terrain slope; climate measured as d) mean summer temperature and e) mean summer precipitation; and management measured as f) local grazing intensity and g) remoteness (i.e., distance to the farm building). At the upper end of each panel, the significance of the difference between regions is given (ns: not significant, * $p<0.05$, ** $p<0.01$, *** $p<0.001$). Identical letters indicate no significant difference ($p>0.05$) among study farms, as tested by Tukey post-hoc comparisons. Grey values at the bottom show coefficients of variation (CV; standard deviation in percentage of the mean) among study plots within each farm.

piecewise structural equations modelling is available in the appendix in Table A.3). First, there were several trade-offs among the ES themselves: High forage quality led to lower colour abundance, and both forage quantity and quality negatively interacted with plant diversity. On the other hand, high plant diversity led to high colour abundance and pollinator resources, which in turn showed strongest positive interactions between each other.

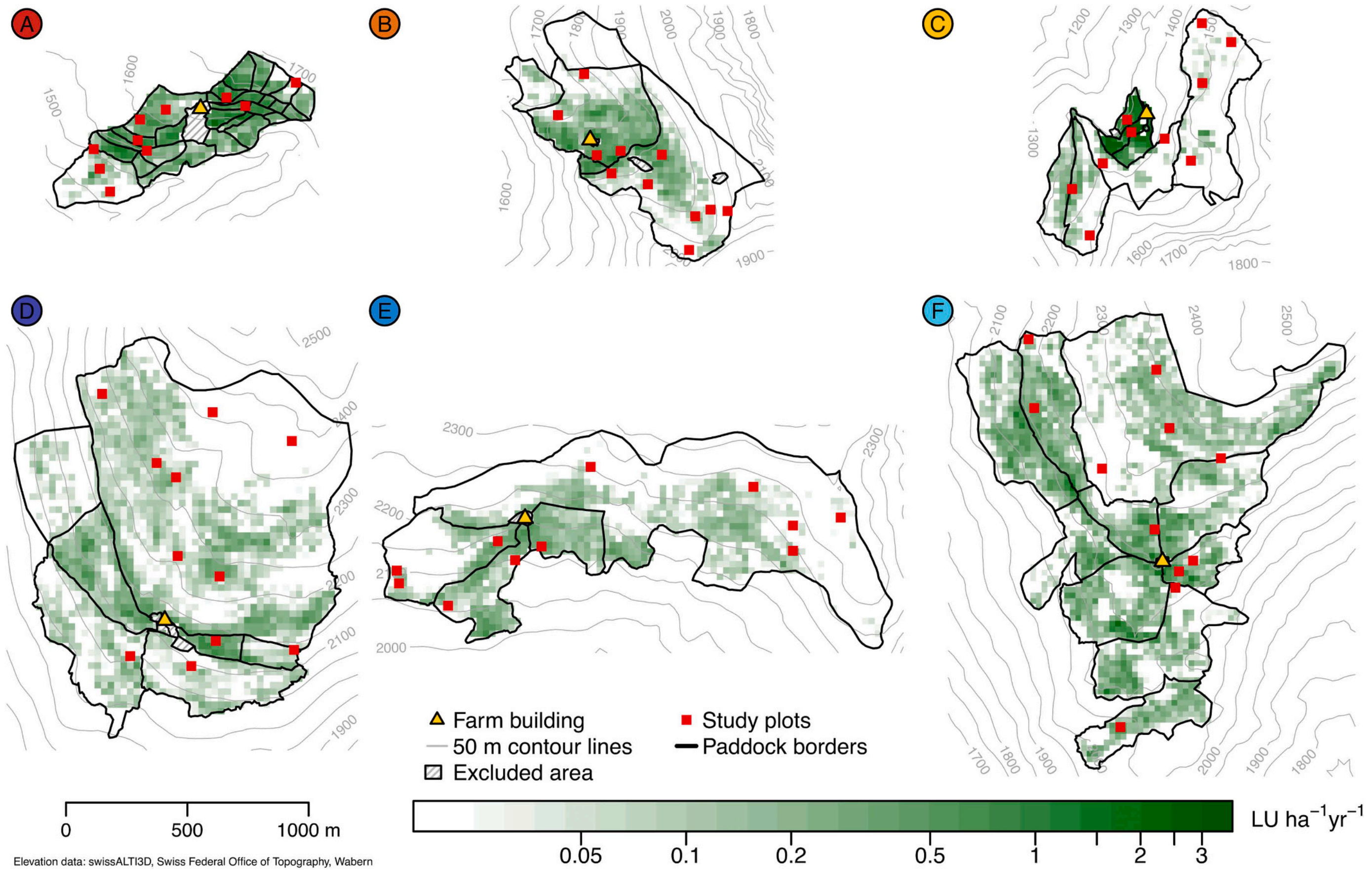
Furthermore, ES were clearly influenced by various explanatory factors: soil fertility increased forage quantity and was itself enhanced by soil pH. In turn, the higher the soil pH, the higher was the plant diversity, the colour abundance and the amount of resources for pollinators. Steep plots were on average less fertile, offered less forage quantity and quality and stored less carbon than flat ones. Warm places provided higher forage quantity and better forage quality, but less pollinator resources than colder ones. A high precipitation reduced plant diversity. The farther away a plot was from the farm building, the more plant species were recorded, the lower was the forage quantity and the less it was visited by cattle. Beyond that, high forage quantity and quality attracted cattle, i.e. the local grazing intensity was increased.

