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Actors' diversity and the resilience of social-ecological systems to global change

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ABSTRACT

Biological diversity is known to enhance the resilience of ecosystems to environmental change. It is however unclear whether a high diversity of social actors analogously increases the capacity of social-ecological systems to maintain the provision of ecosystem services while undergoing socio-economic and climate changes. Based on an empirically informed agent-based modelling approach, we demonstrate that both the number of actors (*actors richness*) and the diversity of their abilities and skills characterizing their management capabilities (*actors' functional diversity*) are key determinants of the resilience of social-ecological systems to global change. A high complementarity among *actors' functional diversity* helps buffering vulnerable mountain systems against socio-economic and climate change. *Actors' response diversity* can mediate an abrupt shift in the social-ecological system, leading to new trade-offs in ecosystem services. Our results highlight the importance of considering both the diversity and the complementarity of actors' management capabilities to ensure the provision of ecosystem services in the face of uncertain global change.

MAIN

Biological diversity has been shown to enhance resilience of ecosystem functioning[1-3]. Besides species richness, functional diversity is a key determinant of ecosystem resilience[4-6]. In analogy to the positive relationship between biodiversity and ecosystem functioning, several authors have demonstrated a link between the diversity of social actors with their manifold decisions and actions and the resilience of coupled social-ecological systems[7-13]. Actors' network ties[14, 15], their heuristics[16, 17], and their ability to adapt[18] and learn[19, 20] have been linked to the robustness and resilience of social-ecological systems[21]. While social actors have diverse possibilities and strategies to interact with ecosystems[22, 23], it is unclear how humans as agents of change with their individual characteristics, their interactions and their adaptive responses influence the resilience of social-ecological systems to broader socio-economic and climate changes and hence the capacity of such systems to maintain the provision of demanded ecosystem services.

Mountains are among the most sensitive social-ecological systems in the world. Characterized by steep vertical gradients[24] and socio-economic transitions[25], they experience the impacts of climate change and economic globalization faster than many other social-ecological systems. Changes in their repositories of biological and cultural diversity[26] have far-reaching consequences for the long-term provision of ecosystem services essential to over half the planet's human population[27]. Given the continued degradation of ecosystems, it would thus be prudent to understand the role of social actors in managing these types of early warning social-ecological systems to increase the likelihood of responding to the growing demands for ecosystem services in the face of global change.

Recent advances in social-ecological modelling allow better exploring complex coupled human-nature systems[28, 29]. Agent-based modelling has been shown to be particularly useful to simulate the dynamic interactions between local actors' behaviour and regional as well as global settings[30, 31] and to elucidate the influence of interactions among various actors and environments on the delivery of ecosystem services[32,33]. Since these models do not have to fulfil equilibrium criteria, they can feature discontinuous behaviour and cross thresholds between regimes. Here, we combine ideas from biodiversity science with social-ecological modelling approaches to demonstrate the importance of actors' diversity for enhancing the resilience of social-ecological systems to global change. We define resilience as the capacity of social-ecological systems to absorb and reorganize while undergoing climate and socio-economic changes so as to still maintain the flow of demanded ecosystem services[34]. Using the fully coupled social-ecological agent-based model ALUAM-AB, we simulate the dynamics of two mountain agropastoral systems and the related ecosystem services' response trajectories. We assess ecosystem services trade-offs in various states in which the systems tend to remain. Such states, in which a social-ecological system has the same function, structure, identity, and feedback, are defined as 'basins of attraction'. Data for informing, calibrating and validating ALUAM-AB were obtained from extensive ecological experiments, process-based ecological modelling, farmers surveys, choice experiments, and spatial data analyses conducted in the frame of a large eight-year inter- and transdisciplinary project in both a local and a regional study site in Switzerland[35]. We apply both long-term changes in climate and socio-economic trajectories (presses) and extreme events (pulses) on the social-ecological systems[36] to assess the amplifying impact of discrete pulses, when superimposed on the underlying presses of climate and socio-economic changes[37, 38] until 2035.

We investigate various diversity measures[2, 5, 6, 39] to capture the dimensions of diversity most relevant to social-ecological systems' stability and functionality. In addition to traditional diversity measures such as species richness, i.e., actors richness, we also assess changes in actors' functional diversity based on their functional traits. We define actors' functional traits by farmers' management capacities[40] with their drives and motivations, their abilities and skills, characterizing their decision-making processes and their interactions with the environment and other actors. Besides applying new production technologies (e.g. irrigation), farmers can increase (or reduce) their land size and adjust land-use intensities to adapt to the presses and pulses. In analogy to evidence from ecology, we expect that actors' functional traits determine how their responses to presses and pulses influence social-ecological processes, and how these changes in the social-ecological processes ultimately enhance the resilience of the social-ecological systems to global change. We demonstrate (1) the positive correlation between actors richness and ecosystem services as well as actors' functional richness and ecosystem services under various socio-economic and climate presses and pulses, (2) the importance of actors' functional divergence, i.e., spatio-temporal complementarity among actors for buffering against socio-economic and climate change, and (3) the role of actors' response diversity in maintaining the long-term provision of ecosystem services.

