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Projections of intertidal estuarine seagrass distribution under climate change scenarios using a Bayesian network approach

Gotzon Mandiola [a,b,*], Ibon Galparsoro [a], Mireia Valle [c], Joxe Mikel Garmendia [a], Roland Garnier [a], Javier Franco [a], Ángel Borja [a], Guillem Chust [c], Sarai Pouso [a], Juan Bald [a], José A. Fernandes-Salvador [c]

[a] AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Herrera Kaia, Portualdea z/g, 20110, Pasaia, Gipuzkoa, Spain
[b] University of the Basque Country (UPV/EHU), Plentzia, Bizkaia, Spain
[c] AZTI Marine Research, Basque Research and Technology Alliance (BRTA), Txatxarramendi Ugartea z/g, 48395, Sukarrieta, Spain

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ABSTRACT

Seagrasses have declined worldwide at accelerated rates mainly due to human pressures. Moreover, climate change (e.g. sea level rise) and consequent effects, increase uncertainty about the future evolution of seagrass spatial distribution and biomass. Among other adaptive measures, habitat conservation and restoration can help to adapt and mitigate the adverse effects of climate change in marine and transitional ecosystems. In the research presented, we assess the potential future spatial distribution of *Zostera noltei* coverage under climate change scenarios adopting the Oka estuary (Basque Country), as a case study. For that purpose (i) a conceptual model was developed to illustrate *Z. noltei* system structure accounting for the environmental conditions, human activities, and climate change effects; (ii) the conceptual model was operationalised into a Bayesian network model; (iii) the main environmental variables and human activities that influence the spatial distribution of *Z. noltei* were identified; and (iv) suitable areas for *Z. noltei* considering climate change scenarios (i.e., SSP1-2.6 and SSP5-8.5) were projected. The resulting model showed a high-performance capacity (89.1% of correctly classified instances, and 0.96 area under the curve). Depth is the main environmental variable conditioning *Z. noltei* coverage distribution. The future projections under climate change scenarios show that the *Z. noltei* area is expected to shift landward with sea level rise and that the potential gains of seagrass area will be constrained by anthropogenic barriers. The presented approach and model, demonstrate the capacity of projecting future seagrass distribution under climate change scenarios. The obtained results are a relevant source of information for management, applicable to planning and prioritisation of the most suitable areas for seagrass conservation, and the adoption of restoration actions in estuaries.

1. Introduction

Seagrasses are marine flowering plants present all around the globe, that provide important ecosystem services (Cullen-Unsworth et al., 2014; Nordlund et al., 2016, 2018). In the last decades, seagrasses have declined worldwide at accelerated rates due to multiple factors, such as environmental changes, water quality degradation, disease, coastal modification, mechanical damage, overfishing, and land-sea interactions (Waycott et al., 2009; Manca et al., 2024). Although declining, European seagrass meadows have shown a recent trend reversal (de los Santos et al., 2019), and some signs of recovery have been reported (Dunic et al., 2021). However, the effects of sea level rise increase the uncertainty about the future evolution of seagrasses distribution and biomass (Capistrant-Fossa and Dunton, 2024).

Habitat restoration can help to support and enhance the natural capacity of marine and transitional ecosystems to adapt and mitigate unwanted consequences of climate change (Manea et al., 2023). As stated by the European Nature Restoration Law (NRL) (European Commission, 2022; Hering et al., 2023), restoring marine and terrestrial ecosystems and the species they host will help increase biodiversity, securing nature's contributions to people, limiting global warming, and building up resilience and strategic autonomy. Therefore, restoration is necessary in achieving the current United Nations Sustainable Development Goals (United Nations, 2015), within the Decade of Ecosystem

* Corresponding author. AZTI, Marine Research, Basque Research and Technology Alliance (BRTA), Herrera Kaia, Portualdea z/g, 20110, Pasaia, Gipuzkoa, Spain.
E-mail addresses: gmandiola@azti.es, gmandiola001@ikasle.ehu.eus (G. Mandiola).

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Restoration (Waltham, 2020; Meli et al., 2023), and the European Green Deal (Wolf et al., 2021).

In this context, effective conservation and restoration strategies of habitat-forming species such as seagrasses, which can mitigate climate effects, are considered a type of nature-based solution (Duarte et al., 2020; Gattuso, 2021). Nature-based solutions are a collection of approaches that take advantage of natural processes to reduce emissions and help adapt to climate change (Cohen-Shacham et al., 2016; Gattuso, 2018). Targeted habitats for marine nature-based solutions include seagrasses, saltmarshes, mangroves, kelp forests, coral reefs and shellfish reefs, which can buffer local communities from the negative effects of warming, coastal erosion, habitat loss, and ocean acidification (Duarte et al., 2013; Ramesh et al., 2019; James et al., 2023). In addition, such habitats provide ecosystem services that benefit humans in multiple ways: they can act as key nursery areas supporting biodiversity (including commercially important species), provide natural refuges and feeding grounds, improve seawater quality, reduce coastal erosion and flood risk, function as carbon sinks (regulating climate), and can sustain tourism and cultural activities (Cooley et al., 2022). Despite the important contribution of habitat-forming species to the ecosystem structure and functioning, seagrasses need ambitious global restoration and recovery targets (Gómez-Gras et al., 2021; Buelow et al., 2022).

Zostera noltei is one seagrass species that forms meadows mainly within the intertidal zone, which makes them particularly vulnerable to the effects of climate change as temperature increase and sea level rise (Valle et al., 2014; Ondiviela et al., 2020). By the end of the 21st century, the suitable habitat of *Z. noltei* is expected to shift 888 km northward between 20°N-70°N latitudes and 30°W-60°E longitudes under seawater warming scenarios (Valle et al., 2014). In the Basque Country (northern Spain), *Z. noltei* is currently the uniquely occurring seagrass species, naturally present only in 3 out of 12 estuaries (Valle et al., 2011), with Oka estuary hosting the larger *Z. noltei* area (Valle et al., 2022). Historic records indicate that at least five of the estuaries were formerly vegetated by seagrass (Garmendia et al., 2023). However, they were negatively affected by poor water quality combined with the physical destruction of suitable habitats due to human interventions such as urbanisation and artificialisation of estuaries (Cearreta et al., 2004; Borja et al., 2016; Bilbao et al., 2022). Moreover, the Oka estuary has been the target of professional and recreational fishers for decades, who have mainly exploited bivalves, but also worms and crustaceans in areas where *Z. noltei* seagrass meadows are present (Garmendia et al., 2021). During the last years, monitoring data demonstrate that the water quality has improved in the estuary (Bilbao et al., 2022), allowing successful seed planting and transplanting restoration actions, based on restoration plans that encompasses on feasibility and pre-project planning, project designing, pre-restoration tasks, and restoration/monitoring (Valle et al., 2022; Garmendia et al., 2023).

Climate change effects, such as sea level rise, will also affect *Z. noltei* distribution in estuaries, increasing the suitable intertidal area availability up to the limits imposed by anthropogenic barriers (Valle et al., 2014). In this context, the implementation of emerging modelling techniques can be helpful to assess the future projection of the distribution of seagrasses (Nordlund et al., 2024), as well as support management strategy plans. Previous studies modelled the habitat suitability under scenarios of climate change of seagrass, but did not consider human activities (Valle et al., 2014), and it is known that anthropogenic disturbance caused by harvesting, urban wastewater discharge, nutrient and sediment loading, chemical contamination, eutrophication, and land reclamation is hampering the natural recovery of *Z. noltei* seagrass beds (Cabaço et al., 2008; Han et al., 2012; Calleja et al., 2017; Garmendia et al., 2017, 2021; Branco et al., 2018; Espel et al., 2019; Román et al., 2019, 2024; Vieira et al., 2020).

This research aims to project *Z. noltei* distribution under climate change scenarios using a Bayesian network modelling approach. This approach was adopted due to its potential to resolve spatial planning conflicts (Coccoli et al., 2018), and to estuarine ecosystem management (Grech and Coles, 2010; Bulmer et al., 2022). The specific objectives established were: (i) to develop a conceptual model to illustrate *Z. noltei* system structure, showing the factors that influence the spatial distribution of seagrass, services provided by seagrass, and potential effects of climate change and restoration actions on seagrass; (ii) to operationalize the conceptual model into a Bayesian network adopting the Oka estuary (Basque Country), as a case study; (iii) to quantify the influence of environmental variables and human activities on the spatial distribution of *Z. noltei* coverage; and (iv) to project suitable areas for *Z. noltei* under climate change scenarios. The resulting model provides relevant information for seagrass conservation and planning of restoration actions in estuaries.

