Guidelines for model adaptation: a study of the transferability of a general seagrass ecosystem DBN model

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Abstract

1. Ecological models are extensively and increasingly used in support of environmental policy and decision making. Dynamic Bayesian Networks (DBN) as a tool for conservation have been demonstrated to be a valuable tool for providing a systematic and intuitive approach to integrating data and other critical information to help guide the decision-making process. However, data for a new ecosystem are often sparse. In this case, a general DBN developed for similar ecosystems could be applicable, but this may require the adaptation of key elements of the network.

2. The research presented in this paper focused on a case study to identify and implement guidelines for model adaptation. Our study adapted a general DBN of a seagrass ecosystem to a new location where nodes were similar, but the conditional probability tables varied. We focused on two species of seagrass (*Zostera noltei* and *Z. marina*) located in Arcachon Bay, France. Expert knowledge was used to complement peer-reviewed literature to identify which components needed adjustment including parameterisation and quantification of the model, and desired outcomes. We adopted both linguistic labels and scenario-based elicitation to elicit from experts the conditional probabilities used to quantify the DBN.

3. Following the proposed guidelines, the model structure of the general DBN was retained, but the conditional probability tables were adapted for nodes that characterised the growth dynamics in *Zostera spp.* population located in Arcachon Bay, as well as the seasonal variation on their reproduction. Particular attention was paid to the light variable as it is a crucial driver of growth and physiology for seagrasses.

4. Our guidelines provide a way to adapt a general DBN to specific ecosystems to maximise model reuse and minimise re-development effort. Especially important from a transferability

perspective are guidelines for ecosystems with limited data, and how simulation and prior predictive approaches can be used in these contexts.

Keywords: complex systems, seagrass, model transfers, ecosystems management.

1 Introduction

Seagrass ecosystems are widely recognised as crucial ecosystems in the coastal zone, with essential functions contributing to multiple marine ecosystems (Hemminga and Duarte, 2000; Pachauri et al., 2014). As plants living in shallow coastal waters, seagrass are typically subjected to anthropogenic stressors, such as water quality degradation and coastal development (Cambridge and McComb, 1984; Orth et al., 2006). Consequently, understanding the risks posed to these systems and how they respond to successive disturbances is essential for improved management (McCann, Marcot and Ellis, 2006). However, dealing with ecological problems is inherently complex since ecosystems are composed of heterogeneous, complex networks with nonlinear relationships and limited predictability (Folke et al., 2004; Starfield, 1997). This is due to multiple interactions that occur within ecosystems and between system components across temporal and spatial dimensions (Green et al., 2005).

A model integrating for disparate data and capturing uncertainties and complexities inherent in natural systems is a Dynamic Bayesian Network (DBN) (Marcot and Penman, 2019). DBNs are temporal extensions of Bayesian networks, which are probabilistic graphical models that use a set of random factors (variables of interest) to represent a system (Fig. 1). Each variable within the DBN network is presented as a node with directed links forming arcs that express causal relationships quantified with conditional probabilities (Koski and Noble, 2011). The conditional probability table (CPTs) describes the probability of being in a particular state, given specified values of the associated states of the parent nodes; therefore, the size of each CPT for a node depends on the number of parent nodes and their states (Marcot et al., 2006). CPTs can be obtained from expert elicitation, learned from experimental or observational studies, or generated from a mix of both approaches. The dynamic component allows the model to capture these interactions between variables and changes over time (Friedman, Goldszmidt and Wyner, 2013).

It is common to discretise nodes into states so that the model infers the subsequent probability distribution over those defined states for each node. Discretisation provides a way to capture decision thresholds pertinent to management and represents an implicit recognition of the uncertainty in the model and available data. The establishment of states within each node is done using recognised classifications, management thresholds, or guidelines. In contrast, when this information is not available, expert knowledge must define node states and thresholds (Pollino et al., 2007).

The value of DBNs as a tool to assist in the management of seagrass ecosystems has been demonstrated in numerous studies where network structures capture nonlinear, dynamic processes in response to natural and anthropogenic stressors (Wu et al., 2017, 2018; Trifonova et al., 2015; Maxwell et al., 2015). However, for a new ecosystem or less well known ecosystem, it is generally

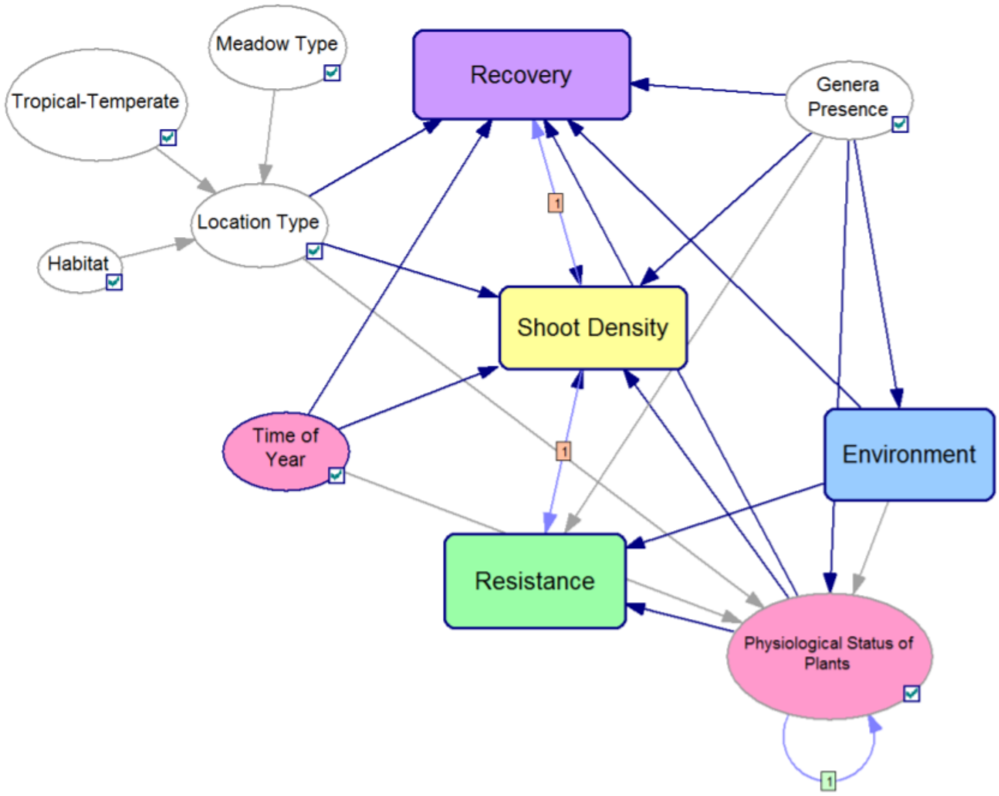


Figure 1: The overall DBN structure. Nodes are ovals and arrows denote causal parent-child relationships in the direction of the arc where a parent node (e.g., Meadow Type) influences a child node (e.g., Location Type); conversely, an absence of a link implies conditional independence. Rounded rectangles denote sub-networks. Nodes are coloured as follows: white for site condition nodes, purple for recovery nodes, green for resistance nodes, blue for environmental nodes, yellow for population (shoot density) nodes, and pink for all other nodes. From "Timing anthropogenic stressors to mitigate their impact on marine ecosystem resilience Supplementary Information" by Wu et al. (2017), Nature Communications 8:1263, Supplementary material, Figure 7.