First, our results show how actors' functional richness helps maintain the flow of ecosystem services under socio-economic and climate changes both at the regional and at the local scale (Figure 1A and Figure 1B). Mountain farmers' functional richness is highly correlated to ecosystem services provision under combined socio-economic and climate presses and pulses scenarios. The richness of the management capacities of the farmers allows responding to changes in commodity prices, farm structural change, abolishment of agricultural direct payments, and climate change to maintain the flow of demanded ecosystem services. The positive relationship between actors richness and flow of ecosystem services (Figure 1C and

Figure 1D) stresses the presence of key actors’ functional traits in supporting ecosystem services provision under global change, while the concave relationship between functional richness and ecosystem services stresses the complementarity of the different actors’ strategies to buffer against the presses and pulses. The stronger saturating relationship between functional richness and ecosystem services at the regional scale highlights the fact that there are more functionally redundant actors at the regional scale than at the local scale.

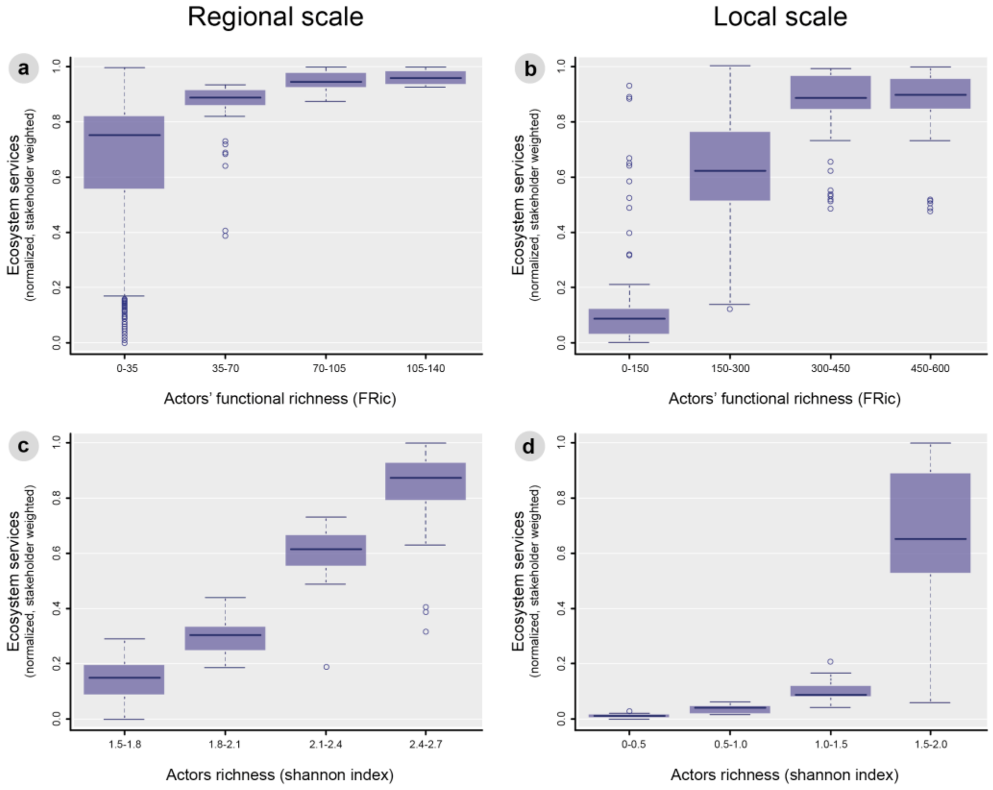

Figure 1. Actors’ functional richness (FRic) (1a and 1b) and actors richness (1c and 1d) highly correlate with the flow of demanded ecosystem services. *The boxplots summarize the results of 440 socio-economic and climatic scenarios. The boxes span the first and third quartile, the band is the median of all values and the whiskers are drawn down to the 10th percentile and up to the 90th. Outliers below and above the whiskers are drawn as individual points. The scatter among communities with equal numbers of actors results from the diverse management capabilities of the actors.*