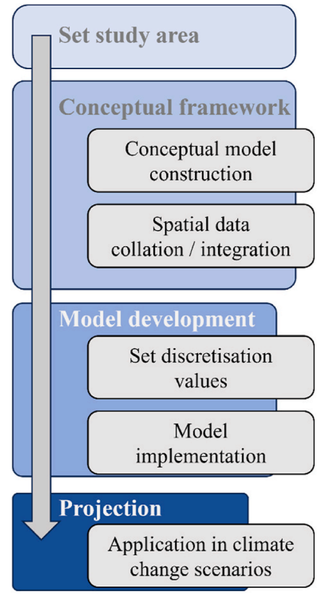

Fig. 1. Workflow for the construction of a model to project *Zostera noltei* coverage distribution under climate change scenarios. Adapted from Gacutan et al. (2019).

2. Material and methods

The research followed the workflow of (i) setting the study area, (ii) defining a conceptual framework, (iii) model development, (iv) and projecting climate change scenarios (Fig. 1).

2.1. Study area

The Oka estuary, located in the Basque Country (SE Bay of Biscay) (Fig. 2), was adopted as a case study for the development and implementation of the approach presented. Currently, natural intertidal populations of *Z. noltei* are present in Oka, Lea and Bidasoa estuaries, with Oka the estuary which hosts the largest seagrass area (Valle et al., 2022). The variety of relevant ecological features present in the estuary is acknowledged by its declaration as Biosphere Reserve by UNESCO in 1984, and RAMSAR Convention on Wetlands in 1993. In addition, it was included in Natura (2000) European Network of Protected Areas in 2000 as a Special Protected Area (ES0000144) and in 2004 as Special Area for Conservation (ES2130007). In particular, *Z. noltei* is listed as an endangered species within the Basque country (Aizpuru et al., 2010) and is included in the Catalogue of Threatened Species (Eusko Jaurlaritza, 2011). Garmendia et al. (2023) identified this estuary as a good donor for the restoration of *Z. noltei* in other estuaries.

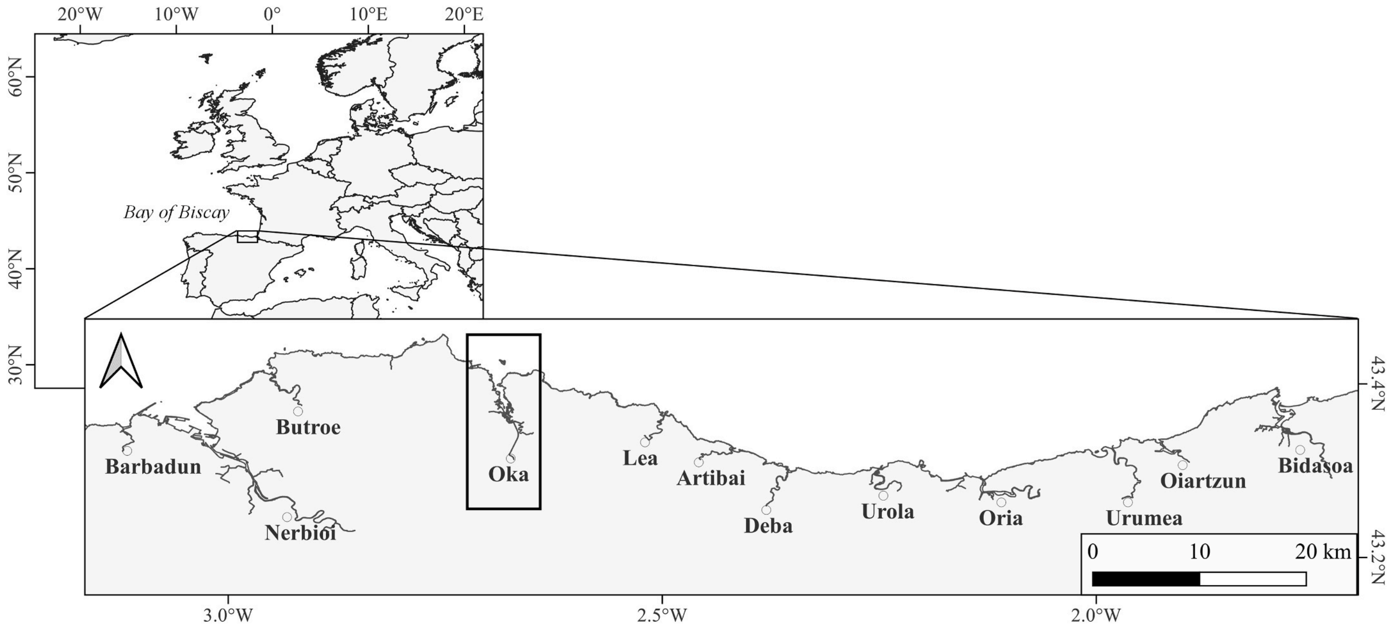

Fig. 2. Basque coast location in the Bay of Biscay and the 12 main estuaries in the Basque coast; the small rectangle corresponds to the Oka estuary.

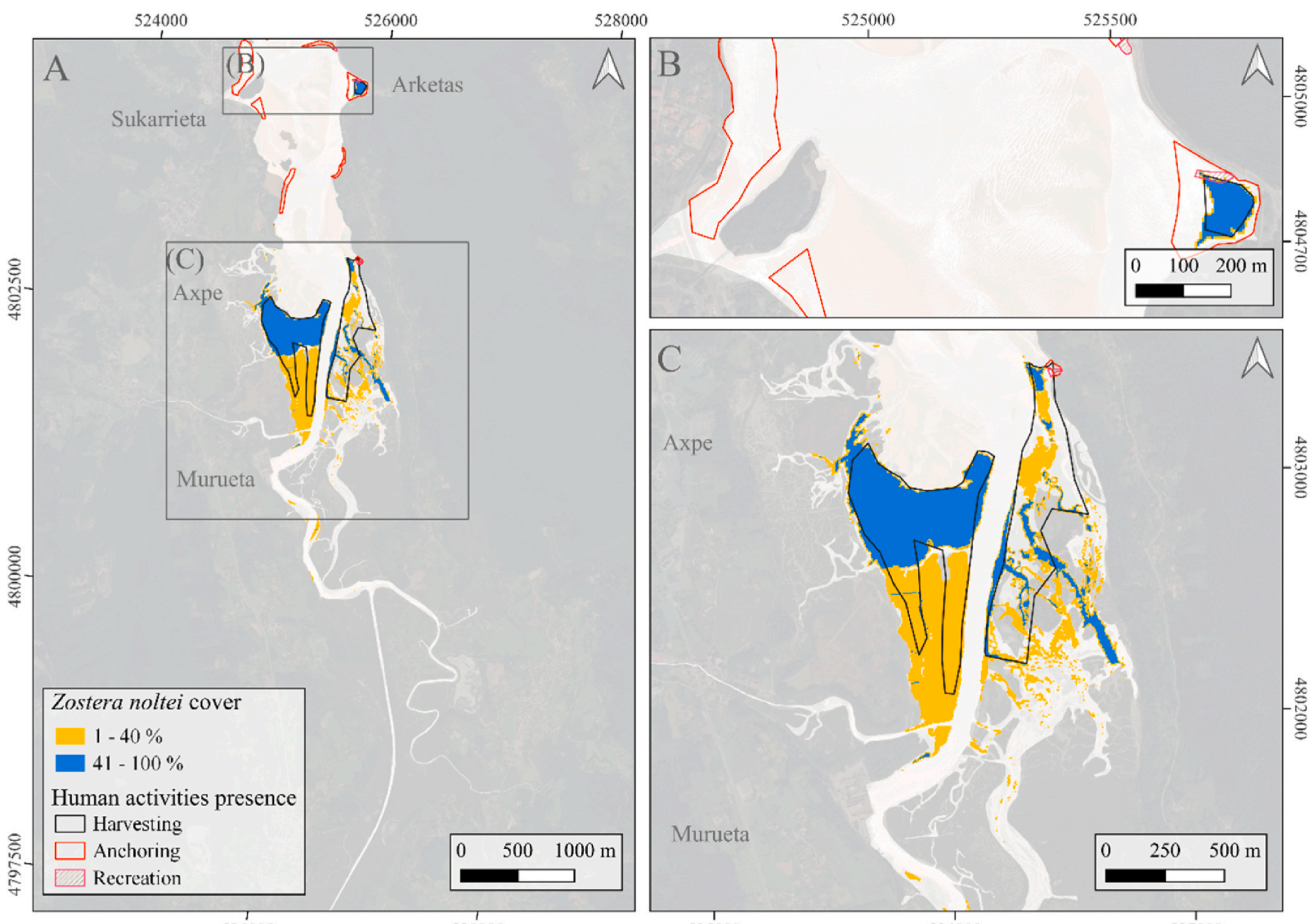

Fig. 3. Spatial distribution of the percentage of coverage of *Zostera noltei* and main human activities in the Oka estuary.

