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ORIGINAL ARTICLE

A quantitative approach to the understanding of social-ecological systems: a case study from the Pyrenees

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Abstract

Mountains are social-ecological systems exposed to multiple climatic and socioeconomic drivers. The Pyrenees are a clear example of the concomitant challenges that these regions face, as they are exposed to stressors linked to depopulation, an economic shift towards tourism, and climate change. To understand how these multiple stressors affect the system's resources, it is useful to study them from a social-ecological system (SES) perspective. Focusing on a Pyrenean SES, we use piecewise structural equation modeling and network analysis to quantitatively describe the interactions between water resources, biodiversity, and the social and economic elements of the system. Our results show that the current economic focus and dependency on tourism severely impact water resources and biodiversity. Future climatic scenarios forecast a worsening of the pressures on the hydrological system and may threaten winter tourism. Actions to alleviate the pressures on water and biodiversity and to increase socioeconomic resilience are a priority. We argue that such actions will have to include both a diversification of the region's touristic offer and of the economy, coupled with a more sustainable use of water resources. Our findings highlight the importance of studying the interactions and causal relationships between SES elements. This can help gain a comprehensive understanding of how the SES functions and its sustainability challenges.

Keywords Social-ecological systems · Mountain areas · Climate change · Sustainable resource management · Quantitative network · Modularity · Interactions

Introduction

Climate change severely threatens mountain ecosystems, particularly at high elevations (Hock et al. 2019). Mountains provide many ecosystem services to human populations living in and outside them (Palomo 2017; Hock et al. 2019). Foremost among these services at a global scale is freshwater supply. This is especially relevant in Mediterranean countries, where summers are hot and dry, and human settlements and activities heavily depend on mountain water resources (Beguería et al. 2003; Grima and Campos 2020). The joint effects of climate and land-use change have already prompted a general decrease in water yield and runoff in Mediterranean rivers over the last decades (Beguería et al. 2003). Mountain regions also greatly contribute to the Earth's biodiversity. They are considered biodiversity hotspots, home to a wide range of endemic, rare, and threatened species (Rahbek et al. 2019). Mountains comprise roughly 30% of the terrestrial area identified as Key Biodiversity Areas (KBAs), and a large portion of mountain areas is under protection (Rodríguez-Rodríguez et al. 2011).

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Elevational and phenological changes in mountain species due to climate change exacerbate their risk of extinction (McCain and Garfinkel 2021; Vitasse et al. 2021), and cause a radical reorganization of ecological communities and food webs (Lurgi et al. 2012).

In parallel to environmental challenges, mountain regions are undergoing important socioeconomic changes (Hock et al. 2019), with impacts on ecosystem services and the associated upstream and downstream human settlements (Palomo 2017). In particular, Mediterranean alpine systems in Europe have experienced difficulties adapting to these changes. The agricultural sector has become increasingly marginalized (Ustaoglu and Collier 2018), and local economies have gradually shifted their focus to the service sector, mostly tourism, for local economic development (del Mármol and Vaccaro 2015; Heberlein et al. 2002). This has additionally prompted the integration of mountain regions into increasingly urbanized and globalized societies (Vaccaro and Beltran 2009). Consequently, both local depopulation due to agricultural abandonment and growing urban development to accommodate tourism coexist in the same space. Farmland abandonment, urbanization, and the establishment of protected areas and ski resorts have led to important demographic and socio-professional changes (Jiménez-Olivencia et al. 2021; Pallarès-Blanch et al. 2014; Vaccaro and Beltran 2009) and to important impacts on the surrounding environment (Beguería et al. 2003; Jiménez-Olivencia et al. 2021).

To adapt to such socioeconomic and environmental changes, mountain territories and communities are experiencing a profound reorganization process. To properly address the challenges that these territories are facing, interdisciplinary theoretical concepts such as social-ecological systems (SES) are especially relevant. They bridge the gap between social and ecological research by integrating interactions between humans and nature, as well as the drivers influencing them, under a common framework (Ostrom 2009; Virapongse et al. 2016; Klein et al. 2019). One of the primary goals of the SES theory is to understand how socioeconomic and ecological factors interact and give rise to sustainability challenges (Berkes and Folke 1998). To address this, scholars have formalized the SES theory using various frameworks and approaches (Colding and Barthel 2019). Among these, Ostrom's Social-Ecological Systems Framework (SESF) stands out as one of the most widely adopted frameworks, due to its power to describe or analyze SES functioning and to diagnose sustainability challenges.

Social-ecological system theory is partly rooted in complex system theory, since SESs are understood as intricate networks of interacting elements (Ostrom 2009). However, there is a lack of empirical studies applying complex theory, such as exploring the connections between variables and performing network analyses (Nagel and Partelow 2022). Until now, efforts have mainly focused on identifying important variables driving SES outcomes, with far less emphasis given to measuring how these variables interact (Villamayor-Tomas et al. 2020). Most works addressing variable relationships have employed pairwise relationships, without considering intermediate or confounding variables (Nagel and Partelow 2022). Moreover, Villamayor-Tomas et al. (2020) noted that most scholars studying interactions between SES variables had taken a descriptive approach and did not provide a clear reasoning behind the inferred causal relationships. Therefore, there is a need to explore new methodologies that facilitate the application of complex theory to social-ecological systems, with a focus on modeling connections between variables.

The Pyrenees mountains offer a clear example of a region with interconnected socioeconomic and ecological variables under multiple stressors. An economic shift towards tourism, declining population numbers, and climate change are all impacting the region's natural resources (Pallarès-Blanch et al. 2014; Lasanta et al. 2013; López-Moreno and García-Ruiz 2009). However, studies investigating the direct and indirect interactions among these stressors and the region's natural resources, such as water and biodiversity, are lacking. As it occurs in other regions, most SES studies in the Pyrenees are sector-specific and often rely on qualitative survey data (e.g., Muñoz-Ulecia et al. (2021); Fernández-Giménez et al. (2022)). Whereas these studies yield valuable insights on the locals' perception of vulnerability, they provide little information regarding the interactions among the elements of the system.

The main goal of this article is to diagnose and understand key sustainability challenges in a Pyrenean SES, with a focus on modeling the interactions among the SES elements. We use structural equation modeling, a quantitative approach, to model the intricate relationships among a comprehensive set of social-ecological factors, including hydrological, land use, climatic, environmental, biodiversity metrics, and socioeconomic elements. Complex network analysis tools are also used to identify tightly connected variables, as well as variables that act as important links between different parts of the SES. This methodological approach facilitates measuring how SES variables affect each other both directly and indirectly, and helps understand the overall functioning of the system. This is used to identify the main drivers of economic growth in the region and assess their impacts on water resources and biodiversity. Based on these findings, we suggest potential adaptation strategies for a sustainable development of the region.

