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Maintaining biodiversity promotes the multifunctionality of social-ecological systems: holistic modelling of a mountain system

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Abstract

Monitoring the provision of multiple ecosystem services (ES) in social-ecological systems is a major challenge. Most tools usually tackle the problem by modelling individual ES, but do not perform a holistic analysis of a dynamic and integrated system. We developed a discrete-event model (DORIAN) and explored its potential for assessing biodiversity and multifunctionality of a mountain ski resort subjected to a changing climate. We represented this social-ecological system as a network comprising 16 binary components and 51 processes that define component interactions. We identified 22 economy- and ecology-related ES, depending on the presence/absence of components. We simulated six scenarios representing different economic, environmental and climatic situations and calculated a score (the sum of proxies for ES or biodiversity), corresponding to the level of biodiversity and multifunctionality. Results showed that climate change reduced the system’s multifunctionality and increased the number of degraded states, as well as the trajectories from healthy to degraded states. With increasing levels of biodiversity, only ecology-related ES were boosted at low biodiversity levels, while both high levels of ecology and economy-related ES were maintained at high biodiversity levels. This result demonstrates the importance of conserving high biodiversity in a social ecological system, for an optimal “biodiversity – multifunctionality” win-win strategy.

Keywords: biodiversity, ecosystem service, social-ecological system, discrete-event model, qualitative modelling, mountain, economy.
The concept of ecosystem services (ES), that bridge both biophysical and economic processes in a social-ecological system, has been increasingly incorporated into management scenarios related to ecosystem governance and landscape planning (Costanza et al., 1997; de Groot et al., 2010; MEA, 2005; Lescourret et al., 2015). Within the current context of a changing climate, researchers and decision-makers have struggled to find ideal models for predicting and optimizing highly complex bundles of ES in social-ecological systems, hindering the adoption of ES into national policies (Bernués et al., 2019; de Groot et al., 2010; Washbourne et al., 2020). Although understanding social-ecological systems is critical for climate change-adapted ES management and biodiversity conservation initiatives, the inclusion of biodiversity as an ecological factor affecting these systems is deficient in most studies (Rissman and Gillan, 2016). As biodiversity loss is a modern day grand challenge (Future Earth, 2014), the success of addressing this challenge lies in suitably quantifying the contribution of biodiversity to multifunctional social-ecological systems.

Models are useful tools to assess ES values and the multifunctionality of a system under study (Nelson et al., 2009; Neugarten et al., 2018; Shoyama et al., 2017). Most ES models aim to quantify individual indicators within a bundle of ES. Usually, these models are either process-based or empirical and are tightly ES or ES-indicator dependent (e.g., see Merritt et al. (2003) for a review of models of sediment transport and erosion control and Manzoni and Porporato (2009) for a review of models of soil carbon sequestration and climate regulation). By coupling several specialized ES models, multiple SE can be independently quantified and then articulated to trace their spatiotemporal dynamics and trade-off patterns (Elkin et al., 2013; Lafond et al., 2017). While such an approach has greatly enhanced our understanding of the multifunctionality of socio-ecological systems, it can be criticised due to its lack of a holistic
treatment of a system that is multi-scale and contains tightly interdependent components. Another drawback of such an approach is the poor consideration of the dynamic nature of a system, that evolves over time and often shifts to another system subjected to anthropogenic pressure, e.g., management and disturbance (Fraterrigo and Rusak, 2008). Therefore, the suitability of existing ES models, that are often developed or calibrated for certain situations but are used in other situations, is questionable. Additionally, this modelling approach can sometimes be time-consuming and technically difficult due to the high interdisciplinary level, unbalanced multisource data, model availability and a high dependence on multi-sectorial cooperation. As a consequence, most results on system multifunctionality from different studies are rarely comparable, due not only to the use of contrasting models and ES proxies, but also because of the diverse ranges of ES categories. If we are to determine and compare management scenarios for different complex social-ecological systems, we need a robust model that allows the exploration of a large number of ES using a generic methodology.

Novel modelling approaches based on the concept of networks have emerged recently, that could provide an alternative solution for the modelling of complex ecological process and ES bundles. These models aid decision-making through e.g., the development of decision trees (Crossman et al., 2010; Delphin et al., 2013; Zerbe et al., 2013), Bayesian belief networks (Aguilera et al., 2011; Landuyt et al., 2013; McDonald-Madden et al., 2016), artificial neural networks (Larsen et al., 2012), social networks (Puga-Gonzalez and Sueur, 2017), optimisation networks (Xiao et al., 2018), Boolean qualitative networks (Kristensen et al., 2019) and Petri nets (Di Giusto et al., 2019; Gaucherel et al., 2017; Gaucherel and Pommereau, 2019). These modelling approaches share a similar concept in that individual components’ simple behaviours are governed by basic laws that can lead to a sophisticated behaviour of the whole network. These models, that are sometimes semi-quantitative or even
Qualitative, differ in terms of network configuration and parametrization. For example, Bayesian belief networks simulate whether one or multiple events will occur, based on a probabilistic network composed of variables and conditional dependencies (Aguilera et al., 2011; Landuyt et al., 2013; McDonald-Madden et al., 2016). Decision trees, sometimes considered as non-flexible and as simplified Bayesian belief networks, are usually devoted to the diagnosis of an event, into which probabilistic conditions and stochastic processes could be incorporated if desired (Crossman et al., 2010). Several types of network-based models, such as Bayesian belief networks and decision trees, are promising with regard to the coupling of quantitative ES models (Delphin et al., 2013; Fontana et al., 2013; Pérez-Miñana, 2016). But these models are classified as quantitative ES models based on the theory of Bayesian statistics, even though sometimes their diagnostic outputs are qualitative.

Qualitative models, such as Boolean qualitative networks (Kristensen et al., 2019) and discrete-event models (Di Giusto et al., 2019; Gaucherel et al., 2017, 2019), have recently been developed to describe complex ecosystems. The conceptual approach behind such qualitative models is that they avoid making any subjective assumptions concerning parameters’ prior distributions and/or ranges, the choices of which are a potential source of bias. Instead, by setting Boolean rules or discrete rules accounting for the interactions among components and by rigorously handling them, they aim at grasping the holistic nature of a system’s behaviour. Unlike e.g., Boolean qualitative networks that involve one-to-one interactions between components for a rule (Kristensen et al., 2019; Thomas and Kaufman, 2001), discrete-event models are able to model non-dyadic (i.e., not only pair relationships but multi-node) interactions in a single rule, a property mandatory in realistic socio-ecosystem functioning. Discrete-event models are built on the theory of Petri nets, i.e., a classic mathematical tool in computer science that allows the description and analysis of concurrent
processes that arise in systems with many components (Petri, 1966). By setting deterministic rules, yet with several outcomes, discrete-event models enable the exploring all the possible states reached by the system from a given initial state (Gaucherel et al., 2017; Gaucherel and Pommereau, 2019). Discrete-event models have been successfully used to describe pathways of status changes of a complex system in terms of component composition and the underlying processes driving such changes (Gaucherel et al., 2017), suggesting their potential for also tackling questions related ecosystem evolution and simulating ES dynamics.

We developed a discrete-event and qualitative model (named DORIAN) for assessing the long-term maintenance of biodiversity and ES in a social-ecological system. We examined multiple ES and biodiversity at a mountain ski resort in the French Alps, popular for both winter and summer sports, and where forestry and hunting also provide income for the local community. This small mountain town is susceptible to anthropogenic pressure linked to climate change and tourism, which is damaging the local environment, and so is a suitable case study on which to test our model. Using the discrete-event modelling approach, we ask:

(i) how changes due to anthropogenic pressure (i.e., climate change) modify a system’s provision of multiple ES?

(ii) what is the role of biodiversity in the maintenance of a highly complex ES bundle and the system’s multifunctionality?

Answering the first question will enable us to better understand a system’s vulnerability with regard to ES provision and allow us to seek adaptive management strategies for a more sustainable social-ecological system (McCarthy et al. 2001). We hypothesize that a changing climate will adversely affect multiple ES provision, but that it is possible to mitigate the adverse effects via management policies. Answering the second question will provide novel data for the global initiatives that focus on including values for biodiversity and ES into
decision-making. Here, we hypothesize that increased biodiversity has a positive impact on multiple ES provision and so promotes multifunctionality.
2 MATERIALS AND METHODS

2.1 The study site

Chamrousse (45°06'33"N, 5°52'28"E) is a ski resort located 30 km from the city of Grenoble (France) and within the Belledonne mountain range, which forms a part of the French Alps. The Chamrousse municipality extends along an altitudinal range from 1400 to 2250 m a.s.l. Chamrousse has 422 inhabitants (data in 2017), but this population can increase to 15 000 during the winter ski season (http://chamrousse.com). The most important economic resource is alpine skiing (the total revenue from the cable cars was 8.17 M€ in the winter of 2015/2016), comprising >90% of the town’s income. To attract tourists, Chamrousse also develops various activities in winter, including cross-country skiing and ice diving. However, natural snow has become more scarce in the French Alps since the 1960s (Durand et al., 2009). From 2005 onwards, the snow pack at Chamrousse was under the critical threshold (i.e., 0.3 m for a minimum period of 100 days), necessary for downhill skiing (Durand et al., 2009). Therefore, Chamrousse was equipped with artificial snow cannons in 2009 to keep ski-slopes open (Spandre et al., 2015), although there are concerns about the negative ecological impact of artificial snow on mountain vegetation and soil quality (Rixen et al., 2004, 2003; Roux-Fouillet et al., 2011). Also, the rise in mean annual temperature and increase in long, dry periods has led to an increase of tree mortality, with diverse implications for forest functioning (Moser et al., 2011; Csilléry et al., 2017).