4. Discussion

4.1. Small-scale gradients are important

Our data demonstrate a large spatial heterogeneity at a small scale in the provision of the six evaluated ES indicators as well as in the factors influencing them. Although there are clear differences in climatic conditions among the two study regions, ES indicators do not differ significantly between regions, except for forage quality. In all other cases, the variability within study farms was higher than differences between regions. Within each single farm, we observed a large gradient of ES provision: there are places offering large amounts of high-quality fodder and substantial carbon storage – and nearby unproductive spots hosting an outstanding biodiversity and beautiful scenery. This goes along with strong small-scale gradients of climate, site conditions and management: For example, within a single farm, we found areas differing in mean summer temperature by up to 2 °C (mainly due to differences in altitude), flat areas in close proximity to areas of more than 80 % steepness, and highly fertile places neighboured by extremely nutrient-poor places. Strong heterogeneity is also revealed by GPS tracking which identified areas never visited by cattle occur right next to areas attracting cattle very much (Homburger et al., 2015).

This multi-level heterogeneity of mountain pastures is especially important for maintaining biodiversity: Of the 327 different plant species growing in the 66 study plots, 309 species were found in less than half of the plots, 204 species in only 10 % of the plots, and 81 plants were even found only once. This underlines how crucial it is to maintain not only the most productive mountain pastures but the entire range of conditions. Small-scale heterogeneity is also important for the recreational value of mountain pastures. Although not explicitly quantified by our hierarchical plot-based investigation, the mosaic-like pattern of different ES provision increases the visual attractiveness of landscapes



Elevation data: swissALTI3D, Swiss Federal Office of Topography, Wabern

Fig. 4. Local grazing intensity on the pastureland of six mountain summer farms during an entire vegetation period measured by high-frequency GPS tracking of cows, discretized onto a 25 m grid. Because of the extreme spatial heterogeneity, data is displayed at a log scale. Red squares indicate the position of the vegetation survey plots, yellow triangles the main farm building.

(Hahn et al., 2018).

4.2. Site conditions and climate clearly influence ES

The second objective of our study was to relate ES indicators and local grazing intensity. It is important to notice that this causality is bidirectional and cannot be disentangled, because grazing responds to multiple ES but at the same time ES respond to grazing. We therefore used allometric line fitting, which (unlike regression) makes no assumption of dependency and distributes error terms equally on both variables.

There are strong allometric relations between ES indicators and local grazing intensity, but the partitioning model revealed that the variation of ES indicators was primarily explained by site conditions and climate. This apparent contradiction can be understood by the fact that both cattle behaviour and ES indicators are influenced by site conditions and climate. Neither of them can practically be modified by farmers: Slope or soil acidity, for example, are given *per se* by topography and geology. Also soil fertility can hardly be enhanced, because in contrast to lowland conditions, manure cannot be distributed at steep or rocky sites and the nutrient holding capacity of shallow soils is low (Donhauser and Frey, 2018). Additionally, on mountain summer farms there normally is only little or no slurry available due to all-day grazing, and mineral fertilizer is too expensive in these low-output systems.

Obviously, climate can also not be influenced locally. However, climate change already alters ES: The observed impact of climate on provisioning ES suggests an overall increase of fodder production in mountain areas with rising average temperature. In fact, an increase of vegetation productivity in mountain regions during the last decades was already demonstrated before (Rumpf et al., 2022). However, lower or less evenly distributed precipitation may limit plant growth, lower forage quality due to changes in vegetation composition, reduce belowground biomass and thereby carbon stock (Möhl et al., 2023; Gilgen and Buchmann, 2009) and lead to a lack of drinking water supply which could reduce grazing intensity.

However, given the large heterogeneity of conditions proofed in our study, we do not expect a uniform reaction of mountain pasture ES to climate change. For example, in some Alpine Foothill regions which suffered from excess humidity in the past, fodder production may benefit from lower precipitation and increasing temperature at regional level (Jäger et al., 2020) whereby flat places with limited percolation may show the largest increase of biomass and fodder quality at local level. On the other hand, dry grasslands in mountain regions of already low precipitation may suffer from additional drought events and increasing temperature (De Boeck et al., 2016; Möhl et al., 2023) going along with increasing evaporation (regional level), especially at steep slopes with low water holding capacity (local level). There, climate change is likely to reduce soil fertility, forage quality, carbon storage and soil stability (Maestre et al., 2022).