2.2. Conceptual framework

2.2.1. Definition of a conceptual model based on expert consultation

A conceptual model was constructed to reflect the links between environmental factors, human activities and climate change effects on the distribution of *Z. noltei*. The conceptual model was built based on the DAPSI(W)R(M) framework (Elliott et al., 2017); which accounts for drivers, activities, pressures, state changes, impacts (on welfare), responses and measures of a socio-ecological system. This framework was adopted due to its ability to link social and ecological elements of a socio-ecological system, examining how changes to the natural system impact human uses and benefits. Five workshops of 1 h each were held with seven local experts during 2023, to construct the conceptual model.

2.2.2. Spatial data collation and integration

Information layers corresponding to the elements identified in the conceptual model were collated: (i) *Z. noltei* spatial distribution; (ii) digital terrain model of the estuary; (iii) hydrodynamic and wave information and (iv) human activities in the estuary.

Data on the *Z. noltei* distribution within the Oka estuary were obtained from a field sampling carried out in August 2021, where the spatial distribution of the species was mapped using a high-precision differential GPS (Trimble R6 GNSS system with Real Time Kinematic (RTK) technologies) (Valle et al., 2022). During the field sampling, data on *Z. noltei* coverage percentage (1–25%; 26–50%; 51–75%; 76–100%) was estimated visually and applying the cover percentage standards from Seagrass-Watch protocols (McKenzie et al., 2003) (Fig. 3).

Bed level data have been obtained from a 20 m resolution bathymetry in the coastal area (year 2009, Basque Government, www.geo.euskadi.eus), a 1 m resolution topo-bathymetry of the estuary mouth (May 2015, Spanish Government) and 1 m resolution topo-bathymetry for the lower and upper estuary from the digital terrain model of the Basque Country (year 2009, Basque Government, www.geo.euskadi.eus).

The hydrodynamic and wave information was obtained from numerical simulations performed with the Delft3D process-based model (Roelvink and Van Banning, 1995). The model was previously implemented and calibrated in the Oka estuary by Monge-Ganuzas et al. (2017). For the present research, the model was run on a fixed bed for mean and extreme (100-year return period) wave and storm surge conditions, mean spring tides, and different sea water levels (current mean sea level and sea level rise scenarios). Mean (extreme) offshore wave conditions were obtained from the historic data of the Bilbao-Vizcaya wave buoy: a significant wave height of Hs = 1.6 m (Hs = 13.6 m), a peak wave period of Tp = 10 s (Tp = 16 s), and a mean direction of 300° (W/NW). Spring tide conditions and mean (extreme) storm surge conditions have been obtained from the data of the Bilbao tidal gauge. The spring tidal range is 3.83 m, and the mean (extreme) storm surge level considered is 0 (0.47 m) (IHOBE, 2020).

Main human activities in the estuary and source of pressure on *Z. noltei* meadows were found to be harvesting (bivalves, worms and crustaceans), recreation, and anchoring (Garmendia et al., 2023) (Fig. 3). The spatial distribution of the harvesting areas was obtained from consultations with the local harvesters. Regarding recreational activities, the access locations for canoes or kayaks were considered. Other activities such as swimming, walking, fishing, or diving were considered not to directly affect the seagrasses because they do not occur in the intertidal areas where the species is present. A layer of anchoring areas was elaborated using five satellite images from Google Earth at different years and seasons.

All the data were integrated into a 5 m horizontal resolution grid, based on the 1 km resolution grid of the European Environment Agency (EEA, 2011). The values of each information layer were projected in the analysis grid. Hydromorphological variables (depth: water depth in m; swell: significant wave height Hs in m; and current: depth-averaged velocities in m/s) were adopted as continuous data, while human activities (anchoring, recreation and harvesting) were considered as present or absent in each cell of the analysis grid. In the case of the information referring to the distribution of *Z. noltei*, a coverage index (CI) was calculated for each cell (Eq. (1)).

$$\mathrm{CI} = \sum \frac{sp.\ coverage}{Total\ coverage} \cdot \frac{sp.\ covered\ area}{Total\ area}, \qquad \text{Eq. 1}$$

Where sp. *Coverage* is the percentage of *Z. noltei* coverage; *total coverage* is 100 (the maximum coverage possible in a cell); *sp. Covered area* is the area occupied by *Z. noltei* in a cell, and the *total area* is 25 (the maximum occupied area in a cell in m^2).

2.3. Model development

A Bayesian Network (BN) model was developed. BNs models are based on the probability theory and provide a well-founded method for dealing with complex systems (Pearl, 1988). They are demonstrated to be especially useful for decision-making in highly uncertain domains such as some marine social-ecological systems (Fernandes et al., 2010; Trifonova et al., 2015; Coccoli et al., 2018). BN have been recognised as a tool for environmental modelling (Aguilera et al., 2011; Tantipisanuh et al., 2014; Boets et al., 2015; Hamilton et al., 2015) and are increasingly being used in the expert domain due to their graphical component, which allows participatory modelling, for instance, to represent causal relationships between different parts of a system (Lauría and Duchessi, 2007; Gacutan et al., 2019). Furthermore, BNs are a powerful tool in the marine planning context due to the potential inclusion of expert knowledge and empirical data (Stelzenmüller et al., 2010), including its use in identifying suitable areas for offshore renewable energy establishment (Pınarbaşı et al., 2019; Maldonado et al., 2022).

A data-driven 'naïve Bayes' (NB), simple and good performing classification method, was chosen to model the habitat suitability of *Z. noltei* (see Supplementary Material for further details on how the NB model was developed). This was chosen due to its capacity to deal with complex real-world problems (Domingos and Pazzani, 1997; Zhang et al., 2003; Duda et al., 2006), performing better than knowledge-supported models in habitat suitability studies (Boets et al., 2015). The conditional probability distributions are represented as Conditional Probability Tables (CPTs), which can be learnt from data, elicited by expert knowledge or both. In the context of scarce data availability, the use of expert knowledge to populate the CPTs is widespread.

The number of variables included in the NB model was reduced from the variables considered in the conceptual model derived from expert consultation due to lack of evidence. For instance, the magnitudes of the pressures generated by human activities on *Z. noltei*, and the magnitudes of human welfare were not possible to assess to feed the model.

The model was composed of nodes representing the predictive variables (i.e., environmental variables conditioning the presence of *Z. noltei*: depth, current velocity, and swell, in mean and extreme wave and tide conditions; and human activities: recreation, anchoring and harvesting); and a response node corresponding to *Z. noltei* coverage distribution.

