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Review

Addressing uncertainty when projecting marine species' distributions under climate change

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Species distribution models (SDMs) have been widely used to project terrestrial species' responses to climate change and are increasingly being used for similar objectives in the marine realm. These projections are critically needed to develop strategies for resource management and the conservation of marine ecosystems. SDMs are a powerful and necessary tool; however, they are subject to many sources of uncertainty, both quantifiable and unquantifiable. To ensure that SDM projections are informative for management and conservation decisions, sources of uncertainty must be considered and properly addressed. Here we provide ten overarching guidelines that will aid researchers to identify, minimize, and account for uncertainty through the entire model development process, from the formation of a study question to the presentation of results. These guidelines focus on correlative models and were developed at an international workshop attended by over 50 researchers and practitioners. Although our guidelines are broadly applicable across biological realms, we provide particular focus to the challenges and uncertainties associated with projecting the impacts of climate change on marine species and ecosystems.

Keywords: ecosystem management, environmental change, fisheries management, future climate, habitat suitability

Introduction

Managing natural ecosystems in this era of global change requires accounting for the ongoing and anticipated impacts of climate change. In general, species are tracking climates poleward (sensu Iverson et al. 2019, IPCC 2022), but the rate, extent, and direction of movement for any individual species is highly uncertain. While the primary application of species' distribution models (SDMs) has been to predict the contemporary distribution of a species based on the spatial variation of environmental covariates, they are becoming a valuable tool to project the potential future distribution of those same species.

In the marine environment, increasing temperatures and other effects of climate change on ecosystems are already impacting species, with changes in physiology and range shifts being among the most recognized (Pörtner and Peck 2010, Pecl Gretta et al. 2017, Fredston-Hermann et al. 2020, Weiskopf et al. 2020). Species will either shift their distribution and attempt to track changing environments, acclimate, or evolve in response to changing conditions, or become extirpated or possibly extinct (Holt 1990, Wiens et al. 2009, English et al. 2021, Tittensor et al. 2021). The three-dimensional marine realm presents some unique challenges to adaptation. For example, the stratification of the water column and the strong correlation between depth and dissolved oxygen can, depending on a particular species' physiological tolerances, limit its ability to shift into deeper depths as conditions warm (Wiens 2016, English et al. 2021, Thompson et al. 2023). Marine species are better able to track climate shifts poleward than terrestrial species due to the lack of physical barriers to movement that exist in the terrestrial realm, such as mountains, river systems, and human development (Lenoir et al. 2020). However, human extractive activities (i.e. fishing) are also shifting poleward, making it difficult to disentangle the different pressures (Pinsky and Fogarty 2012). Despite these challenges, distribution projections are a valuable tool to understand the scope of potential change in future climates (Brodie et al. 2022). While there are many sources of uncertainty inherent to SDM predictions (Araújo et al. 2019, Zurell et al. 2020), the additional uncertainty associated with projections of species' distributions into the future is the focus of this paper. Decisions that are made during the model building process will have a cascading effect on the uncertainty of projections. Projecting SDMs into new time periods, with potentially new climate conditions, introduces three additional sources of uncertainty: 1) climate model uncertainty; 2) emissions scenario uncertainty; and 3) eco-evolutionary uncertainty (Fig. 1). These additional sources of uncertainty stem from the underlying biological and environmental data, the climate projections, as well as the complexity and context dependency of natural ecological systems (Urban 2019). This uncertainty can hamper confidence in model results or interpretation and can include both parametric (uncertainty in model parameters or quantities of interest) and structural uncertainty (model misspecification) (Elith et al. 2002).

Projections can provide critical information to fisheries and conservation managers, such as the identification of areas where species are likely to persist, increase, or decline under climate change (Young and Carr 2015, Sofaer et al. 2018). However, if uncertainty is not accounted for and addressed, there is a risk that species' projections will, at best, fail to be informative for making management decisions and, at worst, lead to poor management decisions by presenting overconfident or inaccurate results (Budescu et al. 2012, Brodie et al. 2022). In this paper, the word uncertainty is used in both the colloquial sense, to describe something that is unknown, and in the statistical sense, to describe the range of probable outcomes. The latter is quantifiable, while the former is not. We argue that to produce rigorous SDM projections that meaningfully inform management decisions, uncertainty must be identified, minimized when possible, and communicated to end users. The themes of this paper were discussed by over 50 researchers and practitioners at an international workshop hosted by Fisheries and Oceans Canada in March 2021. Here, we propose a set of ten guidelines for addressing uncertainties when projecting marine species' distributions under climate change, including identifying the sources of uncertainty, their impacts on the analytical process and results, approaches to manage these uncertainties, and how to appropriately communicate them to end users.

