

A process-based model for multiple ecosystem services in the Venice lagoon under climate change and demographic forcings

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ABSTRACT

Understanding the dynamics and trade-offs of ecosystem services (ESs) represents a crucial step towards a more sustainable management of coastal lagoons. Nonetheless, within ESs modelling, process-based dynamic models had a confined development. This work presents a non-spatial process-based model that represents the dynamics of twelve ESs in the Venice lagoon, grounded in the social-ecological system framework. ESs emerge from the interactions among habitats, fauna, and actors, represented as state variables through a system of ordinary differential equations, forced by climatic and socio-demographic trends. A comprehensive set of data on habitats, fauna, and ESs was considered to parameterise the model, and a numerical simulation covering the years 2000–2080 was performed. Parameters sensitivity was explored through the Morris method. Simulations reveal long-term trends in ESs and state variables, showing a marked long-term decline of lifecycle maintenance and fishing activities, driven by the negative trends of intertidal habitats and fauna. Habitat loss, restoration, and lagoon high-tide regulation influence the lifecycle maintenance ESs, shaping faunal dynamics; nonetheless, the decline in provisioning ESs is also related to the trend in actors, including artisanal and recreational fishers. Simulation outputs and sensitivity analysis showed that the model is capable of representing contrasting feedbacks among different cultural ESs, habitat dynamics and fauna, which are subjected to the exogenous trends in tourists and residents, highlighting leverage points for lagoon management. Comparison with historical data and sensitivity patterns provides guidance for future model development and applications to policy scenarios.

1. Introduction

The idea of estimating the value of nature's contributions to human well-being was introduced at the end of the 1990s by defining the concept of ecosystem services (ESs) (Costanza et al., 1997, 2017; Daily, 1997). After the Millennium Ecosystem Assessment (MA, 2005), ESs have become a recognized management tool, unravelling the multiple ways our societies depend on the natural environment and its ecosystem-level processes (IPBES, 2019). This stimulated the flourishing of a range of tools for assessing ESs, based on different approaches, including correlation and regression analyses, Bayesian networks, system dynamic models (InVEST, EcoServ-GIS, ARIES, SOLVES, ESTI-MAMP, etc.) (Ruiz Agudelo et al., 2020). Among the techniques used for ecosystem services modelling, the family of GIS-based spatial statistic methods has increasingly gained popularity, thanks to their accessibility, user-friendly interfaces and versatility. Process-based dynamic

models had a more confined development, and among the existing ones, only a low number of tools considered extensively the analysis of trade-offs among multiple ESs (Ruiz Agudelo et al., 2020). Nonetheless, predictions based on process-based models have a remarkable applied interest for management and policy making, given the difficulty of relying on future projections without an understanding of the degree of uncertainty and the need for identifying leverage and tipping points (Brugnach et al., 2007; Meadows, 1999; Sterman, 2011). The versatility of process-based dynamic models in representing feedback networks quantitatively, with the possibility to perform tests of sensitivity and accuracy, represents a way to overcome these limitations. A constraint to the development of these types of tools is represented by the difficulty of understanding the dynamic behaviour of socio-ecological systems, which requires multidisciplinary and integrated approaches, aimed at preventing the oversimplification of the complexity of such systems (Bennett and Reyers, 2024; Gain et al., 2020).

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Coastal lagoons are among the most productive aquatic ecosystems, hotspots of biodiversity and wildlife nurseries, and also play a key role in supporting human settlement and activities (Newton et al., 2018). For these reasons, lagoons are affected by high levels of urbanization (Bonaglia et al., 2025) and the ESs they provide are consequently often overexploited (D'alpaos and D'alpaos, 2021; Newton et al., 2018). Lagoons and wetlands are considered key biodiversity hotspots and in the European Union, as such, they have priority in protection and restoration programmes (Directorate-General for Environment and Sundseth, 2015). Climate change is an additional stressor for lagoon ecosystems and their inhabitants that are particularly sensitive to sea level rise and water temperature increase (Fagherazzi et al., 2005; Newton et al., 2018; Pranovi et al., 2013; Zanchettin, 2022). In this context, the Venice lagoon, with many centuries of human interaction, is a very representative case study to understand the dynamicity of a socio-ecological system where human behaviour and the natural environment shape each other (Pranovi et al., 2006; Sarretta et al., 2010; Solidoro et al., 2010). New challenges, driven by human disturbance in the Venice lagoon include mass tourism, sea level rise and the consequent need for protection of the historical town of Venice and its cultural heritage (Bertocchi et al., 2020; Giupponi et al., 2024; Trancoso González, 2018; Umgiesser, 2020). With respect to this latter challenge, the system “Modulo Sperimentale Elettromeccanico” (here-in MOSE) was developed, consisting of an infrastructure that blocks the water from the Adriatic Sea from entering the lagoon during high tide events by closing the inlets with a system of movable gates (Consorzio Venezia Nuova, 2025). These challenges add up to the complex dynamics of an ecosystem that is still far from achieving a good ecological status (ARPAV, 2024).

All these aspects considered, the Venice lagoon seems capable to exemplify the complexity of challenges that coastal lagoons are facing, and modelling the ESs of such socio-ecological system could thus help us gathering more understanding on the possibilities offered by mathematical models for supporting planning and management efforts that are effectively taking into consideration the ecosystem approach ideas (Newton et al., 2018; Rova and Pranovi, 2017; Rova et al., 2019a, 2019b, 2022, 2023). Within this framework, the present work aims at developing a non-spatial quantitative dynamic model for the ecosystem services of anthropized coastal wetland areas, using the Venice lagoon as a representative case study. To do so, the model implements the conceptual socio-ecological system framework (SESF) developed by Ostrom (2009) and translates it into a system of ordinary differential equations. The specific objectives of the work are:

- a) to identify the mathematical model describing ESs as a function of a set of lagoon variables/factors, as habitats, fauna, governance and social actors, and using a comprehensive set of available data on the studied socio-ecological system;
- b) to run a numerical simulation from the year 2000 to the year 2080 and explore the sensitivity of the model state variables to its parameters with the Morris method local sensitivity test.

2. Methodology

2.1. Model layout

The model dynamically represents a set of twelve ESs, emerging from the interactions occurring within the complex social-ecological system of the Venice lagoon. A systemic approach is adopted, describing the variable dynamics by means of gain and loss differential equations. ES identification was based on previous assessments available for the study area (Pranovi et al., 2020, 2021, 2022; Rova et al., 2019a, 2019b, 2022, 2023). They include:

- four regulating ESs, including, lifecycle maintenance (LCM) by the habitat nursery function, N and P removal by vegetated habitats, CO₂

- storage and sequestration by saltmarshes and vegetated habitats, erosion prevention through wind fetch interruption by saltmarshes and sediment stabilization by vegetated habitats;
- four provisioning ESs: clam harvesting, artisanal fishing, recreational fishing and waterbird hunting;
- four cultural ESs: traditional rowing (*Voga alla veneta* in Italian), cognitive development through environmental education activities, tourism in the lagoon, and recreational navigation.

To describe the ES, the model distinguishes among resources, actors and governance, based on the SESF (Ostrom, 2009), which provides a general set of components to describe the system of interest, as visualised in Fig. 1. From this point of view, ESs emerge from the interactions among lagoon resources, actors, and governance under the influence of external forcings (Rova and Pranovi, 2017).

In the case of the Venice lagoon, the resources include ten elements of the seascape (vegetated and unvegetated habitats and lagoon morphology), and six elements of the fauna, which describe the animal species targeted by provisioning ESs. Eleven sets of actors describe the groups of people involved in the flow of the ESs. Governance is represented in the model as management interventions that target seascape elements (e.g. channel dredging), the flow of provisioning and cultural ESs (e.g. regulation of harvesting activities), and climate change adaptation (management of the MOSE system). The model considers two climate-related forcings (sea level rise and water warming) and four demographic ones (demographic trends of the residents of the lagoon and of the lagoon's surroundings, and trends in the number of tourists and university students).

Fig. 2 presents an overview of the model layout, which includes 12 prognostic and 4 diagnostic state variables, grouped in the two subsystems (white boxes) of habitats and fauna. Arrows represent flows between the different model components and between external forcings and model components. A detailed representation of habitats and fauna subsystems is provided in Figs. I and II (Appendix), while ES subsystems are represented in Fig. III (Appendix).

2.2. Model formulation

Model formulation is described by subsequently focusing on the different submodules: i) seascape elements; ii) fauna; iii) actors and governance; iv) ecosystem-services. The seascape module provides a non-spatial representation of the lagoon, which has an overall surface of 543 km². Of this area, 409 km² are covered by aquatic habitat (both intertidal and subtidal), 53 km² are canals, and 81 km² consist of terrestrial habitat to which we refer as tangible cultural heritage, due to the high density of historical buildings spread across the islands of the lagoon. The total surface area remains constant, imposing a spatial constraint. The lagoon intertidal and subtidal areas are subdivided according to their bathymetry, adopting a threshold: intertidal and shallow subtidal areas for depths > 1.5 m, deep subtidal for depths ≤ 1.5 m (Sarretta et al., 2010). The model assumes that the deep subtidal area is not colonisable by vegetated habitats. Distinct habitats were included because of their role in the ESs provision (Rova et al., 2019a, 2022), as shown in Fig. 3, including: saltmarshes, creeks, seagrasses, benthic diatoms, bare bottom, macroalgae, deep subtidal, navigable canals, non-navigable canals, and tangible cultural heritage. The first 6 habitats compose the intertidal and shallow subtidal area.

Following the arrows in Fig. 3, if one considers a generic habitat A that can be converted into habitats B and C, the dynamics are formulated in the model as shown in the following Eq. (1) (overall budget), Eq. (2) (outgoing arrows for the loss), and Eq. (3) (incoming arrows for the gain). Governing equations for each habitat are provided in Table 1, functional expressions are provided in Table III (Appendix), while parameters used are listed in Table 5.

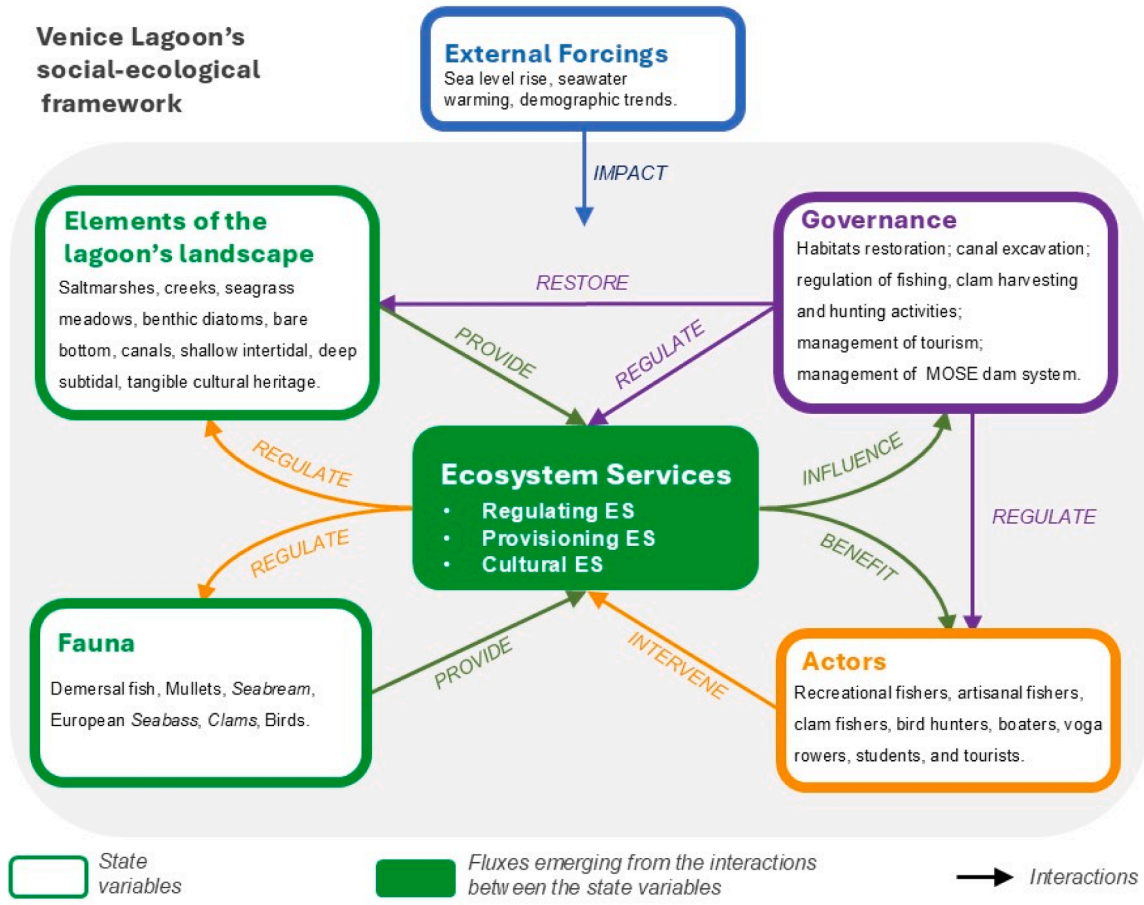


Fig. 1. Application of the socio-ecological system framework to the lagoon of Venice.

$$\dot{A} = \frac{dA(t)}{dt} = growth_A - loss_A \quad (1)$$

$$loss_A = from_{AtoB} + from_{AtoC} \quad (2)$$

$$growth_A = from_{BtoA} + from_{CtoA} \quad (3)$$

The dynamics of the lagoon seascape reflects the habitats natural capacity to colonize/be colonized by other habitats (Eqs III.1 to III.8). The negative effects of human activities (clam harvesting, tourism and recreational navigation, which cause erosion, exacerbating the degradation of the lagoon) are represented in the habitat loss term (Eq. (2) and Table III). Net habitat growth is a function of the available space (Eq. (3) and Table III), of water temperature for vegetated habitats (III.10-III.11), and of sea level rise and MOSE for salt marshes (III.12). It also represents the positive effects of activities, such as environmental education and traditions, that indirectly promote habitat restoration, by raising awareness (f_{sens} , e.g. III.10, Table I). In addition, the model considers the dynamics of canals, which act as waterways for cultural ESs, providing accessibility through navigation. Actors involved in different ESs induce opposite impacts on the state of the navigable canals, by enhancing siltation or by demanding the maintenance and excavation (III.21-III.22).