In the summer, there is a decrease in tourist activities and income from cable cars is only 0.16 M€ (2015 – 2016). Mountain biking and hill-walking are much promoted by the town hall and tourist office, making summer tourism increasingly popular and a high potential. For the rest of the year (spring and autumn), the village is little frequented by tourists. The hunting season starts in the late summer and usually concerns the local community rather than tourists.
Around Chamrousse, there is a wide diversity of landscapes, including small subalpine lakes, low altitudinal peat bogs and mixed montane forest that continuously extends from low altitudes (<1000 m) up to the treeline (at 2000 m). Each type of landscape has natural habitats hosting a rich variety of species that may need protecting now or in the future. IUCN red-listed species include *Aquila chrysaetos* L. (Golden eagle) and *Parnassius apollo* L. (Apollo butterfly). At high elevations, alpine ibexes (*Capra ibex* L.), chamois (*Rupicapra rupicapra* L.), tetra lyre (*Tetrao tetrix* L.) and Arolla pines (*Pinus cembra* L.) are commonly found (https://inpn.mnhn.fr/). While these species attract tourists and help the economic growth of Chamrousse, tourism can cause disturbances to species’ habitats, including pollution due to waste, soil quality degradation due to the use of artificial snow and ecosystem fragmentation due to ski paths and mountain bike trails. Forest harvesting for timber can also drastically change the microhabitat and cause soil loss through erosion and shallow landslides.

Overall, the whole Chamrousse zone provides many ES, beneficial for tourists but also for residents, such as cultural services (mountain beauty, mountain sports and hunting), regulating services (such as the effect of forests on carbon sequestration and erosion control and maintenance of soil fertility), provisioning services (timber, wild food product, fresh water and hunting products). Considering the close link between cultural services and tourism at Chamrousse, here we consider cultural and provisioning services as economy-related ES and regulating and supporting services as ecology-related ES. Such a context makes Chamrousse an ideal mountain town for studying the dynamics of multiple ES and the compromise between economy and ecology under different management scenarios and to examine the role of biodiversity for multiple ES provision.

### 2.2 DORIAN, a discrete-event model


The discrete-event model that we developed, named DORIAN (Discrete-event model for ecOsystem seRvIce AssessmeNt), models a system in a network composed of two sorts of elements:

(i) discrete objects (termed “nodes”) representing tangible and non-abstract components constituting a realistic social-ecological system (Table 1 and S1).

(ii) discrete rules connecting the nodes (termed “edges”), referring to the processes that can occur under the condition of the presence or absence of one or a certain number of nodes that make the functionality of one or certain nodes appear or disappear (Table 2 and S1).

In this qualitative model, each node has binary status: either functionally present in the system (called “ON” and noted as “+”), or functionally absent from the system (called “OFF” and noted as “−”) (Tables 1 and S1). The status of a node depends on the status of the nodes to which it is connected by an edge or edges which are triggered by specific semantics (Tables 2 and S1). The semantics that make the nodes pass from one status to another (Gaucherel et al., 2017; Gaucherel and Pommereau, 2019) can be either rules (R) or constraints (C). A rule is facultative and optional, defined as a process that can (or cannot) be applicable when its condition or conditions of application are met, while a constraint is a mandatory order and always applied in priority (before all rules), as soon as their conditions of application are met (Tables 2 and S1). Semantics can either be simple (i.e., with one-to-one node interaction) or multiple (i.e., several nodes jointly trigger an event affecting other nodes). Each rule or constraint has a unique name composed by the abbreviation of category (R or C) and an identification number (Table 2).

A state refers to ensemble of the nodes’ status (ON or OFF) in a simulation step. The initial condition (Table S1), defined as the first state from which a simulation starts, should be set prior to a simulation by model user (Table 1). During a simulation, each new step consists of
triggering one of the possible semantics based on the existing state, then forming a new state. From the initial condition, the model explores all the possibilities of rules and constraints to form new states. This approach allows either forming new states of the system or going back to a state that already appeared. Such a full exploration provides a state space representing assembly of all the possible states, and thus, the exhaustive system trajectories (Fig. 1a). Each simulated state has its unique assembly of nodes at ON status and mirrors a possible state that the real system may reach. Once it comes to a state that contains no node at ON status or a state when none of the semantics are available to be executed, the state is called a deadlock state (Gaucherel and Pommereau, 2019), and is stable. During the simulation, the model allows the distinguishing of some related states, i.e., strongly connected components (SCC, Fig 1b-d). A SCC reflects an assembly of states in structural stability in which all states have possible two-way circulations from one to the other (Fig. 1d). The whole simulation terminates when all states are either in SCC or deadlocks, or are causally connecting these SCC or deadlocks. The model then records all trajectories reached, and displays them as a state space graph (Fig. 1a).

The networks in DORIAN should not be confused with those in Bayesian network models, in which probabilities, weighting and uncertainties are usually present. Bayesian network models simulate the likelihood that a system may fall into a specific state given the scenario, while DORIAN is non-probabilistic and does not give any likelihood. DORIAN is possibilistic, as it simulates all the possible fates of a dynamic system with a given scenario. DORIAN’s simulation result is mathematically deterministic and finite and, therefore, unique and reproducible.

2.3 Modeling a mountain social-ecological system

2.3.1 Components and processes
To synthesize knowledge about the mountain town of Chamrousse and to reduce the computational cost, we defined the complex social-ecological system into a network composed of 16 nodes corresponding to observed components and 51 edges (42 optional rules and 9 constraints) corresponding to observed processes defining the main interactions among the elements (Tables 1 and 2; Fig. S1). Choosing such a configuration is not random, but a compromise between the model’s simulation cost and degree of resemblance to a real social-ecological system. Each node, either natural- or human-related, and each edge that is related to either biophysical or socio-economic aspects, have a unique ID number and name (Tables 1 and 2; Fig. S1). These edges or processes are determined by common sense (e.g., in the winter, natural snow can fall, i.e., R4), academic knowledge (e.g. artificial snow can adversely affect the environment, i.e., R28 and R38) or information from local stakeholders after a series of interviews were held (e.g., summer activities can attract tourists, i.e., R15 and R16; Table 2). For the interviews, a list of 70 questions was conceived (Table S2) and each question was asked to representatives of the following organisms: Chamrousse Town Hall, Chamrousse Ski Club, Chamrousse Ski freestyle, Ski lifts Chamrousse, French National Federation of Hunters, National Office of Hunting and Wild Animals and a resident professional journalist for a mountain biking magazine. Not all questions could be answered by each representative, but enough data were obtained to construct the list of edges (Table 2). These stakeholders therefore provided information about activities of Chamrousse that are not included in the academic literature, including ski station management, artificial snow cannons, tourism, hunting and timber production. According to Fig. S1, Win (winter, 16 times), Wat (water, 13 times), Res (residents, 9 times) and For (forests, 9 times) were the most frequent nodes involved in rules or constraints as a condition, indicating their fundamental roles in triggering social and ecological processes. Those nodes, that represented flora and fauna [Ffau (10 times), Oflo (9 times), Fflo (8 times) and Ofau (5 times)], tourism [Tou
(tourists; 7 times) and Ski (ski station; 5 times)], were the most frequent involved in rules or constraints as a consequence (Fig. S1), indicating their high susceptibility to environmental changes.

To define the initial state of the system, DORIAN requires an initialization process, in which each node’s state (ON (+) versus OFF (-)) should be defined. At the same time, one can manually comment some semantics, i.e., deciding if one or some of the rules/constraints should be considered or not, to mimic different management possibilities. We elaborated six simulation scenarios (S) that differed in initial states or rules conditioning to mimic different disturbance and/or management policies. The six scenarios could be divided into two groups depending on if climate change occurred (in S2, S4 and S6) or not (in S1, S3 and S5, as control scenarios). In a semantic form, this disparity was caused if both the rule R5 “Win+ (winter) >> Nsn- (natural snow)” and R6 “Win- >> Wat- (water)” were considered (in S2, S4 and S6) or not (in S1, S3 and S5). Activating R5 and R6 mimicked the phenomena of winter snow decline and summer water stress, respectively, as a potential consequence of climate change (Dayon et al., 2018). Alternatively, the six scenarios could be divided into three pairs (S1–S2, S3–S4 and S5–S6), differing in initial states and management policies. S1 and S2 had the same initial states to mimic the natural and non-human situations, while the other four scenarios (S3–S6), had the same initial states to mimic situations under human impact (Table 1). In a semantic form, S3–S6 contained the node Res (residents), while S1 and S2 did not. With the presence of Res in the initial state, all the other human nodes, such as Tim (timber), Tou (tourists), Ski (ski activities) and Asn (artificial snow), could appear later and had possible interactions with natural nodes in S3 and S4, that were the closest to the actual reality of Chamrousse. These components, including Tim, Tou and Asn, could not appear in S1 and S2 due to the absence of Res. Differing from S3 and S4, scenarios S5 and S6 mimicked an extreme management policy in which the ski station was closed and ski activities did not take
place. To reach this point, a reduced number of rules was used, among which the rules related to the ski station and activities were deactivated (R11, R12, R13, R17, R18, R28 and R38) (Table 2).

2.3.2 Ecosystem services

The presence/absence of certain nodes and occurrence of certain interactions among nodes can represent the biophysical or socio-economic processes or interactions, where ES can be produced or removed. Based on the MEA (2005)’s ES list table (Table S3), we rigorously defined all the possible conditions that make each of the ES appear in the context of the Chamrousse case study (Table 3). Accordingly, missing a condition will make the related ES disappear. One ES could be triggered by several possible conditions (Table 3). The list of ES in Table S3 is slightly different from that in the MEA (2005)’s report, as we adapted ES to the Chamrousse situation. For example, we detailed subcategories of the recreational SE to better reflect Chamrousse’s kernel touristic economy (Table S3). Only ES with the number of conditions > 0 were in our case study (Table 3), and not when ES number of conditions = 0 (i.e., several ES in the MEA (2005) list, Table S3).