Guidelines for using SDMs to project marine species

We propose guidelines that support a logical workflow starting from articulating the goals of the study, through the modeling process, both model building and projection, and finally communicating results to other scientists, resource managers, and policy makers. Guidelines 1 and 2 provide advice for the development of sound research. Guidelines 3–6 identify uncertainties associated with model building, including the level of uncertainty acceptable depending on the objective, the uncertainty from input data, relevance of predictors, and the selection of the model. Guidelines 7–10 are specific to projections in new climate conditions and, as described above, deal with climate model uncertainty, emissions scenario uncertainty, and eco-evolutionary uncertainty. For each guideline we have identified key questions for analysts to consider and outline best practices with a focus on how to identify and minimize uncertainty, when possible, and how to transparently communicate the uncertainty that cannot be avoided (Table 1).

1. Frame the research question

Clearly stating the research questions (i.e. the problem, the objectives, and the hypotheses) is essential to ensure that objectives are considered throughout the analysis and support transparent and reproducible SDM results (Araújo et al. 2019, Zurell et al. 2020). A research outline (Table 2) can communicate the intention of the research, explicitly state the scope of the study, help identify any assumptions that may impact the outcome of the study, and support qualitative identification of the tolerance for uncertainty. Different

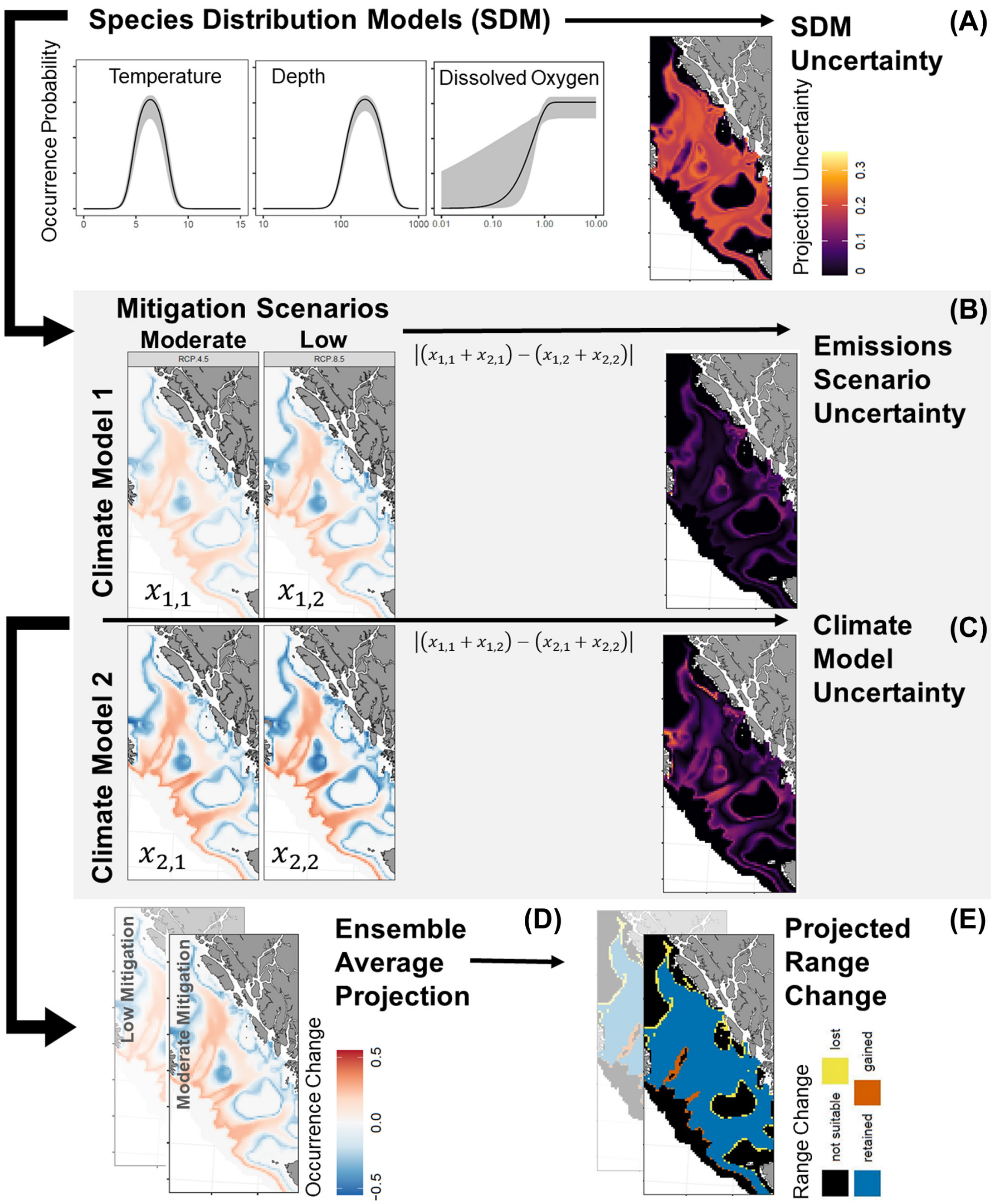


Figure 1. The uncertainty of a species' projected distribution can be broken down into several components of the modeling process, where the uncertainty associated with each component has a cascading effect on subsequent steps. The SDM uncertainty (A; i.e. the uncertainty associated with parameters in the SDM that define the species-environment relationships), and both the emission scenario uncertainty (B; i.e. the difference between projections based on different mitigation scenarios) and climate model uncertainty (C; i.e. the difference between projections based on different climate models – could represent a contrast across multiple global models or multiple regional models) can be mapped separately to illustrate areas of higher or lower confidence to end users. For simplicity, this figure does not include quantifying uncertainty due to internal variability. An ensemble projection (D) is a useful way to present the average projected values across multiple climate models or SDMs, but we recommend that it be presented alongside estimates of these other sources of uncertainty. Uncertainty due to eco-evolutionary processes is not generally quantifiable and is in addition to these other sources of uncertainty. Mapping projected range changes (E) can help to differentiate between areas of lower uncertainty from eco-evolutionary processes (i.e. areas projected to remain suitable) with areas of potentially higher uncertainty (i.e. areas where species are projected to be lost or gained). This figure partitions uncertainty into its individual components rather than propagating uncertainty, which is another good option. This example projection is based on data and outputs from Thompson et al. (2023).

Table 1. Summary of the different sources of uncertainty encountered when projecting species' distribution models (SDMs) into future climates and some recommended approaches to minimize or account for the uncertainty.

Guideline	Source(s) of errors and uncertainty	Recommended approaches
1. Frame the research question	Ambiguous research goals	Clearly state the problem, objectives, hypotheses, and assumptions that may impact the study