4.3. ES are related to, but not clearly influenced by management

As site conditions can hardly be influenced by farmers at high elevation and as climate obviously cannot be directly modified, the question of management impact on ES becomes prominent. Among the management measures implemented on mountain pastures are fencing, chemical and mechanical weed regulation, fertilization, mowing, liming, mechanical shrub removal or drainage of wet areas. However, due

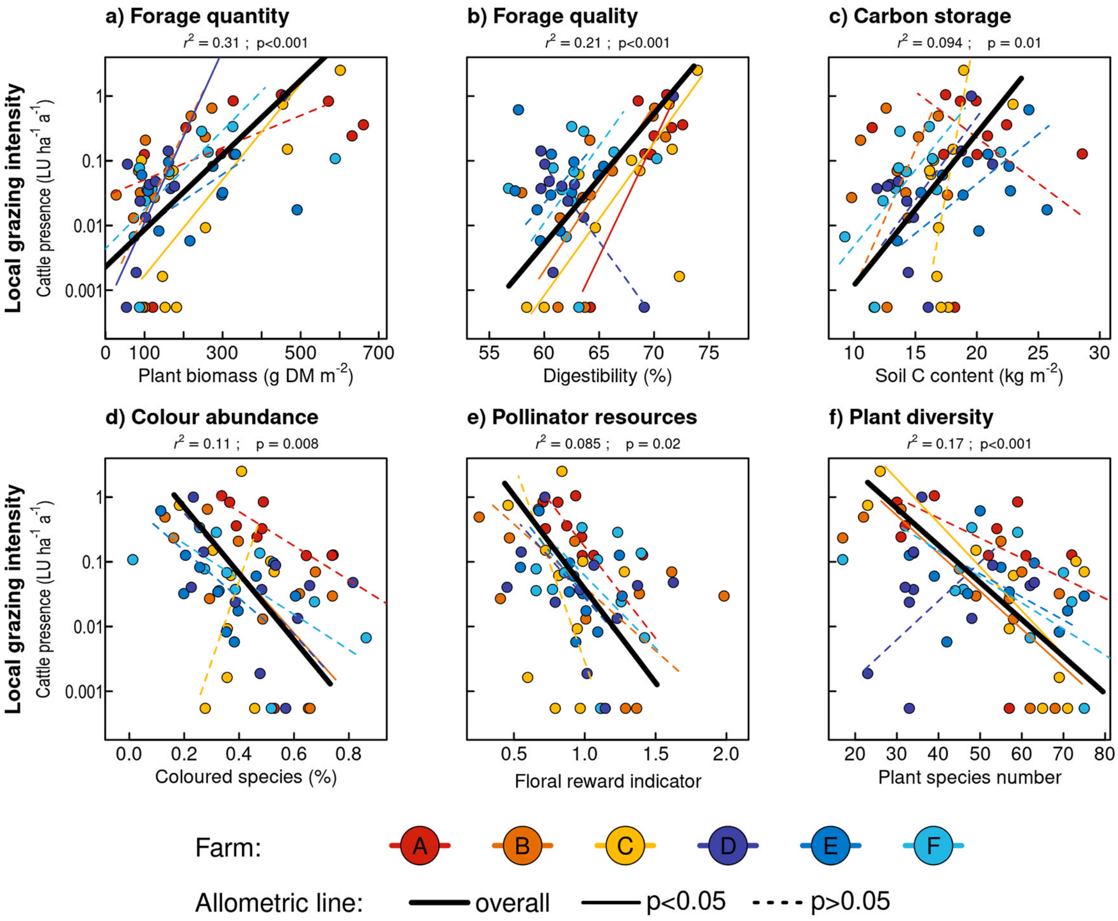


Fig. 5. Allometric relations of local grazing intensity and six ecosystem service indicators. For each indicator the overall allometric line of all study farms (bold black) with its squared correlation coefficient (r^2) and probability (p) is given as well as allometric lines for each study farm (thin coloured lines). Note that allometric line fitting does not indicate causality, but relationship only.

to challenging site conditions, mountains pastures are normally managed as low-input systems and the unfavourable cost-benefit ratio limits the measures actually implemented. Thus, in our study, we chose remoteness as in indicator of all-day pasture care, such as removal of weeds or spreading of manure, as farmers reported to decrease these measures the farther away a pasture is from the main farm building. Beyond these measures, modifying stocking rate and density, and thereby grazing intensity, is the main instrument at hand to modify pasture characteristics. Indeed, there were clear allometric relations between livestock space use and ES. Places providing high forage quality and quantity and storing a high amount of carbon are visited disproportionately frequently, whereas biodiverse areas – attractive for humans and pollinators – were less attractive for cattle. However, allometric relations provide no insights about the direction or even existence of direct causality (Pauler et al., 2020). We suggest a reciprocal interaction and amplification: For instance, high-quality fodder attracts the animals to spend time at a nutrient-rich place *and* fodder becomes attractive due to the frequent presence, because nutrients from faeces are concentrated at places where the animals spend a lot of time.

