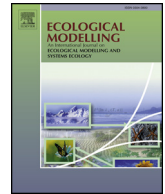




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Review

How to make ecological models useful for environmental management

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ARTICLE INFO

Keywords:

Mechanistic models
Machine learning
Uncertainty
Calibration
Variable selection
Stakeholder
Theory based data science

ABSTRACT

Understanding and predicting the ecological consequences of different management alternatives is becoming increasingly important to support environmental management decisions. Ecological models could contribute to such predictions, but in the past this was often not the case. Ecological models are often developed within research projects but are rarely used for practical applications. In this synthesis paper, we discuss how to strengthen the role of ecological modeling in supporting environmental management decisions with a focus on methodological aspects. We address mainly ecological modellers but also potential users of modeling results. Various modeling approaches can be used to predict the response of ecosystems to anthropogenic interventions, including mechanistic models, statistical models, and machine learning approaches. Regardless of the chosen approach, we outline how to better align the modeling to the decision making process, and identify six requirements that we believe are important to increase the usefulness of ecological models for management support, especially if management decisions need to be justified to the public. These cover: (i) a mechanistic understanding regarding causality, (ii) alignment of model input and output with the management decision, (iii) appropriate spatial and temporal resolutions, (iv) uncertainty quantification, (v) sufficient predictive performance, and (vi) transparent communication. We discuss challenges and synthesize suggestions for addressing these points.

1. Introduction

Environmental management decisions should be based on the current state of scientific knowledge and at the same time account for multiple societal objectives that are of different importance for diverse stakeholders. One important step in environmental decision support is the prediction of consequences of different management alternatives for the fulfillment of the societal objectives (Reichert et al., 2015). Ecological models can be used to support this step as far as ecological objectives are involved. However, so far, this was often not the case, i.e. valuable scientific knowledge is ignored (Addison et al., 2013). In this

paper, we explore why this might be the case and how it could be changed in the future, hence, what components are particularly important and need more attention to make ecological modeling results useful for supporting environmental management.

Two extreme views on ecological models exist: either models are believed to be the solution and redemption of each and every problem without much questioning; or, they are perceived as tools that can be misused to provide any desired prediction and should therefore not be trusted at all. Both extremes may, at least partly, be attributed to missing knowledge on how model building works in general, regarding the specific assumptions towards the model and its potential deficits.

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<https://doi.org/10.1016/j.ecolmodel.2019.108784>

Received 15 May 2019; Received in revised form 5 August 2019; Accepted 6 August 2019

Available online 03 September 2019

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With this paper we want to contribute to a more realistic judgement of the potential for ecological models to support environmental management. We mainly address ecological modelers from various fields regarding modeling approaches and applications that want to increase the relevance of their model results for practice. For potential users from practice this paper offers a summary regarding possible challenges and pitfalls of ecological models that should be considered when using model outputs for decision making.

There are numerous fields of environmental management, where we see an increasing potential for ecological models to support environmental decision making. Examples are the spatial planning for endangered species conservation, biodiversity protection, habitat restoration, and the assessment and management of ecosystem services, alien species, lakes and fisheries, micropollutants (including the registration of chemicals and risk assessment), multiple stressors, global environmental change, and health risks (e.g. from pathogenic microorganisms or antibiotic resistant bacteria). Examples for ecological models in these application fields are provided in the appendix (Table A1).

However, the involvement of ecological modeling in environmental decision making imposes several challenges. First of all, it requires collaboration between environmental decision makers and ecological modelers to develop a common understanding and enable knowledge transfer between science and practice in both directions (e.g. Jakeman et al., 2006; Voinov et al., 2016; Basco-Carrera et al., 2017; Parrott, 2017). Engineering consultants can play a role in this process as well. Additional challenges concern technical issues that are the focus of this paper. Depending on the availability of data and knowledge, various modeling approaches can be used to answer management related questions (Section 2.1). Here we discuss cross-cutting issues that are important regardless of the specific modeling approach. Nevertheless, depending on the choice of the model, they can be more or less challenging to address. The ideal model to support environmental management decisions can be directly linked to management objectives, predicts effects of management alternatives without bias, includes adequate precision and a correct estimate of prediction uncertainty, is transferable in space and time, and is easy to understand. However, real models are usually far from ideal. We identified the following six requirements that we believe are important to achieve this as much as possible:

1. There exists a basic mechanistic understanding of the system regarding causality, which is considered in the model.
2. The model input and output variables are aligned with the management question.
3. The model has an appropriate spatial and temporal resolution to address the management question.
4. The model uncertainty can be quantified.
5. The model has a sufficient predictive performance to be useful for the management problem.
6. The modeling procedure, its assumptions, and its deficits are transparently communicated.

In the following, for each point, we (1) discuss **why** we find it important, (2) review **how** to address it in practice, and (3) provide an outlook about how its implementation could be facilitated in the **future**. The **why** sections address both, model developers and environmental managers that may potentially benefit from ecological models, while the **how** and **future** sections cover technical aspects that are of interest mainly for model developers. Furthermore, we outline a way to integrate the ecological modeling process in the decision making process (Box 1).

2. There exists a basic mechanistic understanding of the system regarding causality

2.1. Why?

A model that is useful for environmental management needs to synthesize the most relevant aspects of our current knowledge regarding the system and how management actions impact relevant system components and processes. The more knowledge exists about the system, the better we can predict its response. Such knowledge can consist of mechanistic understanding and of empirical data. While both are important for any ecological model, various modeling approaches differ in their needs regarding the availability of each one (Fig. 2). Given a specific management question, an appropriate modeling approach should be chosen accordingly (Robson, 2014; Baker et al., 2018). Recently, the increasing availability of (big) data and computational power has allowed complex algorithmic (machine learning/artificial intelligence) models to be developed, seemingly overcoming issues of data and knowledge limitations. Such approaches do not rely on (subjective) prior knowledge and can search for patterns in available data without any prejudice. However, there is a danger of developing models based on easily available data as input variables (also called predictor, explanatory, or independent variables) that are somehow correlated with the model output variables (i.e. response or dependent variables) but without explicit consideration of cause-effect mechanisms. The use of biased input data can lead to biased results. If input variables do not present mechanistically linked attributes of the system, they may have limited practical value for environmental management or even produce false predictions based on spurious correlations in the data. An additional danger when ignoring prior knowledge about important mechanisms is that the dynamic nature of the system is disregarded and important feedback loops between output variables are overlooked (Robson, 2014). Therefore, we consider it important to build on existing mechanistic understanding of a system, and invest in improving it, regardless of which modeling approach is chosen, a mechanistic or a data-driven approach (Dormann et al., 2012). This makes it less likely – but not impossible – that model results are biased and produce false predictions, or correct predictions for the wrong reasons.