Methods

Study site

The study area includes the upper part of the Segre River watershed in Catalonia, from its Pyrenean headwaters to the

Oliana Reservoir, covering a surface area of approximately 1993 km^2 between Alt Urgell and La Cerdanya counties (Figure A1, Supplementary Material, Appendix A). Water from the Segre upper basin is used for domestic consumption, agriculture and livestock farming, aquaculture, snowmaking, and industrial activities, as well as non-consumptive uses, such as recreation and hydropower (Confederación Hidrográfica del Ebro 2015). The area has been suffering from depopulation since the 1960s, in favor of more industrialized areas. From the 1990s onwards, immigration has been the main factor preventing the resident population from declining (Pallarès-Blanch et al. 2014; Guirado González 2014). Since the 1980s, the region has shifted towards an economy focused on the services sector, although agriculture and intensive livestock farming are still present in the region. While Alt Urgell has a more diversified economy, La Cerdanya has specialized into tourism and hosts five ski resorts.

Elements of the social-ecological system

We used Ostrom's SES framework tiers (Ostrom 2009; Vogt et al. 2015) to identify the relevant elements to describe the Pyrenean social-ecological system. Although the framework was originally conceived for common pool resources, its diagnostic power makes it applicable to sustainability challenges beyond this scope (McGinnis and Ostrom 2014). One of its main applications is understanding SES functioning (Partelow 2018). Thanks to the multitier collection of elements provided by this framework, information can be searched systematically, preventing the unintentional omission of potentially relevant elements of the system (Delgado-Serrano and Ramos 2015; Ostrom 2009). For simplicity, the term "variable" is employed in this study to refer to the measurable indicator used to quantify the 2nd-tier variables defined within Ostrom's SESF. Using public databases (see Supplementary material, Appendix A – Data sources and processing), we collected hydrological, climatic, biodiversity, land use, and remote sensing–derived environmental data, as well as socioeconomic variables from the study area. The inclusion criteria were based on the relevance of each variable to describe the social-ecological system (see Supplementary material, Appendix A, Table A3), as well as on data availability (see section 8 - Missing variables, Supplementary material, Appendix A). This resulted in a total of 35 variables measured annually from 2000 to 2020 (Supplementary material, Appendix A, Table A1). Due to the absence of consistent socioeconomic data for the region before the year 2000, the time span of the study had to be restricted to this period. The dataset generated for the current study and the scripts used are available from the corresponding author upon request.

Building the social-ecological network

We hypothesized a network structure based on 67 direct relationships among the 35 social-ecological variables of the system (Supplementary Material Appendix D, Table D2), based both on the available literature (see Supplementary Material Appendix C – Hypotheses) and the authors' expert knowledge of the system. All statistical analyses were performed in R version 4.3.0 (R Core Team 2021), using RStudio version 2023.03.1.

We used the *piecewiseSEM* package to statistically test the set of hypothesized relationships between the variables (Lefcheck 2016). Structural equation modeling (SEM) is a powerful statistical technique that enables the analysis of relationships among variables. By assembling multiple regression models, it connects all variables into a single network, facilitating the testing of multiple hypotheses at once. Moreover, this approach enables the quantification of both direct and indirect relationships, as variables in the network can act as predictors and responses at the same time. A notable advantage of using piecewiseSEM, as opposed to traditional SEM, is that it breaks down the analysis into smaller pieces (sub-models). This flexibility not only allows for a much more manageable handling of non-normal data or other violations of model assumptions, but also makes it possible to conduct the analysis with smaller sample sizes.

We specified and tested the individual regression models for each response variable (Table D2, Supplementary Material D). Continuous response variables and count variables with sufficiently large numbers were fitted using linear regressions. Count data were fitted using generalized linear models (GLMs) with a Poisson distribution. Under and overdispersion in GLMs were tested using the function testOverdispersion from R package DHARMa (Hartig and Hartig 2017), and when encountered, quasipoisson or negative binomial responses were used to account for it. Due to the use of time series data, there could be temporal autocorrelation in some of the response variables. In such cases, autocorrelation was accounted for by running a generalized least squares (GLS) model with first-order autocorrelation (1 year lag). When the assumptions of the GLS were not met, 1-year-lagged residuals were included as an additional predictor in the original model. The assumptions of the linear models were validated using the gvlma package (R Core Team 2021). Heteroscedasticity, i.e., unequal variance of residuals in the model, was accounted for in the GLS model when encountered. The goodness of fit of the linear models was based on the model's R^2 and the global model's significance, as well as the significance of each individual relationship tested. For the generalized linear models, it was assessed based on the pseudo-R^2 (*1-(Residual Deviance/Null Deviance)*) and the significance of each individual relationship tested. Finally, for the generalized least squares models,

the goodness of fit was evaluated by measuring the correlation between the observed values and the fitted values of the response variable, as well as the significance of each individual relationship specified in the model.

To test if our data fit the hypothesized network configuration, all the individual models for each response variable were joined into a single global model using the function *psem()* from the *piecewiseSEM* package (version 1.2.1, Lefcheck 2016). A d-separation test was run to find correlations among variables that were unaccounted for. Correlations that could have a potential causal link were included in the individual models when: (1) the model assumptions remained unaffected; (2) the model fit improved. When the inclusion of the correlated variable in the model affected the relationship with the other variables, we considered those for which the causal link with the response was more robust. All remaining relationships were specified as correlated errors in the model. Goodness of fit of the global SEM model was assessed using the test of directed separation using Fisher's C statistic and its associated *p*-value. Unlike in null-hypothesis methods, a good fit in SEM is indicated by a high *p*-value, i.e., *greater* than 0.05.

Due to the disparity in units and ranges between all included variables, the standardized estimates for each pairwise relationship from the model were used to create a matrix encompassing all interaction coefficients (Table 1). A quantitative social-ecological network depicting the relationships among all variables in our SES was represented using the *igraph* package (Csárdi and Nepusz 2006) and edited using Adobe Illustrator CC19 to display the variable types and modules.

Modularity of the social-ecological network

The resulting network of interactions between social-ecological factors and their corresponding interaction coefficients, revealed by path analysis (see section "Building the social-ecological network"), was analyzed using complex network tools. All relationships with *p*-values < 0.1 were considered for this analysis. We quantified the degree of each node as the number of links it had to other nodes in the network. Modularity analyses are useful for identifying groups of variables that are tightly linked together (modules) and variables that act as connectors between the different modules of the system. This can be helpful, for instance, to identify optimal paths to apply changes in one variable, as well as to see which variables would trigger changes across the entire system if altered. The modularity analysis was

Table 1 Matrix with the independent and dependent variables of the regressions present in the network, with standardized path coefficients from the piecewiseSEM analysis, indicating the strength of the relationship between variables. Colored cells indicate correspondence with hypothesized relationships: blue, the hypothesized relationship was found; red, the relationship was not found; bold standardized coefficients indicate marginally significant relationships (*p*-value<0.1). For clarity, columns (dependent variables) receiving no effect and rows (independent variables) causing no effect were removed from the matrix