The model includes the stocks of 6 different groups of fauna that represent the major target species of provisioning ESs. Manila clam (*Ruditapes philippinarum*), demersal fauna (*Platichthys flesus*, *Solea vulgaris*, *Septia officinalis*, *Zosterisessor ophiocephalus*), mullets (Mugilidae, *Liza* spp.), seabream (*Sparus aurata*), European seabass (*Dicentrarchus labrax*), and hunteable birds of the two families Anatidae (*Anas crecca*, *Anas platyrhynchos*, *Anas acuta*, *Mareca penelope*, *Mareca strepera*, *Spatula*

clypeata) and Rallidae (*Fulica atra*, *Gallinula chloropus*, *Rallus aquaticus*). Fauna dynamics is controlled by the following equations, for a generic fauna group J:

$$\dot{J} = \frac{dJ(t)}{dt} = growth_J + input_J - catch_J \quad (4)$$

$$growth_J = \beta_{LCM} \cdot \left(\frac{LifeCycleMaintenance_t}{LCM_0} \right) \cdot f_k(\Delta T) \cdot r_J \cdot J(t) \cdot \left(1 - \frac{J(t)}{k_J} \right) \quad (5)$$

$$input_J = (in_J \cdot J_0) \cdot \left(\frac{LifeCycleMaintenance_t}{LCM_0} \right) \cdot f_{MOSE} \quad (6)$$

$$catch_{FiJ} = H_J \cdot A_{Fi}(t) \cdot f_{GS_{Fi}} \quad (7)$$

Equations for each group of fauna are presented in Table 1, functional expressions are provided in Table IV (Appendix) and the parameters used are listed in Table 5. The habitats, the ES, and the forcings influence the net growth and loss rate of the fauna. The net growth rate, in Eq. (5), is a function of the species net growth coefficient and carrying capacity density, the water temperature and the state of the habitats providing a nursery function for the species (Kruzić et al., 2012, 2016; Rizzi et al., 2016). Eq. (6) considers the input of marine fauna through lagoon inlets (Table 4 and I). This has been introduced to represent the lagoon as an open system connected to the sea, and to account for the interruption of this connectivity caused by the activation of the MOSE system. In fact, by interrupting the water exchange with the open sea, the operation of the MOSE system impacts the input of fauna and the ES of LCM (Franco, et al., 2006a, 2006b; Umgiesser, 2020). Eq. (7) describes the catches from provisioning ES (see the last part of this section).

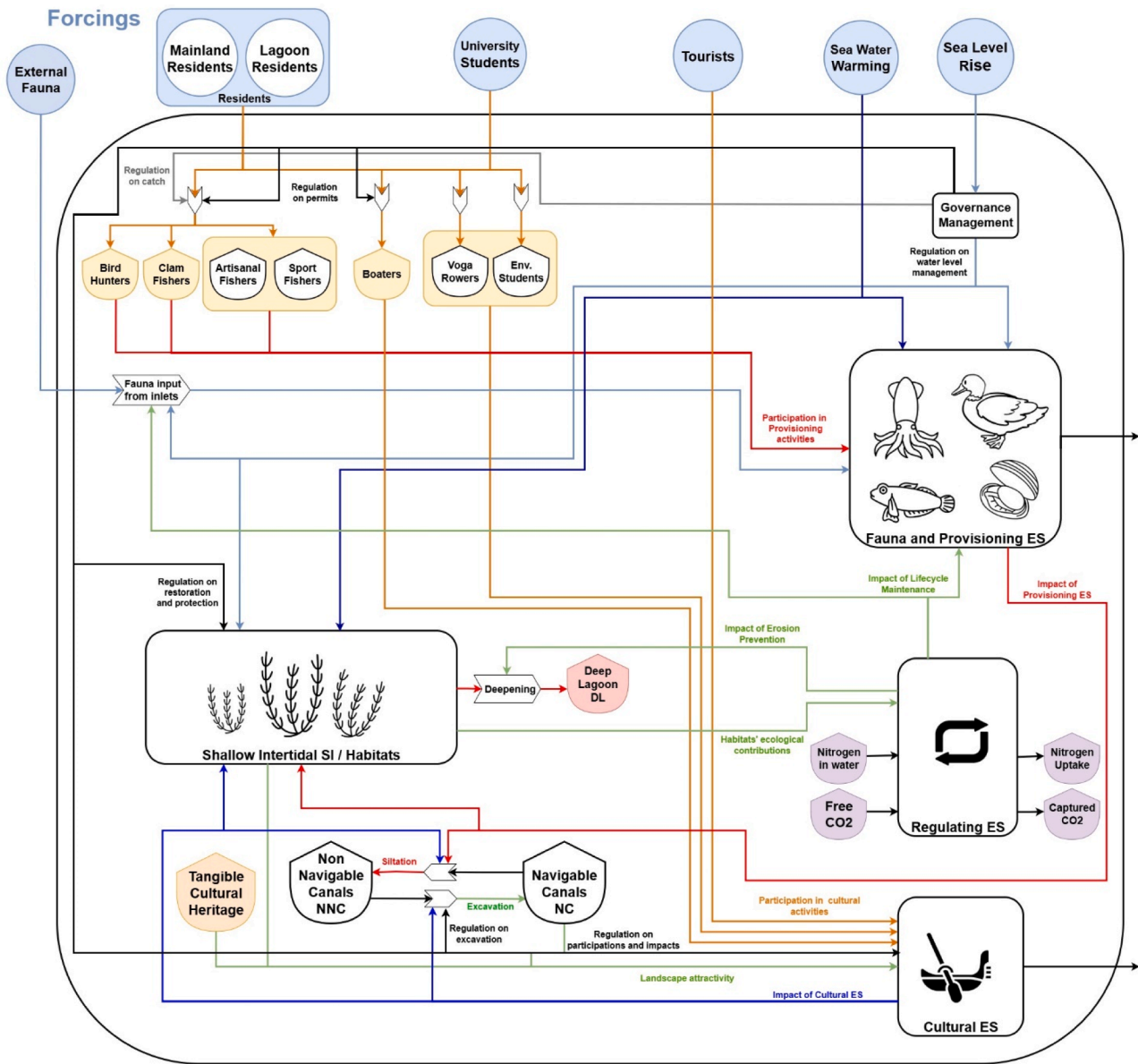


Fig. 2. Model layout. Arrows represent the relationships among the different stocks (drop-shape) and subsystems (white-boxes). For a detailed representation of model subsystems, see Figs. I–III in the Appendix.

Table 2 provides a description of actors and governance elements considered within the model. The demographic forcings are translated into eight groups of actors playing a role in the flow of ESs. Actor groups included are clam, artisanal, and recreational fishers, bird hunters, boaters, voga rowers, environmental education students, and tourists. Governance actions within the system cover different areas of lagoon environmental management, namely MOSE activation, regulation of fishing activities, canal excavation, and habitat restoration.

The model simulates twelve ESs provided by the Venice lagoon, which are described in Table 3. The ecosystem services are estimated as quantitative internal fluxes of the system, using biophysical units and not monetary values, to disincentivise commodification of natural elements (Gómez-Baggethun and Ruiz-Pérez, 2011). Regulating services depend on the habitat extension. The activities involved in provisioning and cultural ESs produce, on the other hand, impacts that contribute to enhancing the erosive processes. Erosion prevention distinguishes two distinct processes and is therefore defined as the sum of Erosion Prevention 1 (wind fetch disruption by salt marshes) and Erosion

Prevention 2 (sediment bio-stabilization by seagrasses and benthic diatoms habitats). Provisioning services are extractive activities, performed by actors insisting on target groups of fauna. The output of these ESs is the yearly catch, and it impacts the fauna population (Eqs. (4) and (7)). Cultural services quantify the activities of different actors (rowers, boaters, students or tourists), expressed as the number of individuals or excursions per year. These services depend on the demographic forcings and on the attractiveness of the lagoon seascape, which is a function of its habitats and cultural heritage. The cultural heritage (HER) is considered constant, assuming that the activation of the MOSE system protects it from flooding. The HER influences the ESs by increasing seascape attractiveness.

2.3. Coding and simulation set-up

The model was coded in R, “4.2.1 (2022-06-23 ucrt)” version. The code is available in open source on the platform GitHub for consultation (GitHub, 2025; VLES_lagoon_ES, 2025). The solution of the system of

ordinary differential equations simulating the dynamics of the lagoon is obtained using the ODE-solver included in the package *deSolve* by applying the function “*ode(y, times, func, parms, ...)*” (Soetaert et al., 2010). The timestep used for simulations is one year, and the simulation covers the period from 2000 to 2080, the year in which the demographic projections used end. This run was aimed at evaluating model stability in the long term. As required in many cases with complex ecosystem models, a spin-up phase to achieve the initial conditions was performed (Thornton and Rosenbloom, 2005). Based on preliminary tests, a time window of 20 years was chosen for the model spin-up.

2.4. Field data on state variables and ES, forcings, and initial conditions

The dataset used to apply the model integrates the results of numerous studies concerning the ecology of the lagoon. The complete description of the parameters and the initial conditions is reported in Table 5 and Tables V, VI (Appendix). Spatially-explicit information is translated from the original sources into non-spatial yearly averages. The equations have been formulated in order to connect in a systemic way available data with a consistency of unit of measure and order of magnitude. Data on fish stock dynamics (growth, carrying capacity and biomass) are derived from *Ecopath* with *Ecosim* and *Ecospace* (Anelli Monti et al., 2021). Data on fishing activities are taken from Riccato et al. (2014) and Boatto et al. (2008), and integrated with the work by Stocco et al. (2024). Clams data are taken from Pessa et al. (2018), while bird hunting data from Licheri and Spina (2005) and Basso and Bon (2018). All biomass data were transformed into density by dividing them by the total surface of the intertidal and subtidal areas combined (409Km²). The quantification of morphological changes and erosion, including the lagoon bathymetry temporal evolution, is derived from studies on sediment dynamics and sediment budget (Sarretta et al., 2010). Trends of sea level rise and the response of the MOSE closures are based on the works by Giupponi et al. (2024), Lionello et al. (2021), Umgiesser (2020). The demographic data, historical and projected, are taken from the Italian National Institute of Statistics (ISTAT, 2024). Ecosystem services assessments comes from the works by Rova et al. (2022, 2023) and Pranovi et al. (2020, 2021). Human actors are modelled based on four exogenous demographic trends: residents of the lagoon, residents in the surrounding mainland, higher-education students, and Venice tourists. These groups are imported as time series of yearly values as described in Table 4. Climatic forcings express the effects of climate change on the local environment, namely, the yearly increase of the average water temperature (*kT*) and the relative sea level rise (*rslr*). These two variables are imported as time series and can have

different trends, depending on the climate-based forcing taken into consideration. Forcings time series are shown in Fig. 4. The numerical boundaries or initial conditions for the model, shown in Tables V, VI (Appendix), were selected to allow the model to qualitatively reach all the historical values available for the model variables. Historical data refer to the period of time between the end of the spin-up phase, in 2000, and 2020. The simulations presented in this work were carried out under the following considerations:

- dynamic climatic trends were included by using the time series of the two forcings: *rslr* and *kT*. We simulated the worst-case climate-change scenario available in the literature, namely RCP8.5. The forcings used by the model are scenario-based projections, that ignore possible internal feedbacks, for example, between the MOSE activation and the water temperature. *kT_{rep}* starts from an initial increase value of 0.02°C per year that is maintained for the spin-up phase until 2019. From 2020 the model assumes a new value based on the scenario, in the case of RCP8.5 it is 0.0525°C. This value was chosen to reach a final value predicted for 2100: +5°C (Bucchignani et al., 2016). *rslr* is imposed as a time series, of yearly values from scenario-based projections by Lionello et al. (2021), covering the period 2001–2100. The value in 2100 is +0.85 m for RCP8.5.
- residents of the mainland surrounding the lagoon time series, *RG(t)* was calculated by making the following assumptions: i) between 1980 and 2000 (spin-up phase) the value of this group is stationary and equal to the value of the year 2001; ii) between 2000 and 2023, the value matches the historical data until 2023 (ISTAT, 2024); between 2024 and 2041 the value matches the available demographic projections of the Italian municipalities until 2041 (ISTAT, 2024); iv) between 2042 and 2080, the demographic projections of the Veneto population are applied (ISTAT, 2024).
- residents of the lagoon islands, *RV(t)* was calculated by making the following assumptions: i) within 1980–2000 (spin-up phase) the value of this group is stationary and equal to the value of the year 2001; between 2001 and 2023 the value matches the historical data. For this timeframe, the partitioning between the islands and the mainland is available (Venice Municipality, 2026). Between 2024 and 2041 the projections of individual municipalities are available, hence *RV(t)* matches the available demographic projections of Italian municipalities until 2040 (ISTAT, 2024). For this interval, the partition between the islands’ and mainland’s residents is calculated by applying the trend of the whole mainland to the last value of Venice mainland and subtracting this time series to the projection of Venice municipality. Between 2042 and 2080 the *RV(t)* decreases with a yearly percentage that is calculated as double the decrease rate of *RG(t)*. This assumption is made to maintain the stronger decrease rate observed in the historical time series of the lagoon residents.
- university students, *US(t)*, value was calculated by adding a constant yearly increase of 250 students, starting from an estimate of about 32 thousand students in 2023 (USTAT, 2026). This produces a slow linear increase that tries to represent the trends and plans of the Venetian colleges.
- tourist arrivals in Venice, *TV(t)*, was obtained by considering the historical trend and extending it in time according to the following assumptions. The value of *TV(t)* matches the historical value in 2019, which corresponds to 5.5 million individuals (Vezzà et al., 2021). The *TV(t)* time series presents a steady increase rate of 3.68% per year, which represents the average increase of the period 2007–2019 (Vezzà et al., 2021). This rate of increase is imposed until 2041. The time-series then proceeds with a yearly rate of 1% from 2042 to 2080.

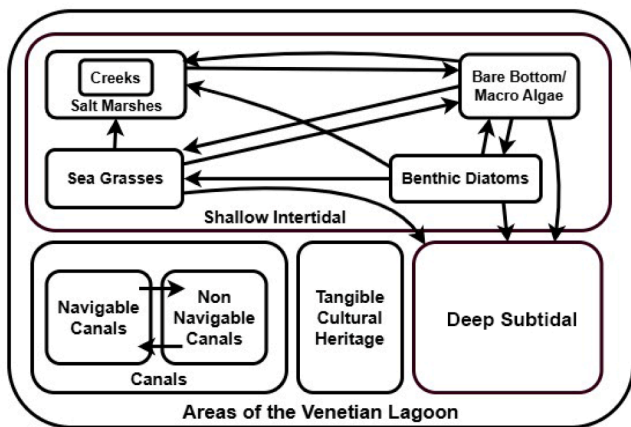


Fig. 3. Elements describing the lagoon seascape (boxes) and relationships among them (arrows). All the elements are described in the model as surface areas. Arrows show the possibilities of the different elements of exchanging surface.

Table 1

Seascape elements and fauna, including names, formulation, brief description, and units. See Tables III and IV (Appendix) for functional expressions, and Table 5 for parameter description.