Secondly, while functional diversity is known to provide options for responding to changes and disturbances in ecological systems[22, 41], we observe in both our social-ecological systems how important the complementarity of actors' management capabilities is for buffering against various presses and pulses. A measure that includes both the relative abundances of the actors and a measure of the pairwise functional differences between the actors is Rao's quadratic entropy[42]. The decline in this measure shows the importance of both actors richness as well as functional divergence of actors for supporting ecosystem services provision under the various presses and pulses (Figure 2). As long as actors' functional traits are complementary and redundant, presses and pulses are buffered and ecosystem services are maintained at both scales (Figure 2A and 2B). Farmers adapt their management strategies based on their traits. If they can no longer cultivate their land due to negative land rents, they will abandon their farms, and the land is assigned to another farm, which has different management capabilities and keeps up the demanded ecosystem service provision (Figure 2, blue scenarios). Continuous strong presses on the social-ecological systems combined with pulses such as accelerated structural change, price, or climate shocks lead to a loss of key actors. The remaining actors are unable to compensate for all the land management activities (Figure 2, orange scenarios). If land is abandoned, it becomes subject to natural vegetation dynamics, and the demanded ecosystem services decline. Under a policy shock scenario, characterized by the abolishment of agricultural direct payments, most of the farmers give up their activity, and the agriculture-dominated landscape shifts to a forest-dominated landscape with a few intensively managed areas (Figure 2, green scenarios). This pattern is even more pronounced at the local scale. The lower redundancy of actors' management capabilities reduces the possibility that land is transferred to other actors and in the case of policy shock scenarios leads to a complete abandonment of agricultural activities. Similar patterns have been observed in various ecosystems and are often described as cross-scale resilience, e.g.[43-45]. A large, functionally diverse community of social actors can thus enable adaptation to slower, ongoing change despite changes in environmental and socio-economic conditions. In our agropastoral social-ecological systems, subsidies for ecosystem services based activities can support actors in rebalancing their activities when market or environmental conditions change. In case, however, presses and pulses are too strong, even highly functionally divergent communities will lose their stability and the system might switch to another state.