Independent \ Dependent	annual volume	annual flow	summer flow	winter flow	max summer ET	max summer NDVI	summer snow	winter snow	roads	urban	meadows bushes fields	bird abundance	bird richness	bird diversity	butterfly abundance	butterfly richness	butterfly diversity	total GDP	agriculture GDP	services GDP	occupation in agriculture	occupation in services	total population	tourism establishments	second homes	water consumption
annual flow	0.567	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
summer flow	0	0.697	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
winter flow	0	0.612	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max summer temperature	0	0	0	0	0.36	0	-0.57	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max winter temperature	0	0	0	0	0	0	0	-0.48	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
winter precipitation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
summer precipitation	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max summer ET	0	0	0.729	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
max summer NDVI	0	0	0	0	0.561	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
summer snow	0	0	0.58	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
winter snow	0	0	**0.304**	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
roads	0	0	0	0	0	0	0	0	0	0	-0.11	-0.94	0	0	0	0	0	0	0	0	0	0	0	0	0	0
urban	0	0	0	0	0	0	0	0	0.613	0	0	-2.62	0	0	0	0	0	0	0	0	0	0	0	0	0	0
meadows bushes fields	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.295	0.216	0.941	0	0	0	0	0	0	0	0	0
forests	0	0	1.411	0	0	0.639	0	0	0	0	-0.82	2.347	0	0	0	0	0	0	0	0	0	0	0	0	0	0
agriculture GDP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.104	0	0	0	0	0	0	0	0
services GDP	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.852	0	0	0	0	0	0	0	0
occupation in agriculture	0	0	0	0	0	0	0	0	0	0	**0.046**	0	0	0	0	0	0	0	0.815	0	0	0	0	0	0	0
occupation in services	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.148	0	0	0	0	0	0
salary in agriculture	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.85	0	0	0	0	0
winter seasonal population	0	0	0	0	0	0	0	0	0	**0.222**	0	0	0	0	0	0	0	0	0	0	0	0	0	0.185	**0.252**	0
summer seasonal population	0	0	0	0	0	0	0	0	0	0.39	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.747	0.59
total population	0	0	0	0	0	0	0	0	0	2E-04	0	0	0	0	0	0	0	1E-04	0	0	0	0	0	0	0	0
tourism establishments	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.021	0	0.023	0.161	0	0	0
second homes	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	-0.11	0	0	0
subsidies	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	**0.301**	0	0	0	0	0
water consumption	-0.42	0	-1.45	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

carried out following the simulated annealing optimization approach to partition the network into connected sub-groups or modules proposed by Guimerà and Amaral (2005), which aims at maximizing the modularity function:

$$M = \sum_{s=l}^{N_M} \left[\frac{l_s}{L} - \left(\frac{d_s}{2L} \right)^2 \right]. \quad (1)$$

where N_M is the number of modules, L is the number of links in the network, l_s is the number of links between nodes in module s, and d_s is the sum of the degrees (number of links to or from that node) of the nodes in module s. The partition of nodes into subsets of the nodes in the network that maximizes M constitutes the modules of the network. In addition to module membership, this approach also allows us to calculate measures of within-module connectivity and participation coefficients, which quantify the degree of connectivity of each node within its own module and the rest of the network, respectively. Within-module connectivity, or simply "connectivity" from now on, is calculated thus:

$$z_i = \frac{k_i - \bar{k}_{s_i}}{\sigma_{k_{si}}} \quad (2)$$

where k_i is the number of links of node i to other nodes in its module s_i, k_{si} is the average of k over all the nodes in s_i, and $\sigma_{k_{si}}$ is the standard deviation of k in s_i. Participation coefficient is defined as:

$$P_i = 1 - \sum_{s=1}^{N_M} \left(\frac{k_{is}}{k_i} \right)^2 \quad (3)$$

where k_{is} is the number of links of node i to nodes in module s, and k_i is the total degree of node i. Large values of P_i (close to 1) indicate that node i has its links uniformly distributed across all modules in the network, whereas P_i close to 0 indicates that all its links fall within the module it belongs to. We calculated modularity M, the corresponding modular partition of nodes (modules), z_i's, and P_i's using the *rnetcarto* library in R (Doulcier and Stouffer 2015; Guimerà and Amaral 2005) on the quantified version of our network (i.e., considering the regression coefficients from path analysis as interaction strengths). Given the stochastic nature of the simulated annealing approach, we ran 100 replicates of the *netcarto* algorithm and kept the best partition obtained among them (i.e., the one yielding the largest modularity score M – Eq. 1).

To assess the importance of nodes within the network, we quantified node-level betweenness centrality. Node betweenness is defined as the fraction of shortest paths between any pair of nodes in the network that traverse it. We quantified this measure for each node in network v as:

$$C_B(v) = \sum_{s \neq v \neq t \in V} \frac{\sigma_{st}(v)}{\sigma_{st}} \quad (4)$$

where s, v, and t are elements of the set V of nodes in the network; σ_{st} is the number of shortest paths from node s to node t; and $\sigma_{st}(v)$ is the number of those paths that traverse node v (Freeman 1979). The larger the $C_B(v)$, the larger the fraction of shortest paths that traverse it, and hence, the more central it is in the network.

Based on their connectivity (z) and participation (P) coefficients, nodes were classified as (1) ultra-peripheral, (2) peripheral, or (3) connectors (Guimerà and Amaral 2005). Ultra-peripheral nodes establish almost all their links within their module (z<2.5; P≈0), peripheral nodes form at least 60% of their links within their module (z<2.5; $0 < P \leq 0.625$), and connectors make at least 50% of their connections in other modules (<2.5; $0.625 < P$).

Finally, we explored the importance of the magnitudes of the relationships in driving modularity results, i.e. we assessed whether a qualitative version of the network and a quantitative one would result in the same modules. For both versions of the network, only the relationships found through the piecewiseSEM analysis explained above were used. In the qualitative version, instead of using the magnitude of the relationships, we only considered the presence/absence of a relationship (1 or 0); in the quantitative version, the path coefficients resulting from the piecewise SEM analysis were used.