Name	Description	Unit	Id
<i>BD</i> $BD = growthBD - lossBD$	Benthic diatoms habitat, corresponding to sediments covered with benthic diatoms. The habitat is modelled as part of the shallow intertidal area. Its surface can increase by covering the area of the bare bottom, or decrease by transferring the loss to bare bottom, to seagrasses, to saltmarshes or to deep subtidal.	[km ²]	1.1
<i>SG</i> $SG = growthSG - lossSG$	Seagrasses habitat, consisting of seagrass meadows of the species <i>Cymodocea nodosa</i> , <i>Zostera marina</i> , <i>Nanozostera noltii</i> and <i>Ruppia cirrhosa</i> . The habitat is modelled as part of the shallow intertidal area. Its surface can increase by colonising the area of the bare bottom or the one of the benthic diatoms, or decrease by transferring the loss to the bare bottom, saltmarshes or deep subtidal (Pastres et al., 2004).	[km ²]	1.2
<i>SM</i> $SM = growthSM - lossSM$	Salt marshes habitat. This complex ecosystem is crossed by the creeks (<i>Ghebi</i> in Italian) and is periodically submerged by tidal movements of the water. The habitat is modelled as part of the shallow intertidal area. Its surface can increase by covering the area of the bare bottom, the seagrasses and the benthic diatoms, or decrease by transferring the loss only to the bare bottom.	[km ²]	1.3
<i>CR</i> $CR = SM \cdot SM_{geom}$	Saltmarshes' creeks habitat. The creeks form an intricate web of natural shallow canals that cross the salt marshes providing a nursery function to many species. Creeks are modelled as a fixed percentage of the area of the saltmarshes. In this way, the growth and loss of this habitat follow directly the dynamics of the saltmarshes.	[km ²]	1.4
<i>SI</i> $SI = SG + BD + SM + BB$	The surface of the lagoon's submerged and intertidal areas with depth lower than 1,5 m, excluding islands and canals. This area comprises the habitats: benthic diatoms, sea grasses, saltmarshes, creeks, and the bare bottom. The area of the shallow intertidal in the model can only decrease in time, by deepening its surface and transforming it into deep subtidal. The deepening effect includes the erosive effect produced by some ESs and simulates the erosion from other causes (net negative sediment budget, wind, commercial navigation and others) (Molinarioli et al., 2009).	[km ²]	1.5
<i>DI</i> $DI = 409 - SI$	This area is considered the deep part of the submerged lagoon, precisely deeper than 1,5 m. The model assumes that local vegetated habitats have difficulties developing in this area because of the depth and the light limitation. In the model, deep subtidal areas can only increase through processes of erosion of the shallow intertidal. The sum of shallow and deep subtidal in the model is a constant area of 409 km ² .	[km ²]	1.6
<i>BB</i> $BB = growthBB - lossBB$	The portion of the shallow intertidal that is empty or colonized by macro algae, that do not provide a substantial biostabilization effect to prevent erosion or shelter to promote LCM.	[km ²]	1.7
<i>NC</i> $NC = excavation - siltation$	The surface of the navigable canals of the lagoon which provides accessibility for navigation. It can be transferred to non-navigable canals through the process of siltation. The sum of navigable and non-navigable canals has a constant area of 53 km ² .	[km ²]	1.8
<i>NNC</i> $NNC = 53 - NC$	This stock represents the non-navigable canals of the lagoon that are not accessible because of their poor state of maintenance. It can be transferred to the stock of navigable canals through excavation. The sum of navigable and non-navigable canals has a constant area of 53 km ² .	[km ²]	1.9
<i>HER</i> $HER = 0$	This stock has an area of 81 km ² and represents the emerged areas of the lagoon (islands). This surface is constant in time and plays a role in the attractiveness of the lagoon for the cultural ESs due to the high density of tangible cultural heritage.	[km ²]	1.10
<i>TA</i> $TA = growthTA - harvTA$	Stock of Manila clams (<i>Ruditapes philippinarum</i>) that are harvested in the lagoon for economic purposes. It has a natural net annual growth that reflects a logistic population dynamic, modulated by the carrying capacity, the water temperature and the hours of activation of the MOSE. It has an annual loss that is caused by the harvesting activities (Pessa et al., 2018; Pranovi et al., 2006; Vincenzi et al., 2011)	[ton km ²]	1.11
<i>DE</i> $DE = growthDE + inputDE - catch_{FA}DE - catch_{FS}DE$	Stock of demersal species (Nekton carnivorous in Anelli Monti et al., 2021), consisting of <i>Sepia officinalis</i> , <i>Solea solea</i> , <i>Zosterisessor ophiocephalus</i> , and <i>Platichthys flesus</i> , that have a natural net annual growth that reflects a logistic population dynamic, modulated by the carrying capacity, the water temperature and the hours of activation of the MOSE. They have an annual loss caused by fishing activities. In addition, there is an annual input of fish from outside the system, that reflects migratory fluxes and depends on the LCM and the closure of the inlets of the MOSE.	[ton km ²]	1.12
<i>MU</i> $MU = growthMU + inputMU - catch_{FA}MU$	Stock of Mulletts (Mugilidae, <i>Liza</i> spp.), that have a natural net annual growth that reflects a logistic population dynamic, modulated by the growth rate, carrying capacity, water temperature and the hours of activation of the MOSE. They have an annual loss caused by fishing activities. In addition, there is an annual input of fish from outside the system, that reflects migratory fluxes and depends on the LCM and the closure of the inlets by the MOSE.	[ton km ²]	1.13
<i>SB</i> $SB = growthSB + inputSB - catch_{FS}SB$	Stock of Seabream (<i>Sparus aurata</i>), that have a natural net annual growth that reflects a logistic population dynamic, modulated by the growth rate, carrying capacity, water temperature and the hours of activation of the MOSE. They have an annual loss caused by fishing activities. In addition, there is an annual input of fish from outside the system, that reflects migratory fluxes and depends on the LCM and the closure of the inlets by the MOSE.	[ton km ²]	1.14
<i>LA</i> $LA = growthLA + inputLA - catch_{FS}LA$	Stock of European seabass (<i>Dicentrarchus labrax</i>), that has a natural net annual growth that reflects a logistic population dynamic, modulated by the growth rate, carrying capacity, water temperature and the hours of activation of the MOSE. They have an annual loss caused by fishing activities. In addition, there is an annual input of fish from outside the system, that reflects migratory fluxes and depends on the LCM and the closure of the inlets by the MOSE.	[ton km ²]	1.15
<i>BI</i> $BI = growthBI + inputBI - huntBI$	Stock of huntable birds which includes the two major families of wintering birds, Anatidae (<i>Anas crecca</i> , <i>Anas platyrhynchos</i> , <i>Anas acuta</i> , <i>Mareca penelope</i> , <i>Mareca strepera</i> , <i>Spatula clypeata</i>) and Rallidae (<i>Fulica atra</i> , <i>Gallinula chloropus</i> , <i>Rallus aquaticus</i>), that are targeted by hunters for recreational purposes. The net annual growth reflects a logistic population dynamic, modulated by the carrying capacity of the population and the water temperature. It has an annual loss that is caused by hunting activities. In addition, the model includes an annual input of birds from outside the system, a forcing condition that reflects migratory fluxes and does not depend on the internal dynamic stock of birds.	[ton km ²]	1.16

Table 2
Actors and governance elements considered in the model. See Table 5 for parameter description.

Name	Description	Unit	Id
A_{TF}	Stock of individuals who practice clam harvesting activities in the lagoon. These are a percentage of the residents. It is assumed that the amount of the target stock affects the actors due to high competition and reduced success. Therefore, the number of actors is modulated by an attractivity factor that depends on the stock of the target fauna divided by its carrying capacity. $ClamFishers = (RVt(t) + RGt(t)) \cdot per_{TF} \cdot (TA / kTA)$	[ind]	2.1
A_{AF}	Stock of individuals who practice artisanal fishing in the lagoon. These are a percentage of the residents in the lagoon and the surrounding mainland. It is assumed that the amount of the target stock affects the actors due to high competition and reduced success. Therefore, the number of actors is modulated by an attractivity factor that depends on the stock of the target fauna divided by its carrying capacity. $ArtisanalFishers = (RVt(t) \cdot per_{AFv} + RGt(t) \cdot per_{AFg}) \cdot \left(\frac{MU + DE}{(kMU + kDE)/30 + MU + DE} \right)$	[ind]	2.2
A_{SF}	Stock of individuals who practice recreational/sport fishing in the lagoon. These are a percentage of the residents in the lagoon and the surrounding mainland. It is assumed that the amount of the target stock affects the actors due to high competition and reduced success. Therefore, the number of actors is modulated by an attractivity factor that depends on the stock of the target fauna divided by its carrying capacity. $SportFishers = (RVt(t) \cdot per_{SFv} + RGt(t) \cdot per_{SFg}) \cdot \left(\frac{SB + LA + DE}{(kSB + kLA + kDE)/30 + SB + LA + DE} \right)$	[ind]	2.3
A_{HUNT}	Stock of individuals who practice bird hunting activities in the lagoon. These are a percentage of the residents in the lagoon and the surrounding mainland. It is assumed that the amount of the target stock affects the actors due to high competition and reduced success. Therefore, the number of actors is modulated by an attractivity factor that depends on the stock of the target fauna divided by its carrying capacity. $Hunters = (RVt(t) + RGt(t)) \cdot per_{HUNT} \cdot \left(\frac{BI}{kBI} \right)$	[ind]	2.4
A_{NAV}	Stock of individuals owning a private leisure motorboat (not rowing or sailing) in a given year. The number of boaters has been increasing in recent decades in counter-tendency to the number of residents. This is due to socio-economic variables that are not part of this system, such as the cost of boats, the cost of fuel and the purchasing power of the Italian population. Therefore, the model estimates boaters as a percentage of the resident population, added to a minimum value to stabilize the value and avoid non-realistic results. $Boaters = (RVt(t) \cdot per_{NAVv} + RGt(t) \cdot per_{NAVg} + USt(t) \cdot per_{NAVg}) + 21000$	[ind]	2.5
A_{ROW}	Stock of individuals who are part of rowing clubs (called <i>remiere</i> and <i>associazioni dei canottieri</i> in Italian) for the traditional “voga veneta” (venetian rowing) inside the lagoon in a given year. The number is calculated in the model as a percentage of the lagoon residents, mainland residents and higher education students, starting from the estimation of the current distribution. $Rowers = RVt(t) \cdot per_{ROWv} + RGt(t) \cdot per_{ROWg} + USt(t) \cdot per_{ROWS}$	[ind]	2.6
A_{EDU}	Stock of students of all ages and levels in the lagoon and the surrounding mainland in a given year. These students are estimated as a percentage of the resident population (corresponding to scholar age) plus a contribution of university students. $EnvironmentalStudents = (RVt(t) + RGt(t)) \cdot per_{EDUr} + USt(t) \cdot per_{EDUs}$	[ind]	2.7
A_{TOU}	Stock of visitors to the lagoon, excluding Venice downtown. It is estimated as a fraction of the tourist arrivals in Venice. The estimation of those who take a trip outside of downtown Venice was reported in the work by Rova et al. (2022) . $A_{TOU} = TV(t) \cdot exA_{TOU}$	[ind]	2.8
per_J	Percentage of potential actors J participating in a given activity. With $J =$ clam fishers, artisanal fishers, recreational fishers of the islands, recreational fishers from the mainland, hunters, boaters of the islands, boaters of the mainland, rowers of the islands, rowers of the mainland, rowers among university students, environmental students among residents of the islands, environmental students among residents of the mainland, environmental students among university students.	[-]	2.9
GS_{CAN}	The management of the canals’ (CN) excavation estimates the weight of management decisions on the intervention rate.	[y^{-1}]	2.10
GS_J	Management intervention on the habitat J, (where $J =$ BD, SM, SG). All three habitats include in their growth equations a parameter that represents the effect of the restoration interventions on the habitat expansion rate. The parameters for the SM and BD are fixed values. The value for the SG is included as a time series assuming different values during the simulation. This was done to replicate the significant impacts of restoration obtained in the last decade by the Life project “LIFE12 NAT/IT/000,331-SeResto. During the period 2014–2018, the surface occupied by SG in the lagoon almost doubled (Sfriso et al., 2019, 2021).	[-]	2.11
GS_{MOSE}	Hours of activation of MOSE in a year as a function of relative sea level rise, estimated from Giupponi et al. (2024) . $GS_{MOSE} = 100 + (\mathfrak{R}_{MO} \cdot (RSLR(t))^3)$ The management of MOSE is included as a parameter that estimates the weight of management decisions on the intervention rate.	[hours y^{-1}]	2.12
\mathfrak{R}_{MO}	Scenario-based response factor of MOSE activation: this can be selected for 110 cm or 130 cm activation thresholds, and for different climate change forcings. $\mathfrak{R}_{MO} = 790$ (threshold 110 cm), 556 (threshold 130 cm) NB: MOSE is active from year 2020.	[-]	2.13
H_J	Per capita harvest rate of J (with $J =$ BI, TA, MU, SB, DE, LA). This refers to the amount of catch that each individual can collect yearly and simulates the current policy restrictions on fishing.	[ton km^{-2} ind $^{-1}$ y^{-1}]	2.14

2.5. Model parameterization and sensitivity analysis

Model parameters are reported in Table 5 and Table II (Appendix). A fine-tuning of parameters was carried out to match historical values of the different variables available for the 2000–2019 timeframe. The tuning was performed manually, by eye-fitting the model outputs to the real data and adjusting the guessed parameters. Initial values of the variables, gathered from the literature, are listed in Table VI (Appendix).

A sensitivity test was implemented adopting the Morris Runna method because of the high number of parameters and the non-linear and non-monotonic nature of the system. This was executed by the ODEmorris function from the package ODEsensitivity, which is compatible with the interface of deSolve. The method computes the values of μ^* and σ for each variable in dependence on the random sampling of each parameter for all timesteps. Where μ^* is the mean of the absolute value of the local variation, useful in the case of the non-monotonic behaviour, and σ is the standard deviation. The sampling is

a random repetition of five hundred values, with the assumption of uniform distribution in a chosen interval. The interval of uncertainty for the carrying capacity (K_j) and the harvest rate (H_j) was derived from the Ecospace model, which assumes an average uncertainty among the biomass of all species of $\pm 25\%$, without assumptions on the distribution ([Anelli Monti et al., 2021](#)). For all the parameters, the interval is set at $\pm 25\%$, assuming a uniform distribution in the interval.

3. Results

3.1. Model-data comparison and long-term behaviour

The temporal evolution of model state variables (solid lines) is shown in Fig. 5, in which the vertical line marks the year 2020, the last year for which experimental measurements (black dots) are available. The habitats present markedly different trends (Fig. 5g–i,k), as reported by recent historical data and correctly reproduced by model simulations,

Table 3
Ecosystem services included in the model. See Table 5 for parameter description.