In all, there were 22 ES identified for Chamrousse, including 6 provisioning, 5 cultural, 7 regulating and 4 supporting ES (Table 3). We classified provisioning and cultural services as economy-related ES (11 in all) and regulating and supporting ES as ecology-related (11 in all). Ecology-related ES refer to the naturally biophysical process-dominated ES that are less directly used for economy, while economy-related ES refer to the human process-dominated ES that can directly supply either lucrative or potentially lucrative goods. For each simulated state, we judged the presence/absence of each ES according to the conditions in Table 3. As each single ES proxy is binary (0 = absence, or 1 = presence), the scores could be considered
as metrics of multifunctionality. Here, multifunctionality reflects the system’s capacity of hosting the number of items of ES to supply, but does not reflect the abundance of ES.

We also created proxies for specific biodiversity indicators by referring to the components in the natural habitat type (Tables 3 and S3). Biodiversity per se can be considered as a supporting ES, but in most cases biodiversity is usually examined separately to investigate its relationship with a single ES or an ES bundle (de Groot et al., 2010; Mace et al., 2012).

Accordingly, the proxies for biodiversity were not counted into the ES scores in this study.

There were four biodiversity proxies in all, forming a gradient of biodiversity level in five modalities: 0, 1, 2, 3 and 4 (Table 3).

2.4 Simulation and post-treatments

The modelling and simulation work was carried out in Python 3.7 and the TINA tool (Berthomieu 2017). For each scenario, the output datasets of DORIAN contained a list of states. For each state, the presence/absence of each node, related SCC, father/son states in evolution, as well the rules that drove such evolution, were all recorded. Then, post-treatments on the model’s outputs, including information extraction, indicator calculation, statistical analysis and plotting, were carried out in R 3.6.3 (R Core Team, 2015).

To characterize the developmental stage of the study system, we illustrated evolution trajectories among SCC that were determined by their sequence order (i.e. the order in which they appear from the initial state in a graph). To quantitatively determine the sequence order of SCC in a scenario, we calculated a confluent index (CI, dimensionless) for each SCC in a network using a derived protocol inspired from the Strahler number for defining river branching (Strahler, 1952) and centripetal protocol used for defining plant root system architecture (Berntson, 1997) (Fig. 1c):

\[
CI_k = -\sum_{i=1}^{Q(k)} (CI_i + 1)\Delta_{i\rightarrow k}
\]  
(Eq. 1)
where, $Cl_k$ is the confluent index of SCC $k$ ($k \in [1, Q]$, where $Q$ is the total number of SCC), $CI_i \leq 0$; $i$ is the iterator counting from 1 to $Q-1$; $\Delta_{i \rightarrow k}$ is a binary variable determining if there is an direct arrow link from $i$ to $k$ (1: presence; 0: absence). Each simulation has only one initial SCC, and we defined $CI_1 = 0$ for the first SCC. Then, $CI_k$ for all the SCC from 1 to $Q$ could be computed one by one. As there are no double direction arrows between two SCC (otherwise they would have formed a bigger SCC), the solution vector is unique for a given SCC network. Then, all the $CI_k$ are ranged in a descending order and the subscript $k$ of each SCC is considered as the sequence order (SO) of the SCC. The descending sequence order ($Q^{th}$, $Q-1^{th}$, ..., $2^{nd}$, $1^{st}$) corresponds to the descending order of CI (Fig. 1c). All the states in the same SCC have the same CI and sequence order as those for their SCC.

To explore the effect of biodiversity on the system’s multifunctionality, we used boxplots and principal component analysis (PCA) to show the relationship among biodiversity and ES scores. To assess the extent to which ecology-related ES are favored relative to economy-related ES, we calculated the proportion of ecology-related ES score in the total ES score ($p_e$, in %), at either the state or SCC level:

$$p_e = \frac{\text{score of ecology-related ES}}{\text{score of ecology-related ES} + \text{score of economy-related ES}} \quad \text{Eq. (2)}$$

Following the IPCC’s standard definition (McCarthy et al., 2001; Füssel and Klein, 2006), here, a system’s vulnerability of ES provision is defined as the degree to which the system under external pressure (e.g., climate change), is susceptible or unable to provide ES. Here, we examined the vulnerability of Chamrousse to climate change (no snowpack and very dry summers) by comparing the ES proxies between treatment and control scenarios. For a given indicator ($i$), its change rate ($V_i$, in %) of the value in the treatment scenario ($M_{i,T}$, referring to climate change), relative to the value in the control scenario SC ($M_{i,C}$, referring to no climate change) can be calculated as:
The examined indicators (i) included total ES score, ecology-related ES score, economy-related ES score and \( p_e \), whose change rate of mean value was calculated for healthy, degraded and all states, respectively. Differentiating healthy and degraded states allowed us to know if a system’s vulnerability under a treatment scenario was dependent on ES scores. To split healthy and degraded states, we used the quantile 50th of the total ES score in all the states that appeared as the threshold.

Besides \( V_i \) for the four ES indicators, we additionally examined the change rates (\( W_j \), in %) of the number of healthy states, number of degraded states and number of degraded trajectories (i.e., a degraded trajectory refers to a path crossing from a healthy state to a degraded state) from the control scenario to the treatment scenario:

\[
W_j = \frac{N_{j,T} - N_{j,C}}{N_{j,C}} \quad \text{Eq. (4)}
\]

Where, \( N_{j,T} \) and \( N_{j,C} \) are numbers of the object \( j \) (which could be healthy states, degraded states or degraded trajectories) in treatment (climate change) and control (no climate change) scenarios, respectively.

\( V_i \) and \( W_j \) could be both considered as metrics of vulnerability at the system scale, but differed in interpretations. A lower \( V_i \) signified a lower ability of the system in treatment for ES supply or for favouring ecology ES. A system is considered less desirable under a treatment scenario when \( W_j \) for healthy states is low and/or \( W_j \) for degraded states or degraded trajectories is high.
3. RESULTS

3.1 State and strongly connected component (SCC) patterns among scenarios

The six scenarios generated unequal numbers of states and SCC (Fig. 2). The natural scenario S1 contained the lowest number of states (88) and SCC (2) (Fig. 2a). The highest numbers of states and SCC were found in different scenarios: 1614 states in realistic S4 and seven SCC in the scenario S6 where skiing was stopped. Scenarios considering the effect of climate change (S2, S4 and S6) always contained more states and SCC than those without climate change (S1, S3 and S5).

All six scenarios generated 4210 states and 28 SCC in total. As identical states and SCC in terms of node composition could appear in different scenarios, we identified 1804 different states and 27 SCCs appeared in all the simulations. The number of states also greatly differed among SCC, ranging from two (SCC T) to 484 (SCC K, L and M) (Fig. 2g). SCC were highly specialized with regard to scenarios, there was only one common SCC (P) that appeared in two scenarios (S4 and S6). Different from SCC, states could be either specialists or generalists: among the 1804 states, 258 were found in only a single scenario, 1118 in two scenarios, 36 in three scenarios and 402 in four scenarios. None of the states was present in all the six scenarios.

Total ES were positively correlated with the confluent index, CI (Fig. S2), upon which was based the sequence order of each SCC (i.e., their trajectory) being determined. The disparities in state and SCC sizes among scenarios resulted in contrasted levels of complexity in terms of trajectories (Fig. 2). The natural scenarios (S1 and S2) had the simplest trajectory with either a simple one-to-one connection (Fig. 2a) or a triangle connection (Fig. 2b), while the human-related scenarios (S3–S6) had more sophisticated trajectories (Figs. 2c-2f). Except for the two natural scenarios (S1 and S2), the number of nodes and ES scores always showed decreasing tendencies from healthy SCC (e.g., Q, R and S in S5) to degraded SCC, especially with regard
to those having lost all ecology-related ES (e.g., T and U in S5; Fig. 2e). Climate change scenarios (S2, S4 and S6) exhibited more sophisticated SCC trajectories than their control scenarios. Except for S1, in all the other scenarios with climate change and/or human impact (S2 – S6), all states could directly reach the degraded SCC (i.e., E, J, O, T and Z; Fig. 2), where ES scores were extremely low after the loss of For (forest) or Soh (topsoil) (Table 3).

3.2 Composition of states and ecosystem services

We presented the spectrum of all the non-repetitive 1804 states that appeared in all the simulations and ranked them in a descending order of total ES score for each of the six scenarios (Fig. S3). Compared to climate change, situation played a more critical role in determining the spectrum structure (including both positioning of a state in the spectrum and number of states) and the number of degraded trajectories (Fig. S3).

By juxtaposing the presence and absence of the components (nodes), biodiversity and ES proxies, we could obtain a full picture of the Chamrousse social-ecological system and dynamics for either a given scenario (Fig. 3) or all scenarios together (Fig. S4). In the example of the realistic scenario with climate change (S4), the presence of biodiversity and ES proxies were strikingly different depending on seasons and ES categories (Fig. 3, part I).

Among the top 12 most frequently present indicators whose presence was higher than 50% (i.e., from fuel to erosion), two thirds were ecology-related ES, including four supporting and four regulating ES (Fig. 3, part I). Among the ten least frequently present indicators whose presence was less than 30% (i.e., from wild to hunting), most were provisioning (four) or cultural SE (three) (Fig. 3, part I). Similar results could be found when all scenarios were plotted with all 27 SCC, composed of 4202 states (Fig. S4, part I).

Regarding the state spectrum with components, ecosystem components differed greatly in their ability to affect biodiversity and ES bundle delivery (Fig. 3, part III and Fig. S4, part
Residents (Res), topsoil (Soh), and forests (For) were the most essential components of the system, as they were present in more than 90% of the states and served as the basis of the biodiversity and ES scores (Fig. 3, part III and Fig. S4, part IV). The nodes of forest flora (Fflo) and water (Wat) were also very important elements of the system, the presence of which resulted in the highest number of ES proxies corresponding to a high ES score (Fig. 3, part III). Timber (Tim) was occasionally present, playing a marginal role in enriching ES (Fig. 3, part III). The highest ES scores (>15) were found in summer states (Win-): the seasonality (oscillation between Win+ and Win-) had a limited role in determining ES scores, despite its importance in influencing the status of several nodes, such as artificial snow (Asn), water (Wat) and ski activities (Ski) (Fig. 3). Natural components were more frequently present than human components, that were more sensitive to the setting of situation (Figs. 3, S3 and S4).