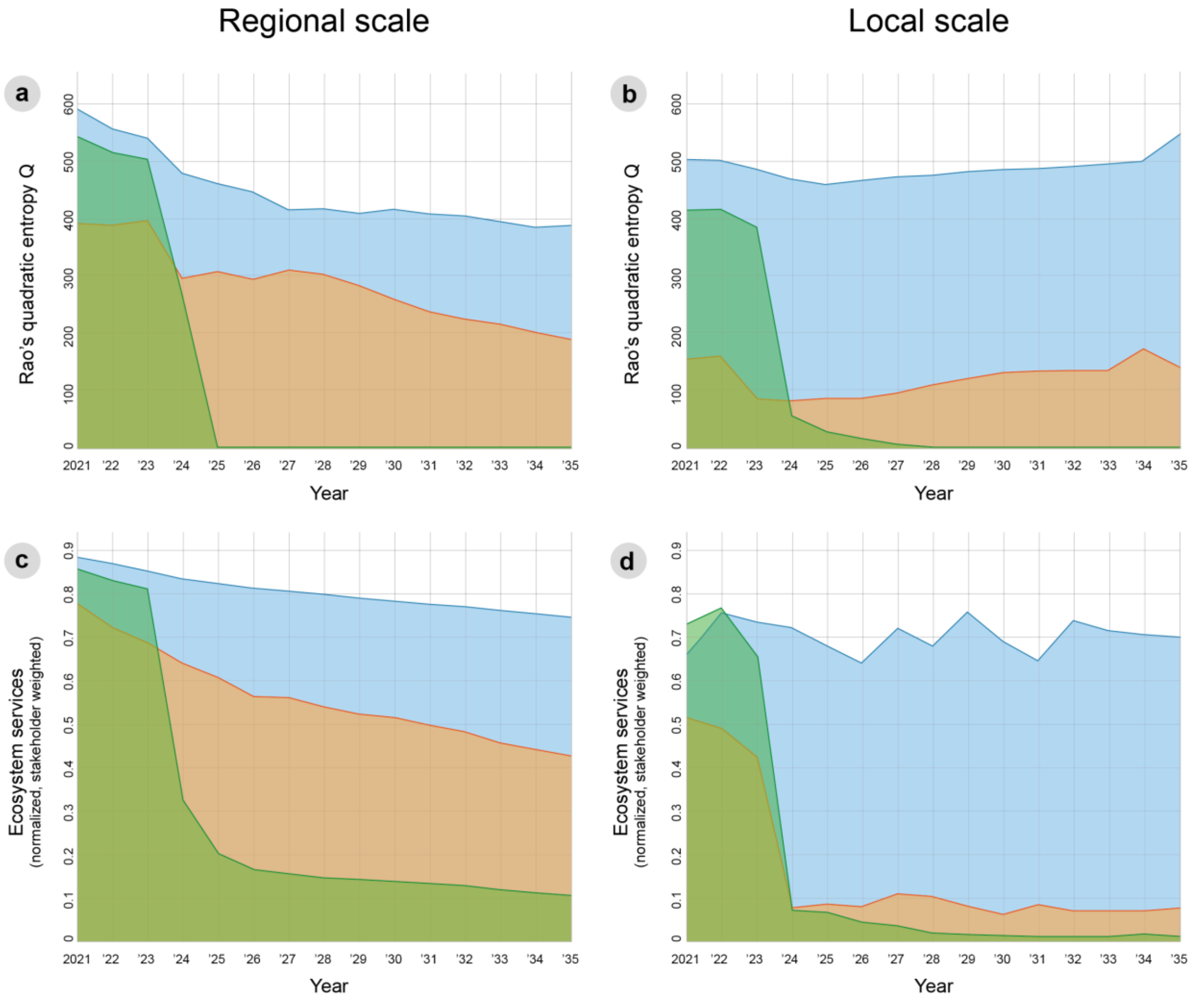

Figure 2. Socio-economic and climatic presses and pulses impact actors' functional divergence (Q) and ecosystem services provision. *Plots a and b show Rao's quadratic entropy (Q) as a measure of both the pairwise functional differences between actors' traits and the relative abundances of the actors under various press/pulse scenarios. Plots c and d show changes in ecosystem services under various press/pulse scenarios. The blue colour represents moderate press/pulse scenarios, the orange colour represents scenarios with strong sustained presses and the green colour scenarios with a strong pulse (policy shock) in 2024.*

Finally, we observe that a drop in actors' response diversity erodes the resilience of the social-ecological system, increasing the likelihood of shifting to an alternative basin of attraction with new trade-offs in ecosystem services. The changes in actors' response diversity reflected by changes in number of farmers, hectare of land per farmer, as well as the amount of different livestock the farmers possess for pasturing, result in non-linear changes in the bundles of ecosystem services (Figure 3). A ball-and-cup model illustrates how the accumulated loss of actors' response diversity triggers abrupt shifts in ecosystem services trade-offs. The depth of the basins of attraction represents the resilience of the social-ecological system to the presses and pulses. The stronger the socio-economic and climate changes reduce actors' response diversity, the more the basin of attraction will shrink. In the initial slow decrease in actors' response diversity, we observe a decrease in food production and in the aesthetics of the landscape, whereas habitat services increase (Figure 3A). Intensive agricultural land is increasingly being replaced by dry meadows with high biodiversity and forest. The combination of strong presses with structural, climate and market pulses leads to a loss of diversity and increases the possibility that the social-ecological system drops into a new state with new ecosystem services trade-offs (Figure 3B). Summer pastures are abandoned and encroached by forest. The low availability of agricultural labour forces cannot buffer the presses and pulses anymore. The further decreasing food production comes along with a further decrease in habitat services as well as a further decrease in landscape aesthetics. Such a synergetic loss of habitat and aesthetic services continues with an increasing loss of actors' response diversity and an accelerated loss in food production (Figure 3C). The loss of actors' response diversity under the strong pulses has eroded the basin of the social-ecological system in the ball-and-cup model to such an extent that demanded ecosystem services are lost.