2.2. How?

While the consideration of knowledge about cause-effect mechanisms is an explicit step when developing mechanistic (process based) models, we think it is also crucial for the development of any data driven, statistical model. This is especially true, if it should inform management decisions. First of all, the explicit consideration of cause-effect mechanisms facilitates the choice of an appropriate model structure (or potential candidate model structures to be tested) including an appropriate description of model errors. For instance, when building a multivariate statistical model, we may have to decide if it should be a linear, generalized linear or non-linear model, and may have to choose a link function and make distributional assumptions. Furthermore, some mechanistic understanding can help with the (pre-) selection of input variables. Actually, the inclusion of input variables can be seen as a formulation of hypotheses, and the selection procedure as a falsification process. This process has major implications on the outcomes of the model and the conclusions for management.

One step in the direction of considering cause-effect mechanisms is the distinction of direct and indirect influence factors. For direct influence factors (e.g. temperature) we have a basic mechanistic understanding of how they influence the output variables (e.g. reproduction of organisms), even if we use empirical functional relationships to parameterize the model and infer the parameters from the data. Conversely, indirect influence factors (e.g. altitude) are those that influence the direct ones and therefore only indirectly affect the output variables. Models that use direct influence factors as input variables

Box 1
How to integrate modeling in a decision support process for management?

To facilitate the use of ecological models for environmental management, the modeling process has to be aligned to the management process. The following procedure illustrates a logical way of integrating modeling in a decision support process (Fig. 1). The procedure consists of 14 steps, the sequence of which can be adapted to the specific situation:

1. explicit definition of management objectives that should be addressed in the decision support process;
2. selection of attributes (i.e. measurable system properties, indicators) and decision criteria (targets) to quantify the fulfillment of the management objectives;
3. selection of output variables of the model that should be identical with or closely linked to these attributes;
4. collection of data of the attributes (model output variables) from the current state of the ecosystem (i.e. observations);
5. evaluation of the current state based on observed attributes to quantify the current degree of fulfillment of management objectives and to identify current deficits (i.e. management objectives that are currently not fulfilled) and needs for action;
6. proposition of management alternatives based on the deficit analysis;
7. collection of data regarding potential model input variables based on current knowledge about cause-effect relationships that will be quantified in the mathematical model;
8. selection of potential model input variables x ; the final selection from potential input variables may be part of the model calibration and validation procedure (step 10);
9. establishment of a model to predict model outputs (attributes) y based on model inputs x and parameters θ ;
10. calibration and validation of the model based on observed input and output variables;
11. identification of “unmanageable” drivers (such as climate or socio-economic variables that are out of scope of local environmental management) that affect input variables and may change in the future;
12. development of (one or several) scenarios for the future change of “unmanageable” drivers;
13. translation of management alternatives and driver scenarios into changes in model input variables and prediction of their effects on model outputs, i.e. attributes of management objectives, and their uncertainty;
14. evaluation of management alternatives under future driver scenarios based on model predictions; identification of trade-offs and synergies regarding the fulfillment of different objectives; identification of potential improvements of management alternatives or identification of new management alternatives (dashed arrow in Fig. 1).

have the potential to be more general (transferable) than models based on indirect influence factors (Guisan and Zimmermann, 2000), but data on direct influence factors is not always available. Validation of the model outcomes with independent data may help evaluating whether the model captures the most important influence factors and cause-effect relationships, or if a good model fit during calibration is just caused by overfitting or confounding variables. To close data gaps in space and/or time, direct influence factors can be predicted through the formulation of models from indirect ones (e.g. water temperature, Hill et al., 2014). However, this introduces additional uncertainty to the model (see Section 5).

Finding a solid mechanistic basis for any modeling approach benefits from a close collaboration between the experts in charge of

gathering data (e.g. field ecologists, experimentalists) who have practical knowledge about the system, and the modelers that are able to express this knowledge in mathematical terms. In addition, more exchange between the different fields of (ecological) modeling could facilitate model comparisons across the range of statistical and mechanistic models. Such a comparison could reveal the advantages and disadvantages of different approaches to address specific management questions and help improving both types of models.

For data rich situations, a promising approach may be to use rather unconstrained, data driven (e.g. machine learning, deep learning) methods for a first exploratory analysis to detect patterns in the data. However, it should be noted that such purely data-driven models may be poor for predicting outside the range of calibration. Therefore, we