3.3 The social-ecological system’s vulnerability to climate change

At the state level, the $V_i$ index showed different tendencies for the four ES scores (Table 4). $V_i$ of ecology-related ES and $V_i$ of $p_e$ were usually negative, signifying that ecology-related ES were in decline due to climate change. In contrast, $V_i$ of economy-related ES were usually positive in the two human scenario pairs (S3 – S4 and S5 – S6), signifying that economy-related ES were increasing when climate change was occurring. Contrasted tendencies between ecology- and economy-related ES rendered a generally negative sign of $V_i$ for total ES when pooling all the situations, but diverse signs of $V_i$ for total ES at the situation-level. Among the three scenario pairs corresponding to three situations (natural for S1 – S2, realistic for S3 – S4, no-ski for S5 – S6), $V_i$ of total ES in the S3 – S4 pair increased by over 30%, but decreased by 20% to almost 40% for S5 – S6 and for S1 – S2, respectively. ES proxies in degraded state subsets showed more sensitivity to a changing climate than those in healthy state subsets, if their absolute values of $V_i$ in the significant cases were compared. Regarding
the total ES, the absolute values of $V_i$ of total ES in the healthy state subsets were small (<11%), even close to 0, as a result of the offset effect of ecology- and economy-related ES.

Yet, in the degraded state subsets, total ES reached very high magnitudes and complex signs of $V_i$: climate change increased total ES by more than 40% for the S3 – S4 pair, but decreased it by 16% for S5 – S6 and by 55% for S1 – S2.

When a changing climate was considered, $W_i$ of healthy states, degraded states and degraded trajectories either increased or remained unchanged (Table S4). Among the three indicators in Table S4, $W_i$ of degraded states and $W_i$ of healthy states increased the most and least, respectively. Among the three situations, the realistic situation (S3 – S4 pair) achieved a better compromise than that when skiing was stopped (S5 – S6 pair), as it had a much smaller $W_i$ of degraded states and trajectories. In climate change scenarios, a number of states with water stress (Wat-) in both summer (Win-) and winter (Win+) were observed, especially in degraded states (Table S5), although Wat- was only triggered in the summer (via R6, Table 2).

3.4 Biodiversity and ecosystem service patterns among scenarios

Compared to the control scenarios (S1, S3 and S5), climate change scenarios (S2, S4 and S6) had comparable economy-related ES scores (Fig. 4b), but only half of the biodiversity (Fig. 4d) and ecology-related ES scores (Fig. 4c), resulting in much lower total ES scores (Fig. 4a).

Not surprisingly, the natural scenarios (S1 and S2) had the highest biodiversity (mean: 2.5 for S1 and 1.2 for S2, Fig. 4d), the highest ecology-related ES score (9.4 for S1 and 5.4 for S2, Fig. 4c) and the lowest economy-related ES scores (mean: 2.0 for S1 and 1.8 for S2, Fig. 4b), leading to a low total ES score (11.4 for S1 and 7.1 for S2, Fig. 4a). Compared to the natural scenarios, the human-related scenarios (S3–S6) resulted in a lower biodiversity score, but higher ES scores (Fig. 4). The highest total ES score was found in S5 (13.8) for control
scenarios, but in S4 (9.6) for climate change scenarios (Fig. 4a). In S4, ecology-related ES declined less due to climate change than that in S6 (Fig. 4c) and the economy-related ES even slightly rose compared to its control scenario (S3) (Fig. 4b). When the ES were presented according to the four categories defined in MEA (2005), regulating and supporting ES (Fig. S5e and S5f) were both more susceptible to climate change than provisioning and cultural ES (Fig. S5c and S5d), thus supporting our classification of economy/ecology-related ES.

When pooling all the scenarios together, there were positive synergetic patterns between the biodiversity score and the scores of ES, including ecology-related ES, economy-related ES and total ES (Fig. 5). Similar results were achieved when all the scenarios were not pooled together (i.e., only in climate change scenarios or only in no climate change scenarios), indicating a limited effect of climate change on such synergetic patterns (Fig. S6). The highest increase in total and ecology-related ES scores occurred when the biodiversity score shifted from 0 to 1 (Fig. 5a and 5c). When the biodiversity score continued to increase from 1 to 4, the increment of total and ecology-related ES scores decreased and reached a stable level (Figs. 5a and 5c). The positive effect of biodiversity on economy-related ES score was present, but to a lower extent compared to that for ecology-related ES (Fig. 5b). When the biodiversity score changed from 0 to 1, no increase in economy-related ES score was found (Fig. 5b). A more pronounced increase in the economy-related ES score was only found with higher biodiversity scores (from 1 to 4; Fig. 5b). An increasing biodiversity score tended to decrease the variance of ecology-related ES scores (Fig. 5c), but had a small effect on economy-related ES (Fig. 5b).

The generally synergetic relationships among the investigated biodiversity and SE indicators were also represented in the principal component analysis with all scenarios included (Fig. S7). All indicators were linked together along the 1st principal component (x-axis) explaining 66.2 % of the total variance. This axis could therefore be interpreted as both gradients of
biodiversity and ES, here in synergy. The 2\textsuperscript{nd} principal component (y-axis) explained 28.1\% of the variance and differentiated economy- and ecology-related ES, corresponding to the phenomenon that certain scenarios (e.g., S1 and S2) and SCC (e.g., A and B) favored ecology over economy.
4. DISCUSSION

4.1 Changes in the provision of ecosystem services in a changing climate (Hypothesis 1)

Our study is one of the first to show how a model can be used to disentangle the trajectories of numerous ES in a complex bundle. In particular, we demonstrated the negative effect of climate change on ecology-related ES in a mountain social-ecological system undergoing anthropogenic pressure. We show that climate change would reduce the system’s multifunctionality through several mechanisms. For example, because of drier summers and a reduced natural snowpack in the winter, water reserves dropped by 40% – 50%, leading to a succession of transitions affecting other processes in which water was an indispensable component (Figs. 3 and S3). Our results are consistent with the literature in that water stress has a negative long-term effect on both mountain prairies and forests, with detrimental effects on ES provision (Deléglise et al., 2015; Hartl-Meier et al., 2014). Our model also showed that in the climate change scenarios (S2, S4 and S6), summer water stress could extend into the winter periods, where a number of states with water deficits (Wat-) were present in the zone of degraded states (Figs. 3 and S3; Table S5). Data on this legacy of summer water stress on winter ecosystem functioning and ES provision are scanty in literature, probably due to the difficulty in establishing causal effects between summer and winter processes via an experimental approach. Therefore, compared to other ES models, our discrete-event model allows us to investigate and anticipate transitional events across periods (e.g. seasons).

The frequency of the natural snowpack (Nsw+) was not very sensitive to climate change, because it could only be triggered in the winter (Win+, Table 3; Fig. 3) and was variable regardless of climate. In contrast, an increase in water reserves (Wat+) could be due to either abiotic (natural snow presence, R8; Table 2) or biotic (difference in water conditions between forests and bogs, R7; Table 2) factors, and so was more sensitive to changes in climatic conditions.
Although a changing climate change had a limited effect on the number and positioning of healthy states in the spectra, it significantly increased the number of degraded states, and so produced more pathways through which a healthy state could shift to a degraded state (Table 4; Fig. S3). The important lesson to learn from this result is that even though a system can be healthy in terms of multifunctionality, it could be more prone to degradation in the context of climate change. This result highlights the necessity to consider a system as highly dynamic where its functions and ES have many possible trajectories: a simple diachronic approach cannot be used to assess the impact of climate change on a system. In spite of the generally negative effect of climate change, economy-related ES scores could be maintained and even show a positive response to climate change (e.g. touristic activities in degraded states) (Table 4). Therefore, DORIAN is useful for examining individually the trajectories of ecology- and economy-related ES scores along the state and SCC evolutions. Additionally, the holistic approach that DORIAN also offers allows the user to determine tradeoffs between ES facing perturbations.

4.2 The regulating role of management in vulnerability mitigation (Hypothesis 1)

To date, the impacts of climate change and management on multiple ES are still inadequately explored in mountain regions (Schirpke et al., 2013). Compared to studies that usually focus on one single landscape (e.g., mountain forests), one single leverage (e.g., forestry management) or one single category of ES (e.g., regulating ES) in a study (Elkin et al., 2015; Lafond et al., 2017; Seidl et al., 2019), a more multidisciplinary approach embracing a multitude of disturbance sources (e.g., management policy and climate change) and a wider range of ES is much needed (Schirpke et al., 2013; Brunner et al., 2017). To tackle such a challenge, our case study that was simulated by DORIAN enriches our knowledge on how management policies could mitigate the effect of climate change on a system’s
multifunctionality. We found that the three modelled situations responded very differently to climate change, validating our first hypothesis (Tables 4 and S4). In the ‘natural’ situation (absence of human beings), healthy states had a low vulnerability to climate change, but this situation is not realistic and so provides limited management indicators for stakeholders. Between the two situations where humans were present, the most realistic situation (with human-related winter activities) was less vulnerable to climate change. Although the ecology-related ES score did not significantly drop when climate change occurred, the economy-related ES score was boosted (Table 4). This phenomenon occurs because human-related skiing activities (Ski) and artificial snow (Asn) were both active in the realistic scenarios. Accordingly, the number of healthy states that were increased was effective against the drop of ecology-related ES scores. In terms of economy, the artificial snow production (Asn+) ensures that tourists (Tou+) come to the town, which in turn activates the skiing (Ski) and cultural ES, even in the absence of the natural snowpack. In the third situation that we modelled (where humans were present but skiing activities did not take place), winter activities were much lower than in the more realistic situation (with human-related winter activities, Fig. 3), and thus could greatly reduce the town’s economic gain.