Name	Description	Unit	Id
Lifecycle Maintenance	Tons of juvenile fish per square kilometre that potentially utilize the natural nursery function provided by saltmarshes, creeks, and seagrasses in a given year. This is modelled as the factor that expresses the density of biomass of fauna supported by those habitats in each square kilometre multiplied by their surface. The value is impacted by MOSE after its activation in 2020. This is crucial for migrating fish species with yearly reproductive cycles entangled in the lagoon's habitats. $LifecycleMaintenance = ((SG(t) + CR(t)) / (DI(t) + SI(t))) \cdot f_{MOSE}$	[ton km ⁻² y ⁻¹]	3.1
Carbon Sequestration	Tons of carbon dioxide captured by salt marshes and seagrasses in a given year. This value depends on the extent of the areas of these two habitats and on the parameters that express their capacity to absorb carbon dioxide. $CarbonSequestration = SM(t) \cdot kC_{SM} + SG(t) \cdot kC_{SG}$	[ton y ⁻¹]	3.2
Water Purification	Percentage of nitrogen loads removed through denitrification per unit of surface area in a year (occurs in seagrasses, benthic diatoms, bare bottom and deep subtidal). This ES depends on the surface of these habitats, multiplied by the parameters that express their estimated capacity to remove nitrogen from the water. $WaterPurification = \frac{SG(t) \cdot kN_H + SM(t) \cdot kN_H + BD(t) \cdot kN_M + BB(t) \cdot kN_M + DI(t) \cdot kN_L}{DI(t) + SI(t)}$	[-]	3.3
Erosion Prevention 1	Surface of the bare bottom that is protected in a given year from wind-driven erosion by the presence of salt marshes, interrupting the wind fetch. This depends on the extension of the bare bottom modulated by the percentage of salt marshes areas contained inside the shallow intertidal. $ErosionPrevention1 = BB(t) \cdot \frac{SM(t)}{SI(t)}$	[km ² y ⁻¹]	3.4
Erosion Prevention 2	Surface of the seagrasses and of the benthic diatoms habitats, which is biostabilized thanks to the presence of vegetation in a year. This depends on a factor of stabilization multiplied by the sum of the areas of the two habitats. $ErosionPrevention2 = (SG(t) + BD(t)) \cdot k_{ep2}$	[km ² y ⁻¹]	3.5
Clam Harvesting	Tons of clams harvested per square kilometre in a given year (wet weight), for economic purposes. This depends on the availability of the resource of target fauna, and the number of actors participating in the activity multiplied by the per capita harvesting rate. $ClamHarvesting = H_{TA} \cdot A_{TF} \cdot f_{GS_{TA}}$	[ton km ⁻² y ⁻¹]	3.6
Artisanal Fishing	Tons of fish caught per square kilometre in a given year (wet weight), for economic purposes. This depends on the availability of the resource of target fauna, and the number of actors (Artisanal fishers) participating in the activity multiplied by the per capita harvesting rate. $Artisanalfishing = \sum_k (H_k \cdot A_{AF} \cdot f_{GS_{SA}})$ (with $k = DE, MU$)	[ton km ⁻² y ⁻¹]	3.7
Recreational Fishing	Tons of fish caught per square kilometre in a given year (wet weight), for recreational purposes. This depends on the availability of the resource of target fauna, and the number of actors (Recreational fishers) participating in the activity multiplied by the per capita harvesting rate. $Recreationalfishing = \sum_k (H_k \cdot A_{SF} \cdot f_{GS_{SA}})$ (with $k = DE, LA, SB$)	[ton km ⁻² y ⁻¹]	3.8
Hunting	Tons of bird quarry per square kilometre in a given year for recreational purposes. This depends on the availability of the resource of target fauna, and the number of actors (Hunters) participating in the activity multiplied by the per capita harvesting rate. $Hunting = H_{BI} \cdot A_{BI} \cdot f_{GS_{BI}}$	[ton km ⁻² y ⁻¹]	3.9
Traditional Rowing	Number of excursions of traditional rowing in a given year. It depends on the number of rowers in the area, modulated by the attractiveness of the activity. This depends on the state of the lagoon at a given time, in terms of the presence of natural habitats, cultural heritage and navigable canals. $TraditionalRowing = A_{ROW}(t) \cdot exA_{ROW} \cdot \left\{ \omega_{nat} \cdot \left(1 + \frac{\omega_{SM-TR} \cdot (SM - SM_0) + \omega_{SG-TR} \cdot (SG - SG_0)}{\omega_{SM-TR} \cdot SM_0 + \omega_{SG-TR} \cdot SG_0} \right) + \omega_{her} \cdot \left(1 + \frac{HER - HER_0}{HER_0} \right) + \omega_{acc} \cdot \left(1 + \frac{NC - NC_0}{NC_0} \right) \right\}$	[exc y ⁻¹]	3.10
Cognitive Development	Number of students participating in environmental education activities in a given year. The number of students in the area is mediated by the attractiveness of the activity. This depends on the state of the lagoon, in terms of the presence of natural habitats, cultural heritage and navigable canals. $CognitiveDevelopment = (A_{EDU}(t) \cdot exA_{EDU}) \cdot \left\{ \begin{array}{l} \omega_{nat} \cdot \left(1 + \frac{\omega_{SM-CD} \cdot (SM - SM_0) + \omega_{SG-CD} \cdot (SG - SG_0)}{\omega_{SM-CD} \cdot SM_0 + \omega_{SG-CD} \cdot SG_0} \right) + \\ \omega_{her} \cdot \left(1 + \frac{HER - HER_0}{HER_0} \right) + \omega_{acc} \cdot \left(1 + \frac{NC - NC_0}{NC_0} \right) \end{array} \right\}$	[ind y ⁻¹]	3.11
Tourism	Number of individuals participating in tourism activities inside the lagoon (excluding Venice downtown) in a given year. It depends on the number of tourists visiting Venice per year, modulated by the attractiveness of the activity. This depends on the state of the lagoon at a given time, in terms of the presence of natural habitats, cultural heritage and navigable canals. $Tourism = (TV(t) \cdot exA_{TOU}) \cdot \left\{ \begin{array}{l} \omega_{nat} \cdot \left(1 + \frac{SM - SM_0}{SM_0} \right) + \omega_{her} \cdot \left(1 + \frac{HER - HER_0}{HER_0} \right) + \omega_{acc} \cdot \\ \left(1 + \frac{NC - NC_0}{NC_0} \right) \end{array} \right\}$	[ind y ⁻¹]	3.12
Recreational Navigation	Number of excursions in the activities of navigation with private motorboats inside the lagoon in a given year. The number of boaters in Venice per year is mediated by the attraction of the activity in the current state of the lagoon by the presence of natural habitats, cultural heritage and navigable canals. $RecreationalNavigation = (A_{BOAT}(t) \cdot exA_{BOAT}) \cdot \left\{ \left(\omega_{nat} \cdot \left(1 + \frac{SM - SM_0}{SM_0} \right) \right) + \omega_{her} \cdot \left(1 + \frac{HER - HER_0}{HER_0} \right) + \omega_{acc} \cdot \left(1 + \frac{NC - NC_0}{NC_0} \right) \right\}$	[exc y ⁻¹]	3.13

decreasing for saltmarshes and increasing for the seagrasses. Saltmarshes habitat showed a 4.3% increase within the first 20 years, followed by a 41.7% decrease during the remaining 60 years of simulation. Seagrasses grew by 80.7% in the first two decades and kept growing until the end of the simulation, showing an overall increase of 170.8%. It is worth noting that seagrasses replicate a discontinuity in the dynamics that in the model was given by a shift in the rate of restoration. Benthic diatoms, although they present a competing behaviour with the

seagrasses (visible from the little drop in correspondence to the acceleration of these latter ones), show an overall increase of 51.9% of the surface during the simulated time window. On the other hand, the bare bottom shows a markedly negative trend, with an overall decrease of 84.1%. The fauna groups (Fig. 5a–f) generally present decreasing trends over the simulated period, with a monotonic behaviour for birds (BI) and clams (TA), and a growth phase followed by a consequent decline for the fish groups (LA, DE, MU, SB). In all cases, model results were able

Table 4
List of external forcings used in the model.

Name	Description	Unit	Id
<i>RV(t)</i>	Residents of the lagoon's islands. The number of individuals living in the insular part of the Venice municipality, which includes Venice downtown and the other islands of the lagoon. These islands' population is considered separately from the mainland population because of its rapid decline and high relevant role in ESs flow. Chioggia municipality is not included in this stock because the data available did not allow to divide the residents of the mainland from the ones on the island.	[ind]	4.1
<i>RG(t)</i>	Residents of the surrounding mainland. This stock includes all the individuals living in the municipalities directly facing the lagoon (<i>Gronda lagunare</i> in Italian). These are Campagna Lupia, Cavallino Treporti, Chioggia, Codevigo, Jesolo, Mira, Musile di Piave, Quarto d'Altino, and the portion of Venice municipality located on the mainland (Mestre-Carpenedo, Marghera, Favaro Veneto e Chirignago-Zelarino).	[ind]	4.2
<i>US(t)</i>	University students. This is the stock of individuals enrolled in high-degree institutes in Venice. The student population of the universities represents a considerable percentage of the local population, especially in the islands. The institutes taken into account are: University Ca' Foscari Venezia, IUAV, Fine Art Academy of Venice, Conservatorio di Musica Benedetto Marcello, IUSVE, and Accademia Teatrale Veneta.	[ind]	4.3
<i>TV(t)</i>	Tourist arrivals in Venice. Number of individuals who spend the night in Venice as visitors. The number of tourists visiting Venice has been increasing in the last decades as declared in the municipality's tourism annual report. The increase from the year 2007 to the year 2019 is highly fluctuating but has a yearly average of 3.68%.	[ind]	4.4
<i>kT_{rep}</i>	Celsius degrees of the average water temperature change from the start of the simulation. This value changes yearly and is included in for RCP8.5 (Bucchignani et al., 2016; Canu et al., 2023).	[°C]	4.5
<i>rslr</i>	The relative sea level rise expresses the meters of changes of the average water level in the lagoon. This value changes yearly and is included for RCP8.5. The sea level rise affects directly the habitats and, from the year 2020, triggers the activation of the MOSE moveable dam system	[m]	4.6
<i>input_J</i>	Annual input of fauna group <i>J</i> from outside the system. (With: <i>J</i> = BI, MU, SB, LA) all the fauna groups excluding the clams, that are reared, have an annual increase of fauna density. Besides the birds that fly in freely, the lagoon is connected to the open sea and allows fish to enter if MOSE is not active. The input depends on the status of LCM and the activation hours of the MOSE for the fish fauna.	[ton km ⁻²]	4.7

to match the values of historical data, with a slight underestimation for the TA value. The fish groups (LA, DE, MU, SB) respond positively to the seagrass restoration by increasing by 17.94% (average among groups within the first 20 years). The following decrease, which shows an evident sensitivity to climate trends, has an average that varies among the groups from -0.8% to 61.45% over the total course of the 80 years.

Regulating ESs (Fig. 6g,h,j,k) show different behaviours, depending on habitat trends, and responding to seagrass restoration interventions. In the Lifecycle maintenance (LCM, Fig. 6g) the discontinuity caused by MOSE, causes a sudden drop in 2020, the year of its activation. Provisioning ES (Fig. 6a,b,d,e) generally present decreasing trends, especially in the case of clam harvesting, which matches the available data and shows a progressive decline, reaching values close to zero at the end of the simulated time window. This behaviour is a consequence of a combined decline of both the resource (see TA in Fig. 5f) and the number of clam fishermen (see Fig. IVc in the Appendix). Artisanal and recreational fishing harvests are stable at the beginning of the simulation, showing a local increase from 2014 to 2018 linked to the interventions of seagrass meadows restoration, and consequent expansion of LCM supporting habitats. After 2020, negative trends of different intensities are predicted for all the provisioning services (Fig. 6a,b,d,e). This is a response, by the rate of secondary production, to the progressive water temperature and sea level increase. Sea level rise increases the frequency of MOSE activation, impacting both LCM and the input of fauna at the inlets. Demographic forcings and the extension of attractive habitats, such as the saltmarshes, are the factors impacting on cultural ES dynamics (Fig. 6c,f,i,l), as exemplified in the trends of traditional rowing, which closely follow the population trends of the lagoon residents (Fig. 4c).

3.2. Sensitivity of model parameters

Results of the sensitivity analysis are reported in Fig. 7, showing for each variable the five parameters with the highest mean for the absolute value of local variation (μ^*). Results are plotted in a standard μ^* and σ plane, with the number of plotted points corresponding to the years of simulation. The parameters μ^* and σ are computed on the distribution generated by the ensemble of model runs. SG, BD, BB, MU, and TA reach higher sensitivity values standard (μ^*), up to 20, approximately 1 order of magnitude higher than the parameters analysed for the other state variables. Also, the σ parameter presents marked variability, ranging between the lowest values for BI (maximum 0.03) and the highest for MU (maximum 12). SG and BD vegetated habitats present a similar set of parameters with higher sensitivity, including the expansion rates ni_SG

and ni_BD , and the intensity of ecosystem restoration, $resSG$ and $resBD$. Interestingly, ni_SG is present within the set of higher sensitivity parameters for BD, marking the importance of interdependencies among habitats in the model. This is also confirmed by the high sensitivities of $resSG$ and $resBD$ for BB habitats, whose dynamics are driven by ecosystem restoration actions, although they do not receive direct interventions. SM show a different behaviour, with parameters associated with tourism impact showing the highest sensitivities (Exa_tou ; D_Tou), presenting lower values for both μ^* and σ . Fauna groups consistently show the highest sensitivity rankings for net growth coefficients, rj , carrying capacity densities, kj , and factors modulating temperature influence on growth, kF . The β_LCM rank among the top 5 sensitive parameters for all the fish groups (MU, SB, LA, DE), although presenting differences. The ratio between sensitivity μ^* and σ presents differences among state variables and within the same state variable for different parameters, as visible from the shapes of the line plots. Habitats, apart from BB, show a direct proportionality between μ^* and σ within all the simulations, while for fauna groups, σ values are constant over a wide range of μ^* .