Identifying such directed cause-effect relations is the great strength of a structural equations model (Shipley, 2016). SEMs are becoming increasingly popular in ecological research (Fan et al., 2016) and here, they allowed us to analyse the hypothesized relationships among all ES and explanatory factors simultaneously. Thereby, we disentangled a broad network of causalities and interactions. As already assumed from the partitioning of variance model, the effect of human-dependent management factors measured in our study was rather small because many of the effects are mediated by site conditions and climate. We found that forage quantity is directly negatively influenced by remoteness as an indicator of farmer's pasture care effort. The closer a pasture is to the shed the more time a farmer normally invests for instance in weed control. Moreover, on many farms livestock is concentrated on few, small paddocks around the farm building during night, where trampling pressure and nutrient excretion are especially high (Koch et al., 2018). The high nutrient supply increases provisioning ES close to the main building. On the other hand, the farther away an area, the higher is the biodiversity. Remoteness also reduced grazing intensity, indicating that cattle avoid long traveling distances (Homburger et al., 2015). Beyond this remoteness-mediated impact, a consistent, but weak correlation among forage quantity and grazing intensity remains. To summarise, we found a clear positive effect of reduced human impact on biodiversity and no direct effect of the observed management factors on carbon storage, aesthetic perception and pollination. So, one may ask the question:

4.4. Is grazing necessary at all?

Yes, it is. Obviously, provisioning services can only be realised by grazing livestock, because only ruminants are able to produce human-edible milk and meat from mountain rangelands where grazing is the only agricultural option. However, other ES depend on continuous grazing, too, even if there is no direct impact visible in our data focusing on open grassland: If there is no more grazing of mountain grasslands, shrub and forest succession sets in, by which pastureland is ultimately lost for food production. There is a shift towards forest-related ES, such as timber production (Schirpke et al., 2020).