2. Build a collaborative community for SDMs in future climates	Irreproducible research or undocumented analytical decisions	Make data, modeling methodology (including purpose-built coding scripts) publicly available
3. Ensure the scope of study is relevant, both in space and time	Extent of study inputs does not accurately represent species' distribution	Use the widest possible spatial and temporal extent available for the species that best addresses the research question
	Scale mismatch	Up or downscale environmental covariates to match the most relevant temporal and spatial scale for the species, either instantaneous or long-term averages. Model comparison can be used to support decisions
4. Identify appropriate species' data	Biases in available data	Incorporate data from additional sources, including species' experts and Indigenous Knowledge; incorporate knowledge of a species' ecology and physical tolerances to improve model outputs
5. Determine relevant climatic and non-climatic environmental variables	Environmental variables may be poor predictors of current species' distribution	Examine species' response to historical climate variability and from physiological experiments; see random effects in Guideline 8
	Assumption of poor model performance when extrapolating into new conditions	Use biological knowledge to select the most relevant environmental variables; consider if the assumption that collinearity between environmental variables will remain the same or shift under future conditions
6. Select the SDM model	Incorrect variable selection and parameterization	Systematic evaluation of a set of candidate models, their model fit, and their predictive power using spatially or temporally held-out data to ensure model is not overfit
7. Identify climate model uncertainty	Internal climate model variability	Internal variability is quantified in Earth System Models by running the same global climate models (GCMs) and scenario multiple times with slightly different initial conditions; temporal averaging of climate projections over multiple decades can help to eliminate the effect of internal variability
	Model uncertainty – global scale	Quantify variability using multiple independent models and the same climate scenario
	Model uncertainty – regional scale	Dynamical or statistical downscaling, regional climate models
	Scenario uncertainty	Compare different scenarios using the same models
8. Identify SDM uncertainty	Natural variation	Acknowledge the influence of natural variation in the physical environment on model calibration; cross-validation
	States of nature	Compare models using different structural assumptions; estimation of parameter uncertainty through bootstrapping, maximum likelihood, Bayesian methods, etc.; spatial and spatial-temporal random effects; review model outputs with species' experts
	Extreme events	Acknowledge the potential for unpredictable events from both climate model uncertainty and eco-evolutionary uncertainty
9. Identify eco-evolutionary uncertainty	Assumption that all individuals have the same environmental response	Assess if environmental response curves vary using spatial-block cross-validation; model sub-populations separately if environmental responses differ
	Current species-environment relationship does not reflect future species-environmental relationship	Acknowledge that actual species' distributions under future climates will inevitably differ from projected potential habitat (i.e. SDM projections are hypotheses); highlight higher certainty in areas where conditions are projected to remain suitable
10. Communication of results and uncertainties	Misinterpretation or dismissal of important findings	Involve end users in the development of the research question; illustrate areas of uncertainty with maps; identify the timescale of outputs as well as both certainties and uncertainties in model outputs