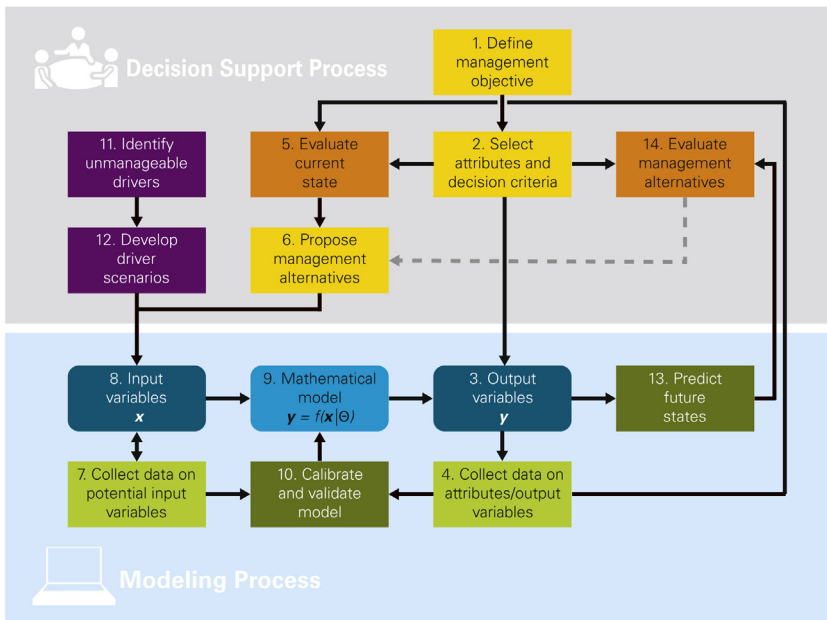


Fig. 1. Schematic representation of the integration of modeling in a decision support process for management. Arrows indicate the flow of information. Similar colors are used for steps that are closely related. Rounded boxes describe the model itself, whereas square boxes describe steps of the decision support and the modeling process. See explanation in the text for each box. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

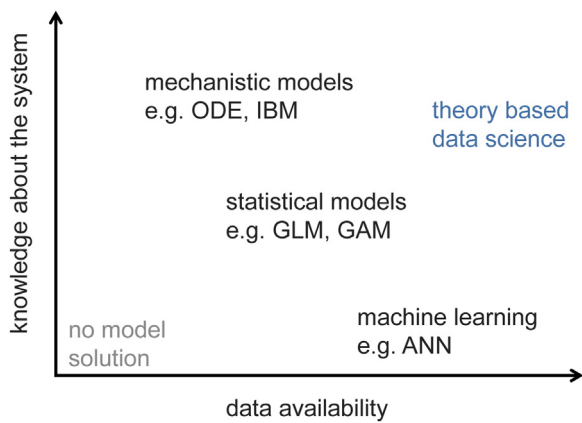


Fig. 2. Requirements of traditional (black) and upcoming (blue) modeling approaches regarding the availability of data and knowledge (ODE: ordinary differential equations; IBM: individual based models; GLM: generalized linear models; GAM: generalized additive models; ANN: artificial neural networks). Note that the transitions between these approaches are rather smooth. See text for further explanations and [Box 2](#) for an elaboration on theory based data science. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

suggest confronting this information with prior mechanistic knowledge about the system in a next step. This could then lead to the development of models that consider mechanistic knowledge and can be used to test hypotheses regarding cause-effect relationships (e.g. [Peters et al., 2014](#); [Feld et al., 2016](#)). Purely data driven models can then serve as a benchmark regarding the predictive performance for models with a more constraint model structure. For rather data poor situations, it might be possible to transfer knowledge from other systems and test it with new data in a Bayesian framework.

2.3. Future changes?

Currently, many machine learning models are good in predicting, if applied within their calibrated range. However, their internal structure is often not accessible and therefore hard to understand. Therefore, they are perceived as “black boxes” ([Castelvecchi, 2016](#)). Attempts in data science to “open the black box” of such purely data driven algorithmic models may help extracting mechanistic understanding from (big) data. This may further develop to what we call “theory based data science” ([Box 2](#), [Fig. 2](#)), where both mechanistic understanding and a flexible structure, which is derived from data analysis, can be combined. Using synergies between complementary modeling approaches will advance mechanistic understanding and predictive performance of ecological models ([Baker et al., 2018](#); [Robson, 2014](#)).

In parallel, the increasing development of large scale experimental facilities (e.g. mesocosms) will contribute to the validation of cause-effect hypotheses, while the use of mechanistic models may contribute to improve experimental design. For example, if a data-driven model detects an effect of an input variable on the abundance of a certain species, a mesocosm study could be set up to manipulate this input variable to verify if it has an effect. In a second step, a mechanistic model could be calibrated to the data of a first set of experiments (e.g. the time series of the development of a population) and the model can then be used to test e.g. the effect of an improved or reduced temporal resolution of the experimental data on the parameter estimates.

Likewise, the implementation of management measures (e.g. upgrade of waste water treatment plans, morphological restoration of rivers, measures to improve the trophic state of lakes) offers the opportunity to use these as large scale experiments and derive monitoring data with a strong experimental design (e.g. before-after-control-impact ([Stewart-Oaten et al., 1986](#))) to strengthen cause-effect linkages, detect

feedback loops, and to validate and improve model predictions.

Further, long-term ecological monitoring programs have started to coordinate their work at regional and global scales, while emphasizing societally relevant information on the sustainable use of natural resources ([Mirtl et al., 2018](#)). The resulting field data is highly relevant, homogeneous and continuous in time, facilitating the identification of causal relationships. The coordination of these different data and knowledge sources requires anticipatory planning, funding that covers a long time horizon, and close collaboration of various experts.

3. The model considers input and output variables that are relevant for management

3.1. Why?

To be useful for environmental management, model outputs have to be aligned with management objectives, while model inputs have to reflect environmental factors that influence the model outputs and are influenced by the management alternatives that are of interest for the decision makers or stakeholders ([Fig. 1](#)). With such a model we can analyze management scenarios by modifying the input variables subject to anthropogenic changes and learning about their potential effects on the management objectives.

For instance, a model describing local species diversity will not be useful for supporting the management objective of stopping a certain target species’ decline in abundance, because the output variable is not aligned to the management objective. On the other hand, a model predicting a target species’ abundance based only on latitude and temperature as input variables, will not be useful either if the potential management alternatives affect water quality. While seemingly trivial, in practice it might be a major challenge to identify and incorporate relevant input and output variables, or output variables with sufficient sensitivity to the input variables that are relevant for management.