4. Discussion

This study considered twelve ESs, including services impacting both at the local and the global scales (fishing activities or nutrient regulation versus carbon retention and sequestration), without neglecting the role of the cultural services in the feedback network. Indeed, the quantitative and dynamic representation of multiple ecosystem services represents an important feature to be considered by planning and policymaking efforts rooted on the Malawi principles (UNEP/CBD, 1998). Despite this, still a marginal number of studies described quantitatively the trade-offs among more than ten coexisting ESs (Ruiz Agudelo et al., 2020). Recent modelling works attempted filling the gap. The dynamic model by Rashidian et al. (2025) successfully described the complexity of a coastal lagoon system. Differently from the present work, the study focused the attention on two specific sectors and on water quality, considering indices related to these subsystems, and not considering habitat and fauna dynamics. Interestingly, one emerging common feature between the present study and the work by Rashidian et al. (2025) is the focus on the conflicting dynamics between activities belonging to the primary sector (agriculture and fisheries) with tourism. A second relevant example is the work by Sharma et al. (2025), who developed a process-based model for a fishpond-reed agroecosystem and used it to compare multiple management scenarios. Spatial scale and focus on a single type of habitat mark a clear difference with the lagoon-scale

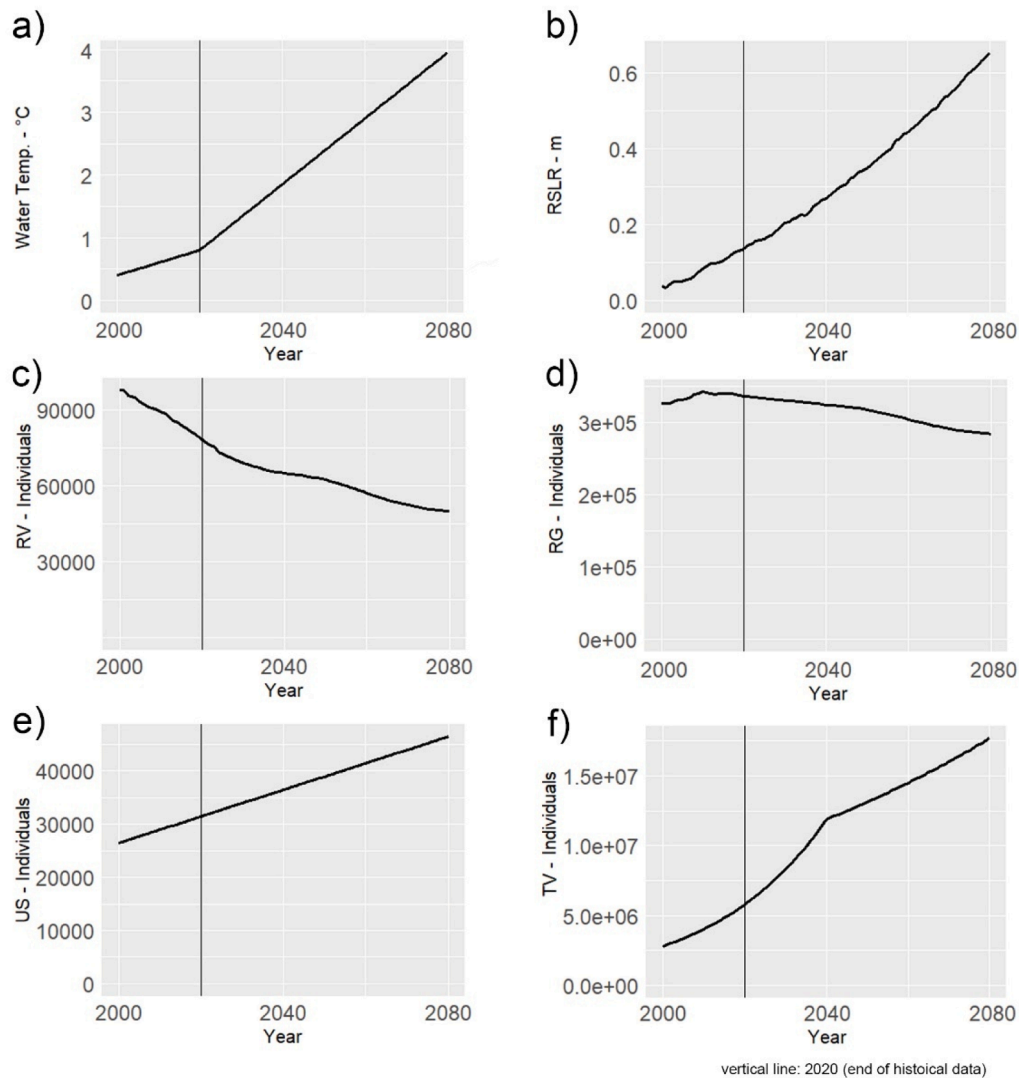


Fig. 4. Time series of forcings used in the simulation. a) Water temperature increase in Celsius degrees. b) rslr: Relative sea level rise in meters. c) RV: Residents of the lagoon islands. d) RG: Residents of the lagoon mainland. e) US: Higher education students. f) TV: Tourists visiting Venice in a year. See text for a detailed explanation on how time series were built.

application considered in the present work. On the other hand, [Sharma et al. \(2025\)](#) included in their model a representation of the food web dynamics based on an Ecopath with Ecosim approach, similarly to the attempt done in the present work. As regards advantages, the deterministic approach adopted by these works, not only provides a clear quantitative overview of the trade-offs among flows, but also enables one to analyse the variability and sensitivity of model state variables to parameters, also representing an element of relevance in a policy-making context ([Brugnach et al., 2007](#)). The following part of this section builds on specific features of the model structure and results, to discuss its strengths and weaknesses, and for guiding its future development and possible management applications.

4.1. Model structure and feedback representation

In terms of structural choices, the complex network of interactions standing behind the provision of ecosystem services described in the model is certainly an extreme simplification of reality, but it presents a level of entanglement that deserves to be described. Some of the internal relationships represented in the layout diagrams, [Fig. 2](#) and [Figs. I–III](#) (Appendix) are visible to the naked eye in the result plots. As can be

seen, the sudden increase of the seagrasses and the decrease of the lifecycle maintenance, both caused by exogenous drivers of restoration and MOSE, propagate to other variables with different intensities. Seagrass growth positively affects the lifecycle maintenance, while the MOSE has a negative impact on it. The lifecycle maintenance, in turn, influences fish stocks dynamics, thus affecting the stock of fishers and hence the fishing activities. Water temperature increase also has a clear role for fauna stocks and consequently for the provisioning ESs, but in this formulation, it has a limited impact on the other services, particularly for the cultural ones. This might be a limitation of the formulation, which links the cultural services to the presence of habitats in the landscape, but not directly to other biodiversity indicators. In fact, biodiversity is pivotal for the emergence of cultural ESs, and its inclusion in this type of model represents a difficult but crucial challenge ([Harrison et al. 2014](#); [Rupprecht et al., 2020](#)). Another important feedback related to cultural services emerges from the sensitivity analysis: the tourist attractiveness of the lagoon depends on the presence of habitats and their accessibility, but tourism results in playing a key role in the progressive loss of saltmarshes and canals (the d_{TOU} parameter was ranked among the highest by the Morris method). On the other hand, other cultural services, such as traditional navigation and

Table 5

Parameters name, description, value and unit of measure.

Name	Description	Value and unit	Id
ni_J	Expansion rate of J (with $J=BD, SG, SM$)	$ni_{BD} : 0.025, ni_{SG} : 0.007, ni_{SM} : 0.00012 [y^{-1}]$	5.1
k_H	Factor of temp. influence on habitat expansion	$0.7 [^{\circ}C^{-1}]$	5.2
k_R	Effect of RSLR on SM	$0.02 [-]$	5.3
GS_J	Management intervention on habitat J (with $J=SG, BD, SM$) NB: interventions on SG are time-dependent to simulate past interventions	$GS_{SG} : var, GS_{BD} : 1.01, GS_{SM} : 1.01 [-]$	5.4
GS_{CAN}	Management intervention on canals	$0.005 [y^{-1}]$	5.5
k_{ER}	Background erosion rate insisting on the bare bottom	$0.0042 [y^{-1}]$	5.6
k_{SA}	Rate of loss of navigable canals surface through siltation	$0.001 [y^{-1}]$	5.7
d_{TA}	Erosive impact of Clam Harvesting	$0.0000046 [km^2 ton^{-1}]$	5.8
d_{TOU}	Erosive impact of Tourism	$0.000000016 [ind^{-1}]$	5.9
d_{NAV}	Erosive impact of Recreational Navigation	$0.0000000057 [ind^{-1}]$	5.10
F_0	Half of initial Bare Bottom $F_0 = \frac{BB_0}{2}$	$94 [km^2]$	5.11
res_J	Percentage of J habitat surface available for restoration per year (with $J=BD, SG, SM$)	$res_{BD} : 0.05, res_{SG} : 0.05, res_{SM} : 0.001 [y^{-1}]$	5.12
k_F	Factor of temperature influence on fauna growth	$0.9 [^{\circ}C^{-1}]$	5.13
β_{LCM}	Response capacity of fauna to LCM	$0.29 [-]$	5.14
$part_F$	Partition proportion of catch between FA & FS for DE	$0.3 [-]$	5.15
r_J	Net growth coefficient for J (with $J=BI, TA, MU, SB, DE, LA$)	$r_{BI} : 0.09, r_{TA} : 2.74, r_{MU} : 0.97, r_{SB} : 1.09, k_{DE} : 1.32, k_{LA} : 0.76 [y^{-1}]$	5.16
k_J	Carrying capacity density of J, the value is estimated as ten times the current reference value of the fauna density for the fish and two times for birds and clams. (with $J=BI, TA, MU, SB, DE, LA$)	$k_{BI} : 0.662, k_{TA} : 27, k_{MU} : 88.2, k_{SB} : 4.5, k_{DE} : 5.6, k_{LA} : 6.9 [ton km^{-2}]$	5.17
H_J	Per capita harvesting rate of J. The value is estimated in order to achieve the provisioning values of the services. (with $J=BI, TA, MU, SB, DE, LA$)	$H_{BI} : 0.0000384, H_{TA} : 0.042, H_{MU} : 0.004462, H_{SB} : 0.0001633, H_{DE} : 0.0003172, H_{LA} : 0.0001925 [ton km^{-2} ind^{-1} y^{-1}]$	5.18
LCM_0	Reference value of LCM, computed using historic values of SG and SM (SM_{old}, SG_{old})	$0.245 [ton km^{-2} y^{-1}]$	5.19
ω_{SM-CD}	% weight of SM on cultural attractiveness	$0.6 [-]$	5.20
ω_{SG-CL}	% weight of SG on cultural attractiveness	$0.4 [-]$	5.21
ω_{her}	% weight of HER on ESs attractiveness	$0.3 [-]$	5.22
ω_{nat}	% weight of natural habitats ESs attractiveness	$0.3 [-]$	5.23
ω_{acc}	% weight of accessibility of the canals on ESs attractiveness	$0.4 [-]$	5.24
ω_{SM-TR}	% weight of the salt marshes on traditional rowing attractiveness	$0.6 [-]$	5.25
ω_{SG-TR}	% weight of the sea grasses on traditional rowing attractiveness	$0.4 [-]$	5.26
k_{ep2}	% of area protected from erosion by SG and BD via bio-stabilization	$0.9 [-]$	5.27
kN_x	% Nitrogen loads removal rate per surface type, with $x = l, m, h$ (l =low, m =medium, h =high)	$l:0.6, m:0.14, h:0.16 [-]$	5.28
kC_L	coefficient of removal of C in L (with $L= SG, SM$)	$k_{CSG} : 725, k_{CSM} : 670 [ton km^{-2} y^{-1}]$	5.29
exA_J	Individual frequency of excursions. (with $J= ROW, EDU, TOU, NAV$)	$ROW : 60.4, EDU : 0.106, TOU : 0.42, NAV : 14.3 [y^{-1}]$	5.30
$perA_J$	Maximum percentage of demographic group J active in the actor group A (with $J = V$ for Islands residents, G for mainland residents, R for all residents, S for higher education students; with $A = TF$ for clam fishers, AF for artisanal fishers, SF for sport fishers, HUNT for hunters, NAV for boaters, ROW for rowers, EDU environmental education students)	$perTF_R : 0.005, perAF_V : 0.0162, perAF_G : 0.00012, perSF_V : 0.026, perSF_G : 0.006, perHUNT_R : 0.00625, perNAV_V : 0.02, perNAV_G : 0.005, perNAV_S : 0.001, perROW_V : 0.027, perROW_G : 0.0017, perROW_S : 0.005, perEDU_R : 0.255, perEDU_S : 0.007 [-]$	5.31

cognitive development, have the possibility to indirectly contrast the loss of habitat, through increasing sensibilization on the importance of habitat restoration (the res_{SG} and res_{BD} parameters). The fact that these four cultural services (recreational navigation is also having a role on the loss of habitat) have contrasting impacts on the habitat dynamics highlights a key mechanism for the Venice lagoon socio-ecological system: the dynamics of the actors benefiting from the different cultural services appear to be governed by two contrasting exogenous drivers, the tourists and residents.

As far as habitats are concerned, we can observe that the simulated restoration and landscape management intervention have an efficacy in contrasting the decline of benthic diatoms and seagrasses. Saltmarshes are most and foremost affected by the impacts of ecosystem services, tourism and navigation (through eq. III.15 Appendix). All these elements reflect the potential of the sensitivity analysis as a tool for understanding model behaviour. The sensitivity test allowed us to rank key parameters driving the dynamics of each state variable. This provides an overview of both the values that are more important to estimate

accurately and the leverage points of a possible sustainable management of the lagoon. One example is the fish fauna, from which the artisanal and recreational fishing services depend, and in which an important role emerged for the β_{LCM} parameter, ranking fourth for SB, LA, DE, and MU. Lifecycle maintenance is directly and indirectly affected by the MOSE, through the exchanges of fauna at the inlets, eq. IV.5 (Appendix), and the saltmarshes growth function, eq. III.12; III.19; III.20 (Appendix). Both these functions are responding to the relative sea level rise, through governance (Eq. (2.12)), thus having a cumulative effect on the decrease of the fauna resource. The negative trend experienced by fish fauna is not only associated with exogenous climate drivers, but also with the harvesting pressure. Harvesting rates respond both to the partitioning of the resource between artisanal and recreational fishermen, and to the governance response to the level of pressure on the resource. These two factors present features deserving further investigation. Indeed, recent studies highlighted the important role played by recreational fishery in the Venice lagoon (Stocco et al., 2024), suggesting also a possible resource response to variable levels of resource partitioning between the

