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

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13

- 14 Abstract
- 15

Monitoring the provision of multiple ecosystem services (ES) in social-ecological systems is a 16 major challenge. Most tools usually tackle the problem by modelling individual ES, but do 17 not perform a holistic analysis of a dynamic and integrated system. We developed a discrete-18 event model (DORIAN) and explored its potential for assessing biodiversity and 19 20 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 21 22 that define component interactions. We identified 22 economy- and ecology-related ES, depending on the presence/absence of components. We simulated six scenarios representing 23 24 different economic, environmental and climatic situations and calculated a score (the sum of 25 proxies for ES or biodiversity), corresponding to the level of biodiversity and that 26 multifunctionality. Results showed climate change reduced the system's multifunctionality and increased the number of degraded states, as well as the trajectories 27 from healthy to degraded states. With increasing levels of biodiversity, only ecology-related 28 ES were boosted at low biodiversity levels, while both high levels of ecology and economy-29 30 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 31 "biodiversity - multifunctionality" win-win strategy. 32

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Keywords: biodiversity, ecosystem service, social-ecological system, discrete-event model,
 qualitative modelling, mountain, economy.

36

37 **1 INTRODUCTION**

The concept of ecosystem services (ES), that bridge both biophysical and economic processes 38 in a social-ecological system, has been increasingly incorporated into management scenarios 39 related to ecosystem governance and landscape planning (Costanza et al., 1997; de Groot et 40 al., 2010; MEA, 2005; Lescourret et al., 2015). Within the current context of a changing 41 42 climate, researchers and decision-makers have struggled to find ideal models for predicting 43 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 44 et al., 2020). Although understanding social-ecological systems is critical for climate change-45 adapted ES management and biodiversity conservation initiatives, the inclusion of 46 47 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 48 Earth, 2014), the success of addressing this challenge lies in suitably quantifying the 49 50 contribution of biodiversity to multifunctional social-ecological systems.

51 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 52 quantify individual indicators within a bundle of ES. Usually, these models are either process-53 54 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 55 (2009) for a review of models of soil carbon sequestration and climate regulation). By 56 coupling several specialized ES models, multiple SE can be independently quantified and then 57 articulated to trace their spatiotemporal dynamics and trade-off patterns (Elkin et al., 2013; 58 59 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 60

treatment of a system that is multi-scale and contains tightly interdependent components. 61 62 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 63 pressure, e.g., management and disturbance (Fraterrigo and Rusak, 2008). Therefore, the 64 suitability of existing ES models, that are often developed or calibrated for certain situations 65 but are used in other situations, is questionable. Additionally, this modelling approach can 66 67 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 68 cooperation. As a consequence, most results on system multifunctionality from different 69 70 studies are rarely comparable, due not only to the use of contrasting models and ES proxies, 71 but also because of the diverse ranges of ES categories. If we are to determine and compare 72 management scenarios for different complex social-ecological systems, we need a robust 73 model that allows the exploration of a large number of ES using a generic methodology.

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75 Novel modelling approaches based on the concept of networks have emerged recently, that 76 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 77 (Crossman et al., 2010; Delphin et al., 2013; Zerbe et al., 2013), Bayesian belief networks 78 79 (Aguilera et al., 2011; Landuvt et al., 2013; McDonald-Madden et al., 2016), artificial neural networks (Larsen et al., 2012), social networks (Puga-Gonzalez and Sueur, 2017), 80 optimisation networks (Xiao et al., 2018), Boolean qualitative networks (Kristensen et al., 81 2019) and Petri nets (Di Giusto et al., 2019; Gaucherel et al., 2017; Gaucherel and 82 Pommereau, 2019). These modelling approaches share a similar concept in that individual 83 84 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 85

qualitative, differ in terms of network configuration and parametrization. For example, 86 Bayesian belief networks simulate whether one or multiple events will occur, based on a 87 probabilistic network composed of variables and conditional dependencies (Aguilera et al., 88 89 2011; Landuvt 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 90 the diagnosis of an event, into which probabilistic conditions and stochastic processes could 91 be incorporated if desired (Crossman et al., 2010). Several types of network-based model, 92 93 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). 94 95 But these models are classified as quantitative ES models based on the theory of Bayesian statistics, even though sometimes their diagnostic outputs are qualitative. 96

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98 Qualitative models, such as Boolean qualitative networks (Kristensen et al., 2019) and 99 discrete-event models (Di Giusto et al., 2019; Gaucherel et al., 2017, 2019), have recently 100 been developed to describe complex ecosystems. The conceptual approach behind such 101 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 102 bias. Instead, by setting Boolean rules or discrete rules accounting for the interactions among 103 104 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 105 106 interactions between components for a rule (Kristensen et al., 2019; Thomas and Kaufman, 107 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 108 109 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 110

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:

- 125 (i) how changes due to anthropogenic pressure (i.e., climate change) modify a126 system's provision of multiple ES?
- (ii) what is the role of biodiversity in the maintenance of a highly complex ES bundleand 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

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- 135 decision-making. Here, we hypothesize that increased biodiversity has a positive impact on
- 136 multiple ES provision and so promotes multifunctionality.

137

138 2 MATERIALS AND METHODS

139 **2.1** *The study site*

140 Chamrousse (45°06'33"N, 5°52'28"E) is a ski resort located 30 km from the city of Grenoble 141 (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. 142 Chamrousse has 422 inhabitants (data in 2017), but this population can increase to 15 000 143 during the winter ski season (http://chamrousse.com). The most important economic resource 144 145 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 146 147 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., 148 2009). From 2005 onwards, the snow pack at Chamrousse was under the critical threshold 149 150 (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-151 slopes open (Spandre et al., 2015), although there are concerns about the negative ecological 152 impact of artificial snow on mountain vegetation and soil quality (Rixen et al., 2004, 2003; 153 Roux-Fouillet et al., 2011). Also, the rise in mean annual temperature and increase in long, 154 155 dry periods has led to an increase of tree mortality, with diverse implications for forest functioning (Moser et al., 2011; Csilléry et al., 2017). 156

In the summer, there is a decrease in tourist activities and income from cable cars is only 0.16 M \in (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, 162 163 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 164 165 hosting a rich variety of species that may need protecting now or in the future. IUCN redlisted species include Aquila chrysaetos L. (Golden eagle) and Parnassius apollo L. (Apollo 166 butterfly). At high elevations, alpine ibexes (Capra ibex L.), chamois (Rupicapra rupicapra 167 L.), tetra lyre (Tetrao tetrix L.) and Arolla pines (Pinus cembra L.) are commonly found 168 169 (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 170 171 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 172 change the microhabitat and cause soil loss through erosion and shallow landslides. 173

174 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), 175 176 regulating services (such as the effect of forests on carbon sequestration and erosion control 177 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 178 179 at Chamrousse, here we consider cultural and provisioning services as economy-related ES 180 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 181 compromise between economy and ecology under different management scenarios and to 182 183 examine the role of biodiversity for multiple ES provision.