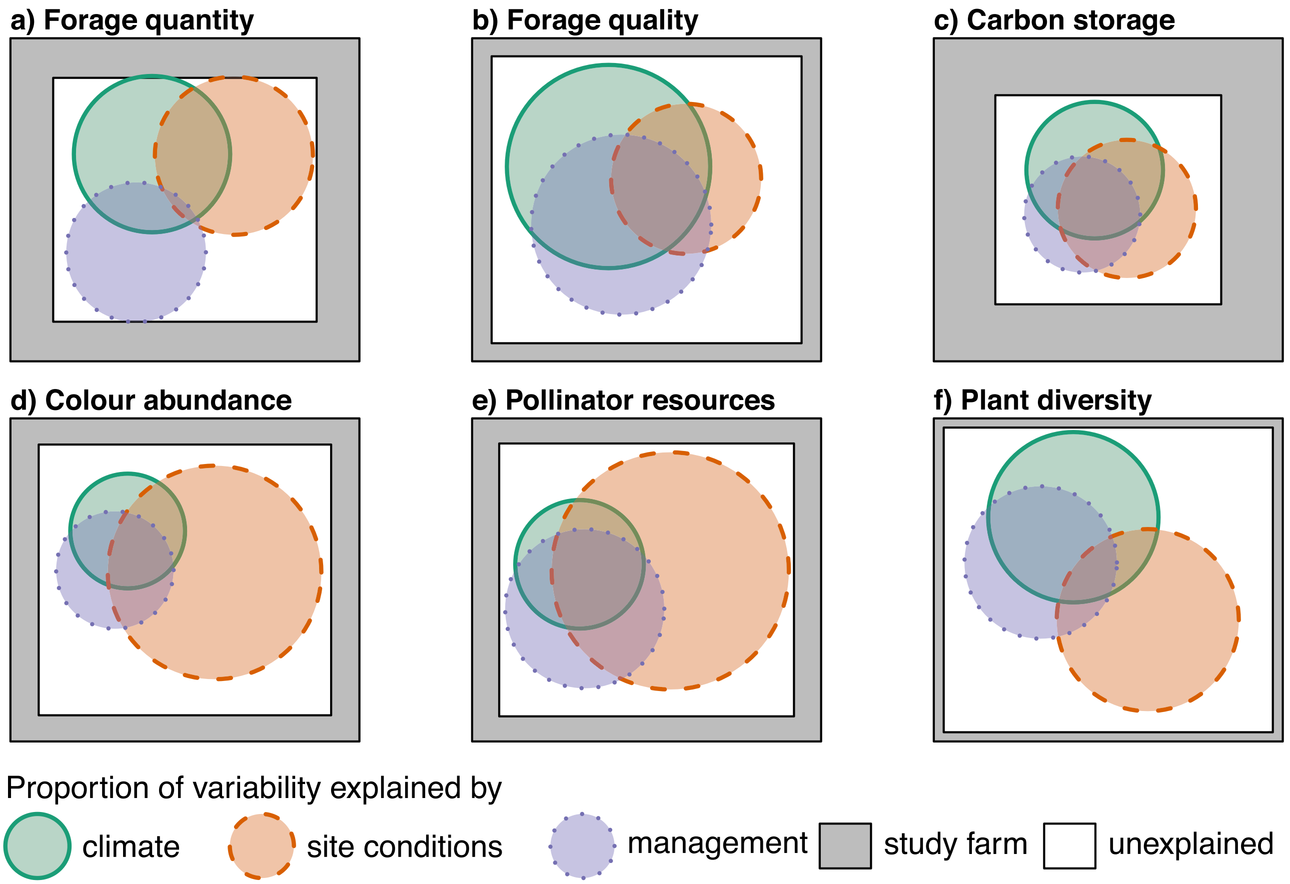


Fig. 6. Partitioning of explained variation of six ecosystem service indicators in linear models by the three groups of explanatory factors: climate, site conditions and management (coloured circles). The larger a circle, the more variation is explained by the respective factor. Overlapping circle sectors indicate interactions. Study farm was included as random effect (grey frames).

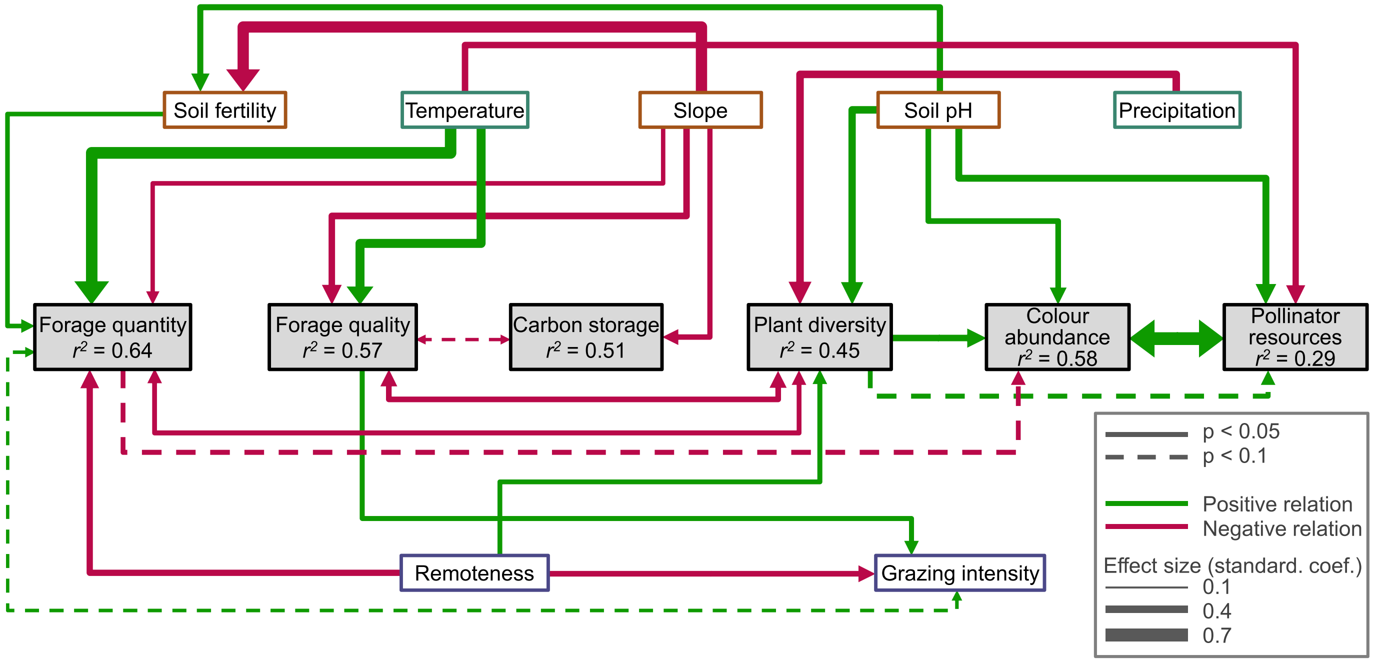


Fig. 7. Structural equation model of six ecosystem service indicators (grey boxes) in response to site conditions, climate and management factors (white boxes). Red arrows denote negative, green arrows positive relationships. Arrow width is scaled according to the standardized regression coefficients. Conditional r^2 for component models are provided in the boxes of response variables. Relationships with $p \geq 0.1$ are not displayed, but available in the appendix (Fig. A.1).