not feasible to collect sufficient empirical data to represent the whole spectrum of scenarios (Clark, 2001; Yates et al., 2018). The DBN framework provides a pragmatic approach for combining limited data from different sources and also including relevant expert knowledge through a formal elicitaion process (Uusitalo, 2007). Experts' opinions can be used to inform the model structure and parameterisation of the ecosystem variables, which are represented as nodes in the network (Pitchforth and Mengersen, 2013).

The challenge considered in this paper is to adapt a DBN developed for one ecosystem to a new ecosystem. This aligns with the idea of model transferability, which involves retrofitting a previously developed model to suit a new context (Vanreusel, Maes and Van Dyck, 2007; Hadayeghi et al., 2006; Rapacciuolo et al., 2012). This study presents an example of transferring a DBN developed for a global seagrass ecosystem involving three genera to a specific site with two seagrass species. The model was adapted using expert information and the limited data available for the new system. Based on this example, general guidelines are introduced to adapt an existing DBN to a new context and validate the new model with limited data. A novel approach for evaluating the transferability of such a DBN is also presented. The proposed method and lessons learned in this study can also be applied to other sites and help guide the reuse and adaptation of different models, especially for locations with limited data.

2 Materials and Methods

A DBN model was developed by Wu et al. (2018) to predict the resilience of seagrass meadows to dredging disturbances. The model focused on the following genera and locations, (1) *Amphibolis* at Jurien Bay, Australia, (2) *Halophila* at Hay Point, Australia, and (3) *Zostera* at Pelican Banks, Gladstone, Australia. This model considered whole-of-system interactions, including light reduction due to dredging (the hazard), the duration, frequency and start time of dredging, as well as ecosystem characteristics such as the life-history traits expressed by genera and local environmental conditions. The general DBN model was also applied to predict how dredging timing, duration, and intensity affect the resilience of seagrasses belonging to similar genera at 28 sites distributed worldwide (Wu et al., 2017). However, species-specific variations, as well as the application of the general mmodel to specific locations, have not yet been explored. Therefore, we attempted to assess the model transferability from global to local scale and from genera to seagrass species.

2.1 Arcachon Bay Case Study

Our case study includes two *Zostera* seagrass species located in Arcachon Bay, France: *Z. marina* and *Z. noltei*. Arcachon Bay is a tidal ecosystem, sheltering Europe's largest seagrass bed of dwarf grass (*Z. noltei*) (Auby and Labourg, 1996). This species colonises soft sandy to muddy sediments of shallow sheltered bays, often in intertidal areas. In the shallow subtidal sector around the channel edges, another species, *Z. marina* (eelgrass) grows forming smaller beds (Cognat et al., 2018). Seagrass mapping between 1989 and 2007 showed a severe decline of Zostera spp. from 2005, an estimated 33% reduction for *Z. noltei* (from 68.5 km^2 to 45.7 km^2) and 74% (from 3.7 km^2 to 1.0 km^2) for *Z. marina* meadows (Plus et al., 2010).

Although studies have suggested that factors such as climate change, eutrophication, increased geese grazing, wasting disease, herbicide contamination, or dredging activities may explain this decline, the exact reason for the loss of seagrass in Arcachon Bay is still unclear (Cognat et al., 2018; Plus et al., 2010). Therefore, transferring a whole-of-system DBN model, which integrates analysis of interactions and feedbacks across different components of the system to Arcachon Bay, provides a way to understand the ongoing seagrass dynamics and allow projections to support future decision making. Furthermore, such a model could be used to simulate and assess different management scenarios to support decision makers.

2.2 Overview of the Guidelines

Our proposed guidelines have three main stages: knowledge acquisition, revision and design phase, and site application (Fig. 2). The first stage focuses on identifying local knowledge, and available data for the study area. The second stage reviews the model structure such as how nodes are linked and what states should be assigned to each node. Furthermore, key elements in the functioning of the environmental system are identified. The third stage is the Site Application, which is subdivided into three steps that are iterated through until the best possible local model is obtained given local knowledge and available data. In the first step, the DBN is quantified using expert elicitation and/or available data. The proposed adaptation of the model is validated in the final step against observed data, ensuring that the model response reflects both the data and local knowledge.