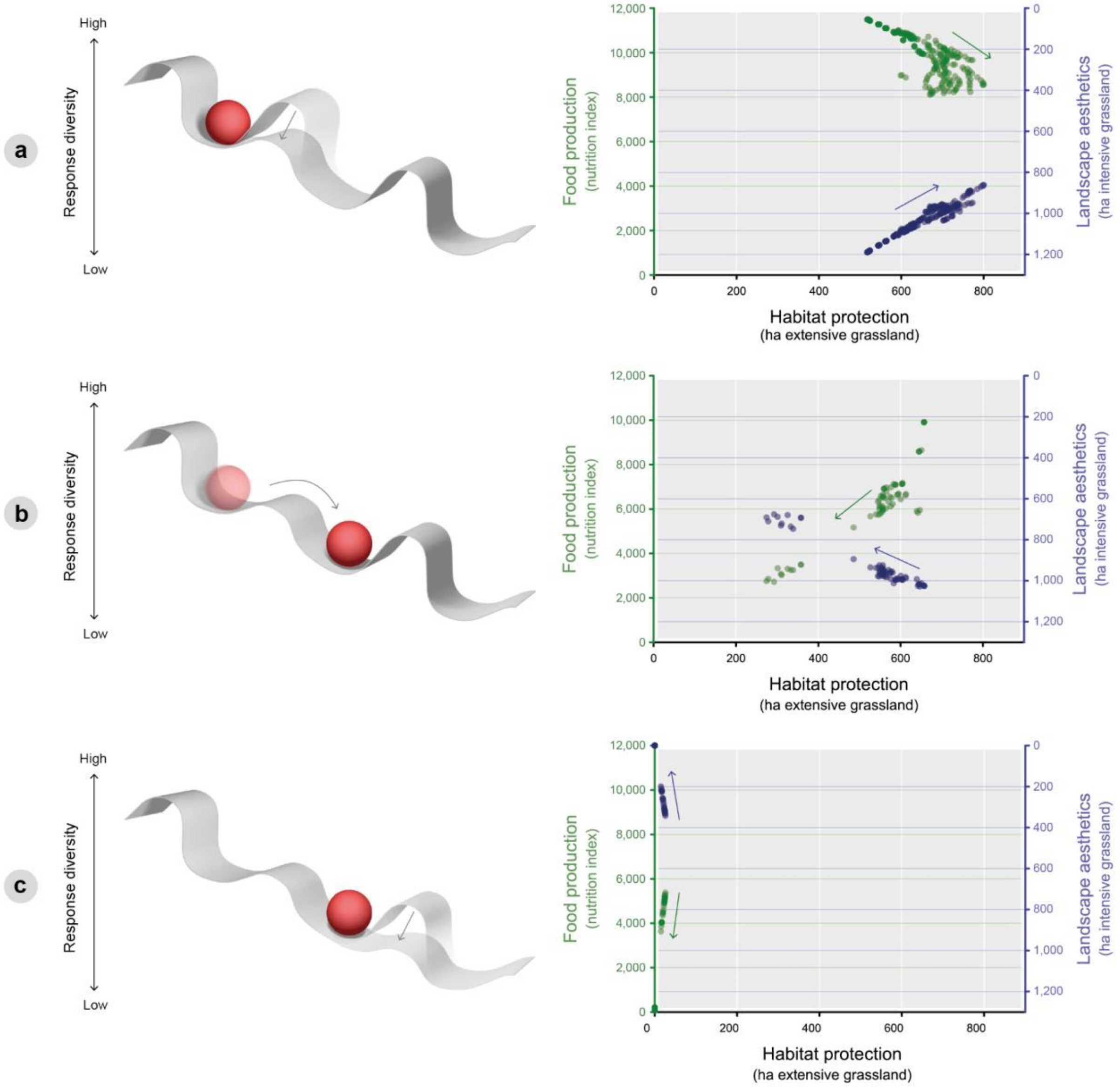

Figure 3. Relationship between presses/pulses and response diversity, showing that an accumulated loss of response diversity triggers a shift in the social-ecological system state and related ecosystem services trade-offs. *The ball-and-cup model of resilience shows different states of the social-ecological system in which the system tends to remain, thus representing various basins of attraction (a-c correspond to the same colors as in Figure 2 with a = blue scenarios, b = orange scenarios, and c = green scenarios). Trade-offs are shown at a regional scale between a provisioning service (food production), a regulation and a maintenance service (habitat protection) and a cultural service (landscape aesthetics). Arrows in the trade-off graphs show the temporal change within one state of the social-ecological system.*

In summary, our results suggest that a high diversity of farmers with manifold management capabilities is essential for maintaining the provision of ecosystem services under various socio-economic and climate presses and pulses in mountainous social-ecological systems. We particularly observe that actors' functional diversity is not responding linearly to global change. Similar non-linear patterns between response diversity and shifts in ecosystem state have been observed in biology and similar disciplines[10, 46-48] and their importance for predicting the behaviour of human-dominated environments[28, 49] has been stressed. Such relationships have relevant implications for designing policy strategies[50] and call for a better understanding of the interactions between the adaptive capacities of humans and changes in ecosystems and ultimately the impacts on the trajectory of ecosystem services provision.