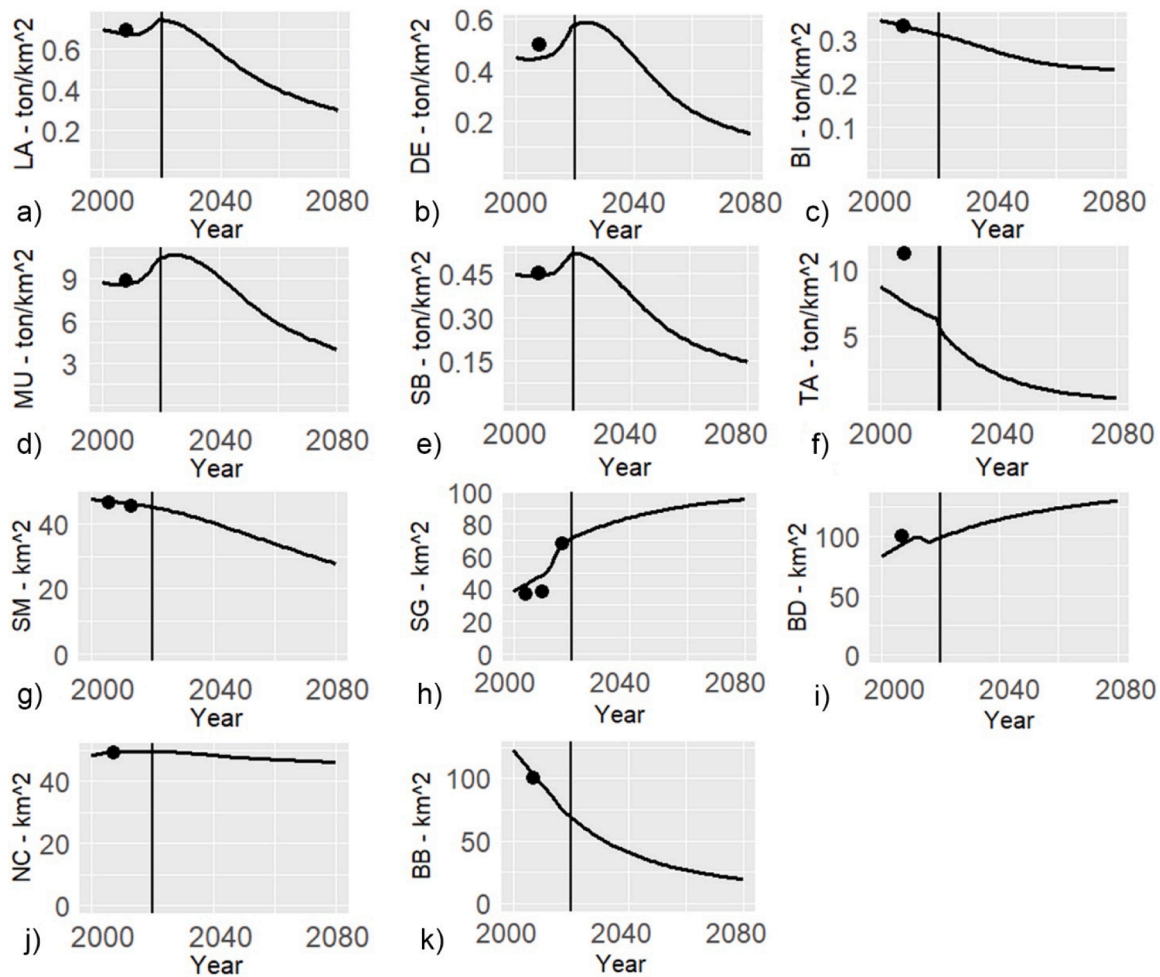


Fig. 5. Plots of the numeric solutions for the state variables. The black vertical line marks the year 2020, which separates the phase of comparison with historical data from the phase of future projections. The variables are: a) LA (seabass), b) DE (demersal), c) BI (birds), d) MU (mullet), e) SB (seabream), f) TA (clam), g) SM (salt marshes), h) SG (sea grasses), i) BD (benthic diatoms), j) NC (navigable canals), k) BB (bare bottom).

two activities (partF), a parameter which in our current formulation is fixed. Regarding the governance response to the pressure on the resource, the model parameterization sets this threshold to half the carrying capacity value, an estimation which may be refined by including further management considerations (Boatto et al., 2008; Riccato et al., 2014). Indeed, for birds, clams and mullets it can be seen the importance of the number of actors involved in the activities, which dynamics are primarily driven by the number of residents in the lagoon and the surrounding mainland (Eqs. (2.1), (2.2), (2.3), (2.4)) but are further modulated by the decrease of the resource.

4.2. Caveats and limitations

As concerns weaknesses, the model presented constitutes the first attempt at representing the Venice lagoon under an integrated quantitative socio-ecological approach, and simplifications were necessary to obtain this formulation. A first important simplification is the non-seasonality of the timesteps that ignore the strong oscillations in the ecological processes (e.g. Rismondo et al., 1997; Bernardi-Aubry and Acri, 2004; Celussi et al., 2009; Franzoi et al., 2010; Baldan et al., 2023). Secondly, we included only the species directly targeted by ESs, while it

is obvious that the ecological processes involved comprehend many other species that define biodiverse areas and are crucial to the well-being of the whole system (Cardinale et al., 2012). Third, the model does not consider the spatial dimension of such a variegated environment, in which heterogeneity and temporal mismatch between ESs supply and demand represent important features for capturing the overall system dynamics (Zulian et al., 2018). One interesting feature that partly compensates these simplifications of the lagoon community ecology is the attempt to use the ESs model in combination with a spatial food web model, which results are based on a long-term development effort (Pranovi et al., 2003; Libralato and Solidoro, 2009; Brigolin et al., 2011; 2014; Anelli Monti et al., 2021). On the other hand, it is worth remarking here that the inter-dependency between the food-web and the ESs models was carried out off-line and one-way, thus neglecting potential feedbacks of the ESs cascade on the resources. Identifying possible solutions to overcome this limitation must be a priority in the future model development agenda. In line with this, it is relevant to highlight a further caveat: in this study, it was not possible to perform a formal validation of the model against a data set independent from the one used for tuning purposes. The coherence of model behaviour was assessed by verifying the agreement with the field data of state variables,

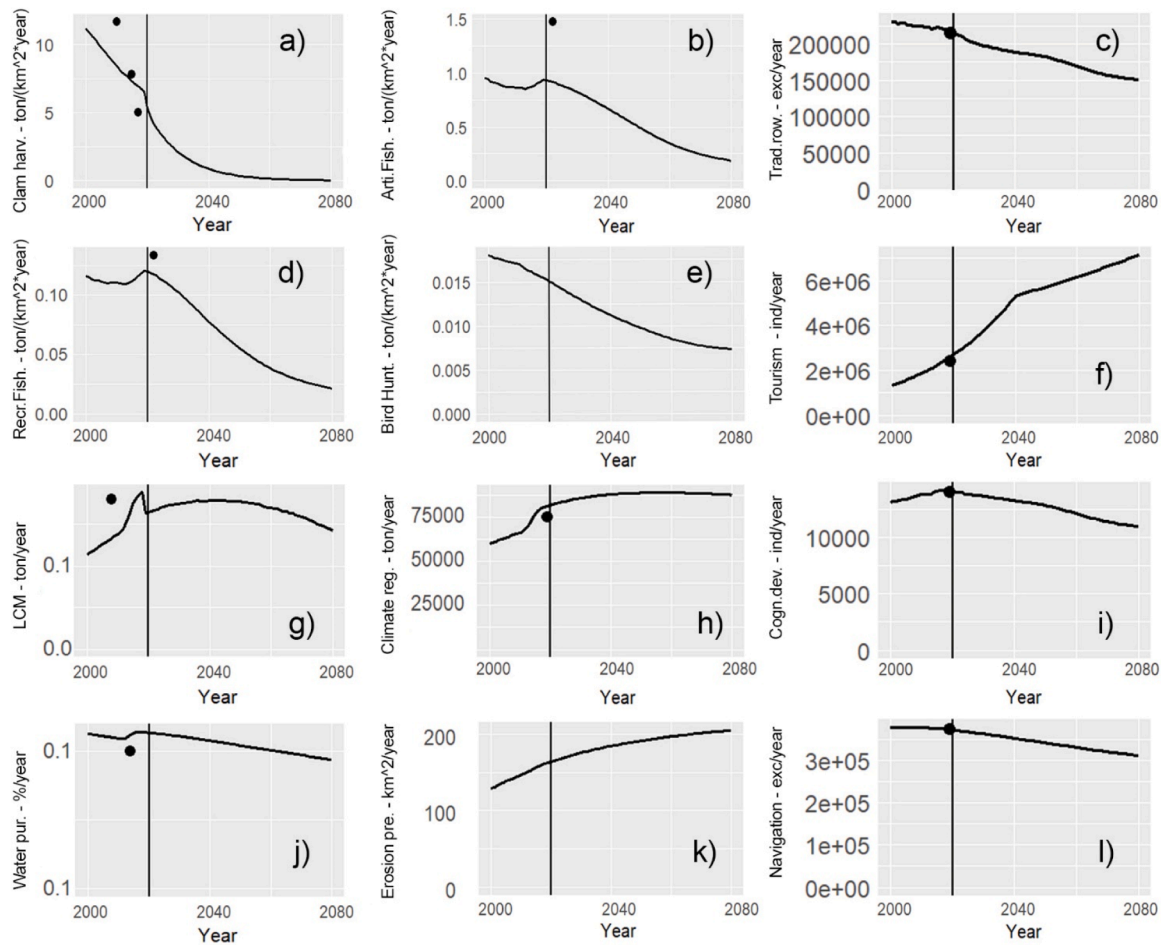


Fig. 6. Plots of the numeric solutions for the Ecosystem Services (ES). The black vertical line marks the year 2020, which separates the phase of comparison with historical data from the phase of future projections. The ES plotted are: a) Clam Harvesting, b) Artisanal Fishing, c) Traditional Rowing, d) Recreational Fishing, e) Bird Hunting, f) Tourism, g) LCM, h) Climate Regulation, i) Cognitive Development, j) Water Purification, k) Erosion Prevention, l) Navigation.

ESs, and actors, which are characterized by different units of measure and order of magnitude. The highest model-data discrepancy is 22%, observed for clams. In this way, we ensured that the model currently identified, with its mathematical formulation and parameterization, is capable to reproduce simultaneously the dynamics of these quantities and, for a subset of these for which more field data were available, to reproduce the observed direction and magnitude of temporal trends. As for habitats, apart from seagrasses, no clear trends have been deducible from the existing data, but it was possible to assess the capability of correctly reproducing the habitat surface orders of magnitude. With respect to fauna, besides the decreasing values of TA, existing literature does not describe in clear terms the trends for the other groups - historical data are available for the amounts of fish sold in the fish/seafood market, but not directly referring to the standing stock. A relatively stable condition was therefore considered reasonable for the first years of simulation, until the visible impacts of seagrass restoration occurred, before 2020. Indeed, further assessment of the model long-term behaviour against contrasting scenarios of forcings will be beneficial. This could ideally be accompanied by the replication of the model application in other lagoon socio-ecological systems, for which a comprehensive assessment of habitats, fauna, ecosystem services, and actors is available.

5. Conclusions

Based on the socio-ecological system framework, this work identified a non-spatial model describing the dynamics of twelve ESs in the Venice lagoon, and ran a numerical simulation for the time period 2000–2080. Within the same period, a sensitivity analysis was performed, thus identifying the highest ranking parameters in shaping the system dynamics. The model was compared with a comprehensive set of *in-situ* data concerning state variables and simulated services. The code used for model simulations is freely accessible through GitHub ([VLES lagoon ES, 2025](#)). Outputs and sensitivity analysis showed that the model is capable to represent contrasting feedbacks among different cultural services, habitat dynamics and fauna, which are subjected to the exogenous trends in tourists and residents. Habitat loss and restoration, and mobile gates closures (MOSE) influence the lifecycle maintenance service, thus shaping the dynamics OF fauna compartments. Nonetheless, the decline in fishery provisioning service is also related to the trend in actors, including artisanal and recreational fishermen.

The adequacy of model results was assessed by verifying the agreement with *in-situ* data for state variables and ecosystem services available, with the observed trends. The capability of reproducing the order of magnitude of the different quantities and the consistency in the long-term

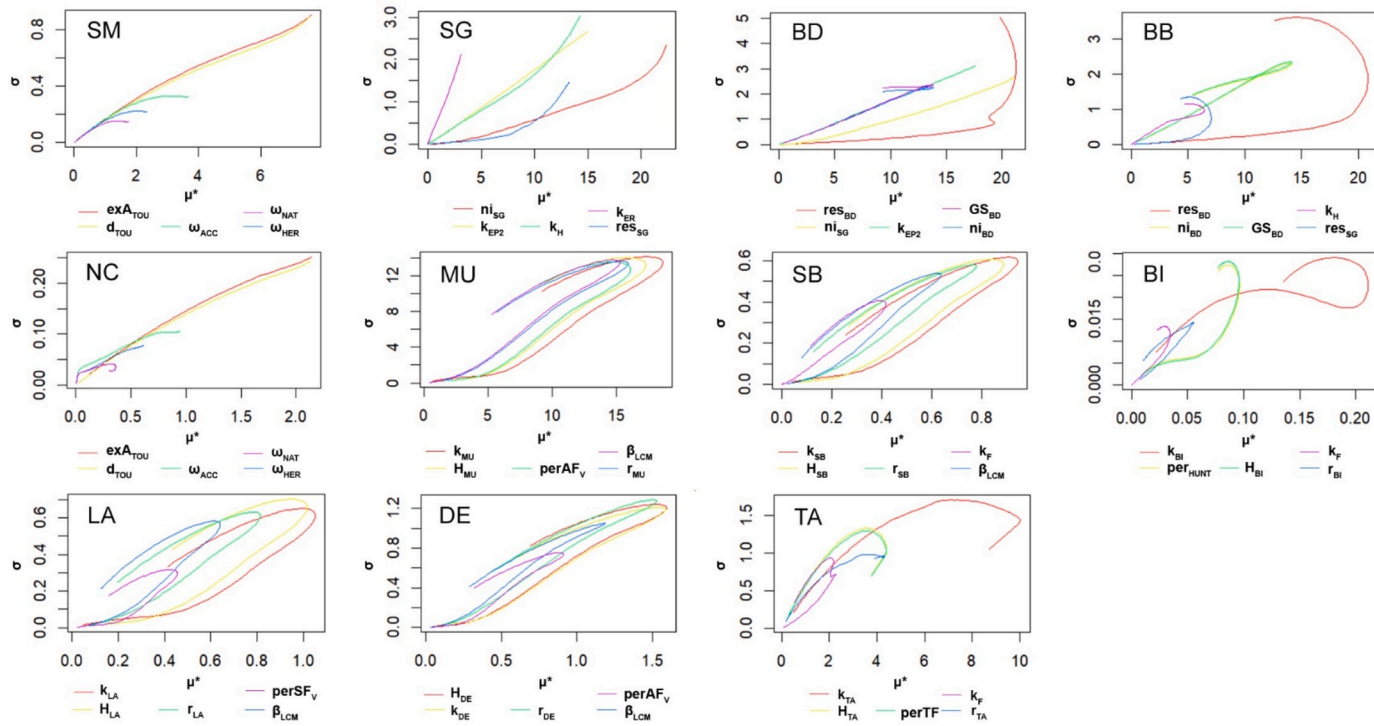


Fig. 7. Plots of the Morris method sensitivity analysis for the state variables. In the plot are shown only the curves of the five parameters with highest μ^* , in a standard μ^* (mean of the absolute of the local variation) and σ (standard deviation) plane. The variables are: LA (*Dicentrarchus labrax*), DE (demersal), BI (birds), MU (mulletts), SB (seabream), TA (clam), SM (salt marshes), SG (sea grasses), NC (navigable canals), BD (benthic diatoms), BB (bare bottom). The parameters included can be found in [Table 5](#).

behavior were considered as additional indicators of model coherence. Additional model validation against an independent set of field data and further testing of the long-term model behavior under alternative scenarios are important future steps, in view of using the model as a management support tool. We also underline the importance of linking the application of this type of model to the results of site-specific spatial food web models, in order to capture community interactions, and advocate for further work on integration between the present model and the existing spatial food web models of the Venice lagoon.