3.2. How?

The alignment of model input and output variables with the management questions requires a clear understanding of management objectives and an agreement about how to measure their fulfillment based on attributes of the system (e.g. fish biodiversity, measured as the number of different fish species occurring in the respective catchment). Furthermore, it requires an identification of important drivers that can be linked to potential management alternatives to be considered (e.g. longitudinal connectivity to be increased through the removal of barriers or water quality to be improved by upgrading wastewater treatment plants towards the removal of micropollutants). This can be reached by a dialogue between modelers, decision makers and stakeholders, e.g. within a co-design process. Multi-criteria decision analysis and problem structuring methods can support this phase (e.g. [Keeney, 1982, 1996](#)). The next step is then to develop a conceptual model that describes the cause-effect linkages between the drivers that are affected by the management alternatives and the ecological variables that can be linked to the management objectives (see [Section 2.2](#) on direct and indirect influence factors).

Depending on the management situation, decision makers may be interested in learning about the relative importance of (anthropogenic) stressors to identify deficits and potential management alternatives to address them. In other situations, they might be interested in predicting the effects of already identified management alternatives. In both cases, models can be useful, if they include important input variables that may influence the fulfillment of the management objective. This is true even if some of the input variables are out of scope of local management (e.g. socio-economic or climate variables), and even if they are difficult to project into the future (e.g. land-use or technological changes). In such cases, model based scenario analysis can be used to conditionally predict the potential effects of the respective management alternatives,

Box 2

Suggestions to advance theory based data science

We define “theory based data science” as research field in which synergies between data driven and theory driven modelling approaches are used to gain new systems understanding from data. There are many possible ways to advance this emerging field. Below we list some that we find promising in the scope of ecological modelling.

- The sequential combination of data driven and mechanistic models is a way forward to gain new insights from data and advance theory development (Baker et al., 2018). Data driven models can be used for data exploration to discover patterns and gain insights in the predictive power of different combinations of explanatory variables (see next point). These insights can be confronted with the current state of knowledge about potential mechanisms and inspire the generation of new mechanistic hypotheses, which can be tested experimentally and lead to a refinement or extension of mechanistic models. The data driven models can serve as a benchmark for predictive performance that can be achieved without constraints by the model structure. The systems understanding, which is synthesized in mechanistic models, can inspire the acquisition of new data that can be fed into the data driven models.
- Attempts made to open the “black box” of machine learning models to derive understanding about their functioning can be subsumed under the keywords “explainable/interpretable artificial intelligence” or “interpretable machine learning”. Due to the complexity of machine learning algorithms, such as deep neural networks, the human mind is not able to grasp the interactions of their internal mechanisms. However, several techniques are being developed to make the behavior and predictions of machine learning systems understandable to humans (e.g. Montavon et al., 2018; Papernot and McDaniel, 2018; Molnar, 2019). A very simplistic way towards understanding the contribution of different input variables is the sequential exclusion of each of them to analyse the loss in predictive performance. In addition, independent of the modelling approach, it is always possible to produce partial dependence plots, where the model outcome is plotted against each input variable (or combinations of two), to gain some insight into the model behaviour.
- Two opposing strategies can be and have been applied to deal with the complexity of ecosystems that makes it challenging to make predictions. One is to increase the complexity of mechanistic models to describe more processes and accounting for various sources of stochasticity in the system to provide a more realistic description of natural systems. The second strategy is the opposite approach that tries to identify predictable, universal phenomena that are transferable across a large range of systems (also referred to as “complex systems theory”). An example for such reductionist approaches is the identification of scaling laws that can be used to explain macroecological patterns (e.g. Banavar et al., 2007) and to indicate if a system may be close to a critical state associated with a phase transition. Such universal laws can then be implemented in mechanistic models to reduce the number of parameters to be estimated and to increase their transferability. An example is the metabolic theory of ecology based on allometric scaling (Brown et al., 2004) that is used in mechanistic food web models for lakes and streams (Brose et al., 2006; Boit et al., 2012; Schuwirth and Reichert, 2013).

taking into account various assumptions about future changes in variables that cannot be controlled by the decision makers. Such an approach can help in the process of identifying cost-effective management alternatives, i.e. alternatives that reach defined management targets with the least costs. Moreover, it allows us to identify management alternatives that are robust to future, “unmanageable” changes. However, this might require to consider additional input variables which may increase model complexity. Ideally, robust management alternatives, aimed at mitigating local or regional impacts, will be developed while considering larger scales or global changes. The challenge consists in balancing model complexity (considering many variables and their interactions to increase realism) and model simplicity (highlighting the most relevant factors to increase understandability and reduce development, computation, and maintenance costs) (e.g. Fulton et al., 2004; Bunnefeld et al., 2011). A framework for assessing model structure adequacy was recently proposed by Getz et al. (2018).

In our view, the interaction with the decision makers (Guisan et al., 2013) and/or experts in the field is vital to test the plausibility of the models: through repeated iterations testing different management strategies – which represent different input variables at different intensities implemented at different spatio-temporal scales – the performance and realism of ecological models and their outcomes can be improved. Such trial and error exercises are actually one of the advantages of ecological models, as *in silico* hypothesis testing can save resources and time.

3.3. Future changes?

New data analysis approaches in addition to recent developments in remote and *in situ* sensing are already delivering a wide range of variables that describe anthropogenic impairments on ecosystems (Bush et al., 2017). Novel datasets incorporate a large variety of highly relevant input variables into environmental models, including global annual land-use/land-cover changes (ESA Climate Change Initiative – Land Cover), regional climatic conditions at a daily temporal resolution

(Haylock et al., 2008) and global freshwater-specific predictor variables (Domisch et al., 2015). Furthermore, remote sensing techniques are capable of providing detailed information on local conditions (such as water temperature patterns recorded by drones). A large untapped potential remains to be explored and tested in this domain (Pettorelli et al., 2014), see Jones et al. (2016) for an example. Such large datasets describing variables that govern ecosystems along the hierarchy of different nested scales are becoming widely available, also to the general public, due to open access policies and on-line repositories.