However, shrubs (above the tree line) and forest (below the tree line) cannot compensate the ES provided by mountain pastures (Prangel et al., 2023) and ecosystem diversity is much lower (Schirpke et al., 2020). For instance, aesthetic appraisal of dense shrublands is worse than for open landscapes or mosaics of pasture and wood (Soliva et al., 2010). Consequently, tourism and recreation depend on mountain pastures grazed by livestock – the only "instrument" that is able to sustainably prevent shrub encroachment on steep and rocky sites. Moreover, shrub stands have higher evapotranspiration than mountain grasslands, resulting in lower runoff with negative consequences for drinking water supply and hydro-electric potential (van den Bergh et al., 2018). However, carbon storage could benefit from the higher standing biomass of shrub stands (Seeber et al., 2022). On the other hand, green alder – the by far most common shrub overgrowing former mountain pastures (Pauler et al., 2022) – emits the highly potential greenhouse gas nitrous oxide (Smith et al., 2021), massively reduces biodiversity (Zehnder et al., 2020) and even prevents forest establishment. Management influences the *amount* of mountain pasture ES only little, but it is their mandatory precondition by preventing shrub encroachment.

5. Conclusion: you can't have it all (at the same place)

Besides the small direct impact of the observed management factors on ES realisation, the applied statistical techniques revealed significant relationships of mountain pasture ecosystems, such as slope reducing soil fertility, forage quantity, forage quality and carbon storage, likely due to a fast downstream water and nutrient runoff. Warm temperatures increase forage quantity and quality of mountain pastures. On the contrary, warm temperatures decrease pollinator resources and high precipitation reduces plant diversity: Under such more favourable growing conditions, some very competitive plant species benefit – often generalists and grasses without nectar – whereas many specialised, insect-pollinated herbs are outcompeted. Accordingly, highly productive places (i.e., high forage quantity and quality) are species-poor and aesthetically less attractive. There are clear trade-offs among production-related ES and conservation-related ES.

Our data highlighted the importance of small-scale heterogeneity in both ES indicators and explanatory variables. Thus, it is crucial to observe them at small scale, to disentangle their relations. This is the only study determining the actual local grazing intensity across multiple contrasting grazing zones and applying a broad range of statistical techniques to understand the complex network of grazing and ES in mountain pastures.

We demonstrated that trade-offs among ES prevent the realisation of all ES at the same place. However, the special value of mountain pastures lies in their high heterogeneity which is not only known to enhance biodiversity in the farmed landscape – irrespective of measured at small or large scale (Benton et al., 2003) – but also to increase resilience of grassland-based systems (Dumont et al., 2022). Compared to lowland pastures, the enormous heterogeneity of mountain pastures may complicate farm practice, but allows to realise a broad bundle of contrasting ES at the same time in close proximity. Famers can support this heterogeneity by differentiated stocking to maintain biodiversity and a plethora of services provided by mountain pasture ecosystems.

CRediT authorship contribution statement

Michael Scherer-Lorenzen: Writing – review & editing, Supervision. **Manuel Kurt Schneider:** Writing – review & editing, Visualization, Supervision, Software, Project administration, Methodology, Investigation, Funding acquisition, Formal analysis, Data curation, Conceptualization. **Andreas Lüscher:** Writing – review & editing, Supervision, Resources, Project administration. **Hermel Homburger:** Validation, Methodology, Investigation. **Caren Manuela Pauler:** Writing – review & editing, Writing – original draft, Visualization, Methodology, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

The data are available on https://zenodo.org/doi/10.5281/zenodo.10912681

Data on Ecosystem services in mountain pastures: a complex network of site conditions, climate and management (Original data) (Zenodo)

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Appendix

Allometric relations calculated by standardized major axis estimation

Table A.1
Output of standardized major axis estimation of allometric relations between local grazing intensity and six ecosystem service indicators. Level describes the relationship across or within the six study farms A-E and n the number of observations available.

ES indicator	Level	n	Intercept	Slope	r^2	p-value
Forage quantity	Overall	63	−6.08	0.013	0.311	<0.001
	A	10	−3.55	0.0057	0.291	0.108
	B	11	−7.13	0.029	0.355	0.0532
	C	10	−8.1	0.017	0.488	0.0247
	D	11	−7.55	0.0306	0.505	0.0142
	E	10	−5.57	0.00928	<0.001	0.995
	F	11	−5.43	0.014	0.282	0.0929

(*continued on next page*)

Table A.1 (*continued*)