Our results show that although certain economic activities can mitigate negative effects of climate change on ES provision, regardless of situation, even a healthy and stable state with high multifunctionality could directly jump to a degraded state with low multifunctionality without passing through any intermediary states (e.g., SCC F → J in S3 or Q → T in S5; Fig. 2). Such a phenomenon could occur if certain key components (e.g., forest and topsoil) become absent or dysfunctional (Figs. 3 and Fig. S3). In addition, this trajectory was not sensitive to climate change (Fig. S3), meaning that irrational practices (e.g., clear-cutting of forest or agriculture on steep slopes causing erosion and topsoil loss), that were harmful to fundamental components, could immediately make the system collapse.
4.3 Effect of biodiversity on multifunctionality (Hypothesis 2)

Results from our model scenarios showed that a system with no biodiversity at all could only provide small amounts of ES of any category (Fig. 5). This result is well in agreement with many studies showing that significant biodiversity loss due to e.g., pollution and habitat degradation, can lead to serious ecological dysfunction and social-economic problems (Cardinale et al., 2012; Díaz et al., 2006; Hooper et al., 2012). However, while a positive effect of increased biodiversity on the overall ES level of a system is clear, the relationship between biodiversity and each ES category is questionable (de Groot et al., 2010). Studies testing the effect of high biodiversity on different social-ecological systems found it can be positively, neutrally, or negatively associated with different functions or ES (Chan et al., 2007; Loreau, 2001; van der Plas et al., 2016). But most of these studies examined biophysical process-based ES, not economy-related ES. Here, our results provide new evidence, showing that increased biodiversity improved the total ES score, but it had a minimal effect on economy-related ES (Figs. 5 and S6). At the same time, biodiversity was found to favour the system’s stability with regard to the supply of ecology-related ES, as the variance of ecology-related ES scores at higher biodiversity levels was lower (Fig. 5c). Yet, such a phenomenon was absent for economy-related ES (Fig. 5b). These results are due to the ecology-related ES corresponding to biophysical processes that depend on the presence of natural elements (i.e., soil, water, forest and bogs). The absence of these elements suppressed not only most of the supporting and regulating services, but also other elements that depend on them (e.g. flora and fauna). Economy-related SE were more related to anthropological components (e.g., tourists, logging and ski activities) despite some dependency on natural elements. We found that, with increasing biodiversity, only ecology-related ES were boosted at low biodiversity levels, while high-level ecology- and economy-related ES were both
maintained at high biodiversity levels. This result highlights the primary importance of conserving high biodiversity in a social ecological system, for an optimal “biodiversity – multifunctionality” win-win strategy.

For fulfilling the Sustainable Development Goals of United Nations, associating biodiversity conservation with socio-economic improvements for communities has been launched in the Man and the Biosphere (MAB) Programme of UNESCO (Persha et al., 2011). Although the importance of integrating a “biodiversity – multifunctionality” win-win strategy against both ecological and/or economical risks is major (Chan et al., 2007; Xiao et al., 2018), the current theoretical framework of biological conservation still inadequately juxtaposes multiple ES, especially economy-related ES, to the equally high level of importance given to biodiversity (Xiao et al., 2018, 2019). One of the major reasons is due to the lack of information on the provisional and feedback links between biodiversity and their interactions, and ecosystem functions and services (Xiao et al., 2019). Our model shows that the interwoven biophysical and social-economic aspects share several components (e.g. habitat, tourists and ski activities), and that a holistic approach is necessary when studying a social-ecological system. Therefore, we propose that the theoretical concept or practical roadmap of biological conservation is revised by either expanding the paradigm to include social-economic aspects or to create a new, parallel but complementary paradigm. This paradigm would concern social-economic conservation, that tackles the vulnerability of social-economic aspects of a system.

4.4 Advantages and limitations of DORIAN for ecosystem service modelling

To investigate the vulnerability of ES provision to climate change, previous studies have mostly quantified ES values and occasionally their magnitudes and spatiotemporal patterns. ES provision is then compared in treatment and control scenarios of climate change (e.g.,
Schröter et al., 2005; Elkin et al., 2015). However, finding robust and data-supported case studies and well-calibrated quantitative ES models is usually difficult, thus hindering our understanding of the effects of climate change and biodiversity on multiple ES relationships in social-ecological systems. Here, with the discrete-event model *DORIAN*, we propose an alternative, but complementary approach to assess multiple ES without the necessity to quantify any ES value.

Although stakeholders and policy-makers need quantitative ES values for diagnosis and decision-making, knowing the trajectory and fate of ES is even more important than their value in the global change context (e.g. knowing if a system is a carbon sink or source, rather than how much carbon is stored, Mao et al., 2019). Therefore, a qualitative and discrete-event model has a specific niche when examining complex bundles of ES. As *DORIAN* simulates fully all the states of a system, as well as the pathways or trajectories among states, important ecological concepts, such as multifunctionality and disturbance (e.g. climate change in our case study), can be rigorously defined and quantified. Therefore, by using *DORIAN*, we avoided characterizing ES in one or several snapshot-like states of a system as is usually performed by many quantitative ES models e.g., Schröter (2005). *DORIAN* can also investigate the legacy effect of a process as it occurs, as well as the potential consequences over time. These legacy effects (e.g. the influence of summer water stress on winter ES in our case study), are usually ignored in quantitative ES models due to limited data. *DORIAN* therefore provides a feasible and efficient way to include ES when tackling the question of multifunctionality of a system.

A common criticism of discrete-event models is that assumptions are over-simplified because of the binary status of components and qualitative processes. In a discrete-event model, while model configuration is qualitative at the component and process levels, simulations and post-
analyses are quantitative at the network system level. Both quantitative ES models and
discrete-event models mimic a simplified reality, as in any model, but they differ in their
focus of description of a system. A quantitative ES model, which can be either probabilistic
(i.e., frequentist or Bayesian) or deterministic, focuses on the description of the inherent
biophysical and social driven processes in one or several components, triggering the ES of a
system under one or several states. A discrete-event model however, makes the inherent
processes as simple as possible (e.g., by using binary values to represent presence and
absence), but gives more focus on the extensive interactions between components within or
across states. Therefore, discrete-event models can be used to model highly complex social-
egological systems (e.g., large interaction networks with hundreds of components and
rules/constraints intervening at multiple scales) and to focus on changes over the long term. In
our case study, 22 services from all four ES categories (MA, 2005) were included in DORIAN,
but all the listed ES in either MEA (2005) or in TEEB (Kumar, 2010) criteria could be
included if desired (Tables 3 and S3). This methodology for ES modelling (Table 3) is generic
and can be standardized and transposed to other case studies, enabling valuable comparisons
to be made across different types of ecosystems and social-ecological systems. It is to be
noted that DORIAN has the potential to be coupled with quantitative ES models, provide that
the latter could be calibrated and validated in all or several specific states. In the current
definition of multifunctionality, relative importance among ES is not yet represented, but can
be taken into account in the optimisation of desired systems and management scenarios,
provided that multisectorial decision-makers could provide such information on the priority of
ES.
The paired component interactions in a discrete-event model require users to identify and
define relevant components and processes. We were able to represent the complex
Chamrousse social-ecological system using only 16 components (e.g. type of landscape, taxa
and anthropogenic activities), that interacted via 51 processes. This simplification enabled us
to reach a compromise between our research question and the available computational
capacity. Processes may have different confidence levels according to the reliability of
sources of knowledge. We did not include the estimation of confidence levels when applying
the model to the Chamrousse case study, as we considered that the knowledge used to
parametrize the processes was robust and testing the effect of confidence level of rules was
not the objective of this study. Such an issue could be tackled by conducting uncertainty
analyses, which consist in creating extra scenario pairs with activated or deactivated
semantics mimicking the uncertainty process.

An advantage of discrete-event models is that any spatial or time scale can be investigated, as
any ecosystem component can be included. However, ecological and anthropogenic processes
can be short- or long-term, or even both, e.g., destruction of a forest. In our case study, we did
not differentiate between time scales, therefore, direct comparisons between stable states are
difficult. However, our objective was to identify the potential degradation of states and system
vulnerability in diverse situations. To better integrate the temporal scale into DORIAN, we
suggest characterizing connectivity among states or SCC, which can partially reflect the
concept of time by indicating the orders of occurrence for processes.

Validating results from DORIAN’s simulations on the dynamics of a system is another
challenge, as independent ground-truth data on socio-ecological systems are still scanty.
Moreover, these data may never exist, as some states that occurred in the model’s results may
never occur in reality. However, conducting such exploratory model simulations would still
be highly useful, as it can provide valuable information on a system’s fate and anticipate
catastrophic events due to certain management practices.

5. CONCLUSION
Using a discrete-event model, DORIAN, we examined modifications in the provision and trajectories of ES in three diverse situations in a mountain social-ecological system subjected to climate change (dry summers and warm winters with reduced snowpack). The degree of human impact differed in each situation, and scores (total number of biodiversity and ES proxies) were calculated for each scenario simulated. Climate change reduced the system’s multifunctionality (ES scores decreased), and increased the number of degraded states, as well as the trajectories from healthy to degraded states. Certain economic activities, e.g., skiing, could mitigate the negative effect of climate change on overall ES provision. However, DORIAN showed that even a healthy and stable state with high multifunctionality could directly jump to a degraded state with low multifunctionality without passing through any intermediary states. Such a phenomenon could occur if certain key components become absent within the system. With increasing levels of biodiversity, only ecology-related ES were boosted at low biodiversity levels, while both ecology- and economy-related ES were maintained at high biodiversity levels. This result highlights the primary importance of conserving high biodiversity in a social-ecological system, for an optimal “biodiversity – multifunctionality” win-win strategy. The holistic modelling approach with DORIAN is methodologically generic and provides a novel and alternative solution to assess the multifunctionality of social-ecological systems without the necessity to quantify any ES.