Increasing the spatio-temporal resolution of input variables should help improving the robustness of the models and the accuracy of the output. This in turn fosters the support of environmental management decisions. However, larger model extents and improved variable resolution may also increase the challenge of uncertainty quantification (Section 5). Furthermore, untangling the effect of large-scale overriding factors and their interplay with local conditions may be challenging.

Besides increasing the resolution of independent, environmental variables, it is necessary to additionally invest in improving the temporal, spatial, and taxonomic resolution of the response variables (i.e. biological variables). High-throughput DNA sequencing methods (e.g. metabarcoding) will provide new opportunities and challenges in this regard (Bush et al., 2017; Hering et al., 2018). Furthermore, openly accessible data repositories (Wilkinson et al., 2016) will contribute to the availability of biological data. Some of them cover the global scale and all taxa (e.g. GBIF; www.gbif.org), while others provide information of specific geographic regions and ecosystem types (e.g. Schmidt-Kloiber and Hering, 2015).

4. The model has an appropriate spatial and temporal resolution for addressing the management problem

4.1. Why?

For adequately addressing a management question, ecological models need to account for the (often administratively determined)

temporal and spatial scales relevant for the management situation. However, in addition, the ecology and natural dynamics of the system need to be considered, with the model's resolution reflecting a balance between the scale of the management problem and the level of ecological detail needed to produce meaningful time and space units (Rahbek, 2005; Elith and Leathwick, 2009; Martínez-López et al., 2016). For example, a nationwide biodiversity management strategy planned for the next 50 years might benefit from a species distribution model representing general and macro-scale patterns and processes using coarse spatial grid units and decadal time steps, while little value would be added by including diurnal migration patterns of species to this model. A site specific management plan, however, might benefit from the explicit inclusion of diurnal migration patterns in order to identify specific habitat units in need of protection. Hence, avoiding a mismatch in scale between model, management plan and ecological processes is an important cornerstone for creating models representing ecological processes of management relevance.

Increasingly, models are used to make predictions towards new locations or into the future. The models are then applied outside the domain in which they were developed, requiring careful consideration of model uncertainties and associated predictive performance under these new conditions. Hence, the decision about a suitable spatial extent and time horizon is crucial.

4.2. How?

A first step towards identifying the appropriate scales is to map the processes, dependencies, drivers and pressures that are relevant for the management problem in a conceptual model (linkage map). Prior to any data analyses, such linkage mapping provides a comprehensive overview of dependencies. This assists in increasing the mechanistic foundation of the model, allowing for the selection of causally linked influence factors and the appropriate spatial and temporal resolution in which they operate. Moreover, spatial dependencies and temporal lag-effects can be identified, where the source may be spatially and/or temporally disconnected from the impact. This is for instance the case in considering effects of micro-plastics which can travel long distances, often changing in toxicity due to fragmentation, sorption of pollutants and fouling by potentially pathogenic communities along the way, before accumulating at sink locations far away from original sources (Vermeiren et al., 2016). After carefully filtering the most relevant processes (in collaboration with experts in the field), the potential input variables should become clear as well as the appropriate scale that should match the output variable to reduce uncertainties in the model.

A conceptual model can be developed with input from stakeholders, experts, and the literature. This helps identifying the adequate breadth (coverage of important aspects) and depth (level of detail) of the model to answer the management question. Note that the focus might need to be widened to capture the full range of relevant processes. For instance, the spatial scale of a model (and thus the spatial scale of the input data) can be broader than the spatial area in which it will be applied in order to provide a better coverage of certain environmental variables. This is of particular relevance when predictions to new environmental conditions (e.g. increased temperature or reduced pollutant concentrations) are made, which are not included in the current area to be managed (avoiding e.g. non-analogue climates in future predictions). In such cases visualization techniques can support the exploration of model behaviour and predictions to novel environments (e.g. Zurell et al., 2012). However, data might not always be available at the appropriate spatial and temporal resolution, or within the range of the environmental variables in which the model will operate. In such cases uncertainty assessment (as discussed in Section 5) becomes of paramount importance.

4.3. Future changes?

We are in an exciting era of increasing data availability (e.g. stemming from wireless real time monitoring systems, eDNA analyses, remote sensing images over large spatial extents and at short time intervals) and capacity to collect and store these data, which can dramatically increase the spatial and temporal resolution of ecological data and thereby ecological models. The flexibility and dynamic features of models may particularly benefit where time-series of both input and output variables are available. The appropriate curation and documentation, and continuous work on incorporating these data into useful ecological models is crucial to benefit best from them. The latter includes mapping linkages between management actions and ecosystem properties and ecosystem processes in conceptual models, and formalizing and testing these links in (temporally and spatially explicit) quantitative models.

5. Model uncertainty can be quantified

5.1. Why?

All models are prone to various sources of uncertainty. In addition to inherent stochasticity of environmental systems, uncertainty originates from model inputs (explanatory variables), model structure, and model parameters (Knutti, 2008). Even observed data used for model calibration and validation are subject to uncertainty owing to imperfect sampling and measurement procedures. To allow environmental managers to interpret model results correctly and draw robust conclusions, it is essential to provide an estimate of model uncertainty along with the expected value of model outcomes (Fischhoff and Davis, 2014; Buisson et al., 2010; Uusitalo et al., 2015). Only then well informed decisions can be made. Even if uncertainty bounds between management alternatives largely overlap, it might be possible to take a clear decision, if it is evident that some of the alternatives lead to changes in the desired direction (Reichert and Borsuk, 2005).

Uncertainty information helps decision makers to develop realistic expectations regarding the predicted effects of management alternatives (Wardekker et al., 2008) and allows considering their own risk attitude (Keeney, 1982). So called "risk neutral" decision makers prefer the alternative with the highest expected value, independent from its uncertainty. "Risk averse" decision makers, on the other hand, prefer alternatives with a lower uncertainty, even if their expected value is slightly lower compared to other alternatives with higher uncertainty. Additionally, a description of uncertainty facilitates the learning process (Wardekker et al., 2008) and adaptive management. Being transparent about the uncertainty of predictions finally increases credibility of scientists.