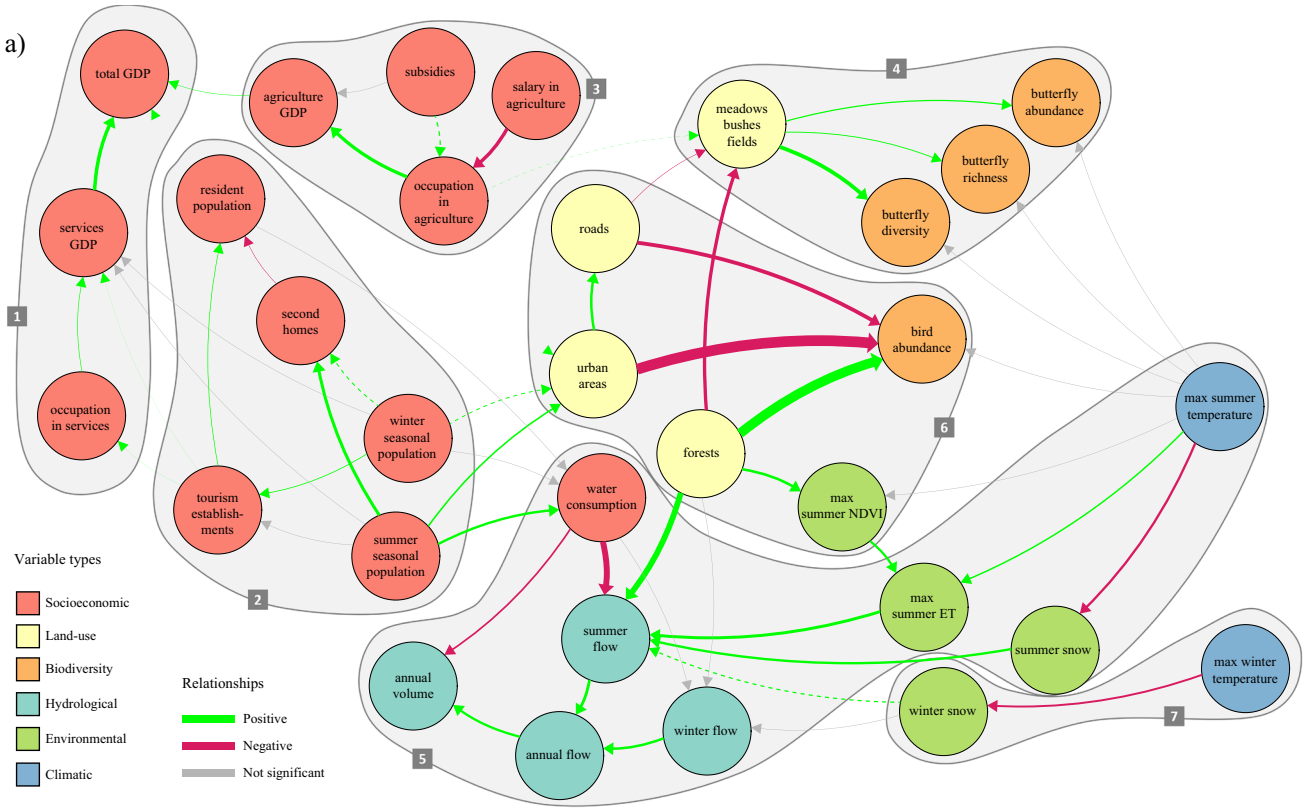
Results

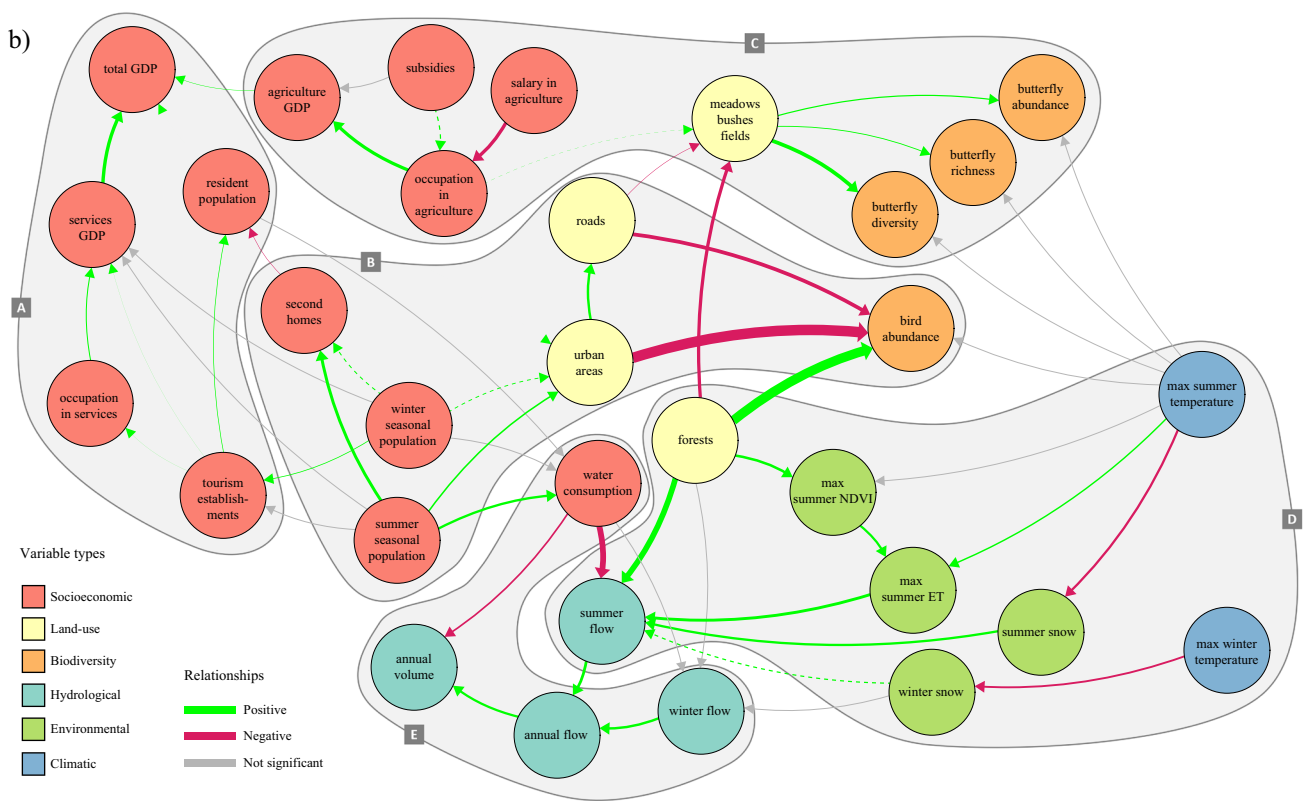
A good fit was found between the data and the hypothesized network configuration (Fisher's C statistic=1172.25, AICc=1122.32, df=1156, p-value=0.363, 578 independent claims), with a total of 37 significant (p-value<0.05) and 5 marginally significant (p-value<0.1) relationships out of the 67 hypothesized relationships (Table 1, Fig. 1, Figure E1 Supplementary Material Appendix E). The results for all the hypothesized individual relationships, as well as the model specifications of linear, generalized linear, and generalized least square models, can be found in Table D1 and Table D2 of Appendix D, respectively.

Relationships between socioeconomy, biodiversity, and water

Drivers of economic growth

Total GDP of the region is heavily influenced by the services sector GDP (coefficient=0.85, p-value<0.01), mildly by the agriculture sector GDP (coefficient=0.10, p-value<0.01) and barely by the r*esident population* (coefficient=1e−4,


a)
total GDP
services GDP
occupation in services
1
agriculture GDP
subsidies
salary in agriculture
occupation in agriculture
3
resident population
second homes
winter seasonal population
tourism establish-ments
summer seasonal population
2
meadows bushes fields
butterfly abundance
butterfly richness
butterfly diversity
4
roads
urban areas
bird abundance
forests
water consumption
max summer NDVI
6
max summer temperature
max summer ET
summer snow
max winter temperature
winter snow
7
summer flow
annual volume
annual flow
winter flow
5
Variable types
Socioeconomic
Land-use
Biodiversity
Hydrological
Environmental
Climatic
Relationships
Positive
Negative
Not significant


b)
total GDP
services GDP
occupation in services
A
agriculture GDP
subsidies
salary in agriculture
occupation in agriculture
resident population
second homes
winter seasonal population
tourism establish-ments
summer seasonal population
B
C
meadows bushes fields
butterfly abundance
butterfly richness
butterfly diversity
roads
urban areas
bird abundance
forests
water consumption
max summer NDVI
max summer temperature
D
max summer ET
summer snow
max winter temperature
winter snow
summer flow
annual volume
annual flow
winter flow
E
Variable types
Socioeconomic
Land-use
Biodiversity
Hydrological
Environmental
Climatic
Relationships
Positive
Negative
Not significant