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Tables

Table 1 Nodes and initial states set for each simulation scenario for the case study of Chamrousse

Table 2 Rules (R) and Constraints (C) for the case study of Chamrousse

Table 3 Biodiversity and ecosystem service list and their triggering conditions

Table 4 Comparison of ecosystem service proxies between control (no climate change) and treatment (climate change) scenarios

Figures

Figure 1 An example of a state space (a), strongly connected component (SCC) space (b), calculation of confluent indices (in text) and sequence orders (in circles) of SCC (c) and evolution between states within and across SCC (d). In (c), $CI_x$ and $SO_x$ represent the confluent index and sequence order of the SCC $x$, respectively. In (d): purple dots represent natural components and orange dots represent human components. Squares represent status (red for presence and grey for absence) of components in each of the five states (0, 1, 3, 2 and 4) from Scenario 3. The curves on the top of spectra represent the evolution between states, and arrows indicate their directions. The text in italics and red colour beside each curve represents the rule/constraint or rules/constraints conducting the evolution between two states, including R1 ($Win+ >> Win-$); R2 ($Win- >> Win+$); R10 ($Res+, Win-, For+ >> Tou+$); R14 ($For+, Res+ >> Tim+, Gap+$); R16 ($Win-, Res+, Bog+ >> Tou+$); R19 ($For+, Tim- >> Gap-$) and C5 ($Win+, Ski- >> Tou-$). States 0, 1 and 3 belong to the same SCC (i.e., SCC F), as they can shift between each other. States 2 and 4 belong to the other SCC, as they are irreversible to the states in SCC F.

Figure 2 Evolution of itineraries of strongly connected components (SCC) per scenario. Subplots from (a) to (f): each SCC has a unique label (in capital or small Latin letters); identical SCC in different scenarios share the same label (e.g., SCC P in scenarios 4 and 6); the arrows with arrow head in the middle represent the evolution of itineraries from one SCC to another. Subplot (g) summarizes the number of states contained in each SCC. The filled colour in each of the circles in (a-f) and bars in (g) represents the average of the total ES scores of all states in a SCC (0 as minimum and 20 as maximum among all the states). The negative direction along the y-axis is the sequence order (SO) of SCC reflecting SCC evolution.

Figure 3 Analysis of state spectra with ecosystem services (ES) and components. The figure shows an example of scenario 4 containing 1614 states of out of all the 1814 states appearing in the social-ecological system of Chamrousse. The figure consists of three parts (marked on the right from top to bottom): (I) – spectrum with biodiversity and ES proxies (red: present; grey: absent), (II) – evolution of total ES score and trajectories among the states and (III) – spectrum with the status of components (red: ON; grey: OFF). In (I) and (III), the order of the states from left to right represents the descending order of the total ES score; the hollow parts
signify the absence of the states in the present scenario; values on the right are percentages of a proxy or a component appearing in all the states of the scenario 4 and are ranged in a descending order from top to bottom. Regarding the evolution of the total ES score in (II), thick and thin sections correspond to the metric of the present scenario and of all the six scenarios, respectively; the vertical dashed blue line of the state ID 948 at $P_{50} = 10$ splits the pools of healthy and degraded states; translucent grey arcs represent degraded evolution trajectories between two states (only paths crossing the line at state ID 948 are shown).

Figure 4 Variations of biodiversity and ecosystem service (ES) scores (total ES, economy- and ecology-related ES) per scenario. For each boxplot, the thick horizontal line and point “X” inside the box represent the median and mean of data points, respectively. Low and top edges of the box correspond to the 25th and 75th percentile data points, respectively. Low and top horizontal lines correspond to the 10th and 90th percentile data points, respectively. Point clouds over boxplots allow a visual check of the quantity of states, each of which corresponds to one point. In (a), the total number of states per scenario is shown on the top of each boxplot.

Figure 5 Variations of ecosystem service (ES) scores (total ES, economy- and ecology-related ES) as a function of biodiversity gradient. For each boxplot, the thick horizontal line and point “X” inside the box represent the median and mean of data points, respectively. Lower and top edges of the box correspond to the 25th and 75th percentile data points, respectively. Lower and top horizontal lines correspond to the 10th and 90th percentile data points, respectively. Point clouds over boxplots allow a visual check of the quantity of states, each of which corresponds to one point. Points of different colours represent different scenarios. In (a), total numbers of states per scenario are shown on the top of each boxplot.

Supplementary tables and figures

Table S1 Terminology and acronyms related to the model
Table S2. List of questions prepared for town hall employees and private stakeholders at Chamrousse
Table S3 Ecosystem services (ES) included in the case study based on the full ES list of MEA (2005)
Table S4 Comparison of state conditions between control and treatment scenarios
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Figure S1 Relationship between semantics (rules and constraints) and nodes for the case of Chamrousse
Figure S2 Scatter plot between total ecosystem service (ES) score and confluent index of all the strongly connected components (SCC).

Figure S3 Analysis of state spectra with ecosystem services and components of for each of the six scenarios along all the 1814 states appearing in the social-ecological system of Chamrousse. Each subplot presenting one scenario consists of two parts. The lower part shows the spectrum of states with the status of components (red: ON; grey: OFF). The order of the states from left to right represents the descending order of the total ecosystem service (ES) score. The hollow parts signify the absence of the states in the present scenario. The order of components from top to bottom represents the descending order of the percentages of nodes in status ON calculated with the data of all the six scenarios. Values on the right of the spectrum indicate the percentage of the nodes for the present scenario. The upper part shows the evolution of total ES score, where thick and thin sections correspond to the metric of the present scenario and of all the six scenarios, respectively. The vertical dashed blue line of the state ID 948 at $P_{50} = 10$ splits the pools of healthy and degraded states. Translucent grey arcs represent degraded evolution trajectories between two states (only paths crossing the line at state ID 948 are shown).

Figure S4 Analysis of state spectra for components and ecosystem service (ES) of all the strongly connected components (SCC), as well as the states that they contain, of the social-ecological system of Chamrousse. The figure consists of four parts (marked on the right from top to bottom): I – spectrum of biodiversity and ES proxies (red: present; grey: absent), II – score of ES and composition between economy- and ecology-related ES, III – evolution trajectories among the states belonging to different SCC, IV – spectrum of components. In I and IV, every thin vertical slice corresponds to a state (4202 states in all for 27 SCC); the numbers on the right are percentage of a proxy or a component appearing in all the states and are ranging in a descending order from top to bottom. In II, numbers on the top of each bar refer to total ES and the colours in the bar represents the proportion of ecology-related ES (light pink) against economy-related ES (deep pink). In III, only degraded trajectories (i.e., a path linking a healthy state and a degraded state) are shown. In IV, numbers below the spectrum indicate the numbers of states in SCC.

Figure S5 Variations of biodiversity and ecosystem service (ES) scores (total, provisioning, cultural, regulating and supporting) per scenario. For each boxplot, the thick horizontal line and point “X” inside the box represent the median and mean of data points, respectively. Low and top edges of the box correspond to the 25th and 75th percentile data points, respectively. Low and top horizontal lines correspond to the 10th and 90th percentile data points, respectively. Point clouds over boxplots allow a visual check of the quantity of states, each of which corresponds to one point. In (b), the total number of states per scenario is shown on the top of each boxplot.

Figure S6 Variations of ecosystem service (ES) scores (total ES, economy- and ecology-related ES) as a function of biodiversity gradient and climate change. For each boxplot, the thick horizontal line and point “X” inside the box represent the median and mean of data
points, respectively. Lower and top edges of the box correspond to the 25\textsuperscript{th} and 75\textsuperscript{th} percentile
data points, respectively. Lower and top horizontal lines correspond to the 10\textsuperscript{th} and 90\textsuperscript{th}
percentile data points, respectively. Point clouds over boxplots allow a visual check of the
quantity of states, each of which corresponds to one point. Points of different colours
represent different scenarios. S1, S3 and S5 correspond to control scenarios with no climate
effect, while S2, S4 and S6 correspond to treatment scenarios with climate change
effect.

Figure S7 Principle component analysis (PCA) of biodiversity and ecosystem service (ES)
variables at both state and strongly connected component (SCC) levels. Hull convex polygons
represent the ranges of scenarios (S1 – S6). Letters represent the names of SCC.
### Table 1

<table>
<thead>
<tr>
<th>Category</th>
<th>ID</th>
<th>Name</th>
<th>Acronym</th>
<th>Scenarios</th>
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<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td>1 &amp; 2</td>
</tr>
<tr>
<td>Natural</td>
<td>1</td>
<td>Winter or summer</td>
<td>Win</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>Natural snow</td>
<td>Nsn</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>3</td>
<td>Water</td>
<td>Wat</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>Topsoil with organic horizon</td>
<td>Soh</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>5</td>
<td>Bogs</td>
<td>Bog</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>6</td>
<td>Dense forest</td>
<td>For</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>7</td>
<td>Forest gaps</td>
<td>Gap</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>8</td>
<td>Forest fauna</td>
<td>Ffau</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>9</td>
<td>Forest flora</td>
<td>Fflo</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>10</td>
<td>Aquatic or open area fauna</td>
<td>Ofau</td>
<td>+</td>
</tr>
<tr>
<td></td>
<td>11</td>
<td>Aquatic or open area flora</td>
<td>Oflo</td>
<td>+</td>
</tr>
<tr>
<td>Human</td>
<td>12</td>
<td>Residents</td>
<td>Res</td>
<td>-</td>
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<tr>
<td></td>
<td>13</td>
<td>Timber</td>
<td>Tim</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>14</td>
<td>Tourists</td>
<td>Tou</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Ski activities (including infrastructure</td>
<td>Ski</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td></td>
<td>and path)</td>
<td></td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>15</td>
<td>Artificial snow</td>
<td>Asn</td>
<td>-</td>
</tr>
</tbody>
</table>