5.2. How?

While information on model uncertainty is indispensable for decision making (Warmink et al., 2010), uncertainty is often difficult to quantify. Most tangible is the quantification of input and parameter uncertainty. First, uncertainty estimates for all model input variables and parameters have to be collected. This uncertainty can be described by probability distributions (Reichert et al., 2015). In a second step, input uncertainty has to be propagated through the model to the outputs. For non-linear models, Monte Carlo simulation is the standard approach. However, it may be computationally demanding depending on the model runtime.

Several methods exist to infer parameters and their uncertainty from data. This is sometimes called inverse modeling. If no prior knowledge about the model parameters (and their uncertainty) exists, but there is enough data for model calibration, parameters can be inferred using Frequentist statistics (Neyman, 1937), e.g. maximum likelihood estimation (see standard textbooks). However, this is only

possible if all parameters are identifiable from the data. Parameters may be unidentifiable due to a lack of sensitivity of the model to some of the parameters or due to correlations among parameters, i.e. if several combinations of parameter values lead to the same model output. Based on certain assumptions, it is possible to derive estimates of confidence intervals for parameters and model outputs, e.g. using a profile likelihood approach (Montoya et al., 2009). Ideally, the model is validated with independent data (Section 6).

Whenever prior knowledge about parameter values is available (e.g. from previous model applications, experiments, or ecological theory (e.g. Robson et al., 2018)) and data for calibration exist, Bayesian Inference can be applied. It offers a consistent framework to combine both, prior information and data, to derive the best predictions possible based on the current state of knowledge (Gelman et al., 2014; Ellison, 2004). It allows to consistently update the information when new data becomes available. Many software tools exist that facilitate Bayesian inference (see Krapu and Borsuk, 2019), such as Winbugs (Lunn et al., 2000), JAGS (Plummer, 2003), or Stan (Carpenter et al., 2017), and can be run on, or linked to, various platforms for statistical computing, e.g. R (R Core Team, 2019). However, a solid mathematical understanding of the underlying concepts is needed to choose an adequate setup of the inference algorithm and to identify and solve numerical problems, e.g. regarding efficiency and convergence. Bayesian inference is even more computationally demanding than just forward propagation of uncertainty, as it requires a larger number of model runs. It may become infeasible if a single model run consumes much computation time (e.g. several minutes), and/or when the posterior parameter distribution has a complex structure, which increases the number of required model runs.

Although structural inadequacy (i.e. model structure error) makes a large contribution to total uncertainty of environmental models (Refsgaard et al., 2006), this aspect is still underrepresented in current practice in some fields of ecological modeling (e.g. mechanistic ecosystem models), while it is popular in others (e.g. species distribution models (Araujo and New, 2007)). In recent years, a number of studies employed multi-model ensembles to (also) consider structural uncertainty in analyses of environmental management scenarios (Lenhart et al., 2010; Ramin et al., 2012; Trolle et al., 2014). Although the approach of multi-model ensembles is promising, it is not without limitations (Janssen et al., 2015). A practical problem (especially with mechanistic models) is the considerable effort needed for setting up and running multiple models in parallel. In other fields (e.g. in species distribution modeling), different challenges exist: One of them is to check whether the calibration leads to reasonable results in all models in the ensemble, and whether they are in accordance to our current mechanistic understanding, e.g. if coefficients have the correct sign or response curves have an adequate shape. A conceptual problem lies in the subjective choice of models and a possible underestimation of uncertainty, if the chosen models are too similar. A recent review confirms that model averaging is particularly useful if the covariance between models is low (Dormann et al., 2018). As discussed in the previous sections, scenario analyses can help exploring the robustness of model outcomes to future changes that are too hard to predict.

5.3. Future changes?

The current push for increasing computational resources and the development of more efficient algorithms such as Approximate Bayesian Computation (e.g. Albert et al., 2015) will facilitate solving inference problems that were computationally too expensive in the past. The use of high performance computing methods that allow parallelization and the use of supercomputers will contribute to this development (e.g. Sukys and Kattwinkel, 2017). The development of emulators – simplifications of the original simulation models that speed up simulation times for the costs of additional uncertainty – are another line of current research that might facilitate the quantification of

uncertainty for slow models (e.g. Carbajal et al., 2017).

The increasing availability of high-resolution data makes the formulation of models even more challenging, because basic statistical assumptions, e.g. with regard to the independence of observations, may no longer hold and more sophisticated formulations of error models may be required, e.g. to consider autocorrelation. Furthermore, with improved measurement techniques, intrinsic (environmental and/or demographic) stochasticity of the system may dominate over measurement error. Therefore, the development of stochastic ecological models will gain importance. Examples are stochastic differential equations and individual based (also called agent based) models for population dynamics that consider demographic stochasticity. Applying Bayesian inference to such stochastic models is a huge challenge and the development of efficient algorithms is becoming a research area of increasing importance (Kattwinkel and Reichert, 2017).

Joining mathematical and computational skills with the ecological knowledge about the system and an understanding of the management problems is a considerable challenge. Consequently, there is a great need for inter- and transdisciplinary collaboration to effectively progress towards useful and applicable ecological modeling (e.g. Voinov and Bousquet, 2010; Basco-Carrera et al., 2017; Parrott, 2017; Martínez-López et al., 2019). In addition, educating scientists from various fields in data science, including Bayesian statistics, will facilitate knowledge transfer and collaboration among different disciplines.

6. The model has sufficient predictive performance

6.1. Why?

Any model that aims at informing environmental management objectives should have a decent predictive performance, as otherwise it is useless. In addition, two aspects are important: model sensitivity to the specific management case (Getz et al., 2018) and transferability (Schroeder and Richter, 1999; Mieleitner and Reichert, 2006; Randin et al., 2006; Wenger and Olden, 2012; Yates et al., 2018) (also called universality or generality), making the model applicable across a wide range of management cases or areas.