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185 2.2 DORIAN, a discrete-event model

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186 The discrete-event model that we developed, named *DORIAN* (Discrete-event model for 187 ecOsystem seRvIce AssessmeNt), models a system in a network composed of two sorts of 188 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).

195 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 196 noted as "-") (Tables 1 and S1). The status of a node depends on the status of the nodes to 197 198 which it is connected by an edge or edges which are triggered by specific semantics (Tables 2 199 and S1). The semantics that make the nodes pass from one status to another (Gaucherel et al., 200 2017; Gaucherel and Pommereau, 2019) can be either rules (R) or constraints (C). A rule is 201 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 202 203 always applied in priority (before all rules), as soon as their conditions of application are met 204 (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 205 constraint has a unique name composed by the abbreviation of category (R or C) and an 206 207 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 211 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 212 form new states. This approach allows either forming new states of the system or going back 213 214 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 215 216 simulated state has its unique assembly of nodes at ON status and mirrors a possible state that 217 the real system may reach. Once it comes to a state that contains no node at ON status or a 218 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 219 allows the distinguishing of some related states, i.e., strongly connected components (SCC, 220 Fig 1b-d). A SCC reflects an assembly of states in structural stability in which all states have 221 possible two-way circulations from one to the other (Fig. 1d). The whole simulation 222 223 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 224 225 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.

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234 2.3 Modeling a mountain social-ecological system

235 2.3.1 Components and processes

To synthesize knowledge about the mountain town of Chamrousse and to reduce the 236 computational cost, we defined the complex social-ecological system into a network 237 composed of 16 nodes corresponding to observed components and 51 edges (42 optional rules 238 239 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 240 compromise between the model's simulation cost and degree of resemblance to a real social-241 242 ecological system. Each node, either natural- or human-related, and each edge that is related 243 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 244 245 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 246 series of interviews were held (e.g., summer activities can attract tourists, i.e., R15 and R16; 247 248 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, 249 250 Chamrousse Ski Club, Chamrousse Ski freestyle, Ski lifts Chamrousse, French National 251 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 252 253 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 254 included in the academic literature, including ski station management, artificial snow 255 cannons, tourism, hunting and timber production. According to Fig. S1, Win (winter, 16 256 257 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 258 259 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 260

(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 264 each node's state (ON (+) versus OFF (-)) should be defined. At the same time, one can 265 manually comment some semantics, i.e., deciding if one or some of the rules/constraints 266 should be considered or not, to mimic different management possibilities. We elaborated six 267 simulation scenarios (S) that differed in initial states or rules conditioning to mimic different 268 disturbance and/or management policies. The six scenarios could be divided into two groups 269 270 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+ 271 (winter) >> Nsn- (natural snow)" and R6 "Win- >> Wat- (water)" were considered (in S2, S4 272 273 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 274 275 change (Dayon et al., 2018). Alternatively, the six scenarios could be divided into three pairs 276 (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 277 278 scenarios (S3–S6), had the same initial states to mimic situations under human impact (Table 279 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), 280 Tou (tourists), Ski (ski activities) and Asn (artificial snow), could appear later and had possible 281 282 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 283 284 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 285

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).

289

290 2.3.2 Ecosystem services

The presence/absence of certain nodes and occurrence of certain interactions among nodes 291 292 can represent the biophysical or socio-economic processes or interactions, where ES can be 293 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 294 295 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 296 in Table S3 is slightly different from that in the MEA (2005)'s report, as we adapted ES to the 297 298 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 299 300 conditions > 0 were in our case study (Table 3), and not when ES number of conditions = 0301 (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, 7 302 regulating and 4 supporting ES (Table 3). We classified provisioning and cultural services as 303 economy-related ES (11 in all) and regulating and supporting ES as ecology-related (11 in 304 all). Ecology-related ES refer to the naturally biophysical process-dominated ES that are less 305 directly used for economy, while economy-related ES refer to the human process-dominated 306 307 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 308 309 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).

319

320 **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 confluential 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):

334
$$CI_k = -\sum_{i=1}^{Q-1} (CI_i + 1) \Delta_{i \to k}$$
 (Eq. 1)

335 where, CI_k is the confluential 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; $\Delta_{i \to k}$ is a binary variable determining if 336 337 there is an direct arrow link from i to k (1: presence; 0: absence). Each simulation has only 338 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 339 (otherwise they would have formed a bigger SCC), the solution vector is unique for a given 340 341 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 342 (Qth, Q-1th, ..., 2nd, 1st) corresponds to the descending order of CI (Fig. 1c). All the states in 343 the same SCC have the same CI and sequence order as those for their SCC. 344

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 economyrelated 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:

350
$$p_e = \frac{\text{score of ecology-related ES}}{\text{score of ecology-related ES} + \text{score of economy-related ES}}$$
 Eq. (2)

351 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 352 under external pressure (e.g., climate change), is susceptible or unable to provide ES. Here, 353 354 we examined the vulnerability of Chamrousse to climate change (no snowpack and very dry 355 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 356 357 climate change), relative to the value in the control scenario SC ($M_{i,C}$, referring to no climate 358 change) can be calculated as:

359
$$V_i = \frac{M_{i,T} - M_{i,C}}{M_{i,C}}$$
 Eq. (3)

The examined indicators (*i*) included total ES score, ecology-related ES score, economyrelated 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:

370
$$W_j = \frac{N_{j,T} - N_{j,C}}{N_{j,C}}$$
 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.

379 3. RESULTS

380 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 387 terms of node composition could appear in different scenarios, we identified 1804 different 388 states and 27 SCCs appeared in all the simulations. The number of states also greatly differed 389 among SCC, ranging from two (SCC T) to 484 (SCC K, L and M) (Fig. 2g). SCC were highly 390 391 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 392 393 generalists: among the 1804 states, 258 were found in only a single scenario, 1118 in two 394 scenarios, 36 in three scenarios and 402 in four scenarios. None of the states was present in all the six scenarios. 395

396 Total ES were positively correlated with the confluential index, CI (Fig. S2), upon which was 397 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 398 trajectories (Fig. 2). The natural scenarios (S1 and S2) had the simplest trajectory with either a 399 400 simple one-to-one connection (Fig. 2a) or a triangle connection (Fig. 2b), while the humanrelated scenarios (S3–S6) had more sophisticated trajectories (Figs. 2c-2f). Except for the two 401 402 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 403

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).