2.3.1. Set discretisation values

Entropy reduction and clustering approaches were used to discretise and assess the predicted power of each node for interpretability and robust parameter estimation. Overfitting was avoided by limiting the number of discretisation intervals to three and using 10-fold stratified cross-validation or 10cv (Pearl, 1988; Arthur and Vassilvitskii, 2007; Fernandes et al., 2009, 2010). In 10cv, the data is portioned in 10 parts, where each part is used for testing once and the rest for training of the model. Therefore, the estimated performance is the average of 10 learned models with different test data. As a result several performance metrics are obtained as average of 10 partitions of train-test data: the correctly classified instances, Area Under the Curve (AUC) true positive

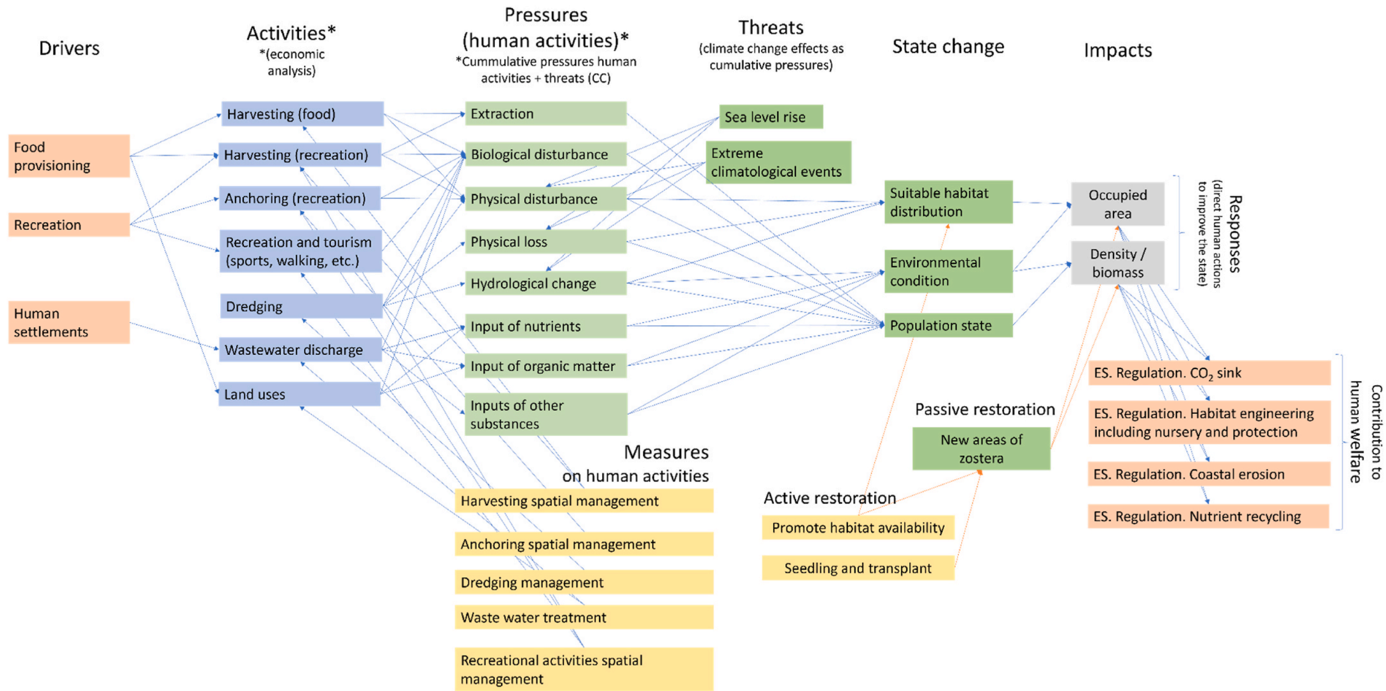

Fig. 4. Conceptual model of *Zostera noltei* system considering Drivers, Activities, Pressures, Threats, State changes, Impacts on human Welfare, and Responses as Measures (DAPSI(W)R(M) framework from Elliott et al. (2017)).

rates and false positive rates, of the model (John and Langley, 1995; Witten et al., 2016).

2.3.2. Model implementation

The final model was implemented in Netica Bayesian network software (Norsys Software Corp.; https://www.norsys.com/). Firstly, the network structure was defined and the parameters (i.e., the conditional probabilities) were inferred from the data. Secondly, a probabilistic inference of variable values was performed to obtain the posterior distribution of the outcomes. Finally, a sensitivity analysis was performed to rank nodes effect on the target node and identify if variables were sensitive or insensitive to another variable (in this case, *Z. noltei* coverage). This analysis makes possible to assess how is the influence of the variables considered on the *Z. noltei* coverage. The sensitivity to findings was quantified by mutual information, used to measure the effect of one variable on another (Pollino et al., 2007; Korb and Nicholson, 2010).

Table 1
Node names, type, states and the discretisation values used for the naïve Bayes development are specified. "L" and "M" in node states column is referring to "Lower than" and "More than", respectively.

Node	Type	Node states	Discretisation intervals
Depth (m) mean condition	Environmental variable	1.L_1.1 2.1.1_4.24 3.M_4.24	[min - 1.1) [1.1–4.24) [4.24 - max]
Depth (m) extreme condition	Environmental variable	1.L_2.26 2.2.26_5.49 3.M_5.49	[min - 2.26) [2.26–5.49) [5.49 - max]
Current (m/s) mean conditions	Environmental variable	1.L_0.41: 2.0.41_0.7 3.M_0.7	[min - 0.41) [0.41–0.7) [0.7 - max]
Current (m/s) extreme conditions	Environmental variable	1.L_0.37 2.0.37_0.78 3.M_0.78	[min - 0.37) [0.37–0.78) [0.78 - max)
Swell "Hs (m)" mean conditions	Environmental variable	1.Zero 2.L_0.05 3.M_0.05	0 (0–0.05) [0.05 - max]
Swell "Hs (m)" extreme conditions	Environmental variable	1.Zero 2.L_0.24 3.M_0.24	0 (0–0.24) [0.24 - max]
Harvesting	Human activity	N Y	No presence Presence
Anchoring	Human activity	N Y	No presence Presence
Recreation	Human activity	N Y	No presence Presence

2.4. Projections in climate change scenarios

Two global scenarios defined by the IPCC (2023) were considered to project *Z. noltei* habitat distribution: the low-emission scenario SSP1-2.6 and the high-emission scenario SSP5-8.5. These two scenarios were selected due to their difference in social future evolution, enabling to project a sustainable path, and a fossil-fuelled development path (O'Neill et al., 2017). Projections of the environmental condition variables in the SSP1-2.6 scenario were obtained for 0.25 m of sea level rise in 2050, and in the SSP5-8.5 for 1 m of sea level rise in 2100. As it was not possible to assess the spatial distribution of variables representing the human activities in the scenarios considered, it was assumed to remain the same under both scenarios.

NB was applied under climate change scenarios, obtaining the probability of *Z. noltei* coverage at each cell of the analysis grid. Finally, maps of the distribution of *Z. noltei* coverage suitability under climate change scenarios were produced assigning the most probable *Z. noltei* coverage value.

3. Results

3.1. Conceptual model

The model representing the *Z. noltei* system in the estuary is composed of 38 elements and 71 links between them representing eight