It is possible that a model that has an acceptable predictive performance is still not sensitive to the relevant management action. This can have different reasons and therefore different implications for management. First, the model output variable may not be much affected by the management action. This means that the management action would not be efficient to improve the ecological state of the system and other management alternatives should be considered. Second, the input variable that is affected by the management may have too much measurement error or is too weakly linked to the management action, while other explanatory variables not linked to management still lead to an acceptable predictive performance. This would mean that the management effect is underestimated by the model, and the data on the input variables need to be improved to better assess the effect of the management actions.

Model transferability can be important for two reasons: First, high transferability regarding the geographic area of application, and also regarding the management application increases the confidence in the mechanistic foundation of the model (because it is less likely that the model just works due to spurious correlations, see Section 2). Second, a model with a larger transferability may be more useful for environmental management, because it can be applied to more management cases. This makes it easier to justify the time and effort that is invested into model development and application.

6.2. How?

Model validation is crucial to assess the predictive performance. It is one of the most important steps during model development, possibly requiring to re-formulate the model or to acquire additional data.

Commonly used validation techniques vary among disciplines from cross-validation, bootstrapping to jack-knifing, and often use a random splitting of the data for calibration or validation (Araujo et al., 2005). Independent validation data that has not been used for calibration helps identifying model accuracy and potential overfitting (i.e. using a too complex model to reach a good fit to the calibration data while having a bad predictive performance for independent validation data). A non random-split of the data to groups that are spatially, temporally or otherwise distinct may be used to assess model transferability and to avoid overfitting in the absence of data from independent sampling campaigns (Wenger and Olden, 2012). Commonly used methods to assess goodness-of-fit, model accuracy, and predictive performance are model deviance from calibration and validation data, respectively, plotting/mapping the model residuals, or using multiple metrics that evaluate the model from different perspectives (e.g., sensitivity and specificity), which largely vary between application fields. A comparison of the model with an appropriate null model (e.g. a model without input variables) highlights the explanatory power of the considered input variables and therefore helps judging its value for supporting the management decision. Additionally, it is important to consider that even if models perform well, this does not mean that model outputs are ecologically meaningful, as e.g. high model evaluation scores do not necessarily go hand in hand with a useful model output (Section 2, Domisch et al., 2013; Elith and Graham, 2009). This caveat is even more challenging when transferring the model in space or time for e.g. management or future scenarios (Araujo et al., 2005). Here, an appropriate selection of scale (Section 4) may help to identify possible shortcomings. In general, starting with a simple model helps understanding the model structure and its behavior, as well as gaining confidence into the model. Model complexity can be increased step-wise by re-assessing the predictive performance, whether it has improved regarding sensitivity to the targeted management objective or increased transferability.

6.3. Future changes?

In the absence of adequate data/knowledge to generate models that have a satisfying predictive performance, environmental managers and decision makers often have concerns regarding the robustness of model outputs and do not take model predictions (under different scenario assumptions) into consideration. This calls modelers to scrutinize the mechanisms and/or acquire better data to improve the model and to assess practical implications of model results on decision making. In the future, data availability will increase, which will help improving the predictive performance of models, allow testing further hypotheses about cause-effect relationships and targeting additional management objectives, whose effects on the system could not be predicted before. We expect that model validations will be more rigorous in the future along with a data availability at higher spatial and temporal scales.

7. The modeling procedure, model assumptions, outcomes and deficits are transparently communicated

7.1. Why?

An understandable and transparent communication about the whole modelling process is central for deriving realistic expectations regarding the potential of models for supporting management. In pesticide risk assessment for example, which can be viewed as a form of prospective environmental management, ecological models are slowly becoming part of the assessment process that was so far mostly based on laboratory test and field studies (Forbes et al., 2011; Schmolke et al., 2010a). However, interviews with stakeholders from industry (the applicants for the registration of new products), regulating authorities, and academia revealed missing trust in models on the one hand and contradicting but high expectations on the other as main obstacles for

making models a widely used method in this field (Hunka et al., 2013). Thorough and comprehensible documentation and communication would help preventing unrealistic expectations and building trust into models. Likewise, it may foster the credibility of science in general, if the scientific method of modeling is not perceived as a “black box” but as a tool that can be understood and discussed.

The same applies to model results and their uncertainty. For potential end-users, the model results have to provide a clear message that is very easy to understand and communicate. Presenting model uncertainty to stakeholders in an understandable way might be a particular challenge and requires an adequate (visual) presentation. Model results must always be interpreted in light of the question the model was built to answer and the assumptions and simplifications made during the model development: If, and only if, a model was a perfect description of the modeled system (which is never the case), the model results would completely reproduce the system's behavior. Although this textbook rule is plausible, it can easily be forgotten. Hence, clearly stating model assumptions fosters the correct interpretation of results (Gregg and Chan, 2014). At the same time, it allows challenging these (subjective) assumptions.

Furthermore, model documentation and communication can serve as additional quality control for modelers, because potential flaws in the conceptual model or in the implementation might be noticed during the process of preparing model descriptions. Likewise, an accessible and comprehensive model description can support the learning process, as it facilitates the discussion of our current understanding about cause-effect relationships among peer modelers as well as with experts and stakeholders.

7.2. How?

Two points are of major importance for a transparent communication of the whole modeling process: First, models for environmental management and decision support should best be developed in close collaboration with decision makers and stakeholders (Hunka et al., 2013). Thereby, the aim but also the limitations of the model could be clearer for all parties from the beginning. It also prevents a situation where end-users receive output from a “black box” that is difficult or impossible to interpret. One crucial aspect of such a collaboration is to overcome transdisciplinary language barriers. In some cases, consulting companies can play a role to bridge between science and practice and to establish long-term collaborations.

Second, careful documentation of the model itself, but also of the background of its development, implementation, and validation, is needed. Standard protocols for the whole documentation (e.g. TRACE (Schmolke et al., 2010b)) or tailored for certain model types or research questions (e.g. for individual-based models (Grimm et al., 2010) or for population viability analyses (Pe'er et al., 2013)) may be helpful. Typically, different levels of documentation are needed to satisfy a heterogeneous audience of modelers, other scientists, practitioners, and decision makers. While a scientific journal article (including a complete mathematical description of the model) matches the expectation of the first group, it does not necessarily suit the other groups. A graphical representation of the model, e.g. using conceptual diagrams, will be appreciated by all groups.