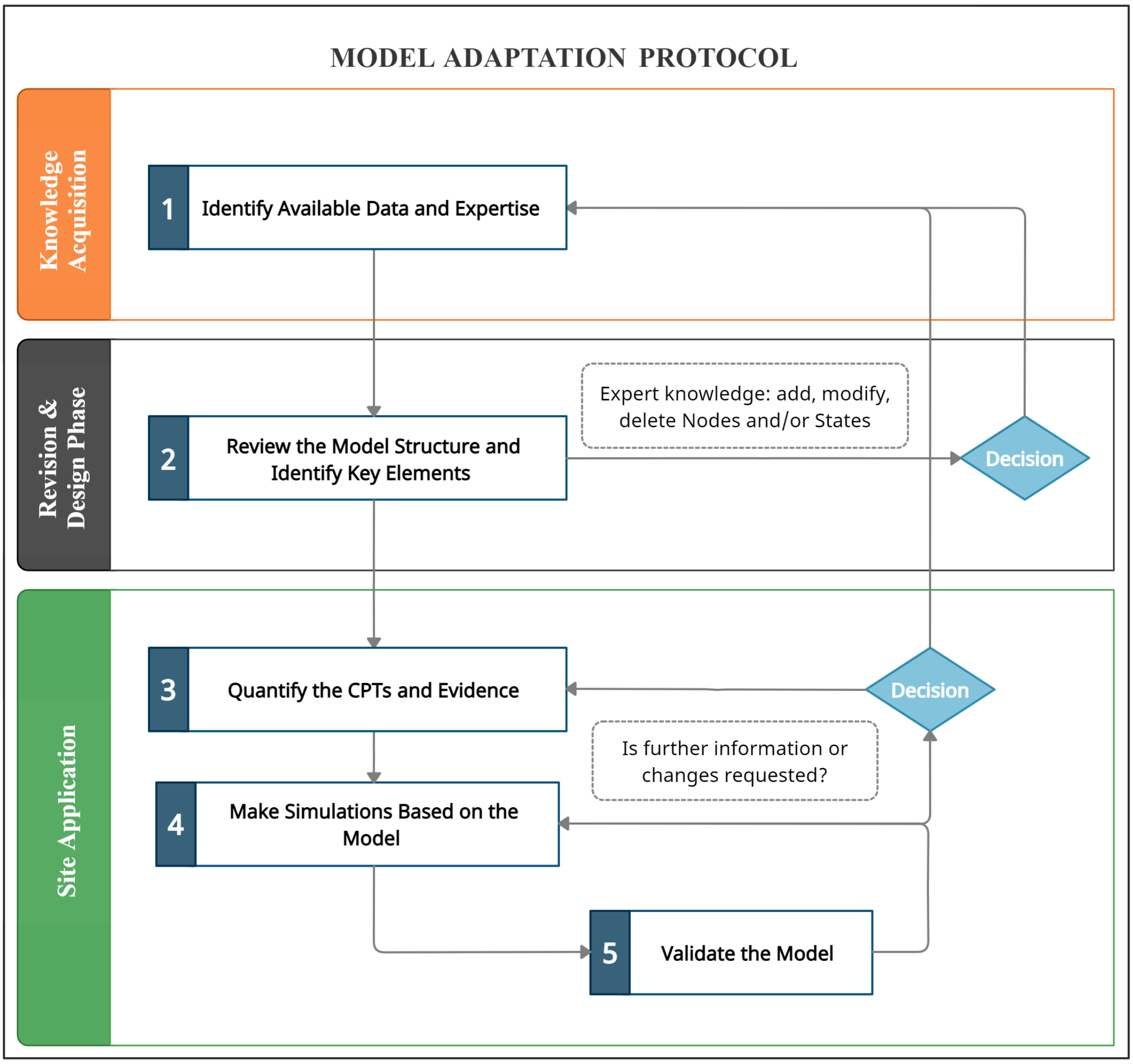


Figure 2: Stepwise methodology flowchart for adapting an existing model through combined observation data, literature, and expert knowledge.

Step 1: Identify Available Data and Expertise

Insufficient and incomplete data is a widespread problem in environmental research, principally when information on the system in question is poorly studied. Therefore, when proposing to transfer an existing model to another context, an important step is to identify what data and expertise are available. The amount of data available and expert knowledge for that system will determine whether the model can be transferred or not. In that regard, in the absence of data, the transferability of the model is not possible. On the other hand, the process of transferring a model becomes appropriate with sufficient data and suitable expertise available.

In data-restricted case studies, the inclusion of experts' knowledge is particularly beneficial to overcome data limitations, strengthen and/or adjust networks, assign states of nodes, and provide estimates of the parameters (Pitchforth and Mengersen, 2013). A structured expert elicitation can be employed to update the model, and available data can also be included as well as used for validation and threshold tuning.

Step 2: Review the Model Structure and Identify Key Elements

The revision and design phase involves reviewing the existing model structure where a set of links representing the causal relationships between nodes is assessed through expert elicitation. Then, expert knowledge and peer-reviewed literature are utilized to identify which components (nodes and states) needed adjustment. Finally, with the key elements (nodes and arcs) identified, the conditional relationships of these elements need to be quantified using conditional probability tables (CPTs).

The use of expert knowledge and peer-reviewed literature may be necessary to identify which components of the DBN are likely to need adjustments to adapt the model to another context. For example, after identifying the species of interest, experts and literature can be consulted to list those factors that might help or hinder the success of management goals. It should be kept in mind that the structure of the DBN should give an overview of the whole environmental system, so begin by evaluating if the causal influence of nodes (and states) represents the most critical variables in the system as a whole.

Step 3: Quantify the CPTs and Evidence

A CPT underlies every node in a DBN, in which the data (expressed as probabilities) used to fill the CPTs must describe how a node changes in response to changes in its parents. As the DBN is a network, the effect of changing any variable is transmitted right through the network in congruence with the relationships expressed by the CPTs. Thus, when transferring a DBN to another context, the CPT for those nodes that have undergone adaptations need to be assessed and adjusted if required to fit the new case data. Aside from the CPT adjustments, it is also important to update the evidence, which is the new data entered into the DBN.

Step 4: Make Simulations Based on the Model

Having the CPTs quantified, the behaviour of the DBN model can be tested by trying different combinations of input values, such as altering the states of some nodes, to assess the posterior marginal probabilities across the entire network. If the model shows unrealistic behaviour, consider modifying the CPTs, by either combining, splitting, or redefining the nodes and/or states of the nodes, or readjusting the overall structure of the model until it provides a reasonable response.

Step 5: Validate the model

The model validation phase is used to evaluate the confidence in the model components, such as factors, the structure, discretisation and quantification (Wu et al., 2017). Thus, a validation approach must be conducted to compare the predicted-state probabilities for a key response variable against observed state probabilities derived from data. One way to validate the model is through the mean squared error (MSE) metric, which is used to compute distances between the model predicted-state probabilities and observed data. The lower value of MSE indicates better model performance, and hence the more accurate the model predictions.

2.3 Guidelines in the Context of the Case Study

In accordance with the general guidelines, the methodology used to adapt the model to our case study is presented below, broken down into three stages where all steps and decisions are presented.

2.3.1 Knowledge Acquisition

Step 1: Identify Available Data and Expert Knowledge

Because local ecological knowledge is crucial, specialists with good knowledge of seagrass and marine ecology in Arcachon Bay were consulted. During the elicitations, the modellers were responsible for guiding the experts through the tasks, encouraging discussion, and presenting results and analysis back to the experts. In addition, modellers worked collaboratively with domain experts in establishing relevant literature, data, and key biological and environmental processes that needed to be adapted for the case study. Communication with all experts was carried out entirely online, via Zoom and e-mail, since face to face meetings were not feasible due to global pandemic travel restrictions.

The empirical data used here was provided by IFREMER (the French Institute for Research and Sea Exploitation) collected from nine sampling sites distributed over the whole of the Bay selected for their different depths, environmental conditions, and seagrass density (Cognat et al., 2018). Although we have data for nine sites, only four sites, FONT, GAIL, ILE, and ROCH, were considered for tuning model parameters (light thresholds) and validation analysis because these sites were considered to be in good physiological condition and historically had not declined (Florian Ganthy, pers. comm.).