409

410 **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).

416 By juxtaposing the presence and absence of the components (nodes), biodiversity and ES 417 proxies, we could obtain a full picture of the Chamrousse social-ecological system and 418 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 419 ES proxies were strikingly different depending on seasons and ES categories (Fig. 3, part I). 420 421 Among the top 12 most frequently present indicators whose presence was higher than 50% 422 (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 423 presence was less than 30% (i.e., from wild to hunting), most were provisioning (four) or 424 425 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). 426

427 Regarding the state spectrum with components, ecosystem components differed greatly in 428 their ability to affect biodiversity and ES bundle delivery (Fig. 3, part III and Fig. S4, part

IV). Residents (Res), topsoil (Soh), and forests (For) were the most essential components of 429 430 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 431 432 (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, 433 part III). Timber (*Tim*) was occasionally present, playing a marginal role in enriching ES (Fig. 434 435 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 436 importance in influencing the status of several nodes, such as artificial snow (Asn), water 437 438 (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). 439

440

441 **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 442 443 of ecology-related ES and V_i of p_e were usually negative, signifying that ecology-related ES 444 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-445 related ES were increasing when climate change was occurring. Contrasted tendencies 446 between ecology- and economy-related ES rendered a generally negative sign of V_i for total 447 ES when pooling all the situations, but diverse signs of V_i for total ES at the situation-level. 448 Among the three scenario pairs corresponding to three situations (natural for S1 - S2, realistic 449 450 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 451 452 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 453

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 459 trajectories either increased or remained unchanged (Table S4). Among the three indicators in 460 Table S4, W_i of degraded states and W_i of healthy states increased the most and least, 461 respectively. Among the three situations, the realistic situation (S3 - S4 pair) achieved a 462 better compromise than that when skiing was stopped (S5 - S6 pair), as it had a much smaller 463 W_i of degraded states and trajectories. In climate change scenarios, a number of states with 464 water stress (Wat-) in both summer (Win-) and winter (Win+) were observed, especially in 465 466 degraded states (Table S5), although Wat- was only triggered in the summer (via R6, Table 2). 467

468

469 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) 470 had comparable economy-related ES scores (Fig. 4b), but only half of the biodiversity (Fig. 471 4d) and ecology-related ES scores (Fig. 4c), resulting in much lower total ES scores (Fig. 4a). 472 Not surprisingly, the natural scenarios (S1 and S2) had the highest biodiversity (mean: 2.5 for 473 S1 and 1.2 for S2, Fig. 4d), the highest ecology-related ES score (9.4 for S1 and 5.4 for S2, 474 475 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 476 477 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 478

479 scenarios, but in S4 (9.6) for climate change scenarios (Fig. 4a). In S4, ecology-related ES 480 declined less due to climate change than that in S6 (Fig. 4c) and the economy-related ES even 481 slightly rose compared to its control scenario (S3) (Fig. 4b). When the ES were presented 482 according to the four categories defined in MEA (2005), regulating and supporting ES (Fig. 483 S5e and S5f) were both more susceptible to climate change than provisioning and cultural ES 484 (Fig. S5c and S5d), thus supporting our classification of economy/ecology-related ES.

485 When pooling all the scenarios together, there were positive synergetic patterns between the 486 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 487 together (i.e., only in climate change scenarios or only in no climate change scenarios), 488 indicating a limited effect of climate change on such synergetic patterns (Fig. S6). The highest 489 increase in total and ecology-related ES scores occurred when the biodiversity score shifted 490 from 0 to 1 (Fig. 5a and 5c). When the biodiversity score continued to increase from 1 to 4, 491 492 the increment of total and ecology-related ES scores decreased and reached a stable level 493 (Figs. 5a and 5c). The positive effect of biodiversity on economy-related ES score was 494 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 495 (Fig. 5b). A more pronounced increase in the economy-related ES score was only found with 496 497 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 498 economy-related ES (Fig. 5b). 499

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 2nd 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.

508 4. DISCUSSION

509 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 510 511 numerous ES in a complex bundle. In particular, we demonstrated the negative effect of 512 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 513 514 multifunctionality through several mechanisms. For example, because of drier summers and a 515 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 516 517 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 518 on ES provision (Deléglise et al., 2015; Hartl-Meier et al., 2014). Our model also showed that 519 520 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 521 522 of degraded states (Figs. 3 and S3; Table S5). Data on this legacy of summer water stress on 523 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 524 525 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). 526

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 533 healthy states in the spectra, it significantly increased the number of degraded states, and so 534 produced more pathways through which a healthy state could shift to a degraded state (Table 535 536 4; Fig. S3). The important lesson to learn from this result is that even though a system can be healthy in terms of multifuctionality, it could be more prone to degradation in the context of 537 climate change. This result highlights the necessity to consider a system as highly dynamic 538 where its functions and ES have many possible trajectories: a simple diachronic approach 539 540 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.

547

548 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 549 explored in mountain regions (Schirpke et al., 2013). Compared to studies that usually focus 550 551 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; 552 Lafond et al., 2017; Seidl et al., 2019), a more multidisciplinary approach embracing a 553 multitude of disturbance sources (e.g., management policy and climate change) and a wider 554 range of ES is much needed (Schirpke et al., 2013; Brunner et al., 2017). To tackle such a 555 556 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 557

multifunctionality. We found that the three modelled situations responded very differently to 558 climate change, validating our first hypothesis (Tables 4 and S4). In the 'natural' situation 559 (absence of human beings), healthy states had a low vulnerability to climate change, but this 560 561 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 562 human-related winter activities) was less vulnerable to climate change. Although the ecology 563 -elated ES score did not significantly drop when climate change occurred, the economy-564 related ES score was boosted (Table 4). This phenomenon occurs because human-related 565 skiing activities (Ski) and artificial snow (Asn) were both active in the realistic scenarios. 566 Accordingly, the number of healthy states that were increased was effective against the drop 567 of ecology-related ES scores. In terms of economy, the artificial snow production (Asn+)568 ensures that tourists (Tou+) come to the town, which in turn activates the skiing (Ski) and 569 570 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 571 572 activities were much lower than in the more realistic situation (with human-related winter 573 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 574 575 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 576 without passing through any intermediary states (e.g., SCC F \rightarrow J in S3 or Q \rightarrow T in S5; Fig. 577 2). Such a phenomenon could occur if certain key components (e.g. forest and topsoil) 578 579 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 580 581 forest or agriculture on steep slopes causing erosion and topsoil loss), that were harmful to fundamental components, could immediately make the system collapse. 582