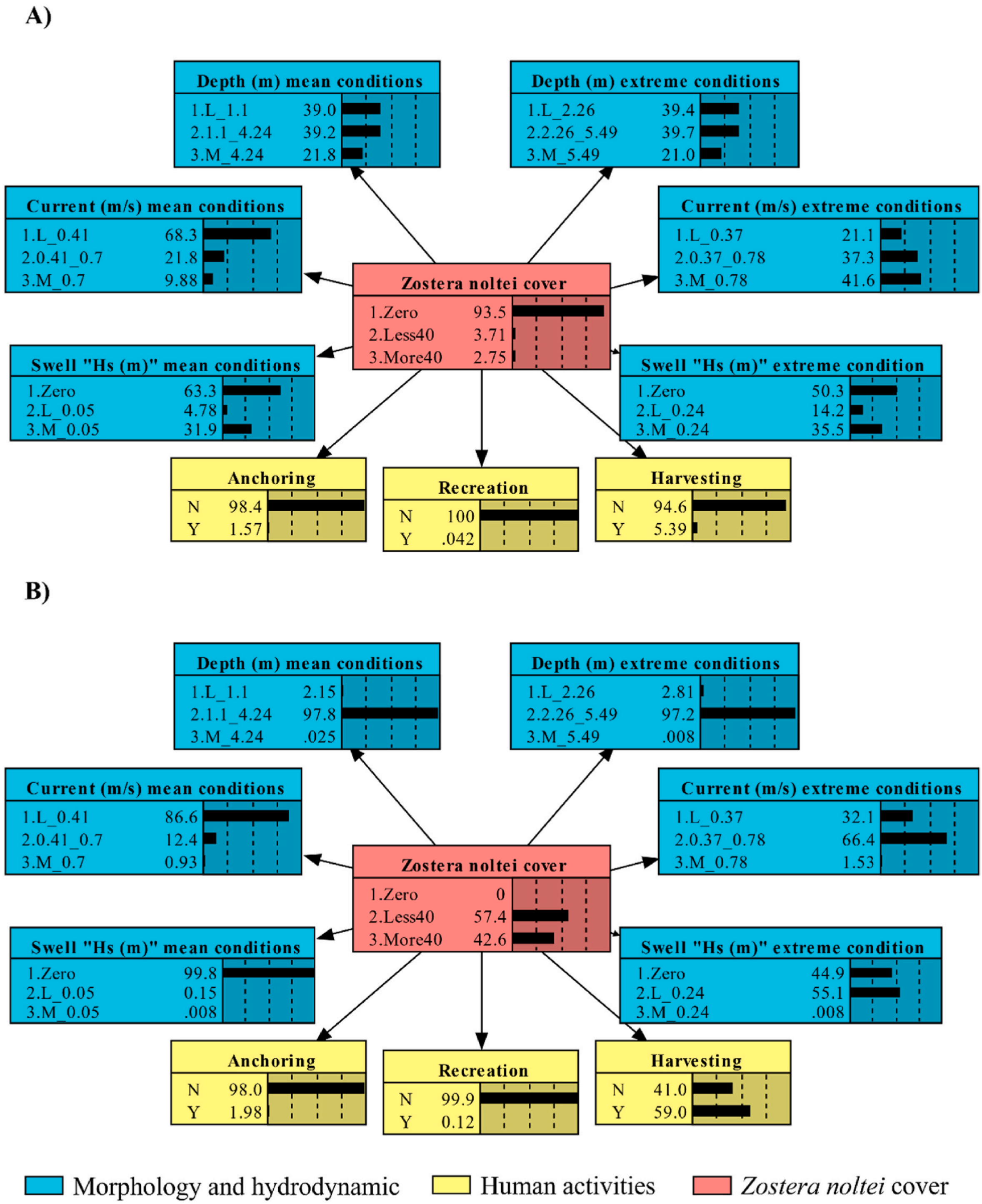

Fig. 5. A naïve Bayes network representing the main factors conditioning the *Zostera noltei* spatial distribution and coverage: in all the estuary (A), and in areas of *Z. noltei* presence (B). All variables were discretised into three states except human activities, which were discretised in two states (i.e., presence/absence). See Table 1, for the codification of states for each node in the model.

dimensions of the DAPSI(W)R(M) framework (Fig. 4). Three drivers (i.e., food provisioning, recreation, and human settlements) are linked to eight human activities carried out in the estuary (i.e., harvesting for food and bait for recreational fishing, anchoring, recreation (e.g. canoeing), dredging, wastewater discharge and land uses), producing eight types of pressures (i.e., extraction of organisms, biological and physical disturbance, physical loss, hydrological change, and inputs of nutrients, organic matter and other substances). Climate change effects were treated as threats that would produce cumulative pressures derived from "sea level rise" and "extreme climatological events". The cumulative effects of pressures produced by human activities and climate change were considered as impacts that would affect suitable habitat distribution, and thus, occupied area and density or biomass of *Z. noltei* (i.e., population state). In terms of potential management responses, active restoration interventions were considered as the promotion of suitable areas for the settlement of *Z. noltei* together with seeding and transplant; while passive actions were related to management measures applied to human activities, to reduce and mitigate impacts on *Z. noltei*, and

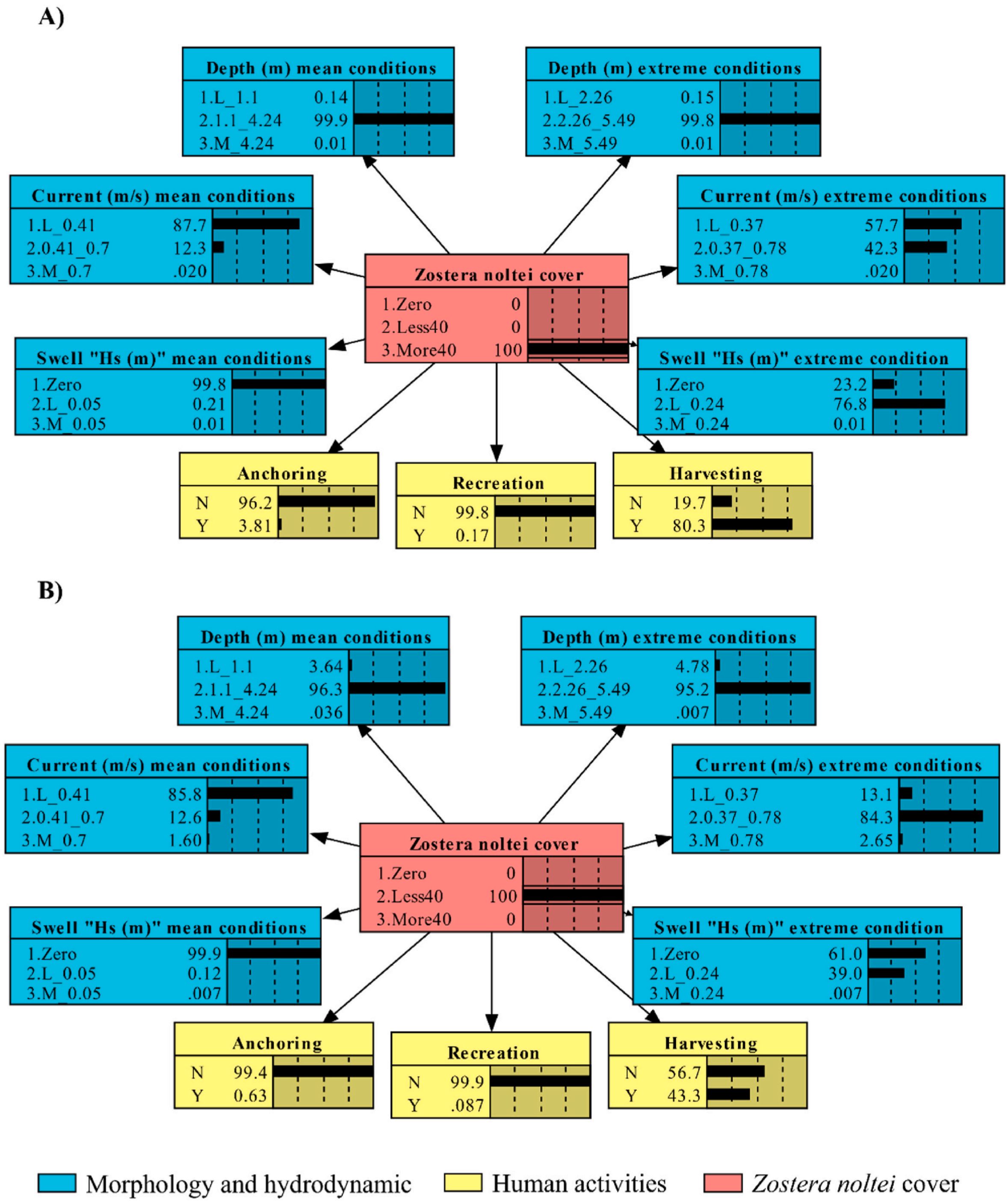

Fig. 6. A naïve Bayes Network representing the probability propagations for 41–100% *Zostera noltei* coverage (A), and 1–40% coverage (B) in seagrass meadows. See Table 1 for the codification of each state at each node of the model.

consequently, improvement of the environmental conditions. The conceptual model also considered the main ecosystem services derived from *Z. noltei*, under the concept that changes in the species abundance affect their contribution to regulation services such as CO_2 caption and sink, maintenance of nursery habitats, control of coastal erosion, and nutrient recycling.

3.2. Naïve bayes model

The NB model consists of 10 nodes (Table 1), 9 links and 75 conditional probabilities (Fig. 5A). The model accounts for the main environmental and human activity predictors conditioning the distribution of *Z. noltei*.

The model resulted in 89.1% of instances correctly classified, and 0.96 AUC. High true positive rates for high coverage (over 41%) and non-coverage areas were predicted (76% and 91%, respectively); while the false positive rates were very low in areas of high *Z. noltei* coverage (2.6%).