Seagrass shoot density, benthic light and temperature data from a one-year field survey (December 2015 - December 2016) were used to test and validate the model. For each site, measurements of shoot density were collected monthly, while light intensity (µmols m^{-2} s^{-1}) and temperature (°C) were measured continuously at high frequency (10 min sampling rate). Unfortunately, no shoot density and biomass records were available for *Z. marina*, making it impracticable to validate the model for this species. To incorporate light data in DBN inference, we discretised light into states. The probability of light being in one of these states is based on simultaneous requirements of light intensity (mols m^{-2} day^{-1}) and light duration per day (number of hours of saturation and compensation irradiance per day). Therefore, site-specific information was required when establishing critical thresholds for water quality based on the responses of seagrass plants to light availability and minimum light levels. As this information was not available for our study area, we employed expert elicitation based on studies from similar sites in France and peer-reviewed literature to estimate light thresholds and estimate baseline light patterns.

2.3.2 Revision and Design Phase

Step 2: Review the Model Structure and Identify Key Elements

The general DBN that was adapted in this study has a network structure comprised of 34 nodes organised into four themes, resistance (e.g., physiology), recovery (e.g., growth), site conditions (e.g., genera present), and environmental factors (e.g., light) (Fig. 1).The current framework uses hybrid and dynamic BNs containing discrete variables over multiple time stages. Overall, the key inputs for the model are the state probability for light (environmental), the genera and location-specific parameters relating to climate (tropical or temperate), depth and tidal exposure (subtidal or intertidal), and transitory or enduring (persistent) type of meadow (site conditions). The temporal frequency of this DBN model is monthly time steps and at local level.

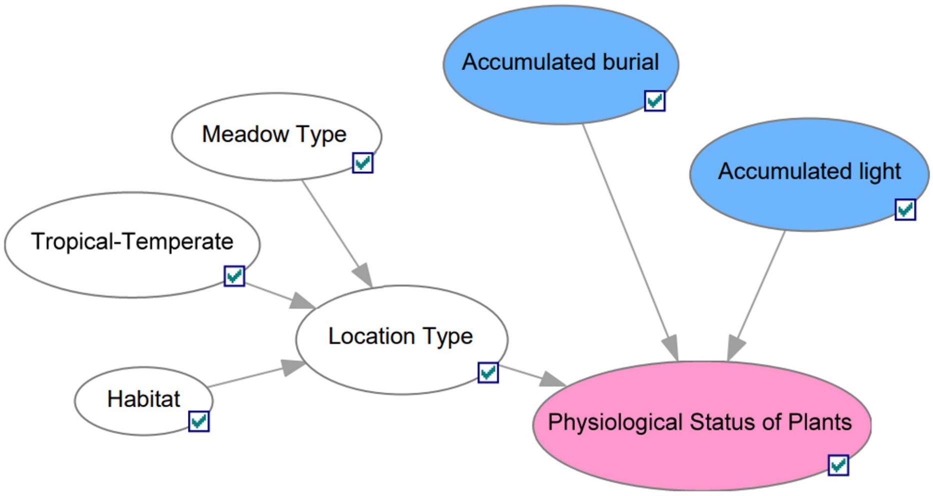
2.3.3 Site Application

Step 3: Quantify the CPTs and Evidence

Expert advice was also sought provide guidelines on node parametrisation, missing data handling and estimates of the conditional probabilities. With regards to parameterisation, experts identified nodes that required updating to adapt the general DBN to the Arcachon case study. The following example shows the CPT quantification process for one node, named physiological status of plants (Fig. 3). Note that other nodes, including accumulated light accumulated burial and location type are parent nodes of the physiological status of plants child node. The elicitation process took the form of scenarios, an intuitive way for experts to make sense of the evidence (Pennington and Hastie, 1993), and linguistic labels of certainty, extremely likely, very likely, likely, 50/50, unlikely, very unlikely, extremely unlikely and impossible. This iterative approach is adopted to maximise cognitive compatibility, as people find it challenging to think of probabilities with several conditioning factors to quantify the DBN (Uusitalo, 2007).

During elicitations, we focused on updating the CPTs for nodes to capture the local growth dynamics of *Zostera spp.* meadows located in the Bay of Arcachon and seasonal variations in their population and life histories. Local knowledge of seagrass growth rates and reproductive success was required to express and calculate the relationships between nodes related to the main drivers of the fitness of seagrass. Temporal variations of growth rates (e.g., light) and sexual reproduction (e.g., flowering shoots, seed production, and seed quality and density) between species and location were considered when updating the relevant conditional probability tables so that the interactions nodes and interactions between nodes captured the local conditions.

Like other plants, the light regime is the primary environmental factor influencing photosynthesis and the growth of seagrass (Dennison, 1987). The light required for growth and survival varies by species, location, and temperature (Kirk, 1994). The maximum photosynthetic rate which promotes plant growth occurs at saturating light conditions (above the light half-saturation point I_k). At lower light values, the compensation irradiance (I_c) level captures when photosynthesis exactly balances respiration and primary metabolism is maintained but not growth. If light falls below I_c, respiration is greater than photosynthesis, and there is not enough light for plant survival (Lee, Park and Kim, 2007). In the existing DBN model, the probability of above or below saturation light is used to capture the optimal and suboptimal light conditions that support seagrass growth. Here, experts propose to test two distinct ways to discretise the light factor to obtain evidence to support the use of a two-state (based only on I_k) or a three-state (I_k and I_c) light model. The thresholds used to discretise the light factor into those states are described below.



Accumulated Light	Accumulated Burial	Location Type	Physiological Status of Plants		
			Good	Medium	Poor
Above Saturation	No Effect	Persistent Temperate InterTidal	Extremely Likely	Extremely Unlikely	Extremely Unlikely
Below Saturation	No Effect	Persistent Temperate InterTidal	Unlikely	Likely	Extremely Unlikely
NA	Effect	Persistent Temperate InterTidal	Extremely Unlikely	Likely	Unlikely
Above Saturation	No Effect	Persistent Temperate InterTidal	Likely	Unlikely	Extremely Unlikely
Below Saturation	No Effect	Persistent Temperate InterTidal	Extremely Unlikely	Unlikely	Likely
NA	Effect	Persistent Temperate InterTidal	Extremely Unlikely	Very Unlikely	Very Likely
Above Saturation	No Effect	Persistent Temperate InterTidal	Very Unlikely	50/50	Unlikely
Below Saturation	No Effect	Persistent Temperate InterTidal	Extremely Unlikely	Extremely Unlikely	Extremely Likely
NA	Effect	Persistent Temperate InterTidal	Extremely Unlikely	Extremely Unlikely	Extremely Likely

Figure 3: Simple model structure representing the relationship between a child node and all its parents and an illustration of a CPT calculation for the node Physiological Status of Plants using expert elicitation. The nodes Accumulated Light, Accumulated Burial and Location Type (parent nodes) represent the causal factors of Physiological node Status of Plants node (child node).