research objectives will have different assumptions. For example, quantified changes in abundance and distribution are necessary for the development of harvest strategies for commercially important species and assume that sampled biomass data are representative of the population (Allyn et al. 2020). Marine spatial planning studies to identify overlap between cetacean distribution and oil and gas exploration activities, however, may only require qualitative

Table 2. Examples of different research outlines to facilitate the next steps of investigation and guidelines presented in this paper.

Research outline	Example 1	Example 2
Problem	Climate is known to elicit movement responses by managed commercial fish species. The lack of knowledge regarding how they will move creates uncertainty in harvest management advice and the associated risk to achieving management objectives in the future	Climate change will impact the availability or distribution of habitats for marine species, such as cetaceans. Identification of areas that are likely to support high biodiversity is necessary for biodiversity and habitat protection initiatives
Objective	Projecting the distribution of a commercial fish species in future climates to support stock assessment and fisheries management	Identifying areas along the coast that are projected to support high biodiversity for marine protected area (MPA) designation
Question(s)	How might distributions of important managed species change within a management zone?	Are there biodiversity hotspots in the study area? Are there habitats for the species or species' assemblages under study that may remain generally stable over time?
Uncertainties (one example)	Cannot assess all life stages of a commercial fish species (e.g. juvenile) due to gaps in life history knowledge and/or limited juvenile species' observations	Interactions between species may prevent some species from predictably tracking their climate niche
How will the above uncertainty impact the analysis?	Incomplete environmental response curves due to lack of juvenile observations; unrealistic confidence around projections	Projected and realized changes in biodiversity may differ

changes in occupancy over time for decision making purposes (Sahri et al. 2021). Laying out the study plan provides a clear communication tool for all parties involved in the research and its outcomes.

2. Build a collaborative community for SDMs in future climates

Teams with multidisciplinary expertise (e.g. biology, oceanography, climate science, statistics, data management, computer science) are essential to properly develop SDM projections and address the associated uncertainty. Each step of the SDM analysis process (goal setting, data selection, model building, model evaluation and validation, interpretation of results, and communication of results) may require a unique set of experts to guide decisions. For example, data selection for a single-species' SDM projection would not only involve species' experts with a strong statistical background but would also require collaboration with oceanographers and climatologists. Modeling steps in the analysis could involve additional support from statisticians and computer scientists that include both biological and climate modeler expertise. Connections among communities of practice working on common objectives and building complementary tools can increase efficiency, reduce duplication of effort, and boost outcomes of research findings (Gomez et al. 2021). Collaborative efforts can both facilitate, and be facilitated by, improved accessibility of all predictors, species' data, and model results. Bio-ORACLE is an example initiative aggregating geophysical, biotic, and climate layers with common spatial resolution (Tyberghein et al. 2012, Assis et al. 2018). The Fisheries and Marine Ecosystem Model Intercomparison Project (Fish-MIP ver. 1.0) is an example of a cross-sectoral network that brings together the marine ecosystem modeling community to produce consistent ensemble medium- and long-term projections of marine ecosystems using common scenarios and standardized outputs (Frieler et al. 2017, Tittensor et al. 2018). Both of these initiatives highlight the importance of making all input data, modeling methodology (including code), and decisions made during the analysis process publicly available to facilitate reproducible research and greater collaboration (Nephin et al. 2020, Zurell et al. 2020, Nature Editorials 2022).