583

584 **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 585 586 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 587 degradation, can lead to serious ecological dysfunction and social-economic problems 588 (Cardinale et al., 2012; Díaz et al., 2006; Hooper et al., 2012). However, while a positive 589 590 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 591 592 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., 593 2007; Loreau, 2001; van der Plas et al., 2016). But most of these studies examined 594 595 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 596 597 minimal effect on economy-related ES (Figs. 5 and S6). At the same time, biodiversity was 598 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, 599 600 such a phenomenon was absent for economy-related ES (Fig. 5b). These results are due to the 601 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 602 603 not only most of the supporting and regulating services, but also other elements that depend 604 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 605 606 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 607

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 611 612 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 613 importance of integrating a "biodiversity – multifunctionality" win-win strategy against both 614 615 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, 616 especially economy-related ES, to the equally high level of importance given to biodiversity 617 (Xiao et al., 2018, 2019). One of the major reasons is due to the lack of information on the 618 provisional and feedback links between biodiversity and their interactions, and ecosystem 619 620 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 621 622 activities), and that a holistic approach is necessary when studying a social-ecological system. 623 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 624 or to create a new, parallel but complementary paradigm. This paradigm would concern 625 social-economic conservation, that tackles the vulnerability of social-economic aspects of a 626 system. 627

628

629 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 639 640 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 641 642 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 643 fully all the states of a system, as well as the pathways or trajectories among states, important 644 645 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 646 647 avoided characterizing ES in one or several snapshot-like states of a system as is usually 648 performed by many quantitative ES models e.g., Schroter (2005). DORIAN can also investigate the legacy effect of a process as it occurs, as well as the potential consequences 649 over time. These legacy effects (e.g. the influence of summer water stress on winter ES in our 650 case study), are usually ignored in quantitative ES models due to limited data. DORIAN 651 therefore provides a feasible and efficient way to include ES when tackling the question of 652 multifunctionality of a system. 653

654

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 658 discrete-event models mimic a simplified reality, as in any model, but they differ in their 659 focus of description of a system. A quantitative ES model, which can be either probabilistic 660 661 (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 662 system under one or several states. A discrete-event model however, makes the inherent 663 processes as simple as possible (e.g., by using binary values to represent presence and 664 absence), but gives more focus on the extensive interactions between components within or 665 across states. Therefore, discrete-event models can be used to model highly complex social-666 ecological systems (e.g., large interaction networks with hundreds of components and 667 rules/constraints intervening at multiple scales) and to focus on changes over the long term. In 668 our case study, 22 services from all four ES categories (MA, 2005) were included in DORIAN, 669 670 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 671 672 and can be standardized and transposed to other case studies, enabling valuable comparisons 673 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 674 675 the latter could be calibrated and validated in all or several specific states. In the current 676 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, 677 provided that multisectorial decision-makers could provide such information on the priority of 678 ES. 679

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 683 to reach a compromise between our research question and the available computational 684 capacity. Processes may have different confidence levels according to the reliability of 685 686 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 687 parametrize the processes was robust and testing the effect of confidence level of rules was 688 689 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 690 semantics mimicking the uncertainty process. 691

692 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 693 can be short- or long-term, or even both, e.g., destruction of a forest. In our case study, we did 694 not differentiate between time scales, therefore, direct comparisons between stable states are 695 difficult. However, our objective was to identify the potential degradation of states and system 696 697 vulnerability in diverse situations. To better integrate the temporal scale into DORIAN, we 698 suggest characterizing connectivity among states or SCC, which can partially reflect the concept of time by indicating the orders of occurrence for processes. 699

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.

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707 **5. CONCLUSION**

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Using a discrete-event model, DORIAN, we examined modifications in the provision and 708 trajectories of ES in three diverse situations in a mountain social-ecological system subjected 709 to climate change (dry summers and warm winters with reduced snowpack). The degree of 710 711 human impact differed in each situation, and scores (total number of biodiversity and ES 712 proxies) were calculated for each scenario simulated. Climate change reduced the system's 713 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, 714 715 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 716 directly jump to a degraded state with low multifunctionality without passing through any 717 intermediary states. Such a phenomenon could occur if certain key components become 718 719 absent within the system. With increasing levels of biodiversity, only ecology-related ES were 720 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 721 722 conserving high biodiversity in a social-ecological system, for an optimal "biodiversity -723 multifunctionality" win-win strategy. The holistic modelling approach with DORIAN is methodologically generic and provides a novel and alternative solution to assess the 724 multifunctionality of social-ecological systems without the necessity to quantify any ES. 725

726

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1037 **Tables**

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

- 1040 Table 2 Rules (R) and Constraints (C) for the case study of Chamrousse
- 1041 Table 3 Biodiversity and ecosystem service list and their triggering conditions

1042 Table 4 Comparison of ecosystem service proxies between control (no climate change) and

- 1043 treatment (climate change) scenarios
- 1044

1045 Figures

Figure 1 An example of a state space (a), strongly connected component (SCC) space (b), 1046 1047 calculation of confluential 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 1048 confluential index and sequence order of the SCC x, respectively. In (d): purple dots represent 1049 1050 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 1051 1052 4) from Scenario 3. The curves on the top of spectra represent the evolution between states, 1053 and arrows indicate their directions. The text in italics and red colour beside each curve 1054 represents the rule/constraint or rules/constraints conducting the evolution between two states, 1055 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-) 1056 and C5 (Win+, Ski- >> Tou-). States 0, 1 and 3 belong to the same SCC (i.e., SCC F), as they 1057 1058 can shift between each other. States 2 and 4 belong to the other SCC, as they are irreversible to the states in SCC F. 1059

Figure 2 Evolution of itineraries of strongly connected components (SCC) per scenario. 1060 Subplots from (a) to (f): each SCC has a unique label (in capital or small Latin letters); 1061 identical SCC in different scenarios share the same label (e.g., SCC P in scenarios 4 and 6); 1062 the arrows with arrow head in the middle represent the evolution of itineraries from one SCC 1063 1064 to another. Subplot (g) summarizes the number of states contained in each SCC. The filled 1065 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 1066 negative direction along the y-axis is the sequence order (SO) of SCC reflecting SCC 1067 1068 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 1076 signify the absence of the states in the present scenario; values on the right are percentages of 1077 a proxy or a component appearing in all the states of the scenario 4 and are ranged in a 1078 descending order from top to bottom. Regarding the evolution of the total ES score in (II), 1079 thick and thin sections correspond to the metric of the present scenario and of all the six 1080 scenarios, respectively; the vertical dashed blue line of the state ID 948 at P₅₀ = 10 splits the 1081 pools of healthy and degraded states; translucent grey arcs represent degraded evolution 1082 trajectories between two states (only paths crossing the line at state ID 948 are shown).