Note: + and - means the node is ON and OFF at initial state prior to simulation, respectively.
<table>
<thead>
<tr>
<th>Category</th>
<th>ID</th>
<th>Semantics of edge</th>
<th>Explanation</th>
<th>Source of information</th>
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<tr>
<td>Constraint (C)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td></td>
<td>Wat- &gt;&gt; Asn-</td>
<td>Without water resources (water table), no artificial snow will be produced.</td>
<td>Common sense</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>Nsn-, Asn- &gt;&gt; Ski-</td>
<td>Without (artificial or natural) snow, no skiing activities will be possible.</td>
<td>Common sense</td>
</tr>
<tr>
<td>3</td>
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<td>Res- &gt;&gt; Tou-, Asn-, Ski-</td>
<td>Without residents, no touristic winter activities will be possible.</td>
<td>Interview with stakeholders</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>Win- &gt;&gt; Ski-, Asn-</td>
<td>In summer, no winter activities, no ski and no artificial snow will be possible.</td>
<td>Interview with stakeholders</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>Win+, Ski- &gt;&gt; Tou-</td>
<td>In winter, tourists will be absent without the ski station and other winter activities.</td>
<td>Interview with stakeholders</td>
</tr>
<tr>
<td>6</td>
<td></td>
<td>For- &gt;&gt; Tim-, Ffau-, Fflo-, Gap-</td>
<td>Without forest, no wood production (logging) and no associated fauna and flora will survive.</td>
<td>Common sense</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>Soh- &gt;&gt; For-, Bog-, Fflo-, Oflo-</td>
<td>Without fertile soils, it will be impossible to maintain forests, bogs and flora.</td>
<td>Common sense</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>Fflo- &gt;&gt; Ffau-</td>
<td>If forest fauna lacks forest flora, they will die or leave the system.</td>
<td>Common sense</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>Fflo-, Oflo- &gt;&gt; Ofau-</td>
<td>If open area fauna lacks any kind of flora, they will die or leave the system.</td>
<td>Common sense</td>
</tr>
<tr>
<td>Rule (R)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>1</td>
<td></td>
<td>Win+ &gt;&gt; Win-</td>
<td>Winter can switch into summer (seasons).</td>
<td>Common sense</td>
</tr>
<tr>
<td>2</td>
<td></td>
<td>Win- &gt;&gt; Win+</td>
<td>Summer can switch into winter.</td>
<td>Common sense</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>Win- &gt;&gt; Nsn-</td>
<td>The arrival of summer can remove the natural snow within the study area.</td>
<td>Observed</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>Win+ &gt;&gt; Nsn+</td>
<td>In winter, natural snow can appear.</td>
<td>Observed</td>
</tr>
<tr>
<td>5#</td>
<td></td>
<td>Win+ &gt;&gt; Nsn-</td>
<td>Climate change can cause late snow events or snowless winter</td>
<td>Observed</td>
</tr>
<tr>
<td>6#</td>
<td></td>
<td>Win- &gt;&gt; Wat-</td>
<td>Climate change can cause summer water shortage</td>
<td>Observed</td>
</tr>
<tr>
<td>7</td>
<td></td>
<td>Win-, For+, Bog+ &gt;&gt; Wat+</td>
<td>In summer, forest and bogs can conserve and renew water resources.</td>
<td>Academic knowledge&lt;sup&gt;1-3&lt;/sup&gt;</td>
</tr>
<tr>
<td>8</td>
<td></td>
<td>Win+, Nsn+ &gt;&gt; Wat+</td>
<td>In winter, natural snow can enhance surface water resources.</td>
<td>Academic knowledge&lt;sup&gt;4-5&lt;/sup&gt;</td>
</tr>
<tr>
<td>9</td>
<td></td>
<td>Wat-, Soh-, For- &gt;&gt; Tou-, Res-</td>
<td>Without fertile soils, forest and water, residents and tourists can leave the system.</td>
<td>Interview with stakeholders</td>
</tr>
<tr>
<td>10</td>
<td></td>
<td>Res+, Win-, For+ &gt;&gt; Tou+</td>
<td>In summer, residents can manage summer activities related to forest.</td>
<td>Interview with stakeholders</td>
</tr>
<tr>
<td>11*</td>
<td></td>
<td>Win+, Nsn+, Res+ &gt;&gt; Ski+</td>
<td>In winter, natural snow can make residents set up and operate ski stations.</td>
<td>Interview with stakeholders</td>
</tr>
<tr>
<td>12*</td>
<td></td>
<td>Res+, Wat+, Win+, Nsn- &gt;&gt; Asn+</td>
<td>In winter, ski stations can produce artificial snow, when the natural snow is absent.</td>
<td>Interview with stakeholders</td>
</tr>
<tr>
<td>13*</td>
<td></td>
<td>Ski+ &gt;&gt; Tou+</td>
<td>Ski stations can attract tourists.</td>
<td>Observed</td>
</tr>
</tbody>
</table>
14 For+, Res+ >> Tim+, Gap+
If forests are present, there can be timber production conducted by residents, resulting in forest gaps.

15 Win-, Res+, For+ >> Tou+
In summer, residents and forest can make summer activities possible.

16 Win-, Res+, Bog+ >> Tou+
In summer, residents and bogs can make summer activities possible.

17* Asn+, Win+, Res+ >> Ski+
In winter, residents can rely on artificial snow to maintain ski stations.

18* Ski+, Tou+ >> For-
Ski activities and tourists can impact forest in short or long terms.

19 For+, Tim- >> Gap-
Without logging, forest regeneration can close forest gaps.

20 Tou+ >> Bog-
Tourists can unfavourably affect bog ecosystem over the long term.

21 Tou+ >> Ffau-, Fflo-
Tourists can unfavourably affect forest fauna and flora over the long term.

22 Tou+ >> Ofau-, Oflo-
Tourists can unfavourably affect the open area fauna and flora over the long term.

23 Wat+, Soh+ >> Fflo+, Oflo+
Flora of forests and of open areas can both grow and prosper when fertile soils and water are present.

24 Wat+, Oflo+ >> Ofau+
Fauna of open areas can grow and prosper when vegetation and water are present.

25 Wat+, Gap+, Soh+ >> Oflo+
The presence of forest gaps and fertile soils can favour the arrival of open area fauna and flora.

26 Wat+, For+, Fflo+ >> Ffau+
Fauna of forest can grow and prosper when vegetation and water are all present.

27 Wat+, Soh+ >> Bog+
Bog can maintain as soon as fertile soils and water are present.

28* Asn+ >> Ffau-, Fflo-, Oflo-
Ski with artificial snow and tourists can unfavourably affect forest fauna and flora.

29 Nsn+ >> Oflo-
Natural snow can suppress flora growth and functioning and cause loss in flora when soil is frozen (of open areas only).

30 Bog+ >> Ffau+, Oflo+
The presence of bogs can favor the recovery or enrichment of forest fauna and open area flora.

31 Ffau+ >> Oflo-
Forest fauna can feed on open area flora.

32 Res+ >> Ffau-
Residents can hunt the forest fauna.

33 Ffau+ >> Fflo-
Forest fauna can feed on forest flora.

34 Tou+ >> Ffau-, Ofau-
Winter activities can unfavourably affect forest and open area fauna.

35 Gap+ >> Fflo-, Ffau-
Opening forest gaps can suppress the growth of forest fauna and flora.

36 Wat+, Fflo+, Soh+ >> For+
Favourable soil and water conditions and presence of forest flora can help the forest to recover over the long term.

Interview with stakeholders
Interview with stakeholders
Interview with stakeholders
Academic knowledge
Interview with stakeholders
Interview with stakeholders
Common sense
Common sense
Common sense
Common sense
Academic knowledge
Academic knowledge
Academic knowledge
Common sense
Interview with stakeholders
Common sense
Academic knowledge
Academic knowledge
Academic knowledge
Academic knowledge
Academic knowledge

47
<table>
<thead>
<tr>
<th>No.</th>
<th>Rule</th>
<th>Description</th>
<th>Academic knowledge</th>
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</thead>
<tbody>
<tr>
<td>37</td>
<td>Tou+ &gt;&gt; Soh-</td>
<td>Tourists can impact the soil fertility over the long term.</td>
<td>Academic knowledge</td>
</tr>
<tr>
<td>38*</td>
<td>Asn+ &gt;&gt; Soh-</td>
<td>Artificial snow can cause decline in soil fertility (organic horizon is degraded).</td>
<td>Academic knowledge</td>
</tr>
<tr>
<td></td>
<td>Wat+, Bog+, Oflo+, Ofau+ &gt;&gt; Soh+</td>
<td>Healthy bog with rich open area fauna and flora can favour soil fertility.</td>
<td>Academic knowledge</td>
</tr>
<tr>
<td>40</td>
<td>Wat+, For+, Fflo+, Ffau+ &gt;&gt; Soh+</td>
<td>If the forest is present and healthy, soil fertility can be guaranteed over the long term.</td>
<td>Academic knowledge</td>
</tr>
<tr>
<td>41</td>
<td>Wat- &gt;&gt; For-, Fflo-, Ffau-</td>
<td>Water stress can damage forest ecosystems.</td>
<td>Academic knowledge</td>
</tr>
<tr>
<td>42</td>
<td>Wat- &gt;&gt; Bog-, Oflo-, Ofau-</td>
<td>Water stress can damage bog and open air ecosystems.</td>
<td>Academic knowledge</td>
</tr>
</tbody>
</table>

Notes: ID with “#” refers to the rule that is deactivated in Scenarios 1, 3 and 5 and activated in Scenarios 2, 4 and 6 to mimic the impact of climate change on snow; ID with “*” refers to the rules that are deactivated in Scenarios 5 and 6 to mimic the situation of no ski activity.