The model captured that *Z. noltei* was present in 6.5% of the estuary. In 3.71% of the area, *Z. noltei* coverage was between 1 and 40%, while in 2.8% of the area, the cover ranged between 41 and 100% (Fig. 5A). Attending only to areas with the presence of seagrass meadows, 57.4% of the area showed 1–40% coverage, while 41–100% coverage represented 42.6% (Fig. 5B).

Table 2
Higher to lower sensitivity variables for *Zostera noltei* coverage based on calculated mutual information.

Variable	Type	Mutual information
Harvesting	Human activity	0.131
Depth in mean condition	Environmental variable	0.083
Depth in extreme condition	Environmental variable	0.080
Swell in extreme conditions	Environmental variable	0.076
Current in extreme conditions	Environmental variable	0.056
Swell in mean conditions	Environmental variable	0.043
Current in mean conditions	Environmental variable	0.011
Anchoring	Human activity	0.001
Recreation	Human activity	0.0001

The marginal probability distribution for high or low *Z. noltei* cover (i.e. the probability that the predictor variable was in that state (or value) when the seagrass cover was high or low), indicated that 99% of the areas of high (41%–100%) *Z. noltei* coverage were found in areas between 1.1 m and 4.2 m depth, and not exposed to wave swell in mean wave and tides conditions (Fig. 6).

In extreme conditions, high coverage areas were found to be distributed between 2.26 m and 5.49 m depth, in zones between zero and 0.24 m of swell in 77% of cases, and not exposed to wave swell in 23% of cases. Areas of high *Z. noltei* coverage were exposed to mean current velocity lower than 0.41 m s^{-1} in 88% of cases and between 0.41 and 0.7 m s^{-1} in 12% of cases; and extreme current velocity lower than 0.57 m s^{-1} in 58%, and between 0.37 and 0.78 m s^{-1} in 42% (Fig. 6A).

According to the marginal probability distributions, 96% of low *Z. noltei* coverage (1–40%) areas were found between 1.1 m and 4.2 m depth, and not exposed to wave swell in mean wave and tides conditions. However, in areas shallower than 1.1 m in mean conditions and shallower than 2.26 in extreme conditions, the probability of finding low *Z. noltei* coverage areas were found to be higher than areas with high coverage. The 99% of low coverage areas were not exposed to swell in mean wave and tide conditions. Under extreme conditions, 61% of the low-coverage areas were not exposed to swell (38% more than high-coverage areas) and 39% of the area was exposed to swell of less than 0.24 (i.e., 38% less than high-coverage areas).

In 85.8% of the area showing low *Z. noltei* coverage, current velocity in mean condition was lower than 0.41 m s^{-1}, between 0.41 m s^{-1} and 0.7 m s^{-1} in 12% and more than 0.7 m s^{-1} in 2% of the area (Fig. 6B). Under extreme conditions, 84% was between 0.37 m s^{-1} and 0.78 m s^{-1}, in 13% lower than 0.37 m s^{-1}, and in 3% more than 0.78 m s^{-1}.

Regarding human activities, biological resources harvesting was spatially overlapping in 80.3% of high *Z. noltei* coverage areas, and in 43.3% of low coverage areas. Anchoring was held in 3.8% of high seagrass coverage areas, and less than 1% of low coverage areas (Fig. 6A and B).

The most sensitive variables to *Z. noltei* spatial distribution were found to be, in order of relevance: harvesting activities, depth in mean and extreme conditions, swell in extreme and mean conditions, current in extreme and mean conditions, anchoring, and recreation. Thus, harvesting and depth showed the greatest weight on seagrass cover in the meadows, contributing to a larger uncertainty reduction (Table 2).

3.3. *Projections of Zostera noltei distribution and coverage under climate change scenarios*

Z. noltei distribution and coverage was projected for SSP1-2.6 and SSP5-8.5 climate change scenarios (Fig. 7 and Table 3). In general terms, the model projects a high probability for the expansion of *Z. noltei* in the estuary.

Excluding projected coverages in wall-enclosed areas, the expected *Z. noltei* distribution is expected to be lost by 15% (0.09 km^2) under SSP1-2.6 scenario and by 6.8% (0.04 km^2) in SSP5-8.5 scenario. Similar seagrass coverage is expected to be maintained for both scenarios, with 60.5% (0.36 km^2) and 61.4% (0.37 km^2) for the SSP1-2.6 and SSP5-8.5 scenarios, respectively. Besides, 93.5% (0.56 km^2) and 218.5% (1.31 km^2) area net gain is expected for SSP1-2.6 and SSP5-8.5 scenarios, respectively. Moreover, the seagrass coverage increases from 1-40% to 41–100% in 32% (0.11 km^2) in the SSP1-2.6 scenario and 45% (0.15 km^2) in the SSP5-8.5 scenario. However, some areas will suffer a reduction in *Z. noltei* coverage, with a 14.3% (0.04 km^2) decrease from 41-100% to 1–40% of the area in the SSP1-2.6 scenario, and in 13.8% (0.035 km^2) in the SSP5-8.5 scenario.

The presence of *Z. noltei* is expected to decrease in certain areas of the estuary (reduction in Arketas area and increase in the western part of the river) (Fig. 8). In contrast, new areas with low and high *Z. noltei* coverage are projected at higher altitudes than the present occurrence (the zone between Axpe and Murueta) (Fig. 8). In the southern area (Murueta), some areas with *Z. noltei* coverage are expected to be lost, and new areas with low coverage will appear (Fig. 8).

4. Discussion

4.1. *Zostera noltei model*

The conceptual model captures the factors interplaying in the *Z. noltei* distribution and provides a strong foundation for data and knowledge gathering. The good performance of the model indicates that it captures the present *Z. noltei* distribution, and that it can be applied in the projection of the seagrass meadows distribution and coverage under climate change scenarios. The performance/predictability capabilities of the produced model are in the range of other seagrass habitat modelling approaches (van der Heide et al., 2009; Wang et al., 2024), and models implemented for other species (Boets et al., 2015; Oh et al., 2019). These models obtained 68–77% of correctly classified instances and 0.7–0.96 AUC, within the model presented in this work performed 0.89 correctly classified instances, and 0.96 AUC. Other models shows BNs have demonstrated to be useful in dealing with the problem of limited data (Tantipisanuh et al., 2014; Hamilton et al., 2015), and data-driven NB models combined with expert knowledge, proved a high predictive performance in high-complexity models (Boets et al., 2015).

The results indicate that invertebrate harvesting is the most influential human activity in the distribution of *Z. noltei* coverage. This is interpreted as a co-occurrence of harvesting and *Z. noltei*. This is because targeted species for harvesting are mainly in areas of *Z. noltei* and thus, seagrass presence is reflecting its role as ecosystem structuring and engineering for some species for benthic invertebrates (Hosack et al., 2006; Bouma et al., 2009; Brun et al., 2009; Grilo et al., 2012; Ricart et al., 2021). The areas where *Z. noltei* is present are dominated by fine-grain sediments which are a suitable sediment type for certain bivalve species such as cockles (*Cerastoderma edule*) and worms (Zorrozua et al., 2015). The area where *Z. noltei* is present shows an annual average of 20–30 people per day harvesting for 4–6 h, and the months between August and October are devoted to the harvesting of bivalves and worms and leisure activities (Garmendia et al., 2021). Biological resource harvesting is a threat to *Z. noltei* due to the disturbance generated by the extraction method (Guimarães et al., 2012; Garmendia et al., 2021), and thus, it is a relevant aspect to be considered when proposing conservation and restoration measures (Román et al., 2020).

The most relevant environmental variables for *Z. noltei* prediction were found to be depth in mean and extreme conditions. Depth ranges determined by our model are in line with previous studies in the estuary, projecting the presence of *Z. noltei* in a depth range of 1–4 m (Valle et al., 2014), and other estuaries worldwide (Ganthy et al., 2013; Azevedo et al., 2016). Other studies showed that hydrology and hydrodynamics are also influential for the *Z. noltei* growth capacity (Cognat et al., 2018).