◂**Fig. 1** Integrated social-ecological network of a mountain ecosystem showing the relationships between 31 social-ecologic variables inferred through structural equation modeling. For clarity, the four variables without any significant (p-value<0.05) or marginally significant (p-value<0.1) relationship with another variable were omitted. Arrows indicate the relationships between variables. Dotted arrows indicate marginally significant relationships (p-value<0.1). For significant and marginally significant relationships, arrow width is proportional to standardized weight coefficients. Shaded background areas indicate **a** the seven modules (labeled with numbers) that emerged when considering relationship magnitudes, i.e., quantitative network; and **b** the five modules (labeled with letters) that emerged when only considering presence or absence of a relationship, i.e., qualitative network. Modules were calculated following the simulated annealing optimization approach to partition the network into connected sub-groups (see details and formulas in "Methods," section "Modularity of the social-ecological network")

p-value=0.02). Both *agriculture GDP* and *services GDP* are mainly influenced by occupation in their corresponding sectors (coefficient *occupation agriculture*=0.81, p-value<0.01; coefficient *occupation services*=0.15, p-value=0.03). *Resident population* is negatively affected by *second homes* (coefficient=−0.11, p-value<0.01) but positively by *tourism establishments* (coefficient=0.16, p-value<0.01). Both seasonal populations increase *second homes*, which has a negative effect on the *resident population*. This results in an indirect negative influence of seasonal populations on *total GDP*. However, there are three additional paths connecting *winter seasonal population* and *total GDP*, all with positive effects (Fig. 1).

Paths from the economic variables to water resources and biodiversity

While most socioeconomic variables have only direct connections with other socioeconomic variables, all population-related variables and *occupation agriculture* act as connectors between socioeconomic variables and biodiversity through their influence on land-use variables (*urban areas* as well as *meadows, bushes, and fields*). Similarly, *summer seasonal population* affects the total *water consumption* (coefficient=0.59, p-value=0.04), which in turn strongly influences hydrological variables (effect on *summer flow*: coefficient=−1.45, p-value<0.01; effect on *annual volume*: coefficient=-0.42, p-value=0.03). As a consequence, direct and indirect paths starting from socioeconomic variables reach all endpoints of the network, ultimately affecting *total GDP*, biodiversity variables, or *water volume* (Fig. 1).

Effects of climatic variables on biodiversity and water resources

Maximum temperatures, through their effect on almost all environmental variables, have an indirect effect on water resources by affecting *summer* (but not *winter*) *flow*, which ultimately influences the water volume in the Oliana reservoir. In contrast, no climatic variable affects any biodiversity variable. Both *summer* (coefficient=−0.57, p-value<0.01) and *winter maximum temperatures* (coefficient=−0.48, p-value=0.03) negatively influence the snow variables. Similarly, neither *summer* nor *winter precipitation* affect any variable of the system (Fig. 1).

The modular structure of the Pyrenean SES

The modularity analysis revealed a total of seven modules (Fig. 1a): (1) the *total GDP and services* module, (2) the *tourism and population* module, (3) the *agriculture* module, (4) the *butterfly* module, (5) the *water* module, (6) the *land use and birds* module, and (7) the *winter snow* module. A simpler pattern, with only five modules, emerges for the qualitative network, in which the magnitudes of the interactions are not taken into account (Fig. 1b). *Resident population* and *tourism establishments*, which are grouped with the other tourism variables in the quantitative network, join the *total GDP and services* module in the qualitative network (Fig. 1b, module A). The seasonal populations and *second homes* are assembled with *urban areas*, *roads*, and *bird abundance* in the qualitative network (Fig. 1b, module B). The *agriculture* module and the *butterfly* module unify into one in the unweighted network (Fig. 1b, module C). Finally, in the qualitative network, *summer flow* is isolated from the rest of the water variables (Fig. 1b, module D), and groups with a large module including all climatic and environment variables instead (Fig. 1b, module E).

Regarding the links between the variables, *summer flow* and *meadows, bushes, and fields* present the highest degree (6 links), followed by *urban areas* (5) (Fig. 1). *Meadows, bushes, and fields* appears to be the most dominant node regarding nodes' centrality in the network (i.e., betweenness) (Fig. 2a), probably because this variable conveys the paths from socioeconomic or land-use variables to all butterfly variables. The same occurs with *urban areas*, as many paths from the socioeconomic part of the network converge to *urban areas* before reaching the biodiversity endpoints located in two different modules. In contrast, despite its high degree and connectivity (Fig. 2b, c), *summer flow* shows a relatively low betweenness (Fig. 2a). This indicates that this variable is highly interconnected within its own module, but plays a relatively minor role in connecting different modules.

Finally, with only three links, *summer seasonal population* connects three different modules: the *tourism and population* module, the *water* module, and the *land use and bird* module (Fig. 1a). Despite being an exogenous variable with among the lowest betweenness and degree values (Fig. 2a, c), *summer seasonal population* is a vital connector at both local (within module) and regional (between modules) levels (Fig. 2b). In fact, *summer seasonal population* is the