<table>
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<tr>
<th>Class</th>
<th>Category</th>
<th>Ecosystem service</th>
<th>Subcategory</th>
<th>Accronym</th>
<th>Triggering conditions</th>
<th>No. of conditions</th>
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<td>Provisioning</td>
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<td></td>
<td></td>
<td></td>
<td>Wild plant / animal products</td>
<td>wild</td>
<td>Res+, Ffau+, Win- or Res+, Flo+, Win- or Res+, Ofau+, Win- or Res+, Oflo+, Win-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Food</td>
<td>Wild plant / animal products</td>
<td>wild</td>
<td>Res+, Ffau+, Win- or Res+, Flo+, Win- or Res+, Ofau+, Win- or Res+, Oflo+, Win-</td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td>Hunted products</td>
<td>hunted</td>
<td>Ffau+, Res+, Win-</td>
<td>1</td>
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<tr>
<td></td>
<td></td>
<td>Fiber</td>
<td>Timber</td>
<td>timber</td>
<td>For+, Tim+, Win-</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Fiber</td>
<td>Wood fuel</td>
<td>fuel</td>
<td>For+, Res+</td>
<td>1</td>
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<tr>
<td>Fresh water supply</td>
<td>Cultural</td>
<td>Aesthetic values</td>
<td>aesthetic</td>
<td>aesthetic</td>
<td>For+, Ski- or Bog+, Ski-</td>
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<tr>
<td></td>
<td>Recreation</td>
<td>Hunting</td>
<td>hunting</td>
<td>Win+</td>
<td>Tou+, Ffau+, Res+</td>
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<tr>
<td></td>
<td>Recreation</td>
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<td>hiking</td>
<td>For+, Tou+, Res+ or Bog+, Tou+, Res+</td>
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<td>Recreation</td>
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<td>bike</td>
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<tr>
<td></td>
<td>Recreation</td>
<td>Skiing</td>
<td>skiing</td>
<td>Tou+, Ski+, Res+, Win+</td>
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<tr>
<td></td>
<td>Ecology-related ES</td>
<td>Regulating</td>
<td>Climate regulation</td>
<td>Global</td>
<td>clim. global</td>
<td>3</td>
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<tr>
<td></td>
<td>Climate regulation</td>
<td>Regional and local</td>
<td>clim. local</td>
<td>For+, Wat+ or Bog+, Wat+ or Soh+, Wat+</td>
<td></td>
<td>2</td>
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<tr>
<td></td>
<td>Water cycling regulation</td>
<td>water cycle</td>
<td>Water purification and waste treatment</td>
<td>For+, Ffau+, Soh+ or Gap+, Oflo+, Soh+</td>
<td></td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>Erosion regulation</td>
<td>erosion</td>
<td>Water purification and waste treatment</td>
<td>For+, Ffau+, Soh+ or Gap+, Oflo+, Soh+</td>
<td></td>
<td>2</td>
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49
<table>
<thead>
<tr>
<th>Pollination</th>
<th>pollination</th>
<th>触发条件</th>
<th>强度</th>
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<tr>
<td>Natural hazard regulation</td>
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<td>Supporting</td>
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<td>Soil formation</td>
<td>soil form.</td>
<td>For+, Wat+, Soh+</td>
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<tr>
<td>Photosynthesis and primary</td>
<td>photosyn.</td>
<td>For+, Wat+, Soh+</td>
<td>2</td>
</tr>
<tr>
<td>production</td>
<td></td>
<td>Bog+, Wat+</td>
<td></td>
</tr>
<tr>
<td>Nutrient cycling</td>
<td>nutri. cyc.</td>
<td>For+, Wat+</td>
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<tr>
<td>Water cycling</td>
<td>water cyc.</td>
<td>For+, Wat+ or</td>
<td>2</td>
</tr>
<tr>
<td>Biodiversity</td>
<td></td>
<td>Bog+, Wat+</td>
<td></td>
</tr>
</tbody>
</table>

| Biodiversity                |             |                  |      |
| Specific diversity          |             |                  |      |
| Forest species              | forest div. | For+, Ffau+, Fflo+, Wat+ | 1 |
| Specific diversity          |             |                  |      |
| Open area species           | open div.   | Ofau+, Oflo+, Gap+, Wat+ | 1 |
| Aquatic species             | aquatic div.| Bog+, Wat+        | 1    |
| Soil species                | soil div.   | Soh+, Wat+        | 1    |

Note: In the column “Triggering conditions,” there was no priority between conditions in case of multiple conditions; see Table 1 for the explanations of the components.
### Table 4

<table>
<thead>
<tr>
<th>Scenario pairs</th>
<th>Mean total ES score</th>
<th>Indicators (i)</th>
<th>Mean economy-related ES score</th>
<th>Mean ecology-related ES score</th>
<th>Mean $p_v$</th>
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<tbody>
<tr>
<td></td>
<td>$M_{cC}$</td>
<td>$M_{cT}$</td>
<td>$M_{rC}$</td>
<td>$V_i$</td>
<td>$M_{cC}$</td>
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<tr>
<td>Control (C)</td>
<td>Treatment (T)</td>
<td>$M_{cC}$</td>
<td>$M_{cT}$</td>
<td>$M_{rC}$</td>
<td>$V_i$</td>
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<tr>
<td>S1 S2</td>
<td>11.7 ± 0.1a</td>
<td>11.7 ± 0.1a</td>
<td>0.0</td>
<td>0.0</td>
<td>2.0 ± 0.0a</td>
</tr>
<tr>
<td>S3 S4</td>
<td>11.7 ± 0.1a</td>
<td>13.0 ± 0.1b</td>
<td>1.3</td>
<td>11.2</td>
<td>4.1 ± 5.6 ±</td>
</tr>
<tr>
<td>S5 S6</td>
<td>13.0 ± 0.1a</td>
<td>14.1 ± 0.1b</td>
<td>1.1</td>
<td>8.3</td>
<td>4.3 ± 4.5 ±</td>
</tr>
<tr>
<td>S1+S3+S5 S2+S4+S6</td>
<td>13.3 ± 0.1a</td>
<td>13.2 ± 0.1a</td>
<td>-0.1</td>
<td>-0.7</td>
<td>2.0 ± 0.0a</td>
</tr>
<tr>
<td>S1 S2</td>
<td>8.9 ± 0.1a</td>
<td>4.0 ± 0.2b</td>
<td>-4.8</td>
<td>-54.5</td>
<td>1.6 ± 3.4 ±</td>
</tr>
<tr>
<td>S3 S4</td>
<td>4.0 ± 0.2a</td>
<td>5.8 ± 0.1b</td>
<td>1.7</td>
<td>43.3</td>
<td>0.0a</td>
</tr>
<tr>
<td>S5 S6</td>
<td>7.0 ± 0.2a</td>
<td>5.9 ± 0.1b</td>
<td>-1.1</td>
<td>-15.8</td>
<td>2.3 ± 3.8 ±</td>
</tr>
<tr>
<td>S1+S3+S5 S2+S4+S6</td>
<td>7.3 ± 0.2a</td>
<td>5.7 ± 0.1b</td>
<td>-1.6</td>
<td>-22.2</td>
<td>2.3 ± 3.4 ±</td>
</tr>
<tr>
<td>All states together</td>
<td>11.4 ± 0.1a</td>
<td>7.1 ± 0.3b</td>
<td>-4.3</td>
<td>-37.7</td>
<td>2.0 ± 0.0a</td>
</tr>
<tr>
<td>S1 S2</td>
<td>7.1 ± 0.3a</td>
<td>9.6 ± 0.1b</td>
<td>2.5</td>
<td>35.4</td>
<td>1.7 ± 3.8 ±</td>
</tr>
<tr>
<td>S3 S4</td>
<td>7.1 ± 0.3a</td>
<td>9.6 ± 0.1b</td>
<td>2.5</td>
<td>35.4</td>
<td>3.7 ± 4.6 ±</td>
</tr>
<tr>
<td>S5 S6</td>
<td>11.9 ± 0.1a</td>
<td>9.5 ± 0.2b</td>
<td>-2.4</td>
<td>-20</td>
<td>0.1a</td>
</tr>
<tr>
<td>S1+S3+S5 S2+S4+S6</td>
<td>12.4 ± 0.1a</td>
<td>9.4 ± 0.1b</td>
<td>-3</td>
<td>-24</td>
<td>4.0 ± 3.9 ± 0.0a</td>
</tr>
</tbody>
</table>

Only healthy states included

Only degraded states included

All states together

Note: for each of the four indicators $i$, values of $V_i = (M_{rT}/M_{rC})/M_{cC}$ are presented in % (see Eq. (3)); mean ± standard deviation were given for $M_{cC}$ and $M_{rT}$; different letters in each pair of columns ($M_{cC}$ and $M_{rT}$) represent the significance at $p<0.05$ level according to student test; letters are independent among rows and indicators. Grey zones highlight the cases where $M_{rT}$ and $M_{cC}$ were significantly different.
Figure 1

(a) State space with trajectory

(b) State space with separate SCC

(c) Graph with labels:
- \( C_l_A = 0; S_l_A = 4^{th} \)
- \( C_l_B = -1; S_l_B = 3^{rd} \)
- \( C_l_C = -3; S_l_C = 2^{nd} \)
- \( C_l_D = -7; S_l_D = 1^{st} \)

(d) Node structure with transitions:
- Node labels: Nsn, Ski, Asn, Win, Tou, Tim, Gap, Wat, Soh, Oflo, Ofau, For, Fflo, Ffau, Bog, Res
- State and SCC labels:
  - State: 0, 1, 3, 2, 4
  - SCC: F, F, F, H, G

Connections:
- R2 and C5
- R10 or R16
- R14
- R14

Figure 1
Figure 2
Figure 3
Figure 4
Figure 5