While the presented results are based on two case studies, it is the first study, which uses context specific information to confirm the importance of both actors richness and actors' functional diversity in determining the resilience of social-ecological systems to retain the provision of demanded ecosystem services under global change. Similar to other European mountain regions, resilience, however, relies heavily on a subsidized agricultural system[51], making the social-ecological systems even more vulnerable to drivers and inhibiting innovations that would support adaptation to changes[52]. Furthermore, interactions with distant social-ecological systems are adding non-linearity to the mountain systems, increasing the complexity of their dynamics[53]. Such patterns can be observed in other Alpine countries and in countries in the Carpathians and central European mountains, in which, more recent political transformations have caused accelerated changes in agriculture [54, 55] and a strong rural-to-urban migration[56]. Developing management strategies for these vulnerable cultural landscapes thus requires a deep, process-oriented understanding of the role of local actors in buffering the uncertain socio-economic and climate changes. While it is not always possible to support the existence of all actors in a region, we believe that a prioritization considering functional singularities and recognizing the adaptive capacities of actors is key for the continuous support of essential ecosystem services. Land use decision makers should be equipped with better information on the role of the social actors in securing ecosystem functioning. It took decades for ecologists to recognize the importance of functional diversity on the resilience of ecosystems to anthropogenic drivers. Given the growing presses on cultural landscapes, we should build our knowledge on the combined insights from ecology and social sciences to better understand the role of diversity as an essential factor fostering the resilience of social-ecological systems to global change.

METHODS

Study sites. Agropastoral mountain systems are social-ecological systems that deliver a suite of important ecosystem services across scales[57, 58]. Locally, they prevent and mitigate natural hazards[54, 59, 60] and provide diverse food and energy resources to dwellers[61]. At the regional or national scale, mountains often have high cultural significance, and scenic landscapes[62-64] and clean air make them target destinations for recreation and tourism. In addition, they are of global significance due to their key role in the water cycle, climate regulation, biodiversity protection[27, 65], and carbon sequestration[66, 67]. The environmental factors and management practices that allowed the creation of these agropastoral mountain systems are, however, massively influenced by global change, resulting in changes in the grassland, forest, and agriculture structure and related ecosystem services[25, 55]. We selected two typical mountain study sites in Switzerland with different histories of socio-economic development and analysed them at different scales (Supplementary Figure 1).

The Central Valais is a drought-sensitive continental inner-Alpine mountain region. Unproductive ground, including rocks and glaciers, accounts for 62% of the area, 20% is covered by forest, 16% by agriculture, and 2% by settlement. The long-established small-scale farming practices, including seasonal alpine grazing, substantially contribute to maintaining the typical character of the landscape and the provision of ecosystem services[68]. However, the importance of agriculture is declining and many farmers give up their businesses, while touristic and industrial activities increase and settlement and infrastructure grow steadily. At this site, we analysed the regional community of initially (in 2001) 251 farmers, which cultivate on average 8 ha and house around seven livestock units, among them many sheep. The farmers are highly dependent on subsidies and more than 90% of the farms are part-time in combination with other economic activities, predominantly in tourism. The agent-based model covered an area of 11’864 paddocks of the size of one ha (details see below).

The Jura Vaudois is a temperature-sensitive oceanic mountain area. The biggest share of land use is forest (57%), followed by agriculture (36%), settlement (4%) and unproductive area (3%). The traditional landscape is a mosaic of open agricultural land, closed forest and typical semi-open woodland pastures; habitat protection and landscape aesthetics are important ecosystem services[69]. Despite strong regional day tourism, the economic performance of the region remains limited and the population is stagnating. In this setting, we studied a local community of fifteen farmers who cultivate on average 48 ha and house around 25 livestock units, predominantly cows. Half of the farmers work full-time and all but one so far have no successor. The agent-based model covered 473 paddocks, in total 475 ha.

The ALUAM agent-based model described by the ODD protocol[70]

Purpose. The purpose of ALUAM-AB is to simulate the effect of socio-economic, climate, and political presses and pulses on actors’ management capabilities, their interactions with the environment and with other actors, and ultimately on the provision of ecosystem services.

State variables. Agents represent types of farmers with specific management capabilities. The description of the agent types in the two case studies are provided in the Supplementary Table 1 for the Valais and Table 2 for the Jura. All actors of a specific agent type have (1) their own state (i.e., land endowment, stable capacity, etc.), which is updated after each yearly simulation period and (2) their own decision-making mechanisms for managing farm resources in form of constraints to an income optimization approach. Information on agents for each case study was derived from interviews with and a survey among local farmers combined with an analysis of agricultural census data. At the local scale, each of the 7 farmers was an own agent described with its/her specific characteristics[71]. At the regional scale, 14 agents were derived from 251 farmers using a PCA with a quartimax rotation and subsequent k-means clustering on 19 farmers' characteristics, including the opportunity costs of labour, additional workforce hired, a threshold for minimum income, farm size, and the intention to increase farm size or livestock housing capacity[72]. The median characteristics for each agent were then fed into the model.