As light intensity thresholds were not well understood in our study area, we used a K-nearest neighbours algorithm (k-NN) (Fix and Hodges, 1989) based on published data to apply to our area of study (See Supporting Information S1, and Table S1). For this approach, since photosynthetic parameters are related to temperature and show seasonal trends, we used the monthly temperature of Arcachon Bay to predict seasonal I_k and I_c thresholds. The saturation and compensation irradiance (I_k and I_c, respectively) obtained from the k-nearest algorithm are summarised for *Z. noltei* in Table 1 (See Supporting Information Tables S2 and S3 for more information on I_k and I_c, estimated for *Z. marina* and *Z. noltei* at the nine sampling sites). Both I_k and I_c were used to assess the number of hours of saturation and compensation light. From that, thresholds for light duration (H_{sat} and H_{comp}) were required to determine the number of hours of saturation and compensation light per day was necessary to classify the daily light as above, below and/or below limitation state. Because this information was unknown for *Z. noltei* located at Arcachon Bay, we employed expert elicitation based on recorded data to set different combinations of H_{sat} and H_{comp} values (Table 2).

Table 1: Average monthly water temperature (Temp, °C), saturation and compensation irradiance (I_k and I_c, µmols photons m^{-2} s^{-1}) estimated for *Z. noltei* located at FONT, GAIL, ILE and ROCH.

	FONT			**GAIL**			**ILE**			**ROCH**		
	Temp	I_k	I_c	**Temp**	I_k	I_c	**Temp**	I_k	I_c	**Temp**	I_k	I_c
Jan	11	174	19	11	174	19	12	174	19	12	174	19
Feb	11	174	19	11	174	19	12	174	19	11	174	19
Mar	13	174	19	13	174	19	14	174	19	13	174	19
Apr	16	305	35	16	305	35	16	305	35	16	305	35
May	20	305	35	19	305	35	19	305	35	19	305	35
Jun	23	254	33	22	254	33	23	254	33	23	254	33
Jul	26	254	33	25	254	33	25	254	33	25	254	33
Aug	27	254	33	25	254	33	25	254	33	26	254	33
Sep	24	254	33	23	254	33	24	254	33	24	254	33
Oct	17	305	35	18	305	35	19	305	35	18	305	35
Nov	14	174	19	14	174	19	15	305	35	14	174	19
Dec	12	174	19	12	174	19	13	174	19	12	174	19

After establishing the light intensity and duration thresholds, it was possible to estimate the number of days of light being in one of those states per month. The proportion of days of above saturation light in a month was represented by $\delta(x^{light}_{abovesat}, t)$ and the probability of above saturation light was encoded as $\delta(x^{light}_{abovesat}, t)$, $t = \{Jan, Feb, \ldots, Dec\}$. The same equation was applied to model the probability of light being below saturation or below limitation. These probabilities were input as evidence to the DBN in simulating scenarios. Finally, we estimated the light conditions for all sites and used it as evidence of our model.

Step 4: Make Simulations Based on the Model

The behavior of the structure was tested by the application of two light models, in which different numbers of states for the light node were used. Furthermore, for each light model, combinations of light thresholds were also considered to assess the posterior marginal probabilities for the shoot

Table 2: The combination of the lengths of daily light periods thresholds (H_{sat} and H_{comp}, hours) for *Z. noltei*. The thresholds are separated for the 2-state model.

Model	**Threshold ID**	H_{sat}	H_{comp}
2-state	Thdl-1	4	-
	Thdl-2	5	-
	Thdl-3	5.5	-
	Thdl-4	6	-
	Thdl-5	7	-
	Thdl-6	7.5	-
	Thdl-7	8	-
	Thdl-8	8.5	-
	Thdl-9	9	-
3-state	Thdl-1	6	8.5
	Thdl-2	6	9
	Thdl-3	6	10
	Thdl-4	6	11
	Thdl-5	6	12
	Thdl-6	7	8.5
	Thdl-7	7	9
	Thdl-8	7	10
	Thdl-9	7	11
	Thdl-10	7	12
	Thdl-11	8	8.5
	Thdl-12	8	9
	Thdl-13	8	10
	Thdl-14	8	11
	Thdl-15	8	12
	Thdl-16	8.5	8.5
	Thdl-17	8.5	9
	Thdl-18	8.5	10
	Thdl-19	8.5	11
	Thdl-20	8.5	12
	Thdl-21	9	8.5
	Thdl-22	9	9
	Thdl-23	9	10
	Thdl-24	9	11
	Thdl-25	9	12

density node. Specifically, we were interested in a key outcome node which was shoot density and its change over time. Thus, it is possible to verify if the predictions obtained from the model are consistent with the current understanding of the system (Chen and Pollino, 2012; Bogaert and Fasbender, 2007; Uusitalo, 2007). Therefore, we simulated different light threshold scenarios for both 2- and 3-state light formulations, and validated model predicted shoot density against observed shoot density. The simulations were conducted for each of the four sites in the Bay. The system response can be sub-divided into two periods, the initialisation period to establish the baseline pattern and the response period. A weighted mean approach was used as a comparative method in which multiple state probability trajectories are aggregated into a single trajectory. The weighted mean follows the approach of Wu et al. (2017).

Step 5: Validate the Model

The MSE was used as a distance metric to compute distances between simulated posterior marginal distribution for shoot density (probabilities for high, moderate, low and zero shoot density) against observed distributions of shoot density. Shoot density data collected in Arcachon Bay (Cognat et al., 2018) were used to validate the prediction of the model (See Supporting Information Table S4). We used a hierarchical ordinal regression analysis to transform the observed data into state probabilities of high, moderate, low and zero shoot density as follows:

$$g(y_{i,t}) = \beta_{0,i} + \beta_{1,i} \sin\left(\frac{t}{6\pi}\right) + \beta_{2.i,Site}$$

Here, we use a Generalised Linear Mixed Model (GLMM) and $g^{-1}(y_{i,t})$ represents the probability of state i (high, moderate, low and zero) of shoot density at time t (month of year). The regression has coefficients β_0 and β_1, which are the global intercept and the slope for the seasonal effect from months t, respectively, and coefficient β_2, which is the random effect used to capture the differences between sites. The model was formulated with the Bayesian framework (Wu et al., 2015) and fitted with Hamiltonian Monte Carlo (HMC) using the R package brms (Bürkner, 2018) using default, flat priors (i.e. uninformed priors).