1083 Figure 4 Variations of biodiversity and ecosystem service (ES) scores (total ES, economyand ecology-related ES) per scenario. For each boxplot, the thick horizontal line and point 1084 "X" inside the box represent the median and mean of data points, respectively. Low and top 1085 edges of the box correspond to the 25th and 75th percentile data points, respectively. Low and 1086 top horizontal lines correspond to the 10th and 90th percentile data points, respectively. Point 1087 1088 clouds over boxplots allow a visual check of the quantity of states, each of which corresponds 1089 to one point. In (a), the total number of states per scenario is shown on the top of each boxplot. 1090

Figure 5 Variations of ecosystem service (ES) scores (total ES, economy- and ecology-related 1091 1092 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 1093 edges of the box correspond to the 25th and 75th percentile data points, respectively. Lower 1094 and top horizontal lines correspond to the 10th and 90th percentile data points, respectively. 1095 Point clouds over boxplots allow a visual check of the quantity of states, each of which 1096 1097 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. 1098

1099

1100 Supplementary tables and figures

- 1101 Table S1 Terminology and acronyms related to the model
- 1102 Table S2. List of questions prepared for town hall employees and private stakeholders at
- 1103 Chamrousse
- 1104 Table S3 Ecosystem services (ES) included in the case study based on the full ES list of MEA(2005)
- 1106 Table S4 Comparison of state conditions between control and treatment scenarios
- 1107 Table S5 Percentage of states with water stress (%) according to different scenarios (S1 S6),
- 1108 health condition (healthy, degraded and all together) and season (summer (*Win-*) and winter
- 1109 (Win+))
- Figure S1 Relationship between semantics (rules and constraints) and nodes for the case ofChamrousse

Figure S2 Scatter plot between total ecosystem service (ES) score and confluential index ofall the strongly connected components (SCC)

1114 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 1115 1116 Chamrousse. Each subplot presenting one scenario consists of two parts. The lower part 1117 shows the spectrum of states with the status of components (red: ON; grey: OFF). The order 1118 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 1119 1120 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 1121 spectrum indicate the percentage of the nodes for the present scenario. The upper part shows 1122 1123 the evolution of total ES score, where thick and thin sections correspond to the metric of the 1124 present scenario and of all the six scenarios, respectively. The vertical dashed blue line of the 1125 state ID 948 at $P_{50} = 10$ splits the pools of healthy and degraded states. Translucent grey arcs 1126 represent degraded evolution trajectories between two states (only paths crossing the line at 1127 state ID 948 are shown)

1128 Figure S4 Analysis of state spectra for components and ecosystem service (ES) of all the 1129 strongly connected components (SCC), as well as the states that they contain, of the social-1130 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 – 1131 1132 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 1133 1134 and IV, every thin vertical slice corresponds to a state (4202 states in all for 27 SCC); the colours represent the presence (red) and absence (grey) of the component in each state; 1135 numbers on the right are percentage of a proxy or a component appearing in all the states and 1136 1137 are ranging in a descending order from top to bottom. In II, numbers on the top of each bar 1138 refer to total ES and the colours in the bar represents the proportion of ecology-related ES 1139 (light pink) against economy-related ES (deep pink). In III, only degraded trajectories (i.e., a 1140 path linking a healthy state and a degraded state) are shown. In IV, numbers below the 1141 spectrum indicate the numbers of states in SCC

1142 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 1143 and point "X" inside the box represent the median and mean of data points, respectively. Low 1144 and top edges of the box correspond to the 25th and 75th percentile data points, respectively. 1145 Low and top horizontal lines correspond to the 10th and 90th percentile data points, 1146 respectively. Point clouds over boxplots allow a visual check of the quantity of states, each of 1147 which corresponds to one point. In (b), the total number of states per scenario is shown on the 1148 1149 top of each boxplot

Figure S6 Variations of ecosystem service (ES) scores (total ES, economy- and ecologyrelated 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 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. S1, S3 and S5 correspond to control scenarios with no climate change effect, while S2, S4 and S6 correspond to treatment scenarios with climate change effect

- 1160 Figure S7 Principle component analysis (PCA) of biodiversity and ecosystem service (ES)
- 1161 variables at both state and strongly connected component (SCC) levels. Hull convex polygons
- 1162 represent the ranges of scenarios (S1 S6). Letters represent the names of SCC

Table 1

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

¹¹⁶⁴ Note : + and - means the node is ON and OFF at initial state prior to simulation, respectively.

Table 2

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

14	For+, Res+ >> Tim+, Gap+	If forests are present, there can be timber production conducted by residents, resulting in forest gaps.	Interview with stakeholders		
15	Win-, Res+, For+ >> Tou+	In summer, residents and forest can make summer activities possible.	Interview with stakeholders		
16	Win-, Res+, Bog+ >> Tou+	In summer, residents and bogs can make summer activities possible.	Interview with stakeholders		
17*	Asn+, Win+, Res+ >> Ski+	In winter, residents can rely on artificial snow to maintain ski stations.	Interview with stakeholders		
18*	Ski+, Tou+ >> For-	Ski activities and tourists can impact forest in short or long terms.	Academic knowledge ⁶		
19	For+, Tim->> Gap-	Without logging, forest regeneration can close forest gaps.	Academic knowledge7-8		
20	Tou + >> Bog-	Tourists can unfavourably affect bog ecosystem over the long term.	Interview with stakeholders		
21	Tou+ >> Ffau-, Fflo-	Tourists can unfavourably affect forest fauna and flora over the long term.	Interview with stakeholders		
22	Tou+ >> Ofau-, Oflo-	Tourists can unfavourably affect the open area fauna and flora over the long term.	Interview with stakeholders		
23	Wat+, Soh+>> Fflo+, Oflo+	Flora of forests and of open areas can both grow and prosper when fertile soils and water are present.	Common sense		
24	Wat+, Oflo+ >> Ofau+	Fauna of open areas can grow and prosper when vegetation and water are present.	Common sense		
25	Wat+, Gap+, Soh+ >> Oflo+	The presence of forest gaps and fertile soils can favour the arrival of open area fauna and flora.	Common sense		
26	Wat+, For+, Fflo+ >> Ffau+	Fauna of forest can grow and prosper when vegetation and water are all present.	Common sense		
27	Wat+, Soh+ >> Bog+	Bog can maintain as soon as fertile soils and water are present.	Common sense		
28*	Asn+ >> Ffau-, Fflo-, Oflo-	Ski with artificial snow and tourists can unfavourably affect forest fauna and flora.	Academic knowledge		
29	Nsn+>> Oflo-	Natural snow can suppress flora growth and functioning and cause loss in flora when soil is frozen (of open areas only).	Academic knowledge ¹⁰⁻¹²		
30	Bog+ >> Ffau+, Oflo+	The presence of bogs can favor the recovery or enrichment of forest fauna and open area flora.	Academic knowledge ¹³⁻¹⁴		
31	Ffau+ >> Oflo-	Forest fauna can feed on open area flora.	Common sense		
32	Res+ >> Ffau-	Residents can hunt the forest fauna.	Interview with stakeholders		
33	Ffau+ >> Fflo-	Forest fauna can feed on forest flora.	Common sense		
34	Tou+ >> Ffau-, Ofau-	Winter activities can unfavourably affect forest and open area fauna.	Academic knowledge ^{6, 15-17}		
35	Gap+>> Fflo-, Ffau-	Opening forest gaps can suppress the growth of forest fauna and flora.	Academic knowledge ¹⁸⁻¹⁹		
36	Favourable soil and water conditions and presence of forest flora can help the forest		Academic knowledge ²⁰		