The current velocity in *Z. noltei* suitable areas tends to be low, both in mean and extreme conditions, which is coherent with the sediment distribution in the estuary. The current velocity affects directly *Z. noltei* growth, morphology and plant architecture, producing larger leaves at

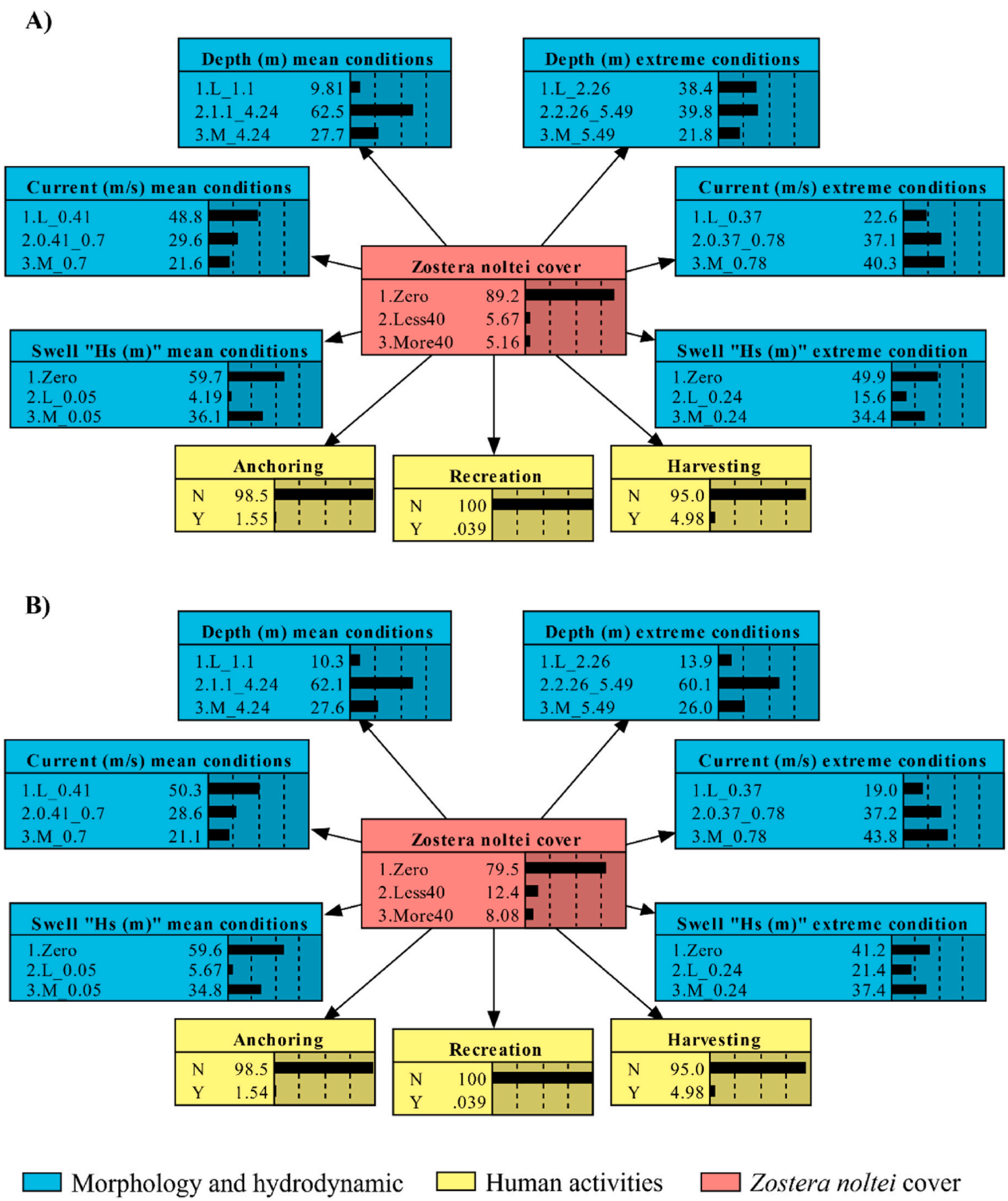

Fig. 7. A naïve Bayes Network representing the main factors and relationships conditioning the *Zostera noltei* distribution and coverage in SSP1-2.6 scenario (A), and SSP5-8.5 scenario (B). See Table 1 for the codification states for each node.

low current velocity locations (Peralta et al., 2006). In turn, high current flows can destroy the seagrass meadows due to erosion (Erftemeijer et al., 2023). *Z. noltei* is more likely to be found in areas not exposed to swell. Seagrass meadows attenuate waves (Paul and Amos, 2011), and a high swell affects negatively *Z. noltei* survival and morphological properties (La Nafie et al., 2012).

4.2. *Zostera noltei distribution projections under climate change scenarios*

The spatial distribution and shift of the most suitable Z. noltei habitat at present and under climate change scenarios are aligned with previous studies of habitat suitability of the species in the estuary (Valle et al., 2011, 2014). In our study, the main expected changes under climate change scenarios are related to sea level rise. This rise favours the availability of estuarine areas landward, potentially offering suitable conditions for the establishment of the seagrass. The projected expansion of the *Z. noltei* under climate change scenarios suggests positive consequences, with the potential increasing contribution of *Z. noltei* to the many ecosystem services it provides. However, projected expansion landward depends on the pace of sea level rise and the sediment accretion of current saltmarshes and on the whole system (Garnier et al., 2022). If saltmarshes are able to accrete in their present locations, which is not taken into account in the model, they will maintain their suitable level of submergence excluding the expansion of *Z. noltei* in these areas.

Table 3
Zostera noltei coverage changes, in area (km^2 and percentage), from present to future climate change scenarios.

Coverage changes from present status	Climate change scenario	
	SSP1-2.6	SSP5-8.5
41–100% loss	0.02 (7.6%)	0.01 (5%)
1–40% loss	0.07 (20.5%)	0.03 (8.2%)
Total loss	**0.09 (15%)**	**0.04 (6.9%)**
41–100% to 1–40% decrease	0.04 (14.3%)	0.035 (13.8%)
1–40% maintained	0.16 (47.4%)	0.16 (46.7%)
41–100% maintained	0.2 (78.1%)	0.21 (81.2%)
Total maintained	**0.36 (60.5%)**	**0.37 (61.4%)**
1–40% to 41–100% increase	0.11 (32%)	0.15 (45%)
1–40% gained	0.36 (106.1%)	0.88 (255.2%)
41–100% gained	0.2 (76.6%)	0.43 (168.9%)
Total gained	**0.56 (93.5%)**	**1.31 (218.5%)**

Therefore, our model is probably slightly overestimating the reduction of saltmarshes and overestimating the expansion of *Z. noltei*.

The results of this study differ from other studies in the Bay of Biscay, where a loss of large seagrass areas is projected in the Bay of Santander with future sea level rise (Ondiviela et al., 2020). The deviations in the results are explained due to differences in the models and variables used, as well as different estuary dynamics. In Ondiviela et al. (2020), the dependency of hydro-geomorphological processes and local rates of sea level indices in coastal ecosystems are emphasised, arguing that in the face of the same threat, the same community in different estuaries may respond differently. However, it must be considered that the potential expansion of suitable areas for *Z. noltei* will not only depend on changes due to sea level rise but also human activities in the estuary and the adaptation of the species to the new environmental conditions (Cearreta et al., 2004; Liria et al., 2009; Monge-Ganuzas et al., 2013; Garmendia et al., 2023). Despite the projected increase of *Z. noltei* distribution under climate change scenarios, other variables that also influence the distribution of the species have not been considered, such as the presence of human-made barriers and activities. Management actions, such as removing obstacles, are needed to ensure the expansion of seagrass meadows under sea-level rise scenario.

4.3. Model capacities and limitations

The model is fed with the results of a process-based numerical hydrodynamic model which has been used to produce flow and wave fields over the entire estuary for mean conditions of the present state, but also for theoretical incurred conditions (extreme conditions, projections). This limits the applicability of the BN model to estuaries for which such hydrodynamic and wave data has been produced, but also allows to study *Z. noltei* distribution without other data collection such as surficial sediment characteristics.