3 Results

3.1 Application of Guidelines to Case Study

In this section, the results from the application of the guidelines for adapting a model to a case study is outlined. The results are broken down into three stages that include sub-elements that can be viewed as a step-by-step process.

3.1.1 Knowledge Acquisition

Step 1: Identify Available Data and Expert Knowledge

Our study had access to both seagrass data, but only limited data, and environmental experts with local knowledge. Therefore, since data was limited and insufficient to 'learn' the DBN model structure, the effort to harness the expert knowledge to adapt the model became critical.

Overall, the key inputs for the model were the state probability for light (environmental), the genera and location-specific parameters relating to climate (tropical or temperate), depth and tidal exposure (subtidal or intertidal), and transitory or enduring (persistent) type of meadow (site conditions). The temporal frequency of this DBN model was monthly time steps and over global spatial locations. The key metric of interest to management was shoot density (number of shoots m^2). Given the importance of local ecological knowledge, we obtained the participation of ten experts in seagrass and marine ecology. Amongst them, six experts came from the Ifremer, France, one from Edith Cowan University, Australia, and one from James Cook University, Australia.

3.1.2 Revision and Design Phase

Step 2: Review the Model Structure and Identify Key Elements

In the existing DBN framework (Wu et al., 2018), the variability in seagrass response was modelled globally across different latitudes, genera and local conditions. However, this model did not capture differences between species at local scales. Therefore, adjustments on factors used to capture the general health and growth of the two *Zostera spp.* are needed, these are summarised in Table 3. For example, although both species are perennial (persistent) in the Bay, *Zostera* beds display significant seasonal variations in density and biomass (Auby and Labourg, 1996). Tolerance and ability to acclimate to different environmental conditions, such as turbidity, salinity regimes and light availability, is also known to vary between species (Peralta et al., 2000; Cognat et al., 2018). For example, to offer better resistance to desiccation during low tide, *Z. noltei* has a narrower leaf than *Z. marina*, as *Z. noltei* covers the large intertidal flats of Arcachon Bay while *Z. marina* only grows in submerged channels (Plus et al., 2010).

3.1.3 Site Application

Step 3: Quantify the CPTs and Evidence

As stated above, based on expert agreement it was unnecessary to change the definition of nodes and the core model dynamics for our case study, so the overall structure of the DBN was retained. The focus was then on changes in the designation of probabilities and correspondents CPTs for these components that reflect the local system of interest (Step 3, Fig. 2). The CPTs were used to capture the uncertainty and variation of multiple associations between species and their environment. To elicit the conditional probabilities for each node of interest from the experts, questions were phrased as follows "If seagrasses were under good conditions of light but show poor physiological status, what is the probability of the plants growing?".

Table 3: This table shows the nodes that have undergone adjustment when transferring the existing DBN to the Arcachon Bay case study. In addition, a definition of the nodes is provided and where the change took place in each node. Definition of the nodes is obtained from "Timing anthropogenic stressors to mitigate their impact on marine ecosystem resilience Supplementary Information" by Wu et al. (2017), Nature Communications 8:1263, Supplementary material, Table 3.

Node	Definition	What has changed?
Accumulated Light	Probability of meeting light requirements for the normal function of the plant representing accumulated variations and effects in that month.	The addition of a third state. The 2-state and 3-state models are compared.
Genera Presence	Categorical, proportion of meadow of that genera.	The current model adds two specific *Zostera* species: *Z. marina* and *Z. noltei.*
Physiological Status of Plants	The physiological status captures the degree to which the plant can function normally.	Node modelled as a function of light factor - CPTs are adjusted when considering a 3-state light model.
Baseline Shoot Density	Best case expected shoot density for a given month given the physiological status of the meadow. Used to explicitly capture large seasonal variations.	The CPTs are estimated for each species separately to capture the different growth strategies between species.
Loss in Shoot Density	Loss in shoot density for that month.	Node modelled as a function of light factor - CPTs are adjusted when considering a 3-state light model.
Seed Density	Density of seeds per m2. States capture the dynamic range in growth rates from fast colonising species to slow persistent species.	The CPTs are adjusted to capture the reproduction cycle for the two species.

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Recruitment Rate from Seeds	Rate of recruitment into the adult population from seeds.	The CPTs are adjusted to capture the reproduction cycle for the two species. Node modelled as a function of light factor - CPTs adjusted when considering a 3-state light model.

The modifications required for the case study included factors that characterised the growth dynamics in *Zostera spp.* population located in Arcachon Bay and the seasonal variation on their reproduction (Table 4). Although adjustments were made to the conditional probabilities for the nodes used to capture the reproduction cycle of the seagrass, such as the seed density and seed recruitment rate factors, the CPTs for those parameters were determined to be identical for both species. This is because the seasonal variation in reproduction does not differ between the two species of *Zostera*. However, the seagrass growth captured via shoot density factor had the CPTs estimated separately for *Z. marina* and *Z. noltei* to capture the different growth strategies between the species. Additionally, nodes used to capture the impact on the seagrass population caused by different light conditions, such as loss in shoot density, physiological status of plants, and seed recruitment rate, have undergone adjustments when quantifying their CPTs for the 3-state of light model (Table 3).

Light availability appears to be a critical factor influencing shoot densities, growth rates, and seagrass physiology. Thus, the light impact on seagrass ecosystems is considered in terms of ecological baselines and as a key stressor to modelling risk. However, determining an appropriate light threshold for seagrasses involves several challenges. First, because obtaining this information (I_k, I_c, H_{sat} and H_{comp}) from regional and seasonal light regimes is uncommon. Second, the tolerance to different light regimes is known to vary between species, as each seagrass species has unique physiological and morphological adaptations to light availability (Dennison et al., 1993).

In our case study, one element used as evidence of the model is the light conditions, which is incorporated in DBN inference via state probability of above saturation, below saturation and/or below limitation light. As light thresholds were not well understood in our study area, a combination of light thresholds was established (Table 2) and then employed to estimate the state probability of light used to build evidence for the model (Step 4, Fig. 2).

Step 4: Make Simulations Based on the Model

In our case study, the model infers predicted-state probabilities for shoot density based on scenarios of different species (*Z. marina* or *Z. noltei*), the light conditions (2- or 3-state) and site-specific parameters relating to depth and tidal exposure (subtidal or intertidal) (Fig. 4). In the absence of light thresholds data, we considered ranges of values based on expert judgments as evidence of light conditions. This process of varying the value of uncertainty one at a time while keeping all other factors fixed helped us to draw conclusions about whether it should have further adjustments.