Scale. At the local level, the landscape units correspond to the plots managed by the farmers. At the regional level, the smallest landscape unit is an area of 100m x 100m. The model was run between 2014 and 2035. Thereafter, uncertainties in agent behaviour becomes too high, as decision-making mechanisms of young farmers in the process of succession may change substantially.

Process overview and scheduling. ALUAM-AB proceeds in annual time steps. The agents allocate their available resources to maximize land rents. Thereby they consider plot-based, farm level, and individual constraints as well as incentives and regulations from the market and policy instruments, which are annual input data to the model. Investments in production capacity made in previous years are considered as sunk costs representing path dependencies of the individual agents. Structural change is modelled using a land market module[71]. The module identifies land units that are no longer cultivated under the existing farm structure due to negative land rents, because an agent does not reach the minimum wage level or if agents retire without successor. The land market module randomly assigns the land units to one of the other agents and then checks whether the price for the land unit is positive. This procedure is repeated until all land units are assigned to an agent or none of the agents is willing to take the land units left on the market. In that case, these are defined as abandoned and subject to natural vegetation dynamics. When land-use allocation is optimal, farm capacities and livestock as well as the age of the agents are updated and the next annual time step is initialized.

Emergence. Changes in the activities of agents emerge from changes in prices, policies and the climate i.e., the spatially explicit climate-induced changes of yield quantities, and depend on the agents' management capabilities. In addition, ecosystem services provision emerges from changing land-use patterns and intensities as well as from structural changes on agent level.

Adaptation. Agents respond to external pulses and presses by adjusting their production activities, applying new production technologies (e.g. irrigation), increasing (or reducing) land size and adjusting land-use intensities. In addition, agents exit the sector if their income falls below a minimum threshold, which was defined based on survey data.

Prediction. The model follows a constraint income optimization approach assuming rational economic behaviour with no direct learning pattern. However, the consideration of empirically derived individual constraints, such as opportunity costs, minimum income wage and limited time resources, includes non-economic goals in the decision-making process.

Interaction. The interaction between agents is based on the land market described above. Interactions between agents and the environment are based on the model linkage with a sub-model: LandClim is a spatially-explicit process-based model that simulates forest dynamics and yields on meadows given different management regimes[73].

Initialization. Initial attributes for agents were defined from surveys, interviews and farm census data (see above). The observed age structure in the case study region was assigned to each agent. The initial allocation of land units to agents is based on a random assignment of parcels in which the share of parcels according to slope and the total area per farm type corresponds to the real world distribution[33].

Input. Spatially explicit data were derived from national data sets or simulated with LandClim. In the baseline setting, policy and socio-economic parameters were derived from scenarios for the European and Swiss[74, 75] agricultural sector. Other scenarios were implemented as described below.

Software requirements. ALUAM-AB runs on Linear Programing Language (LPL) from Virtual Optima and requires ILOG CPLEX Optimization Studio from IBM. LPL academic license is available on purchase at http://www.virtual-optima.com/en/index.html, CPLEX academic license is available at no charge at https://www.ibm.com/software/.

Calibration and validation. We carried out a behaviour reproduction test to assess the model's ability to reproduce the behaviour of observed data in our study site in the Valais. Model validation results of ALUAM had already been published in the original model[75], the agent-based version of the model[72] as well as in[76]. We repeated the model validation test presented in these manuscripts using the newly available census data for the period 2012 – 2015. We describe the error between observed data and simulation output, measured point by point for each simulation run and provide a decomposition of the error using the Theil inequality statistics. The root mean square percentage error (RMSPE) represents the mean percentage difference between simulation and observed data[77]. For model calibration, we used census data from the Swiss Federal Office of Agriculture containing livestock housing capacities and numbers of farms as well as managed land, farmer age, livestock numbers and land in slope categories for each farm type in the year 2000. Model validation uses the development in exogenous input parameters, i.e., prices, costs, and direct payments between the years 2001 and 2015 to test model behaviour. The modelling results with respect to the number of animals (cattle and sheep) and land-use intensities (area of intensive and extensive land-uses) are then compared to the development of these parameters in the census data to assess the single best performance of the model (validation). To compare the different grazing animals, we use livestock units (LU), which represents a nutritional equivalent between sheep (0.17 LU), dairy cows (1 LU), suckler cows (0.8 LU), calves, and heifers (0.4 LU). The total area of extensive grassland and total areas of intensive land-uses serve as indicators for land-use intensities. Extensive land-use covers those management forms that are entitled to ecological compensation payments in Switzerland, namely extensively managed hay meadows, less intensively managed meadows and extensive pastures. Extensively managed meadows and pastures can only be mown or grazed after the 15th of July. Only two cuts or grazing rotations are permitted and no fertilizers are allowed on meadows. Results show a mean percentage error between simulation results and observed census data of 4.9 to 5.7 %, which represents a satisfactory validation of the model (Supplementary Table 3 and Figure 2). More details and the decomposition into bias, unequal variation and unequal covariation based on the mean square error can be found in[72].