It is also important to clarify that factors such as morphological changes that may occur in the estuary due to future changes in the hydrological regime have not been considered. Among others, changes in the distribution of sediments, floods, and nutrients are expected (Ganju and Schoellhamer, 2010; Statham, 2012). The morphology has been maintained constant under sea level rise scenarios, but it is known that the estuary morphology will change with changes in sea level: the Oka is a transgressive estuary and past observations have shown that sedimentation of the different parts of the estuary occurred with sea level rise (Garnier et al., 2022; García-Artola et al., 2023). In the case of temperature, previous analysis in Z. noltei indicated that this factor is not important at the level of Basque estuaries since this species is widely present at both northern and southern latitudes (Valle et al., 2014). Neither salinity has been considered, due to the plasticity of *Z. noltei* to salinity shifts, and the salinity ranges in the estuary (Sousa et al., 2017; García-Artola et al., 2023).

Human activities distribution has been maintained constant under climate change scenarios. However, anchoring areas and recreational activities could change due to sea level rise. Accessibility to harvesting areas can also affect the presence of the activity (Garmendia et al., 2021), but it is expected to migrate as the seagrass meadow distribution changes. Also, the extractive pressure could increase, decreasing the recovery capacity of *Z. noltei*, especially in low shoot density and biomass areas (Román et al., 2024).

Other variables such as light exposure, sediment characteristics or emerged time are relevant factors to consider in seagrass distribution studies (Campbell et al., 2007; Valle et al., 2011; Ondiviela et al., 2020; Guerrero-Meseguer et al., 2021). However, light and emerging time are non-explicitly considered with the depth (Peralta et al., 2002). The availability of data on pressure produced by human activities on *Z. noltei* and species contribution to human welfare has reduced the number of predictive factors considered. Although the plasticity of *Z. noltei* under different environmental conditions has been demonstrated (Sousa et al., 2017), other factors or events not considered may affect the seagrass survival and growth capacity, such as enhanced nutrients, heavy rainfalls, heatwaves, and eutrophication (Burkholder et al., 2007; Cabaço et al., 2008; Cardoso et al., 2008). The inclusion of such factors or events would reduce the projected *Z. noltei* distribution under climate change scenarios, even to non-existent levels. Nevertheless, the model performance is good enough to be applicable for habitat suitability projections under climate change scenarios.

The suitability models can be used to guide conservation and restoration (Grigg et al., 2025). The information provided in this study can be used by managers in human activities planning, identifying critical points that hinder the expansion of seagrass. The assessment of the effects that infrastructures and activities have on the growth of *Z. noltei* could be a next step to establish a nature-based solution strategy, as well as other climatic stressors as more frequent and/or intense extreme events such as floodings, heavy rainfall, and heatwaves or eutrophication.

5. Conclusions

This research provides valuable information for nature conservation and restoration management measures under climate change scenarios. This case study demonstrates the capacity of a spatially explicit NB approach to project future changes in the spatial distribution of estuarine seagrasses. The applied modelling approach showed the capacity to incorporate information and knowledge derived from experts. Despite the limited amount of data for certain variables such as the pressures generated by human activities and the contribution of *Z. noltei* to human welfare, the produced model showed a high performance. Furthermore, the model has been used to project *Z. noltei* distribution under climate change scenarios, providing useful information to support management and restoration actions.

An increase in the distribution of *Z. noltei* is projected in the study area under sea level rise scenarios, but constrained by physical barriers and anthropogenic activities that can affect the potential future expansion. Nature-based solutions such as habitat restoration need to be implemented and appropriately monitored in order to assure the landward migration of the species.

CRediT authorship contribution statement

Gotzon Mandiola: Writing – review & editing, Writing – original draft, Visualization, Methodology, Data curation, Conceptualization. **Ibon Galparsoro:** Writing – review & editing, Writing – original draft, Supervision, Methodology, Conceptualization. **Mireia Valle:** Writing – review & editing, Data curation. **Joxe Mikel Garmendia:** Writing – review & editing, Data curation. **Roland Garnier:** Writing – review & editing, Data curation. **Javier Franco:** Writing – review & editing. **Ángel Borja:** Writing – review & editing, Funding acquisition. **Guillem Chust:** Writing – review & editing, Funding acquisition. **Sarai Pouso:**

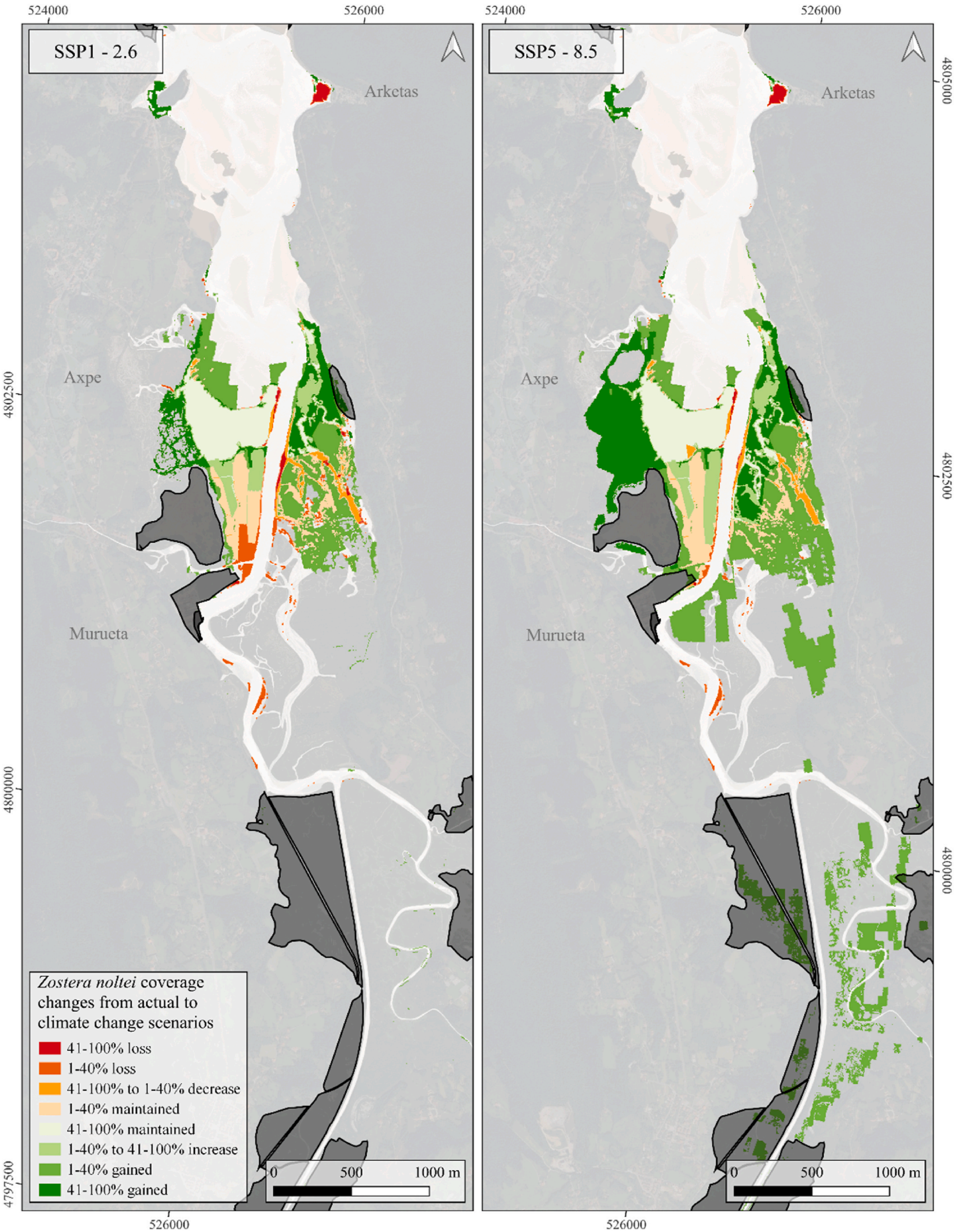

Fig. 8. *Zostera noltei* coverage evolution from present status to future climate change scenarios in the Oka estuary. SSP1-2.6 (left), SSP5-8.5 (right). Black-grey polygons are areas enclosed by walls.

Writing – review & editing. **Juan Bald:** Writing – review & editing, Supervision. **José A. Fernandes-Salvador:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Data curation, Funding acquisition.

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 A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.ecss.2024.109093.

Data availability

Data will be made available on request.

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