Each subfigure comprises two panels, where the top panel shows the state probability trajectories over time for the states indicated, while the bottom panel shows the weighted mean response (assuming a uniform distribution) of the expected value and the interquartile range. As can be seen from Fig. 4, a light saturation threshold I_k that is higher than available light leads to significant decline in shoot density but the level of impact differs by site. For example, when comparing FONT with ILE for $H_{sat} = 8$h, the meadow is driven to zero shoot density for seagrasses located at FONT, while this pattern is not observed at ILE.

Step 5: Validate the Model

The model was validated by comparing simulated scenarios corresponding to unobserved parameters (i.e. light thresholds) with observed data (shoot density and light over time). The MSE in the predicted state probabilities for shoot density compared to observed values lies between 0.01 to 0. 04 across the four sites when considering the H_{sat} of 6 h and 2-state model (Table 4), demonstrating an acceptable fit of the model to the data. Furthermore, the ability of the model to predict seagrass shoot density trends was also validated for the 3-state of light, in which the MSE values are on the order of 0.01 for GAIL and ROCH for H_{sat} of 6 h and H_{comp} of 8.5 (Table 5). For the other two sites, FONT and ROCH, the lowest MSE estimated are 0.02 and 0.01, respectively, is observed when the highest light thresholds are considered. Thus, the 2- and 3-state models demonstrated a similar ability to predict the trends for the *Z. noltei* at Arcachon Bay; nevertheless, because of parsimony and data limitations in a model transferability context, we decided to go with a 2-states light model and H_{sat} of 6 h for Arcachon Bay.

Table 4: MSE for the 2-state model per site (FONT, GAIL, ILE and ROCH) and considering different lengths of daily light periods thresholds (H_{sat}, hours) for *Z. noltei*.

Hsat	FONT	GAIL	ILE	ROCH
4	0.0417	0.0401	0.0405	0.0424
5	0.0399	0.0392	0.0395	0.0409
5.5	0.0390	0.0387	0.0392	0.0403
6	0.0362	0.0145	0.0121	0.0183
7	0.0586	0.0176	0.0434	0.0490
7.5	0.1446	0.0923	0.0785	0.0712
8	0.1977	0.1158	0.0930	0.1327
8.5	0.2848	0.1965	0.1764	0.2553
9	0.2939	0.2904	0.2605	0.2855

4 Discussion

Model transferability and adaptation can be highly beneficial, since methods to enable reusing and adapting models can help with widespread model uptake to support managers and decision makers, especially for sites with limited data. In general, transferring a model to a new context

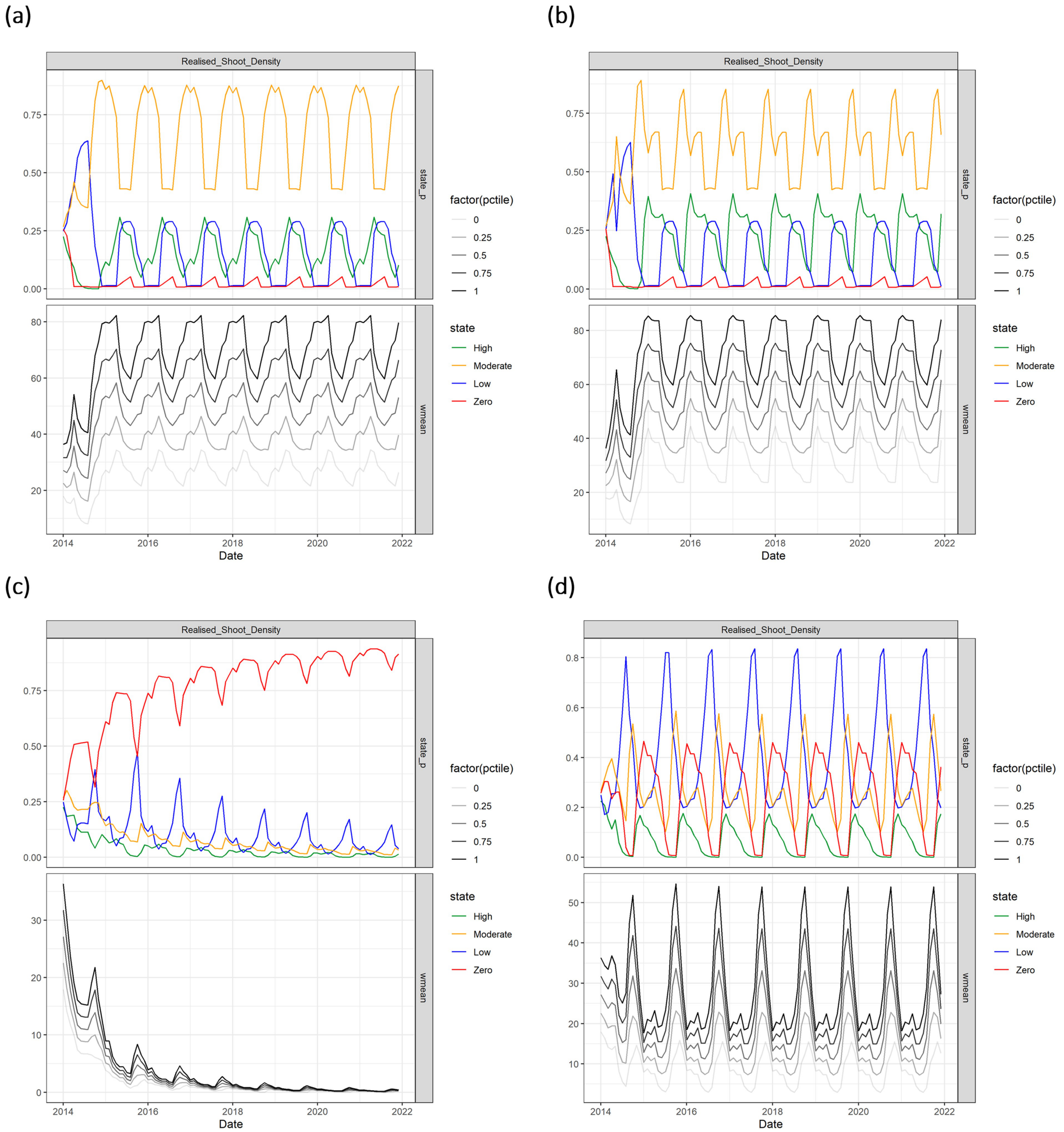

Figure 4: The model predicted-state probabilities for shoot density for *Z. noltei* located at FONT and ILE. The initial 24 months are used for initialisation to allow the system to enter the baseline pattern. Top plots are the probability of each shoot density state, and the bottom plots show the weighted mean of the expected value and the interquartile range. Shoot density state probabilities for seagrass located at **(a)** FONT and **(b)** ILE, when considered H_{sat} of 6 h as light thresholds to estimate the light conditions used as input to the model. Shoot density state probabilities for seagrass located at **(c)** FONT and **(d)** ILE, when considered H_{sat} of 8 h as light thresholds to estimate the light conditions used as input to the model.

can shorten the time and effort to develop a new model by adapting an existing model. Although not a replacement for comprehensive data and studies, model transferability helps to provide predictive evidence on potential future scenarios to support proactive management, such as in the management of resilience. This paper has demonstrated the transferability of an existing general

Table 5: MSE for the 3-state model per site (FONT, GAIL, ILE and ROCH) and considering different lengths of daily light periods thresholds (H_{sat} and H_{comp} hours) for *Z. noltei*.