3. Ensure the scope of study is relevant, both in space and in time

The choice of extent and resolution in both space and time can impact the accuracy of SDM projections and affect their utility to support management decisions (Record et al. 2018). Projecting distributions into future climates assumes that species' distributions across spatial climate gradients will match species' responses to temporal changes in climate. While this assumption is based on a species' distribution being at equilibrium with climate and is, at times, incorrect, it is important to consider how analysis may be limited by both the distribution of sampling within the study area and the environmental range that is being characterized (Pearson and Dawson 2003, Araújo and Peterson 2012).

Applications of SDMs to marine species have often involved fitting models with observations from a subset of the species' range within geopolitical boundaries (Thorson et al. 2015, Laman et al. 2017). While this spatial extent may be appropriate for questions related to regional commercial fish stock assessments, they are ill-suited to climate change applications. Using only a subset of data in space or time will usually lead to truncated species-environment relationships and introduce uncertainty in the fitted SDM parameters (Guillera-Arroita et al. 2015). These models are likely to have reduced transferability when they are extrapolating beyond the range of observed conditions where they are not calibrated or validated, and therefore generate poor distribution projections (Thuiller et al. 2004, Muhling et al. 2020, Charney et al. 2021). To characterize the species-environment relationship, species' observations should be sourced from the widest spatial and temporal extent available that best addresses the research question (Thuiller et al. 2004, Barbet-Massin et al. 2010).

The spatial resolution of appropriate environmental covariates should also be at a biologically relevant scale for the taxa being modeled (Austin and Van Niel 2011). For example, the relevant scale for the relationship between bathymetry and a highly migratory pelagic fish species (e.g. tuna) is likely coarser than that for an intertidal invertebrate (e.g. oyster). One challenge with modeling at an appropriate scale is that the available spatial resolution of environmental covariates may not match the resolution of the species' observations. In these cases, environmental covariates should be up- or down-scaled (Hijmans et al. 2005, Araújo et al. 2019). Unfortunately, future climatic variables are necessarily coarse since they are typically modeled at a global scale and projections are not yet available for all relevant climatic variables. For example, Bio-ORACLE currently only has a quarter of the number of benthic variables available for projections as it does for current distributions (Assis et al. 2018). While downscaling methods can be applied to match the desired scale in an attempt to capture the variability at the scale relevant to the organism, this process may introduce additional uncertainty. Modeling at coarser spatial resolutions than is biologically appropriate can increase uncertainty in projections by over- or under-predicting habitat (Seo et al. 2008, Randin et al. 2009, Willis and Bhagwat 2009, Gottschalk et al. 2011, Franklin et al. 2013). Importantly, the spatial scale at which species' projections are generated should be considered when making management decisions. Coarser resolution models (e.g. 100 km) that do not resolve local topographic features, for example, may not be well suited to support local management decisions (e.g. within a 10 km squared coastal protected area) (Whittaker et al. 2005). Although these coarse models may currently represent the best available knowledge, they should be considered to have a high level of uncertainty due to gaps in finer scale distribution.

The temporal resolution of environmental covariates is another important consideration. Ideally, the temporal resolution of the environmental covariates should match that of the species' data used to build the species-environment relationship (Batalden et al. 2007, Araújo et al. 2019). However, SDM projections also involve a mismatch between current and future species-environment relationships as the projections derived from climatologies (i.e. long-term means) and characterize response to the long-term average (Heikkinen et al. 2006, Bateman et al. 2012). These climatologies ignore interannual variability and exclude extreme weather events, and thus will not be well calibrated to the range of conditions experienced by the species over time, leading to under- or overestimations of species' distribution (Bateman et al. 2012). When possible, comparing inter-annual and long-term climatic variability on a species' current predicted distributions can inform how effectively long-term averages can describe a species-environment relationship (Gardner et al. 2021, Perez-Navarro et al. 2021). Understanding this limitation will allow researchers to qualify the amount of uncertainty in model projections (Whittaker et al. 2005, Heikkinen et al. 2006, Randin et al. 2006).