ES indicator	Level	n	Intercept	Slope	r^2	p-value
Forage quality	Overall	64	−33.1	0.464	0.208	<0.001
	A	10	−59.1	0.822	0.719	0.00195
	B	11	−41.4	0.587	0.417	0.032
	C	10	−39.7	0.544	0.511	0.0202
	D	11	30.2	−0.545	<0.001	0.964
	E	11	−30.7	0.449	<0.001	0.985
	F	11	−37.4	0.547	0.0373	0.569
Carbon storage	Overall	64	−12.2	0.541	0.0936	0.014
	A	10	5.04	−0.326	<0.001	0.964
	B	11	−16.8	0.989	0.063	0.457
	C	10	−45.5	2.41	0.224	0.167
	D	11	−12.5	0.588	0.146	0.247
	E	11	−10.2	0.353	0.187	0.184
	F	11	−10.8	0.542	0.327	0.0658
Colour abundance	Overall	64	2.01	−11.8	0.109	0.0078
	A	10	1.91	−6.08	0.118	0.331
	B	11	1.73	−10.9	0.449	0.0242
	C	10	−14.4	28.6	0.00257	0.889
	D	11	1.58	−10.8	0.142	0.253
	E	11	−0.215	−8.46	0.178	0.197
	F	11	−0.396	−6.3	0.319	0.0702
Pollinator abundance	Overall	64	3.39	−6.67	0.085	0.0194
	A	10	4.75	−6.51	0.231	0.159
	B	11	1.29	−4.5	0.234	0.131
	C	10	8.26	−14.1	0.0109	0.774
	D	11	2.15	−5.73	0.0896	0.371
	E	11	2.77	−6.26	0.154	0.232
	F	11	2.36	−5.16	0.0165	0.706
Plant diversity	Overall	64	3.56	−0.132	0.171	<0.001
	A	10	2.12	−0.0716	0.133	0.299
	B	11	3.38	−0.135	0.505	0.0142
	C	10	5.33	−0.156	0.492	0.0237
	D	11	−9.21	0.138	0.0806	0.398
	E	11	1.37	−0.0821	0.0851	0.384
	F	11	1.81	−0.0929	0.284	0.0914

Partitioning of variation

Table A.2
Percentage of variation in six ecosystem service indicators explained by climate (temperature and precipitation), site conditions (pH, P, slope), management (remoteness and local grazing intensity) and the study farm.

	Forage quantity	Forage quality	Carbon storage	Colour abundance	Pollinator resources	Plant diversity
Climate	7.6 %	10.9 %	5.6 %	3.8 %	3.0 %	9.5 %
Site conditions	10.2 %	5.6 %	5.4 %	24.8 %	26.2 %	18.6 %
Management	10.2 %	7.1 %	2.9 %	4.2 %	6.2 %	5.8 %
Climate+Site conditions	5.8 %	2.0 %	1.2 %	0.1 %	0.1 %	0.1 %
Climate+Management	0.1 %	0.1 %	0.6 %	0.1 %	2.5 %	0.1 %
Site+Management	2.3 %	6.9 %	0.1 %	0.1 %	0.1 %	6.5 %
Climate+Site+Management	0.1 %	6.9 %	5.2 %	4.5 %	7.5 %	2.7 %
Study farm	43.0 %	21.1 %	58.1 %	29.8 %	28.7 %	11.1 %

Piecewise structural equations modelling (SEM)

Table A.3
Output of piecewise structural equation model of six ecosystem service indicators in response to seven explanatory factors.

Response	Predictor	p-value	Standardized coefficient	
Forage quantity	Slope	0.3989	−1.2	
Forage quantity	Soil pH	0.0541	−3.2	
Forage quantity	Soil Fertility	0.0065	4.2	**
Forage quantity	Temperature	0.0113	8.5	*
Forage quantity	Remoteness	0.0015	−4.1	**
Forage quantity	Precipitation	0.3705	−2.8	
Forage quality	Slope	0.0025	−3.9	**
Forage quality	Soil pH	0.3886	−1.3	

(continued on next page)

Table A.3 (*continued*)