The output of the model must be easy to understand by decision makers and stakeholders. A summary report should include concise and robust take-home messages derived from model results and the methodology followed. Nevertheless, a critical assessment of the model should be part of every report, clearly stating the model's provenance, conceptual background, the major simplifications, the associated limitations, and uncertainty of the outputs. It should go without saying that model verification and validation statistics as well as estimates of predictive uncertainty are reported faithfully.

Furthermore, the FAIR principles for data management (Findability, Accessibility, Interoperability, and Reusability; Wilkinson et al., 2016)

should be applied as much as possible to models in order to let them be automatically discovered and used on-line. Public access to the model's source code and documentation serves both verification by and discussion with peer scientists and it provides a basis for continuous development. It is crucial that researchers make their models available and adopt open source modeling tools and methodologies, such as R (R Core Team, 2019), so that models can be further developed by their community of users.

7.3. Future changes?

A promising approach to improved transparency is to separate the concept (mathematical equations) from the actual implementation in a computer code. This has recently led to the development of largely self-documenting mechanistic models, which have the additional advantage to be re-used and portable (Mooij et al., 2014; Kneis et al., 2017). Technologies that support interactive web-based modeling evolve rapidly (Chang et al., 2017; Ooms, 2014). We see this as a great chance to make end-users more acquainted with “their” models and guarantee rapid feedback to developers. We promote the use of online hosting repositories (such as GitLab, GitHub, or Bitbucket) that, additionally to allowing code sharing, include other functionalities such as version control, bug tracking, and wiki services. Hence, they are ideal environments for collaborative model development. Especially for more complex models a collaboration with professional software developers might be beneficial, e.g. to improve code testing, maintenance, or the development of user-friendly interfaces. Additionally, the collaborative development and testing of ‘standard models’ for certain fields, e.g. pesticide risk assessment (e.g. European Food Safety Authority, 2016), coordinated by respected institutions or authorities in the field, may foster agreement on model assumptions and structure. Thereby, they facilitate building trust into models as tools for management. The development of check lists and templates for model documentation will furthermore facilitate model development and communication.

8. Conclusions and final remarks

With this paper, we intend to stimulate a long-needed discussion about how to facilitate the use of ecological models in decision making processes for environmental management. We find this important, because environmental management decisions should be based on the current state of knowledge and there seems to be a gap between the ecological modeling community and environmental managers that often hinders the application of ecological models in environmental decision making. To change this in the future, we outlined how the modeling process could be better aligned to the decision making process (Box 1). Furthermore, we identified and discussed six methodological requirements that we believe are important to make ecological models useful to inform environmental management decisions. A crucial step for achieving these requirements is to foster collaboration and a transfer of knowledge on three different levels:

1. Transdisciplinary collaboration between ecological modelers and environmental managers as well as stakeholders to facilitate the alignment of the model to the management decision (see Box 1), to foster an appropriate interpretation of the results, and to facilitate the implementation of results into the management decision (Parrott, 2017);
2. Interdisciplinary collaboration between ecological modelers and empiricists to foster the integration of empirical data and mechanistic understanding about the system into the models;
3. Intradisciplinary collaboration between ecological modelers from different fields regarding modeling approaches (see Fig. 2, Dormann et al., 2012) but also regarding fields of application (e.g. terrestrial vs. aquatic or marine vs. freshwater ecosystems) to foster the exchange of ideas, methods, and code (Mooij et al., 2010).

To engage in environmental decision making, we as “ecological modelers” should seize opportunities to engage with the public or important stakeholder groups to exchange knowledge. Therefore, it is important to know the policy processes and communication culture of decision makers to identify windows of opportunity to establish collaborations with environmental decision makers. We should use our models to provide knowledge about consequences of management alternatives based on the best available science, as objectively as possible, by showing the advantages and disadvantages of each management alternative, instead of only providing direct recommendations for certain management alternatives. To facilitate this, it is helpful to explicitly separate the objective prediction of consequences from subjective valuations about the importance of management objectives that should be inferred from democratic processes. We have to communicate clearly the benefits of ecological models as well as any model deficits and their potential consequences and treat our models as tools to facilitate iterative learning and support adaptive management. Finally, it should be noted that the sustainable development of ecological models for use in practice requires a stable institutional and personal infrastructure. It can hardly be achieved during short-term projects by persons with temporary employment. With this paper, we hope to raise awareness about challenges and opportunities for increasing the impact of ecological modeling on real world environmental decision making.

Acknowledgements

This paper was initialized during a special session on Ecological Modelling at the 10th Symposium for European Freshwater Science 2017 (<http://www.sefs10.cz/>) and further developed during the AQUACROSS project, funded by European Union's Horizon 2020 research and innovation programme (Grant agreement No. 642317). SD, SDL and MF were partly funded by the “GLANCE” project (Global Change Effects in River Ecosystems; 01 LN1320A) through the German Federal Ministry of Education and Research (BMBF). SDL has received additional funding from the European Union's Horizon 2020 research and innovation programme under the Marie Skłodowska-Curie grant agreement No. 748625. JML acknowledges the support of the Spanish Government through María de Maeztu excellence accreditation 2018–2021 (Ref. MDM-2017-0714). We thank Romina Martin and Sonja Jähnig for stimulating discussions and feedback to an earlier draft. We acknowledge the members of a reading group about data science and machine learning in the department of Systems Analysis, Integrated Assessment, and Modelling at Eawag for insights into emerging fields in data science and inspiring discussions, and Tom Lorimer for comments on the box about theory based data science. We thank Boris Schröder, Thomas Petzoldt, and two anonymous reviewers for their constructive comments to earlier drafts.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <https://doi.org/10.1016/j.ecolmodel.2019.108784>.

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