37	Tou+ >> Soh-	Tourists can impact the soil fertility over the long term.	Academic knowledge ⁶
38*	Asn + >> Soh-	Artificial snow can cause decline in soil fertility (organic horizon is degraded).	Academic knowledge9
39	Wat+, Bog+, Oflo+, Ofau+ >> Soh+	Healthy bog with rich open area fauna and flora can favour soil fertility.	Academic knowledge ²¹⁻²²
40	Wat+, For+, Fflo+, Ffau+ >> Soh+	If the forest is present and healthy, soil fertility can be guaranteed over the long term.	Academic knowledge ²³⁻²⁴
41	Wat- >> For-, Fflo-, Ffau-	Water stress can damage forest ecosystems.	Academic knowledge ²⁵⁻²⁶
42	Wat->> Bog-, Oflo-, Ofau-	Water stress can damage bog and open air ecosystems.	Academic knowledge ²⁷⁻²⁸

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. Numbers in the column "Source of information" refer to the reference sources supporting the argument: 1 – Bragg (2015); 2 – Woo and Valverde (1981); 3 – Sun et al., (2016); 4 – Huss et al., (2017); 5 – Kormos et al., (2014); 6 – Rixen and Rolando (2013); 7 – Bugmann (2001); 8 – Franklin et al. (2002); 9 – Rixen et al., (2003); 10 – Ruess et al., (2003); 11 – Mao et al., (2013); 12 – Drescher and Thomas (2013); 13 – Littlewood et al., (2010); 14 – Minayeva et al., (2017); 15 – Negro et al., (2009); 16 – Andereck (1995); 17 – Gössling (2002); 18 – Spitzer et al., (1999); 19 – Pagès and Michalet (2006); 20 – Diwold et al., (2010); 21 – Moore (1989); 22 – Wallén (1986); 23 – Aber et al., (1990); 24 – Sagot et al., (1999); 25 – Moser et al., (2011); 26 – Rouault et al., (2006); 27 – Bragazza (2008); 28 – Breeuwer et al., (2009).

Table 3

Class	Category	Ecosystem service	Subcategory	Accronym	Triggering conditions	No. of conditions
Economy-	Provisioning	Food	Livestock	livestock	Oflo+,Res+,Win-	1
related ES		Food	Wild plant / animal products	wild	<i>Res+,Ffau+,Win-</i> or	4
			•		<i>Res</i> +, <i>Flo</i> +, <i>Win</i> - or	
					Res+, Ofau+, Win- or	
					Res+, Oflo+, Win-	
		Food	Hunted products	hunted	Ffau+,Res+,Win-	1
		Fiber	Timber	timber	For+,Tim+,Win-	1
		Fiber	Wood fuel	fuel	For+,Res+	1
		Fresh water supply		fresh water	<i>Wat</i> +or	2
					Nsn+	
	Cultural	Aesthetic values		aesthetic	<i>For+,Ski-</i> or	2
					Bog+,Ski-	
		Recreation	Hunting	hunting	Win,Tou+,Ffau+,Res+	1
		Recreation	Hiking	hiking	<i>For+,Tou+,Res+</i> or	2
					Bog+,Tou+,Res+	
		Recreation	Mountain bike	bike	For+, Win-, Tou+, Res+	1
		Recreation	Skiing	skiing	Tou+,Ski+,Res+,Win+	1
Ecology-	Regulating	Climate regulation	Global	clim. global	<i>For</i> +, <i>Wat</i> + or	3
related ES					<i>Bog+,Wat+</i> or	
					Soh+, Wat+	
		Climate regulation	Regional and local	clim. local	<i>For</i> +, <i>Wat</i> + or	2
					Bog+,Wat+	
		Water cycling regulation		water cycle	<i>For</i> +, <i>Soh</i> +, <i>Bog</i> +, <i>Wat</i> +, <i>Nsn</i> +, <i>Win</i> + or	2
					For+,Soh+,Bog+,Wat+,Win-	
		Erosion regulation		erosion	<i>For</i> +, <i>Ffau</i> +, <i>Soh</i> + or	2
					Gap+, Oflo+, Soh+	
		Water purification and waste treatment		waste	<i>For+,Fflo+,Wat+,Soh+</i> or	2
					Bog+, Oflo+, Wat+	