Scenario experiments. ALUAM-AB was run for 20 scenario experiments to explore how climate, socio-economic and political changes affect actors' management capabilities. We defined four press scenarios by applying a formative scenario technique to regionally downscale market and climate information from the four global IPCC SRES storylines[78]. In addition, these gradual presses on the system were combined with four pulse scenarios, which represent disturbances that occur abruptly. We assumed a shock in (1) agricultural markets associated with a sharp fall of commodity prices, in (2) the farm structure characterized by an accelerated farm abandonment and a decrease in the available labour force, in (3) the policy system assuming an abolishment of agricultural direct payments, and in (4) the climate by implementing a sequence of three dry and hot summers associated with a reduction in grassland yields.

For each IPCC press scenario, qualitative levels of social, economic, ecological and policy factors were elaborated and translated into quantitative scenarios to feed ALUAM-AB by adjusting time series of input parameters[50]. The pulse scenarios were implemented accordingly. Shocks were implemented in 2024, and in all but the climatic shock scenario, we assumed no subsequent regeneration of the external drivers (i.e., of markets, agricultural activities on abandoned farms or subsidies).

Calculation of ecosystem services provision. For each year in each model run of ALUAM-AB, we estimated the provision of four ecosystem services covering all three classes of the CICES ecosystem services typology: (1) food provision as a provisioning service, (2) habitat protection as a regulation and maintenance service, (3) cultural heritage and (4) landscape aesthetics as cultural services. Indicators for each service were developed in iterative stakeholder processes. Food provision was calculated by a nutrition index that standardizes food production of differently managed grasslands based on its energy content[75]. Habitat protection was measured with the area of extensive dry meadows which are amongst the most species-rich Alpine habitats and priority ecosystems for biodiversity conservation in Switzerland[79]. Cultural heritage was approximated with the number of farms, as the small-scale structure and abundance of farms links to local traditions and regional identity[80]. Landscape aesthetics were described by the share of three land-use types, which were perceived most dominant by the locals[68].

To calculate an overall provision of ecosystem services, we inferred preferences for the services with a discrete choice experiment among residents in each case study region[68, 80]. For each ecosystem service, marginal utility coefficients were estimated with nested logit models (Supplementary Table 4). These coefficients show how much a change in a service increases or decreases the utility of the landscapes for the residents and were used to calculate a weighted sum of the ecosystem provision in each simulation of ALUAM-AB. Because the values of this sum varied widely across scenarios, we standardized the overall ecosystem services provision to a common scale ranging from 0 to 1 according to the following formula:

$STD = (X - X_{min})/(X_{max} - X_{min})$; where STD is the standardized variable and X, X_{min}, and X_{max} are the target variable and its minimum and maximum value across all scenarios, respectively

Diversity calculations. In analogy to measures in ecology[81, 82], actors' diversity can be described both in terms of number of actors per se and functional diversity [5, 83] based on functional traits, i.e., management capabilities of the actors that influence the performance of the social-ecological system. Actors' functional traits include farming objectives, their attitudes towards off-farm labour and extensive land-use, their management intentions and their farm structural characteristics (Supplementary Tables 1 and 2).

We assessed actors richness with the Shannon Diversity Index (D)[84]. Actors' functional diversity was quantified based on the traits values determined in each scenario annually between 2014 and 2035. Functional diversity distinguishes between richness (functional space occupied by actors), divergence (how diverse are actors in the functional space) and evenness (how regularly each actor occurs in the functional space)[85]. For communities with lower richness, actors' functional richness (FRic) is known to be the best performing index of functional richness[86]. We used only uncorrelated traits and calculated FRic accounting for continuous and categorical traits using the Gower distance[87]. To assess how different the management capabilities of the most abundant actors are, we computed Rao's quadratic entropy Q[88]. We selected Q as the best measure for actors' functional divergence, as functional richness is highly different between both case studies and Q embraces both actors richness and divergence. We also calculated functional evenness based on[86] for the regional case study area (Supplementary Figure 3). All functional diversity measures were computed with the FDiversity software package for the integrated analysis of functional diversity[89].

Data availability

The data used for this study and the ALUAM agent-based model code are available in the ETH Research Collection with the identifier: https://doi.org/10.3929/ethz-b-000221406[90].

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Competing interests

The authors declare no competing interests.

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Supplementary information

Supplementary Tables 1–4, Supplementary Figures 1–3