Response	Predictor	p-value	Standardized coefficient	
Forage quality	Temperature	0.031	5.8	*
Forage quality	Precipitation	0.3174	2.5	
Forage quality	Remoteness	0.4316	−1	
Carbon storage	Grazing intensity	0.8458	0.3	
Carbon storage	Remoteness	0.3201	1.5	
Carbon storage	Forage quantity	0.0546	3.5	
Carbon storage	Slope	0.0495	−3.3	*
Carbon storage	Soil pH	0.2442	2.2	
Carbon storage	Temperature	0.3086	4	
Carbon storage	Soil Fertility	0.8272	−0.4	
Carbon storage	Precipitation	0.3815	−3.1	
Pollinator resources	Grazing intensity	0.3934	−1.4	
Pollinator resources	Remoteness	0.6571	−0.7	
Pollinator resources	Temperature	0.0242	−4.2	*
Pollinator resources	Soil pH	0.0165	4.5	*
Pollinator resources	Plant diversity	0.0595	3.2	
Colour abundance	Grazing intensity	0.9176	−0.1	
Colour abundance	Remoteness	0.5983	0.7	
Colour abundance	Soil pH	0.018	3.7	*
Colour abundance	Forage quantity	0.0553	−3.2	
Colour abundance	Plant diversity	0.0058	4.2	**
Plant diversity	Grazing intensity	0.2393	−1.7	
Plant diversity	Remoteness	0.0264	3.1	*
Plant diversity	Soil pH	0.0021	5.8	**
Plant diversity	Soil Fertility	0.0525	−3.2	
Plant diversity	Slope	0.4785	1.2	
Plant diversity	Temperature	0.3141	2.9	
Plant diversity	Precipitation	0.0388	−5	*
Grazing intensity	Forage quality	0.0273	3.3	*
Grazing intensity	Slope	0.0125	−3.4	*
Grazing intensity	Remoteness	0.0065	−3.7	**
Soil Fertility	Grazing intensity	0.8262	−0.3	
Soil Fertility	Remoteness	0.9872	0	
Soil Fertility	Slope	0	−7.3	***
Soil Fertility	Soil pH	0.0246	3.6	*
∼∼Forage quantity	∼∼Grazing intensity	0.0648	2.3	
∼∼Forage quantity	∼∼Forage quality	0.2704	1	
∼∼Forage quantity	∼∼Plant diversity	0.0117	−3.4	*
∼∼Plant diversity	∼∼Forage quality	0.004	−4	**
∼∼Pollinator resources	∼∼Colour abundance	0	8.3	***
∼∼Carbon storage	∼∼Forage quality	0.0987	−2	

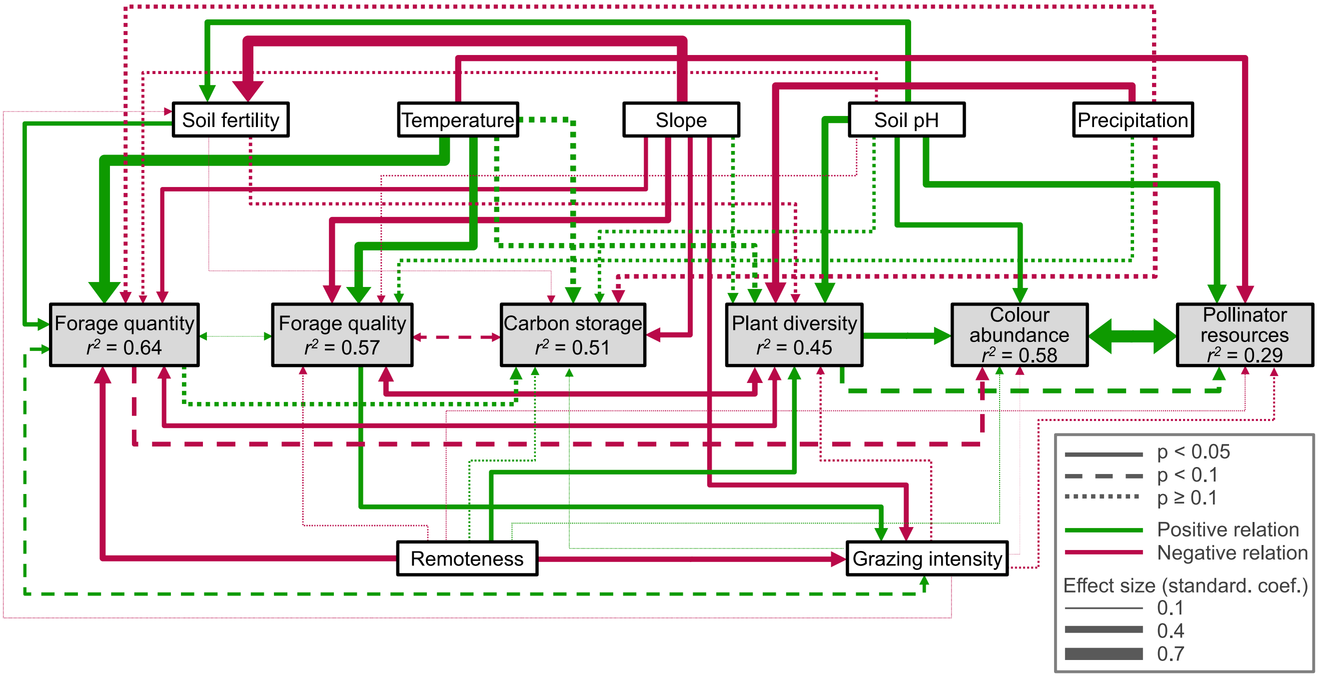

Figure A.1. Complete display of structural equation model of six ecosystem service indicators (grey boxes) in response to site conditions, climate and management factors (white boxes). Red arrows denote negative, green arrows positive relationships. Arrow width is scaled according to the standardized regression coefficients.

Arrow line types indicate probability (solid lines: $p < 0.05$, dashed line: $p < 0.1$, dotted lines: $p \geq 0.1$). Conditional r^2 for component models are provided in the boxes of response variables.

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