		Pollination		pollination	<i>Fflo</i> + or	2
					Oflo+	
		Natural hazard regulation		hazard	For+,Gap-	1
	Supporting	Soil formation		soil form.	For+,Wat+,Soh+	1
		Photosynthesis and primary production		photosyn.	<i>For</i> +, <i>Wat</i> +, <i>Soh</i> + or	2
					Bog+,Wat+	
		Nutrient cycling Water cycling		nutri. cyc.	For+,Wat+	1
				water cyc.	<i>For</i> +, <i>Wat</i> + or	2
					Bog+,Wat+	
Biodiversity	Biodiversity	Specific diversity	Forest species	forest div.	For+,Ffau+,Fflo+,Wat+	1
		Specific diversity	Open area species	open div.	Ofau+, Oflo+, Gap+, Wat+	1
		Specific diversity	Aquatic species	aquatic div.	Bog+,Wat+	1
		Specific diversity	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																	
Soonar	rio pairs	_							Indica	tors (i)								
Scenar	no pans	Mean total ES score		Mean	Mean economy-related ES score			Mean ecology-related ES score				Mean p_e						
Control (C)	Treatment (T)	$M_{i,C}$	$M_{i,T}$	$M_{i,T}$ - $M_{i,C}$	V_i	$M_{i,C}$	$M_{i,T}$	$M_{i,T}$ - $M_{i,C}$	V_i	$M_{i,i}$.C	$M_{i,T}$	$M_{i,T}$ - $M_{i,C}$	V_i	$M_{i,C}$	$M_{i,T}$	$M_{i,T}$ - $M_{i,C}$	V_i
Only healthy states included																		
	~-					2.0 ±	• • • • •				.7 ±							
S1	S2	$11.7 \pm 0.1a$	$11.7 \pm 0.1a$	0.0	0.0	0.0a 2.0 ±	$2.0 \pm 0.0a$	0.0	0.0		0.1a 9.7 ±	9.7 ± 0.1a 8.8 ±	0.0	0.0	$82.7 \pm 0.2a$	82.7 ± 0.2a	0.0	0.0
S 3	S 4	11.7 ± 0.1a	$13.0 \pm 0.1 b$	1.3	11.2	2.0 ± 0.0a	$4.2 \pm 0.1a$	2.2	110.6		0.1a	0.0 ± 0.1b	-0.9	-9.4	$82.7 \pm 0.2a$	$68.4 \pm 0.4b$	- 14.4	-17.4
50	5.			110		4.1 ±	5.6 ±	2.2	11010		.0 ±	8.5 ±	017	211	0217 _ 0124	0011 = 0110		1/11
S5	S 6	$13.0 \pm 0.1a$	$14.1\pm0.1b$	1.1	8.3	0.1a	0.1b	1.5	38	(0.0a	0.1b	-0.5	-5.1	$69.9\pm0.3a$	$60.7\pm0.7b$	-9.2	-13.2
											â							
S1+S3+S5	S2+S4+S6	$13.3 \pm 0.1_{2}$	13.2 ± 0.1a	-0.1	-0.7	4.3 ± 0.1a	4.5 ± 0.1b	0.2	4.5		0.0 ± 0.0a	8.7 ± 0.0b	-0.3	-3.1	69.0 ± 0.32	$67.0 \pm 0.4 b$	-2	-2.9
51-55-55	32+34+30	$15.5 \pm 0.1a$	15.2 ± 0.1 a	-0.1	-0.7		degraded stat				0.0a	0.00	-0.5	-5.1	$09.0 \pm 0.3a$	07.0 ± 0.40	-2	-2.9
						Only	uegruueu siui	es inciuu	ieu									
						$2.0 \pm$				6	.9 ±	2.5 ±						
S1	S2	$8.9 \pm 0.1a$	$4.0\pm0.2b$	-4.8	-54.5	0.0a	$1.6\pm0.0a$	-0.4	-21		0.1a	0.2b	-4.4	-64.2	$77.4\pm0.4a$	$55.4 \pm 1.8 b$	-22	-28.5
62	6.4	10.00	50 0 11	1.7	12.2	1.6 ±	3.4 ±	1.0	110.0		.5 ±	24 01	0.0	1 7	55 4 1 0		-	20.0
S3	S4	$4.0 \pm 0.2a$	$5.8 \pm 0.1 b$	1.7	43.3	0.0a 2.3 ±	0.1b 3.8 ±	1.8	113.2		0.2a •.7 ±	2.4 ± 0.1a 2.1 ±	0.0	-1.7	$55.4 \pm 1.8a$	$38.3\pm0.8b$	17.1	-30.8
S5	S 6	$7.0 \pm 0.2a$	$5.9 \pm 0.1b$	-1.1	-15.8	0.1a	0.1b	1.5	67.7		0.2a	0.1b	-2.6	-56.1	$61.2 \pm 1.5a$	$33.0\pm0.9b$	28.1	-46
G1 G2 G5						2.3 ±	3.4 ±		10.0		.9 ±	2.3 ±		5 0 6			-	20
S1+S3+S5	S2+S4+S6	$7.3 \pm 0.2a$	$5.7 \pm 0.1b$	-1.6	-22.2	0.1a	0.1b		43.9	(0.2a	0.0b	-2.6	-53.6	$61.1 \pm 1.4a$	$37.9\pm0.6b$	23.2	-38
							All states tog	ether										
						2.0 ±				9	.4 ±	5.4 ±						
S1	S2	11.4 ± 0.1a	$7.1 \pm 0.3b$	-4.3	-37.7	0.0a	$1.7 \pm 0.0a$	-0.2	-12.5		0.1a	0.3b	-4.1	-43.1	$82.3 \pm 0.2a$	$66.4 \pm 1.4b$	15.9	-19.3
						1.7 ±	3.8 ±				.4 ±							
S3	S 4	7.1 ± 0.3a	$9.6\pm0.1b$	2.5	35.4	0.0a 3.7 ±	0.0b 4.6 ±	2.1	118.3		0.3a .2 ±	5.8 ± 0.1a 4.9 ±	0.4	8.3	$66.4 \pm 1.4a$	$54.5\pm0.6b$	-12	-18.1
S5	S 6	11.9 ± 0.1a	$9.5 \pm 0.2b$	-2.4	-20	0.1a	4.0± 0.1b	0.9	23.3		0.2 ± 0.1a	4.9± 0.1b	-3.3	-39.7	$68.4 \pm 0.4a$	$45.4 \pm 0.7b$	-23	-33.6
						4.0 ±					.4 ±	5.5 ±					-	
S1+S3+S5	S2+S4+S6	$12.4 \pm 0.1a$		-3	-24	0.1a	3.9 ± 0.0a	-0.1	-1.8	(0.1a	0.1b	-2.9	-34.5	$67.8 \pm 0.3a$	$52.4 \pm 0.4b$	15.4	-22.8

Note: for each of the four indicators *i*, values of $V_i = (M_{i,T} - M_{i,C})/M_{i,C}$ are presented in % (see Eq. (3)); mean ± standard deviation were given for $M_{i,C}$ and $M_{i,T}$; different letters in each pair of columns ($M_{i,C}$ and $M_{i,T}$) 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 $M_{i,T}$ and $M_{i,C}$ were significantly different.