Hsat	Hcomp	FONT	GAIL	ILE	ROCH
6	8.5	0.0254	0.0122	0.0108	0.0164
6	9	0.0295	0.0128	0.0113	0.0175
6	10	0.0336	0.0137	0.0116	0.0175
6	11	0.0363	0.0140	0.0117	0.0187
6	12	0.0363	0.0140	0.0117	0.0175
7	8.5	0.0230	0.0185	0.0168	0.0150
7	9	0.0269	0.0332	0.0287	0.0194
7	10	0.0416	0.0155	0.0423	0.0130
7	11	0.0543	0.0460	0.0425	0.0484
7	12	0.0561	0.0457	0.0427	0.0130
8	8.5	0.0822	0.0471	0.0348	0.0246
8	9	0.0875	0.0409	0.0365	0.0522
8	10	0.1495	0.0738	0.0775	0.0130
8	11	0.1976	0.1032	0.0846	0.1013
8	12	0.2021	0.1239	0.0910	0.0130
8.5	8.5	0.1258	0.0442	0.0418	0.0380
8.5	9	0.1241	0.0504	0.0450	0.0845
8.5	10	0.1887	0.1071	0.0938	0.0130
8.5	11	0.2669	0.1748	0.1263	0.2028
8.5	12	0.2758	0.1869	0.1782	0.0130
9	8.5	0.1247	0.0507	0.0455	0.0604
9	9	0.1356	0.0835	0.1020	0.0990
9	10	0.2045	0.1279	0.1160	0.0130
9	11	0.2798	0.2204	0.1717	0.2348
9	12	0.2911	0.2421	0.2072	0.0130

seagrass ecosystem DBN model to new sites and offered guidelines on model transferability that could be applicable across different contexts and scales around the world.

In the future, substantial losses are expected on seagrass meadows in response to human impact, both through direct proximal impacts affecting seagrass meadows locally and indirect impacts, which may affect seagrass meadows far away from the sources of the disturbance (Duarte, 2002). Thus, the ability to transfer a global model and concepts and apply them to a local case study can help protect and sustainably manage these valuable marine resources such as the seagrass meadows located in Arcachon Bay.

One of the challenges we faced in the study arose in defining the light thresholds to characterise the regional light regime and the lack of extensive empirical data available to validate our model.

Although we have shown that applying such a range of different light thresholds provides valuable insights into the effects of light intensity and duration variability on seagrass ecosystems, determining an appropriate light threshold for seagrasses involves several challenges. For example, light requirements are unknown for many seagrass species, particularly locally-specific thresholds. The light levels can differ over multiple timescales; seagrass light requirements may vary by season and a range of environmental parameters, including water temperature and sediment chemistry (Lee, Park and Kim, 2007; Koch, 2001). Furthermore, the levels of adaptability of the plants to respond to changing environmental conditions can differ among species (Collier, Waycott and McKenzie, 2012).

Bayesian inference necessitates the use of certain prior distributions. Hence, approaches concerned with choosing a proper prior for a statistical analysis has been developed (Kass and Wasserman, 1996; Sarma and Kay, 2020). Generally, experienced experts translate what is known about an application into choosing a probability distribution by reflecting beliefs about the unknown values of certain quantities. For example, Wang et al. (2018) developed effective numerical methods in which history matching specifies a prior distribution from expert-elicited information. As a result, a set of appropriate prior choices can be used as a basis for making a unique prior choice less arbitrary in a sensitivity analysis (Wang et al., 2018). Based on that, an alternative model updating approach is also outlined here (See Supporting Information S2) to apply the calibration of light thresholds, and identify which best light model and threshold fit the empirical data. Although discretisation thresholds can be drawn from experts and literature when there is limited or no data available, finding high-scoring discretisation is difficult or impractical due to a large number of possibilities that need to be verified, which makes this approach beneficial. This methodology has the potential to be particularly valuable to select optimum DBN inputs (e.g., light thresholds) in data-scarce regions.

Another challenge faced in this project was the scarce data to validate the model and the balance between a more detailed model and a practical model that is supported by available data and expert knowledge. For example, discretising the light parameter into three states instead of two did not show better estimates for shoot density values when compared to the data. Furthermore, as there was only data for one species, steps from three to five were possible only for *Z. noltei*, whereas *Z. marina* could only complete steps one to three due to limited data (Fig. 2). Such a systematic set of guidelines can additionally help modellers and experts to identify potential limitations in the scope of the developed models, and where more study and data is needed. Although we focused on transfer of a general DBN to a local site and species, it could also include transfers to other stressors. For example, stressors from new environmental hazards or climate stress, such as heat stress caused by marine heatwaves, can be included in the model to explore changes in seagrass response.

5 Conclusions

Model users are increasingly transferring models to alternative sites where data can be scarce. When transferring a model from one context to a new application context, the effort in developing a model is reduced, and data collection can be less demanding. In this regard, models transferred to novel conditions could provide predictions in data-poor scenarios, contributing to more informed management decisions. In this study, we have demonstrated the transferability of an existing general seagrass ecosystem DBN model to new sites and offered general guidelines capturing the lessons learned here. Moreover, the DBN adapted for the Arcachon Bay case study can also be applied to various other domains in ecology. For example, other stressors can be incorporated into the model, such as effects caused by climate events, to explore changes in seagrass response.

6 Competing Interests

The authors declare that they have no competing interests.

7 Consent for Publication

Not applicable.

8 Ethics Approval and Consent to Participate

Not applicable.

9 Availability of Data and Materials

Validation data used to validate the DBN model for *Zoster noltei* at Arcachon Bay, France (supporting information, supporting tables, Table S4).

10 Authors' Contributions

P.S.H. led the writing of the manuscript. P.S.H. and P.P.-Y.W. designed the model and the computational framework and analysed the data. P.P.-Y.W. was involved in planning and supervised the work. K.Mc. provided expert knowledge and ecological analysis. K.M. aided in the proposed alternative calibration approach. All authors provided critical feedback and helped shape the research, analysis and manuscript.

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