CRedit authorship contribution statement

Stian Rampoldi: Writing – original draft, Software, Methodology, Formal analysis, Data curation. **Silvia Rova:** Writing – review & editing, Validation, Supervision, Methodology, Investigation, Conceptualization. **Fabio Pranovi:** Writing – review & editing, Validation, Methodology, Investigation, Funding acquisition. **Alice Stocco:** Writing – review & editing, Validation, Investigation, Data curation. **Daniele**

Brigolin: Writing – original draft, Validation, Supervision, Methodology, Investigation, Funding acquisition, Data curation, Conceptualization.

Declaration of competing interest

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

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Appendix

Table I
Non-state variables name, description, formula, and unit of measure.

Name	Description	Value	Id
f_{space}	Control variable on Bare Bottom availability $f_{space} = BB(t)/(F_0 + BB(t))$	var [-]	I.1
$fi(\Delta T)$	Variable of temp. influence on habitats expansion $fi(\Delta T) = e^{-kH \cdot waterT(t)}$	var [-]	I.2
f_{RSLR}	Variable of the SM's growth response to the RSLR $f_{RSLR} = e^{-k_R \cdot RSLR(t)}$	var [-]	I.3
f_{MOSE}	Variable % of hours of non-active MOSE in a year $f_{MOSE} = (8765.76 - GS_{MOSE})/8765.76$	var [-]	I.4
f_{sens}	Factor of sensibilization to restoration from cultural services $f_{sens} = \frac{(CognitiveDevelopment + TraditionalRowing)}{(CD_0 + TR_0) + (CognitiveDevelopment + TraditionalRowing)}$	var [-]	I.5
$fk(\Delta T)$	Temperature influence on fauna growth $fk(\Delta T) = e^{-k_f \cdot waterT(t)}$	var [-]	I.6
f_{GS_L}	Clam Harvesting and Bird Hunting availability of the resource J. $f_{GS_L} = \frac{L(t)}{(k_L/2) + L(t)}$ (with $L=BI, TA$)	var [-]	I.7
$f_{GS_{JA}}$	Artisanal fishing availability of the resource J. $f_{GS_{JA}} = \frac{J(t)}{\left(\left(\frac{k_J}{2}\right) \cdot (1 - part_F) + J(t)\right)}$ (with $J= MU, DE$)	var [-]	I.8
$f_{GS_{JS}}$	Sport fishing availability of the resource J. $f_{GS_{JS}} = \frac{J(t)}{\left((k_J) \cdot part_F + J(t)\right)}$ (with $J= SB, DE, LA$)	var [-]	I.9
in_J	Fauna J input coefficient (with $J= BI, MU, SB, DE, LA$) $in_J = 0.02$	var [y^{-1}]	I.10

Table II
Reference values name, description, value, and unit of measure.

Name	Description	Value	Id
SM_{geom}	Percentage of CR in the SM	0.17 [-]	II.1
CD_0	Reference value of students of env. Education per year	19,785 [ind y^{-1}]	II.2
TR_0	Reference value of traditional voga rowers per year	3034 [ind y^{-1}]	II.3
HER_0	Reference value of the surface of tangible cultural heritage	81.644 [km ²]	II.4
SM_{old}	Historic value of the surface of Salt Marshes, extimation for the post-war period	120 [km ²]	II.5
SG_{old}	Historic value of the surface of Sea Grasses, extimation for the post-war period	80 [km ²]	II.6

Equations

Table III
Landscape's equations.

Equation	Id
$growthBB = fromSMtoBB + fromSGtoBB + fromBDtoBB$	III.1
$lossBB = fromBBtoSM + fromBBtoSG + fromBBtoBD + fromBBtoDI$	III.2
$growthBD = fromBBtoBD$	III.3
$lossBD = fromBDtoSG + fromBDtoSM + fromBDtoBB + fromBDtoDI$	III.4
$growthSG = fromBBtoSG + fromBDtoSG$	III.5
$lossSG = fromSGtoBB + fromSGtoSM + fromSGtoDI$	III.6
$growthSM = fromBBtoSM + fromBDtoSM + fromSGtoSM$	III.7
$lossSM = fromSMtoBB$	III.8
$fromBBtoDI = f_{space} \cdot (BB(t) - ErosionPrevention1) \cdot (k_{ER} + (ClamHarvesting \cdot d_{TA} + Tourism \cdot d_{TOU} + RecreationalNavigation \cdot d_{NAV}))$	III.9
$fromBBtoBD = \left(\frac{BB(t) - fromBBtoDI}{FO + BB(t)} \right) \cdot (ni_{BD} \cdot fi(\Delta T) \cdot GS_{BD} + BDO \cdot res_{BD} \cdot f_{sens})$	III.10
$fromBBtoSG = \left(\frac{BB(t) - fromBBtoDI - fromBBtoBD}{FO + BB(t)} \right) \cdot (ni_{SG} \cdot fi(\Delta T) \cdot GS_{SG} + SG0 \cdot res_{SG} \cdot f_{sens})$	III.11
$fromBBtoSM = \left(\frac{BB(t) - fromBBtoDI - fromBBtoBD - fromBBtoSG}{BBO + BB(t)} \right) \cdot (ni_{SM} \cdot fr_{SLR} \cdot f_{MOSE} \cdot GS_{SM} + SM0 \cdot res_{SM} \cdot f_{sens})$	III.12
$fromBDtoBB = (ClamHarvesting \cdot d_{TA}) \cdot (BD(t) - fromBDtoDI)$	III.13
$fromSGtoBB = (ClamHarvesting \cdot d_{TA}) \cdot SG(t)$	III.14
$fromSMtoBB = (Tourism \cdot d_{TOU} + RecreationalNavigation \cdot d_{NAV}) \cdot SM(t)$	III.15
$fromBDtoDI = \frac{BD(t)}{SG(t) + BD(t)} \cdot (SG(t) + BD(t) - ErosionPrevention2) \cdot k_{ER}$	III.16
$fromSGtoDI = \left(\frac{SG(t) - fromSGtoBB - fromSGtoSM}{SG(t) + BD(t)} \right) \cdot (SG(t) + BD(t) - ErosionPrevention2) \cdot k_{ER}$	III.17
$fromBDtoSG = (ni_{SG} \cdot fi(\Delta T) \cdot GS_{SG}) \cdot (BD(t) - fromBDtoBB - fromBDtoDI)$	III.18
$fromBDtoSM = (ni_{SM} \cdot fr_{SLR} \cdot f_{MOSE} \cdot GS_{SM}) \cdot (BD(t) - fromBDtoBB - fromBDtoDI - fromBDtoSG)$	III.19
$fromSGtoSM = (ni_{SM} \cdot fr_{SLR} \cdot f_{MOSE} \cdot GS_{SM}) \cdot (SG(t) - fromSGtoBB)$	III.20
$siltation = (k_{SA} \cdot NC(t) + NC(t) \cdot (ClamHarvesting \cdot d_{TA} + Tourism \cdot d_{TOU} + Navigation \cdot d_{NAV})) \cdot \left(\frac{NC(t)}{NC(t) + NNC(t)} \right)$	III.21
$excavation = (NNC(t) \cdot GS_{CAN}) \cdot \left(\frac{NNC(t)}{NC(t) + NNC(t)} \right) + NC0 \cdot 0.1 \cdot f_{sens} \cdot \left(\frac{NNC(t)}{NC(t) + NNC(t)} \right)$	III.22

Table IV
Fauna equations.

Equation	Id
$growthBI = r_{BI} \cdot fk(\Delta T) \cdot BI(t) \cdot \left(1 - \frac{BI(t)}{k_{BI}} \right)$	IV.1
$growthTA = r_{TA} \cdot fk(\Delta T) \cdot f_{MOSE} \cdot TA(t) \cdot \left(1 - \frac{TA(t)}{k_{TA}} \right)$	IV.2
$growthJ = r_J \cdot \beta_{LCM} \cdot \left(\frac{LifecycleMaintenance_t}{LCM_0} \right) \cdot fk(\Delta T) \cdot J(t) \cdot \left(1 - \frac{J(t)}{k_J} \right)$ (with $J = MU, SB, DE, LA$)	IV.3
$inputBI = in_{BI} \cdot BI_0$	IV.4
$inputJ = (in_J \cdot J_0) \cdot \left(\frac{LifecycleMaintenance_t}{LCM_0} \right) \cdot f_{MOSE}$ (with $J = MU, SB, DE, LA$)	IV.5
$huntBI = H_B \cdot A_{HUNT}(t) \cdot f_{GS_{BI}}$	IV.6
$harvTA = H_T \cdot A_{FT}(t) \cdot f_{GS_{TA}}$	IV.7
$catch_{FAJ} = H_J \cdot A_{FA}(t) \cdot f_{GS_{JA}}$ (with $J = MU, SB, DE, LA$)	IV.8
$catch_{FSJ} = H_J \cdot A_{FS}(t) \cdot f_{GS_{JS}}$ (with $J = MU, SB, DE, LA$)	IV.9

Tuning and Initial Values

Table V

Tuning values for variables and parameters.

Name	Value	Source
Clam Harvesting – 2010	11.64 [ton km ² y ⁻¹]	(Pessa et al., 2018)
Clam Harvesting - 2015	7.8 [ton km ⁻² y ⁻¹]	(Pessa et al., 2018)
Clam Harvesting - 2017	5 [ton km ⁻² y ⁻¹]	(Pessa et al., 2018)
Artisanal Fishing – 2022	1.471 [ton km ⁻² y ⁻¹]	(Rova et al., 2022)
Recreational Fishing – 2022	0.1334 [ton km ⁻² y ⁻¹]	(Stocco et al., 2024)
Climate Regulation (CO ₂ uptake) 2013–2019	74 800 [ton y ⁻¹]	(Rova et al., 2022)
Water Purification (% of nitrogen loads removed) - 2014	12%	(Rova et al., 2022)
Rowing – 2019	215 000 [exc y(1)]	(Rova et al., 2022)
Education – 2019	13 995 [ind y ⁻¹]	(Rova et al., 2022)
Tourism – 2019	2 400 000 [ind y ⁻¹]	(Rova et al., 2022)
Navigation – 2019	372 763 [exc y ⁻¹]	(Rova et al., 2022)
Shallow Intertidal - 1970	331 [km ²]	(Sarretta et al., 2010).
Shallow Intertidal – 2002	291 [km ²]	(Sarretta et al., 2010).
Salt Marshes – 2006	46.54 [km ²]	monitoring from Magistrato alle Acque, year 2006
Salt Marshes – 2013	45.35 [km ²]	monitoring from Magistrato alle Acque, year 2013
Seagrasses – 2004	36.87 [km ²]	(Provveditorato OO. PP. del Triveneto and SELC 2018), (Sfriso et al., 2019)
Seagrasses – 2010	38.06 [km ²]	(Provveditorato OO. PP. del Triveneto and SELC 2018)
Seagrasses – 2017	67.94 [km ²]	(Provveditorato OO. PP. del Triveneto and SELC 2018)
Navigable Canals – 2007	49 [km ²]	(Madricardo et al., 2019)
Tangible Cultural Heritage – 2020	81.644 [km ²]	(Atlante della Laguna, 2026)
BI – 2005	0.33 64 [ton km ⁻²]	(Licheri and Spina, 2005)
TA – 2016	35.1 [ton km ⁻²]	(Rova et al., 2022)
DE – 2008	0.5 [ton km ⁻²]	(Anelli Monti et al., 2021)
MU – 2008	8.82 [ton km ⁻²]	(Anelli Monti et al., 2021)
SB – 2008	0.45 [ton km ⁻²]	(Anelli Monti et al., 2021)
LA – 2008	0.69 [ton km ⁻²]	(Anelli Monti et al., 2021)
Hunters – 2019	1 320 [individuals]	(Pranovi et al., 2022)
Tapes Fishers – 2006	1 041 [individuals]	(Pessa et al., 2018)
Tapes Fishers – 2012	634 [individuals]	(Pessa et al., 2018)
Tapes Fishers – 2017	487 [individuals]	(Pessa et al., 2018)
Artisanal Fishers “tipo A” – 1999	1740 [individuals]	(Rova et al., 2022)
Artisanal Fishers “tipo A” – 2006	1354 [individuals]	(Rova et al., 2022)
Artisanal Fishers “tipo A” – 2012	865 [individuals]	(Rova et al., 2022)
Sport Fishers – 2020	2 500 [individuals]	(Stocco et al., 2024)
Boaters – 2019	24 700 [individuals]	(Rova et al., 2022)
Rowers – 2019	3 034 [individuals]	(Rova et al., 2022)
Environmental st. – 2020	107 514 [individuals]	(ISTAT, 2024)

Table VI

Initial values of the state variables.