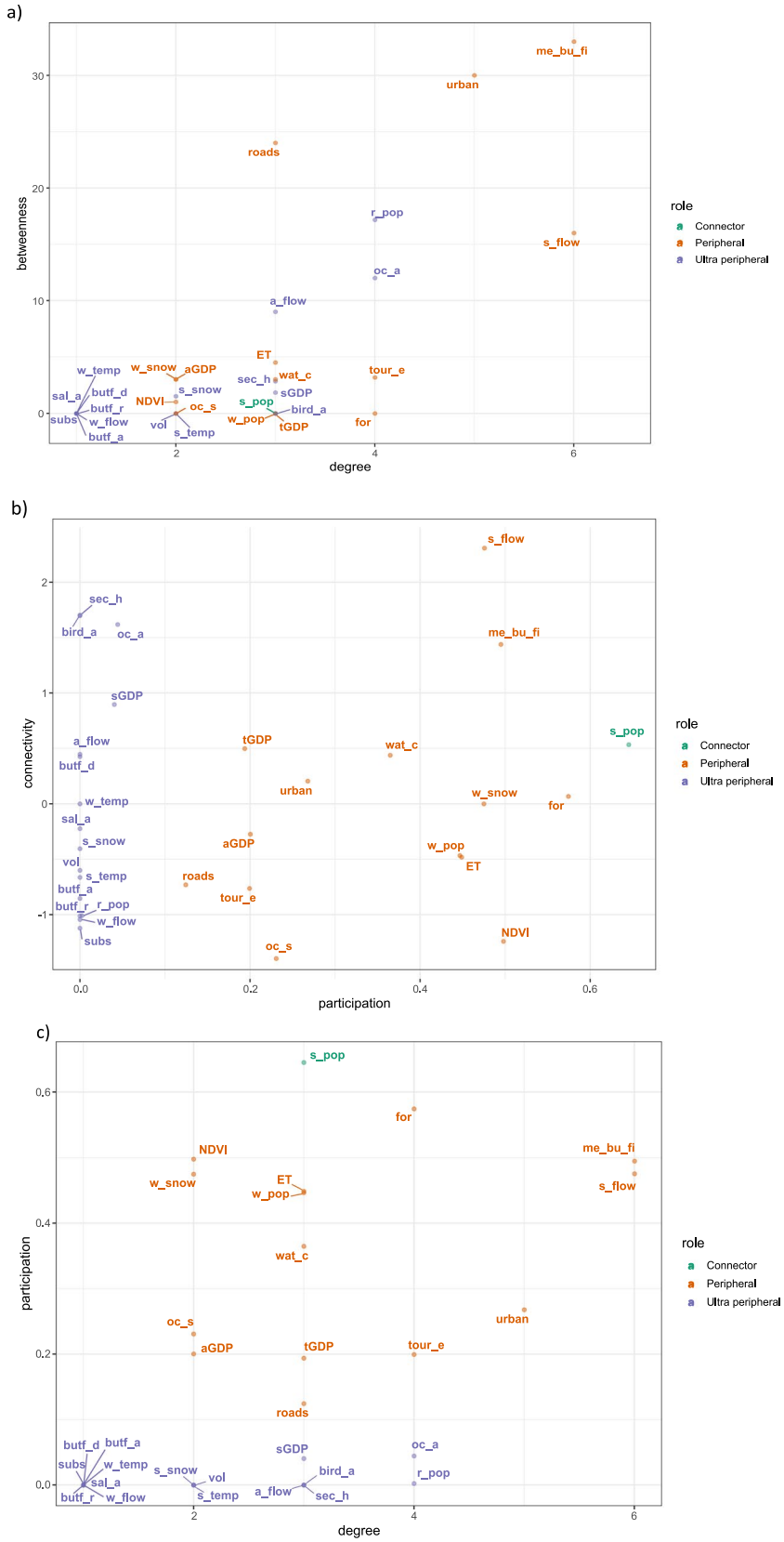


Fig. 2 Relationship between **a** betweenness and degree; **b** connectivity and participation; and **c** participation and degree for each one of the 31 variables included in the modularity analyses. For clarity, the four variables without any significant (p-value<0.05) or marginally significant (p-value<0.1) relationship to another variable were excluded from these analyses. Betweenness quantifies the importance of a node within the network by assessing its role connecting pairs of nodes with each other through the shortest possible path; degree indicates the number of links a node possesses; connectivity quantifies the degree of connectivity of each node within its own module; and participation indicates a node's degree of connectivity with the rest of the network (see "Methods," section "Modularity of the social-ecological network," for further details and mathematical formulas). The peripherality of nodes was calculated based on the quantitative network, i.e., considering relationship magnitudes. Abbreviations: vol for annual volume, a_flow for annual flow, s_flow for summer flow, w_flow for winter flow, s_temp for max summer temperature, w_temp for max winter temperature, ET for max summer ET, NDVI for max summer NDVI, s_snow for summer snow, w_snow for winter snow, urban for urban areas, me_bu_fi for meadows, bushes, and fields, for for forests, bird_a for bird abundance, butf_a for butterfly abundance, butf_r for butterfly richness, butf_d for butterfly diversity, tGDP for total GDP, aGDP for agriculture GDP, sGDP for services GDP, oc_a for occupation in agriculture, oc_s for occupation in services, sal_a for salary in agriculture, w_pop for winter seasonal population, s_pop for summer seasonal population, r_pop for resident population, tour_e for tourism establishments, sec_h for second homes, subs for subsidies, and wat_c for water consumption

only variable classified as a connector, while the rest are all peripheral or ultra-peripheral nodes.

Discussion

The region's economic dependencies and its vulnerabilities

The socioeconomic system in the Segre upper basin of the Pyrenees strongly relies on the services sector to maintain economic growth, particularly on tourism in both summer and winter. Specifically, agrotourism is the main tourist activity in less touristic counties in the Catalan High Pyrenees, such as Alt Urgell, whereas popular destinations such as La Cerdanya rely on a more intensive, snow-oriented tourist model (Campillo Besses and Font Ferrer 2004; Lasanta et al. 2013). It is also evident that both tourism establishments and second homes are influenced by seasonal populations, albeit in different ways. Second homes increase with the number of visitors in both seasons, with a predominant effect of summer visitors. Indeed, in recent decades, many Pyrenean districts have witnessed an increase in the number of second homes due to the growing appeal of the region to urban dwellers seeking mountain retreats for occasional use during weekends and summer holidays (Vaccaro and Beltran 2009).

In contrast, only winter seasonal population seems to have a significant positive relationship with tourism establishments. This clearly indicates the region's focus on snow tourism to promote economic growth in recent decades (Lasanta et al. 2013), although there has been a recent increase in summer-related activities. Ski resorts in the region are currently not economically profitable per se, but they generate benefits by boosting local economies (Campillo Besses and Font Ferrer 2004; Lasanta et al. 2013). Unfortunately, we could not find any data on snow depth or snowmaking for ski resorts in the region, and snow cover—the only available data related to snow—is not a reliable measure of snow depth (Niu and Yang 2007), and much less of snow available for skiing. Thus, we were unable to establish a relationship between snow and ski resort profitability. However, the results show that maximum temperatures in both summer and winter have a negative influence on snow cover in their respective seasons. Due to the increased temperatures caused by climate change, Pyrenean ski resorts rely heavily on artificial snowmaking rather than natural snowfall (Moreno-Gené et al. 2020). Snowmaking is costly and financially unviable in the long run under climate change scenarios and causes significant environmental impacts related to water and energy consumption (Moreno-Gené et al. 2020; Spandre et al. 2019). These drawbacks, along with growing competition from other European resorts (e.g., the Alps), threaten the long-term sustainability of ski resorts in the region (Steiger et al. 2017).

The economic importance of the services sector aligns with the overall shift from a traditional agro-silvo-pastoral economy to a tourism-based economy observed in the Catalan Pyrenees since the second half of the twentieth century (del Mármol and Vaccaro 2015; Guirado González 2014; Pallarès-Blanch et al. 2014). As anticipated, the primary sector and its influence on the local economy are limited (del Mármol and Vaccaro 2015; Guirado González 2014). The marginalized economic role of this sector in the region's current development model is evident from the small contribution of agriculture to the total GDP, as well as the notable segregation of all agriculture variables within a separate module from the region's GDP. Subsidies to agriculture and cattle farming also fail to significantly promote employment in the sector or contribute to its GDP (Lasanta and Marín-Yaseli 2007; Muñoz-Ulecia et al. 2021). Farmers' salaries do not contribute to occupational growth in agriculture, and the negative relationship between these two variables may be attributed to the technification of the agricultural sector, which requires personnel with higher qualifications. Pauw et al. (2007) found that technological advances in agriculture had a negative impact on agricultural employment in South Africa, a phenomenon that could also be occurring in our region. Furthermore, the resident population, which has a modest influence on the region's GDP, is positively affected by touristic businesses. Tourism has played a vital role in mitigating the economic recession in the Pyrenees region and has significantly contributed to countering depopulation (Pallarès-Blanch et al. 2014). However, this trend highlights the ongoing dependence on external elements of the system, namely, visitors and tourists, to sustain the local economy.