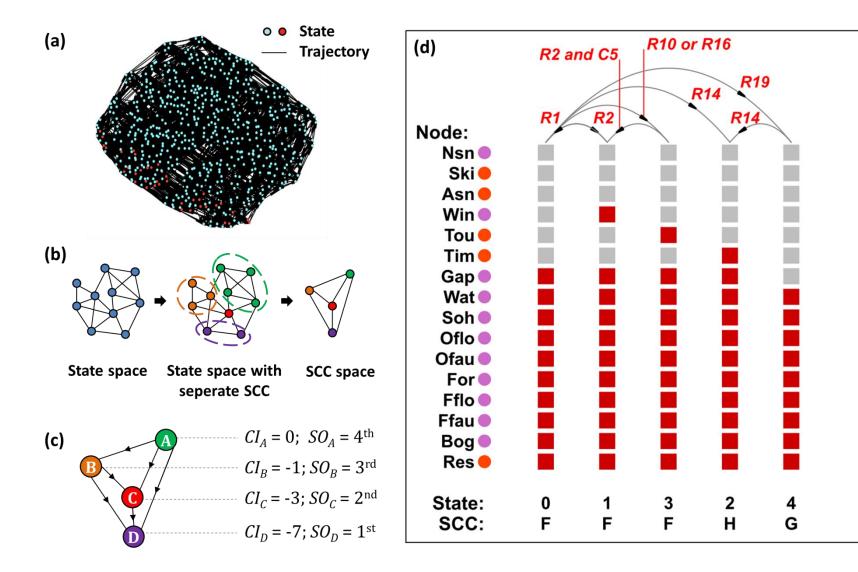


Figure 1

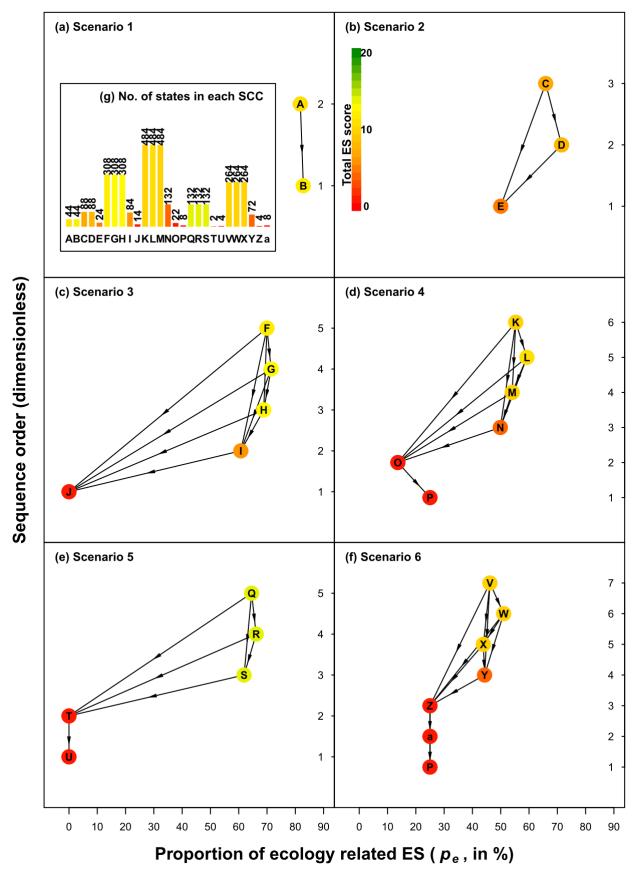


Figure 2

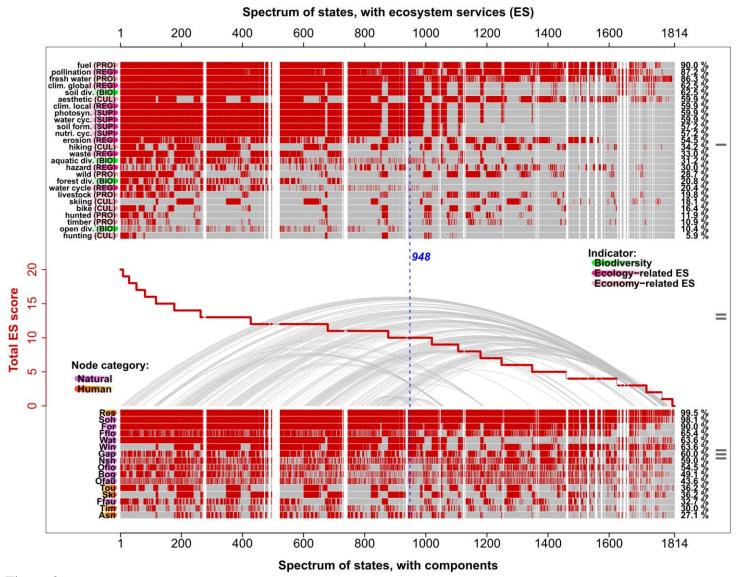
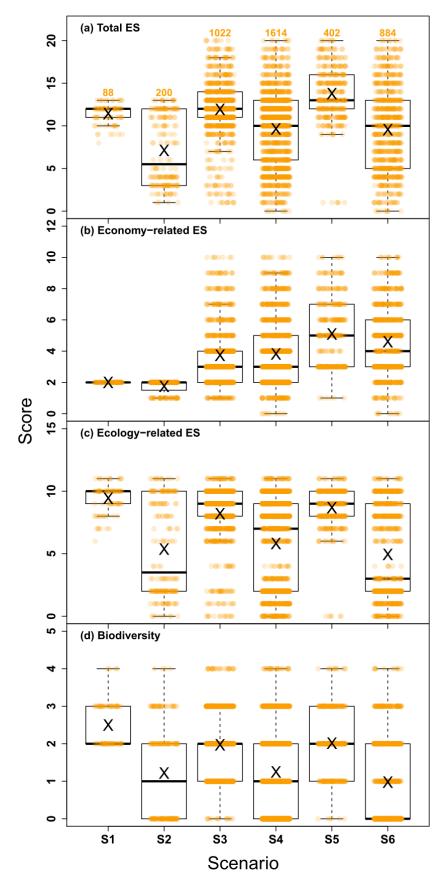
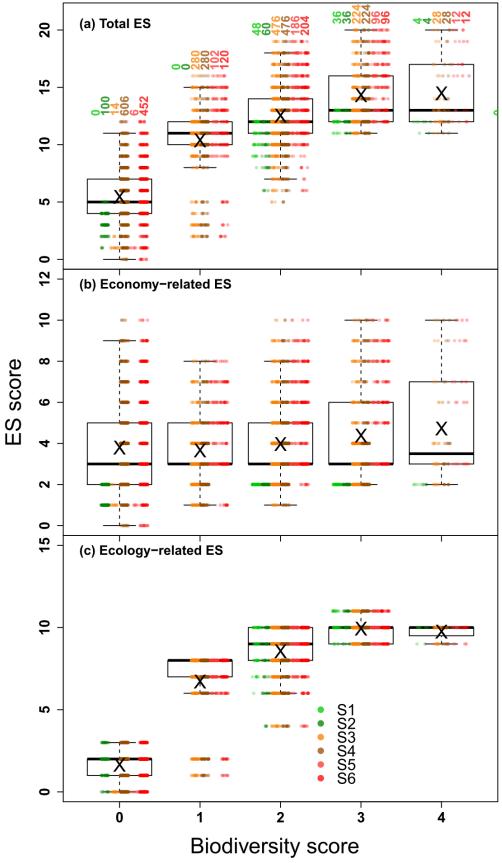


Figure 3









34 Figure 5