Name	Value
BD_0	48 [km ²]
SG_0	18 [km ²]
SM_0	49 [km ²]
BB_0	188 [km ²]
NC_0	40 [km ²]
BI_0	0.331 [ton km ⁻²]
TA_0	11 [ton km ⁻²]
DE_0	0.75 [ton km ⁻²]
MU_0	13.23 [ton km ⁻²]
LA_0	1.035 [ton km ⁻²]
SB_0	0.675 [ton km ⁻²]

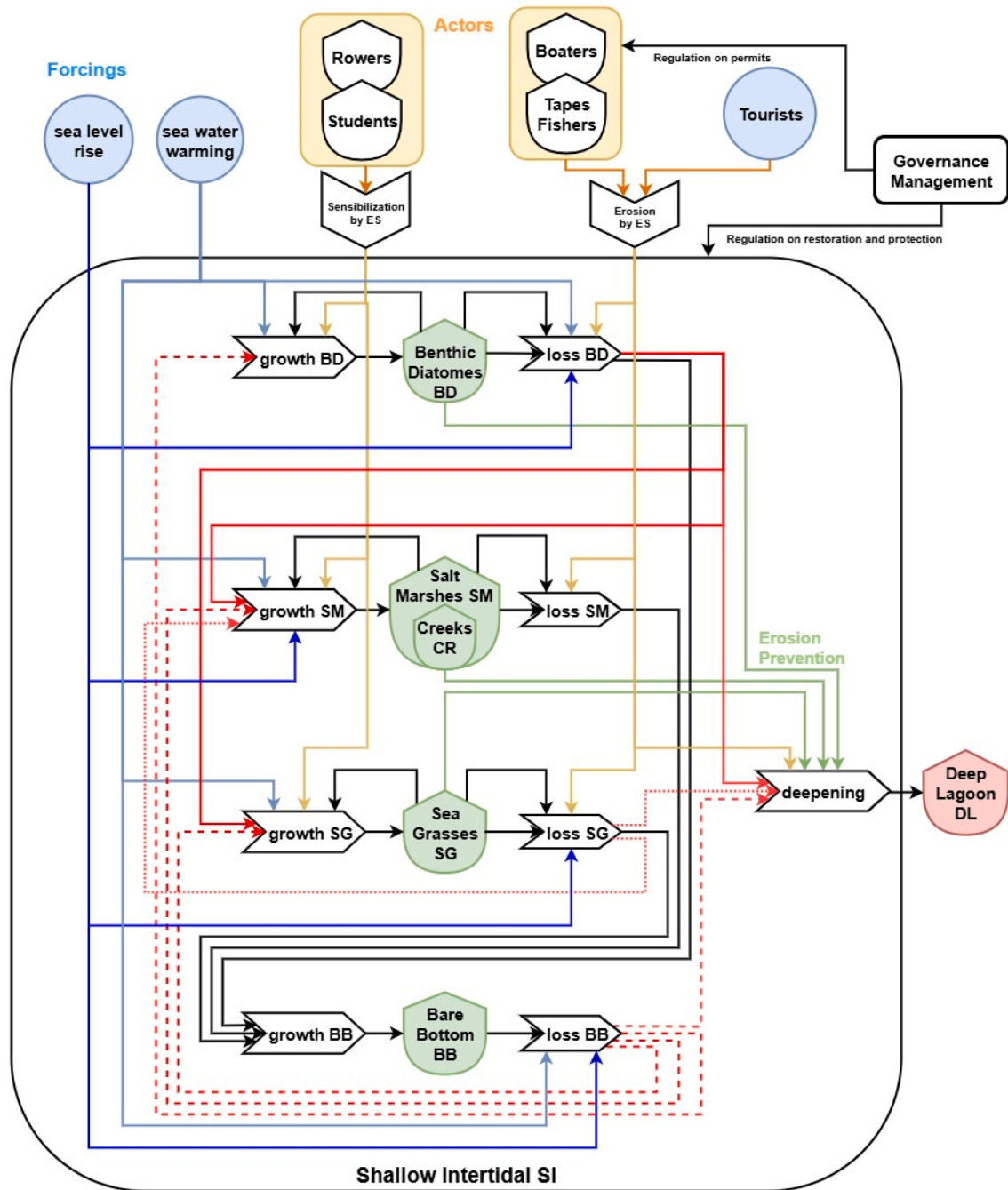


Fig. I. The habitats. In blue are identified the forcings, in yellow the actors, in green the habitats, and in red the output of the subsystem.

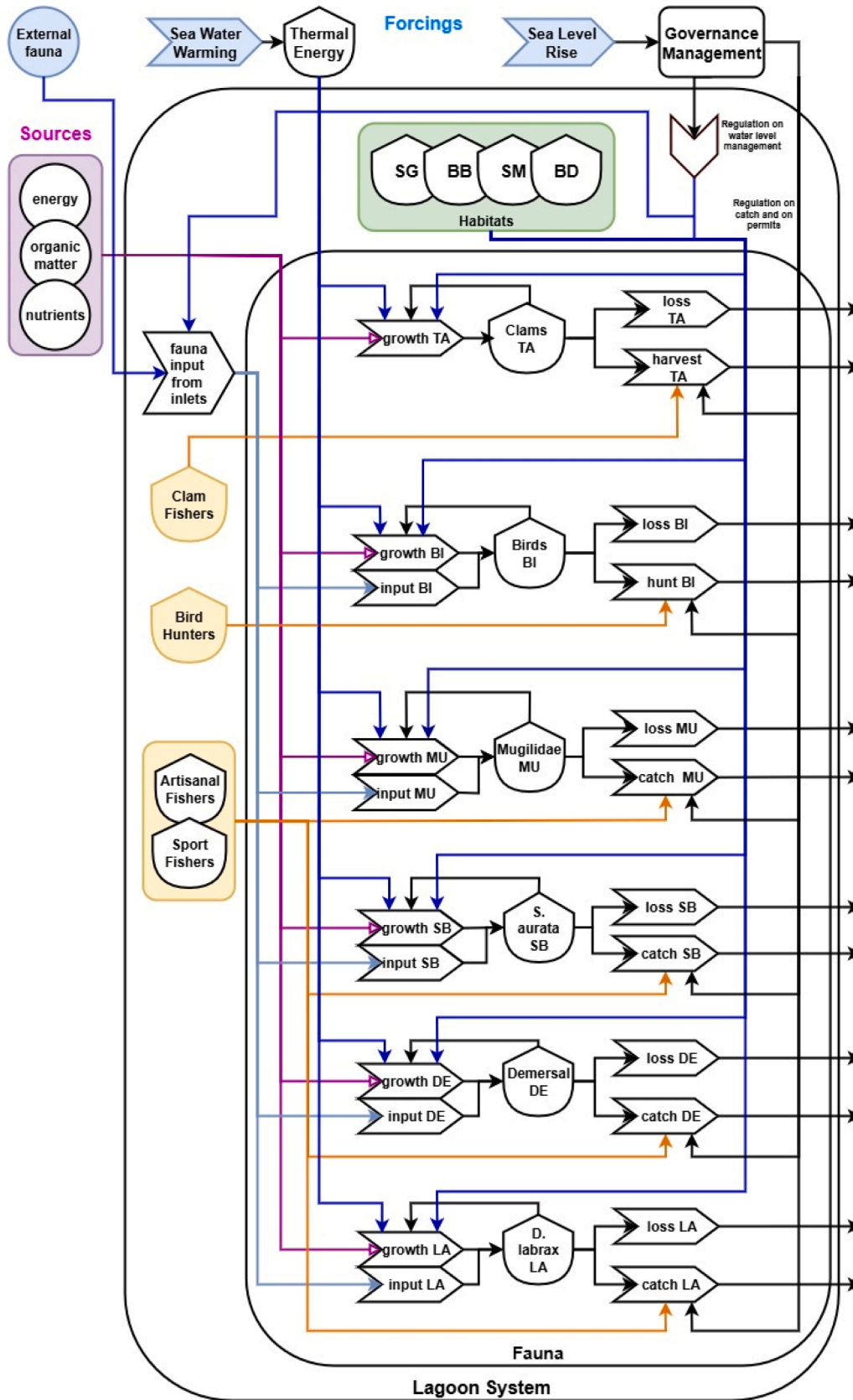


Fig. II. The Fauna. In blue are identified the forcings, in yellow are the actors for provisioning ecosystem services while in green are the habitats (CR=creeks, SG=seagrasses, BD=benthic diatoms, BB=bare bottom), in purple are the sources internal to the system but not taken into consideration by the model formulation.

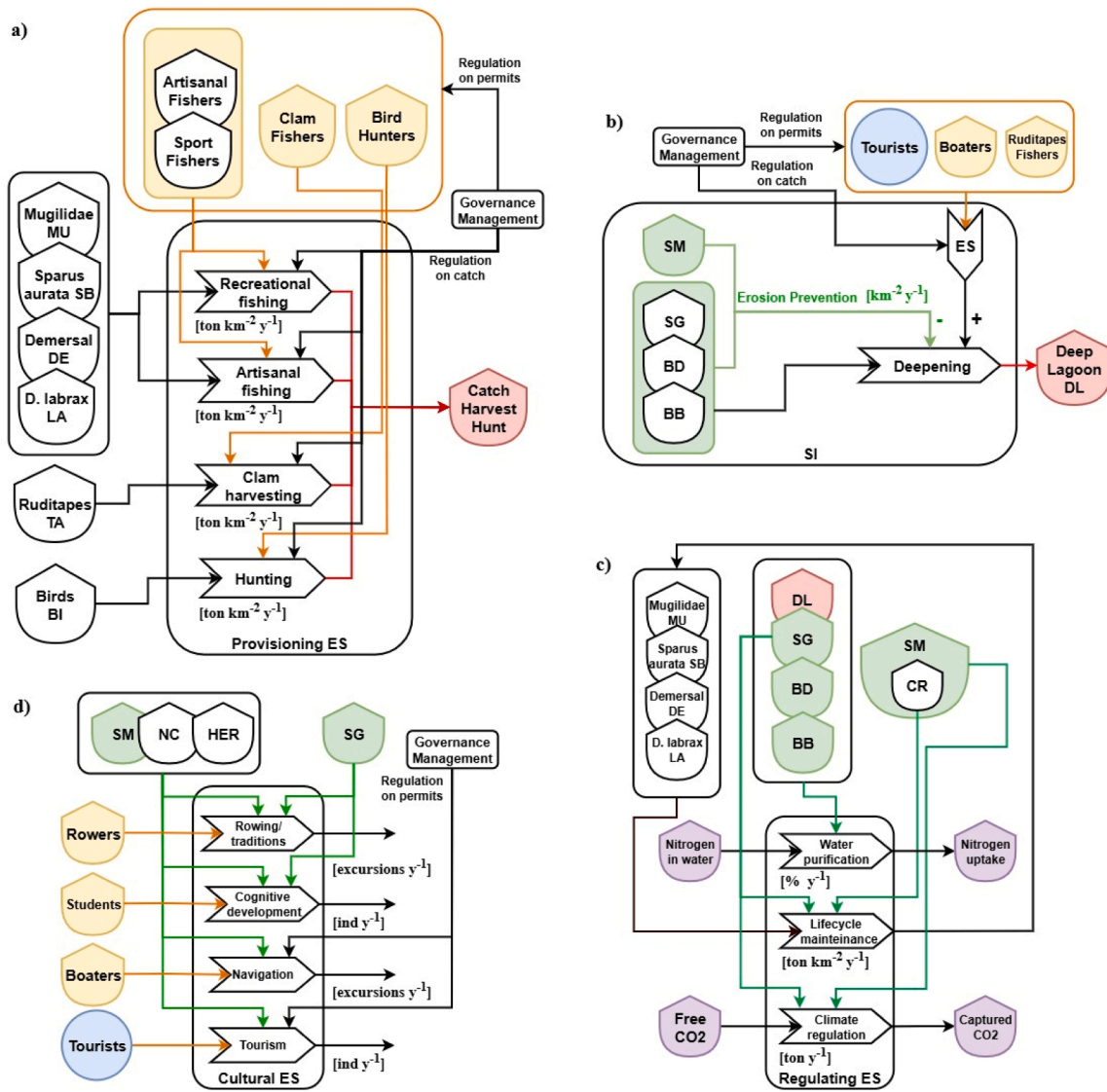


Fig. III. The ecosystem services (ES). A) provisioning ES: the actors are shown with the colour yellow, in red is the output of this subsystem. The ESs are identified as the flow that transforms fauna stock (left side) in catch (right side). These are affected by the stock of the actors, these impacts are shown with the blue arrows. B) erosion prevention ecosystem service. In red is highlighted the output of the subsystem, in blue the forcings. In yellow the internal actors contributing to the erosive processes. The habitats (SM=salt marshes, SG=seagrasses, BD=benthic diatoms, BB=bare bottom, DS=deep subtidal) are involved in this ES, which can accelerate or decelerate the speed of the deepening. C) Regulating ES: The ESs are identified as flows. In the upper part, the stocks of the habitats (CR=creeks) contribute to the services. On the left are placed the stocks that are affected. In purple are the stocks that are not taken into consideration by the model. D) cultural ES: In blue are highlighted the tourists of Venice that are a forcing, in yellow the actors internal to the system. The landscape is influencing, through the blue arrows, these ES (NC=navigable canals, HER=tangible cultural heritage). In green are identified the habitats. The ESs are the flows that transform stocks of potential users into active users.

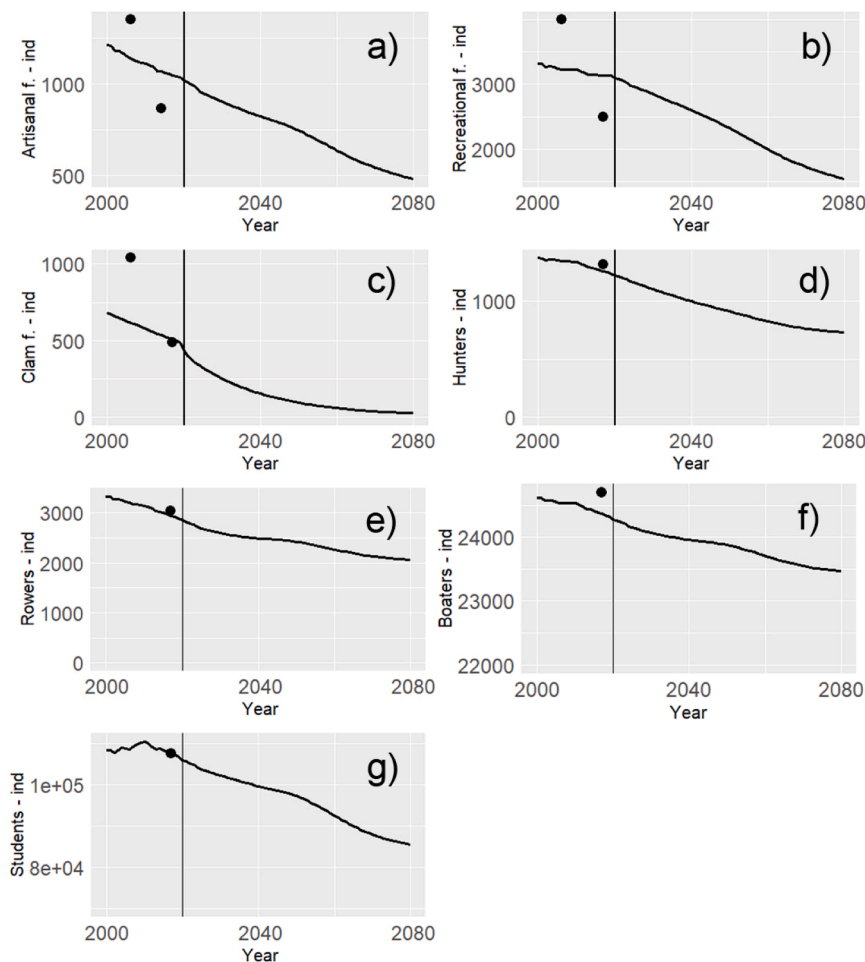


Fig. IV. Plots of the numeric solutions for the actors involved in the ESs. The black vertical line marks the year 2020, which separates the phase of comparison with historical data from the phase of future projections. The actors plotted are: a) Artisanal Fishers, b) Recreational Fishers, c) Clam Fishers, d) Hunters, e) Rowers, f) Boaters, g) Students.

Data availability

The code produced by this research is available through Github. References are included in the text.

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