Threats to water resources and biodiversity

The hydrological system is directly and indirectly influenced by various SES elements. Direct connections to the hydrological system encompass elements related to water demand (water consumption), land use (forest cover), and environmental variables (evapotranspiration and snow cover). The high degree of connectivity of summer flow indicates its significant importance within the water module, and it also highlights the vulnerability of the hydrological system to water scarcity during summer. Apart from forested areas, most of the linked variables are grouped in the same module as this variable, indicating their strong influence on it. When the magnitude of the interactions is not considered, the influence of water consumption on summer flow diminishes, and the latter is grouped in a different module from water consumption and other water variables.

As for the indirect effects, both summer and winter temperatures affect the hydrological system through their

effects on environmental variables. Snow cover is highly variable among years in mountain areas, and there is a general reduction in solid precipitation compared to liquid precipitation in winter, as well as earlier snowmelt linked to climate change (Gössling and Hall 2006; Sanmiguel-Vallelado et al. 2017). The positive effect of both summer and winter snow cover on summer flow, but not on winter flow, reflects the usual seasonal pattern found in Pyrenean rivers: low discharges in winter, when snowpacks above 1600 m.a.s.l. act as water reservoirs, and higher discharges in spring due to snowmelt (López-Moreno and García-Ruiz 2009; Revuelto et al. 2017).

Contrary to our expectations, we found a positive effect of both evapotranspiration (ET) and forest cover on summer flow. It is possible that an increase in snowmelt due to rising temperatures causes more discharges in early spring, masking the negative effects of forest cover or ET on flow (Buendia et al. 2016; Vicente-Serrano et al. 2015). We tried to account for the influence of snow on summer flow, but the only available data related to snow was snow cover. The lack of information on snow depth or rates of snowmelt is most likely behind the inability of our model to capture the total effect of snow on flow changes.

Our biodiversity variables are only affected by land-use variables, particularly forested areas and those related to human expansion. Both urban areas and roads have a strong negative effect on bird abundance. The high betweenness of urban areas shows its strategic role in mediating the effects of tourism-related variables on bird abundance. Moreover, summer seasonal population has the highest participation in the network and influences the land use and bird module and the water module. These modularity analysis results highlight tourism as an indirect driver of habitat loss and fragmentation (Dri et al. 2021; Payne et al. 2020), which also impacts water availability (Hof and Schmitt 2011; Confederación Hidrográfica del Ebro 2015). In contrast, forested areas have a strong positive effect on bird abundance. In the Pyrenees, as well as in many European mountains, agricultural and livestock abandonment has led to widespread afforestation processes, changing habitat composition (MacDonald et al. 2000). Some studies have reported that afforestation and the loss of grassland habitats have had a negative overall outcome for bird biodiversity in other European mountains. For instance, a study on Greek mountains found that bird diversity and richness were negatively affected by afforestation (Zakkak et al. 2014). However, a study of the impact of managed afforestation in open grasslands in Ireland showed an overall positive effect on bird species richness (Graham et al. 2013). Similarly, a study in Galician Spanish mountains found 13 bird species benefited from the afforestation of abandoned farmlands, while only four species were negatively affected (Regos et al. 2016). Despite the absence of a significant association between forested areas and bird richness or diversity, the observed positive effect on abundance implies a potentially beneficial influence of afforestation on this taxonomic group as a whole.

As expected, all butterfly biodiversity variables increase with the extension of meadows, bushes, and fields, which are favorable habitats for this group (Bubová et al. 2015). These habitats are slightly endangered by roads (Stefanescu et al. 2011) but they are mainly affected by direct forest expansion linked to encroachment (MacDonald et al. 2000). Thus, although forests demonstrate a positive association with bird abundance, they have a detrimental effect on all butterfly biodiversity variables. Butterflies are mildly affected by the abandonment of agricultural and livestock practices. Medium to low grazing by livestock and traditional agricultural practices contribute to insect and plant diversity and the maintenance of a heterogeneous landscape (MacDonald et al. 2000), and the progressive abandonment of these practices can endanger these species (Balmer and Erhardt 2000).

When looking at the qualitative unweighted network, the importance of some relationships is over- or underestimated. Forested areas group in a different module than bird abundance, thus underestimating their importance. The opposite occurs for butterflies, as occupation in agriculture groups with all biodiversity variables in the same module, overestimating its effects. The emergence of different modules in the unweighted network highlights the relevance of considering the magnitude of the interactions when analyzing social-ecological networks, to ensure that the relevance of both direct and indirect effects is properly captured.

We did not find any effect of climatic variables on biodiversity. However, this does not mean that the species groups under study are not impacted by climate change. Mountain butterfly populations in Europe and other regions are shifting their habitat ranges in response to the rapidly changing climate (Rödder et al. 2021; McCain and Garfinkel 2021). Moreover, a study carried out in four European mountain regions, including the Pyrenees, reported an overall 7% decline in bird species, and a 10% decline in mountain bird specialists (Lehikoinen et al. 2019). Similar to our study, Nogués-Bravo et al. (2007) did not find a relationship between their diversity variables and temperature changes, as these relationships are difficult to capture. However, alpine habitats that are essential for these species are highly vulnerable to climate change (Seddon et al. 2016). The Millennium Ecosystem Assessment (2005) found that changes in land use and land cover have been the main drivers of terrestrial biodiversity changes in the last half of the century. However, Ostberg et al. (2015) reported that the effects of climate change have now reached the levels of those caused by land-use/land-cover changes. Thus, future biodiversity forecasts should aim to capture the concomitant and potentially synergistic effects of both these drivers in the study region (Santos et al. 2021).

Recommendations for a sustainable management of resources

Warmer winters, earlier snowmelt, decreases in precipitation, and more frequent and severe droughts are expected to change the intra-annual streamflow variations in the Pyrenees (López-Moreno and García-Ruiz 2009; Sanmiguel-Vallelado et al. 2017). According to projections, water demand for domestic supply will increase from 28.07 hm^3/year in 2013 to 38.70 hm^3/year in 2033 in the Segre basin, partly due to seasonal population and services supply (Confederación Hidrográfica del Ebro 2015). Under these projections of drought coupled with increased water demand, focusing on tourism may have conflicting outcomes. On the one hand, it can help revitalize the economy. This has been the solution to slow the demographic recession in Alt Urgell and even revert it in Cerdanya (Guirado González 2014). On the other hand, it aggravates the pressure on water resources and biodiversity. The centrality of urban areas and the high participation of summer seasonal population in the SES highlight these elements' ability to reach multiple endpoints, causing multiple cascading effects that may be difficult to balance out.

Although we did not find a relationship between winter tourism and water consumption, water extraction for snowmaking threatens water resources in mountains (Reynard 2020; Steiger et al. 2022) and is expected to increase with climate change (Rixen et al. 2011; López-Moreno et al. 2014). Our results do reflect, however, that water resources are strongly influenced by visitors in summer, when droughts are more likely (López-Moreno and García-Ruiz 2009). A diversification and deseasonalization of tourism, promoting spring and autumn visitors, could dampen the negative effects of an unreliable snowpack on the local economy (Moreno-Gené et al. 2020) and summer peaks in water demand. However, promoting tourism in the less popular seasons does not necessarily imply fewer visitors in hot summer months, nor in the ski season. Thus, diversification of the touristic offer should go hand in hand with increasingly needed strategies to reduce water consumption (Calianno et al. 2018; Foris and Pleşca 2017).

The region's single focus on tourism has been coupled with the progressive marginalization of the agriculture and livestock sectors. This affected both farmers' income, which heavily depends on subsidies (Muñoz-Ulecia et al. 2021), and the extension of meadows and fields, which contribute to maintaining habitats for butterflies, albeit mildly (Bubová et al. 2015). Promoting a development strategy solely focused on tourism and exacerbating these imbalances between sectors does not seem to be a sustainable economic strategy. An economic model based almost exclusively on a sector can be risky and diminish the socioeconomic stability and resilience of a region (Dissart 2003; Kaulich 2017), as the COVID19 pandemic has recently shown (Pinilla et al. 2021). A general diversification of the economy, not only of tourism, would thus be necessary to strengthen the economic basis of the region. Agriculture focused on local varieties adapted to a dry climate (i.e., current initiatives to recover old varieties of potatoes, apples, and vineyards), as well as extensive livestock farming, are assets that could be further promoted to establish a more resilient and diverse economy. Despite policies such as the Common Agricultural Policy (CAP) attempting to encourage employment in the sector (Muñoz-Ulecia et al. 2021), many farmers have already opted for diversification of their activities. In the Catalan Pyrenees, diversification of farming households towards tourism entails that less of the farmers' well-being is secured through farming itself (López-i-Gelats et al. 2011). Thus, an increased diversification of the activities carried out in the farm usually precedes the abandonment of most, if not all, agricultural practices. To prevent this, it is important that agricultural policies aim at readdressing diversification: instead of diversifying towards activities other than agriculture, the focus should be on strengthening and expanding agricultural practices themselves (López-i-Gelats et al. 2011). However, a word of caution. Although we were unable to quantify water extraction for agriculture, irrigated agriculture is water-demanding and will likely be threatened under climate change scenarios (Haro-Monteagudo et al. 2020). Additionally, intensive agriculture or livestock practices do not contribute to the maintenance of essential habitats for biodiversity, rather the opposite (Dudley and Alexander 2017). Thus, promoting locally adapted crops as the ones mentioned above would increase their survival under climate change scenarios, contributing to both food security, farmers' income, and water use efficiency.

Methodological considerations

Despite the insights gained from our study, it is essential to acknowledge several limitations that may affect the interpretation of our findings. Firstly, some potentially relevant variables could not be included in the study due to data availability issues (see Supplementary material, Appendix A, section 8 - Missing variables). Data availability is a common challenge in SES studies and it often influences the variable selection criteria (Partelow 2018). Probably because of Ostrom's SESF roots in social sciences (Ostrom 2007, 2009), most SES studies focus primarily on socioeconomic variables, with a notably lesser emphasis on ecological ones (Nagel and Partelow 2022; Partelow 2018). In our case, Governance System variables were particularly limiting (see Supplementary Material Appendix A, section 8 - Missing variables for details). Alternatively, some biodiversity variables are quite similar, though not redundant (e.g., diversity, richness, and abundance of butterflies are three

distinct variables). This implies that some Ostrom SESF attributes were over or well represented, such as Ecological Outcomes and Resource System variables, while others were underrepresented or absent, such as Governance System or Interaction variables. This unbalanced representation of the different variable types surely had an influence on the results, particularly those related to the network analysis. For instance, the degree and betweenness value found for the variable *meadows, bushes, and fields* is probably inflated due to this variable's connection to the three butterfly biodiversity variables. Similarly, including new variables could change module configuration, or reduce the magnitude of the effect between variables.

Moreover, it is worth noting that, while one pattern may emerge at the scale of the social-ecological system, trends can differ among and within counties. For example, depopulation has affected mostly small and isolated villages, and the population has been concentrated in larger and more touristic municipalities located in valley bottoms (Guirado González 2014; Pallarès-Blanch et al. 2014). Working at the watershed scale as we did, such spatial patterns were missed. In this respect, we were again limited by the absence of better data. Similarly, not all variables were available on the same spatial scale (see Supplementary material, Appendix A, Table A1), which certainly influenced the magnitude of the relationships between them. In addition to the data availability challenge previously mentioned, scale mismatch is another issue faced by multidisciplinary approaches to environmental management, such as Social Ecological Systems science, and monitoring standards must be developed to homogenize scales among disciplines and facilitate the acquisition of integrated databases (Virapongse et al. 2016).

Finally, developing tools to facilitate computing the cascade effects of changes in elements of the network, as well as incorporating feedback loops (Herrero-Jáuregui et al. 2018; Nagel and Partelow 2022), would bring valuable information to management planners and researchers alike. Our method does not allow for including feedback loops, but it does help measuring the interactions between variables and visualizing cascading effects in a network format. SES networks obtained using the methodology of this study could serve as a starting point for dynamic systems modeling. This could provide decision-makers with quantitative methods to model and evaluate management scenarios.

Conclusions

Taking the Pyrenees as a case study, we have been able to quantitatively characterize a complex network of interacting social-ecological elements. We have shown how such an approach helps understand the direct and indirect relationships among interacting elements, potentially supporting decision-making. In the Pyrenees, promoting all-year-round tourism coupled with strategies to reduce water consumption could contribute to alleviating the current pressure on water resources and biodiversity, while at the same time reducing the dependence on snow tourism. Moreover, efforts to effectively promote employment in the primary sector could help distribute economic wealth among sectors, increasing the system's economic and social resilience. Extensive livestock practices can also favor the maintenance of essential habitats for biodiversity. However, as rainfed agriculture and intensive practices can threaten both biodiversity and water resources, local crops adapted to a dry climate and extensive practices should be promoted. Extrapolated to other mountain systems, our findings highlight the importance of considering social and ecological factors holistically to improve economic and environmental resource management. Furthermore, our results emphasize the need to quantify the relationships between the elements of the system to ensure that both direct and indirect effects between variables are properly captured. Future efforts should aim at gathering socioeconomic data at appropriate temporal and spatial scales to match environmental data, as well as at developing tools to facilitate the incorporation of feedback loops and computing cascade effects on such complex networks. The methodology used in this study could be used as the basis for system dynamics modeling to facilitate data-informed decision-making.

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Data availability The dataset generated for the current study and the scripts used are available from the corresponding author upon request.

Declarations

Conflict of interest The authors declare no competing interests.

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