4. Identify appropriate species' data

While consistent and standardized datasets of presence/absence or abundance are ideal for minimizing uncertainty when building SDMs, they may not be readily available or logistically feasible. Existing data may also be biased to a certain time of year due to logistical constraints or data collection priorities. Alternative information sources may confirm or expand species' observation data. For example, environmental DNA (eDNA) is becoming increasingly viable, particularly for bony fishes (Muha et al. 2017). Advancements in imagery analysis also allow for biological surveys of coastal habitats with remotely piloted aircraft (e.g. drones) (McKee et al. 2021, Monteiro et al. 2021). Citizen science platforms and global databases can provide observational data, trading sample size for potential inaccuracy and spatial bias (Beck et al. 2014, Johnston et al. 2020). Expert and Indigenous Knowledge can also be used in conjunction with survey data to capture the extent of a species' distribution (Merow et al. 2017, Skroblin et al. 2021).

Combining data sources can fill in gaps in any individual dataset. Integrated SDMs incorporate complex statistical structures to combine datasets from different sources can increase the power of a model while still accounting for biases and variances of the individual datasets (Isaac et al. 2020, Rufener et al. 2021). For example, this approach has been used to define the spatio-temporal distribution of killer whales (Watson et al. 2019). However, analysts must consider the biases that may result from differences across data sources. For instance, catchability often varies by fishing gear type, and data collected from fisheries may be non-random and preferentially sampled (Fletcher et al. 2019).

Information on a species' ecology can be used within SDMs to reduce uncertainty in forecasting. For instance, dispersal barriers, ontogenetic shifts, and biotic influences on aggregations (e.g. spawning) affect model accuracy and performance (Robinson et al. 2011). Dispersal barriers are less common in marine systems (Carr et al. 2003), but may be important to incorporate as post hoc constraints to SDM projections for species with lower dispersal capacities (Robinson et al. 2011). Uncertainty may be reduced by splitting observation data between adults and juveniles if a species occupies habitats with different environmental conditions across its life stages (Petitgas et al. 2013). Experimentally derived responses can be applied to compare the fundamental niche of a species relative to the realized niche modeled by SDMs (Martínez et al. 2015, Franco et al. 2018) or incorporated as priors in Bayesian SDMs (Gamliel et al. 2020). Though physiological limits are unknown for many marine species, this information is particularly valuable for SDM projections, as future distributions will be underestimated when observed locations are constrained by non-climatic factors (Araújo and Peterson 2012).

5. Determine relevant climatic and non-climatic environmental variables

There are two key considerations when identifying relevant environmental variables: 1) their ability to describe species' responses to current environmental conditions; and 2) the uncertainties that exist in how those responses may change in future climates (Table 1, guideline 9). Many studies have shown temperature-related variables to be among the most powerful predictors of species' distributions (Bradie and Leung 2017, Bosch et al. 2018). A variety of mechanisms have been identified through experiments, models, and observations of extreme thermal events whereby temperature affects biological processes such as development, dispersal, growth, and species' interactions (O'Connor et al. 2007, Kordas et al. 2011, Sunday et al. 2012, Boyd et al. 2013). Understanding these mechanisms can help to determine the most suitable temporal values (e.g. average daily maximum temperature, warmest month, or cumulative values such as growing degree days). However, data availability and realism must also be considered when selecting climatic variables. If biological knowledge suggests that extreme temperature events contribute to limiting the local-scale distribution of a species, it is necessary to determine whether the spatial and temporal resolution of the data (both from observations and climate models) are sufficient to resolve such events. Global climate models (GCMs) are most suited to projecting changes in the statistics of a climate phenomenon (e.g. mean temperature or the frequency of an event), rather than the magnitude of an extreme event, and the confidence in those extreme event projections can depend on the variable and region (Seneviratne et al. 2012).

Static, non-climatic variables are essential to reduce uncertainty when projecting species' distributions (Willis and Bhagwat 2009). Ignoring non-climatic variables that limit species' distributions increases the risk of overfitting the climatic variables, and over- or under-estimating changes in a species' distribution and extinction risk under climate change (Beaumont et al. 2005, Virkkala et al. 2010, Hof et al. 2012, Zangiabadi et al. 2021). In the marine realm, excluding physical habitat variables such as bathymetry can be problematic as they are often correlated with climatic variables that are difficult to measure or model, such as food availability, but integral to predicting habitat (Luoto and Heikkinen 2008). Unlike climatic variables, static variables can either be used as predictors in a model or explicitly excluded depending on the question and research objective. However, we recommend determining if environmental covariates should be included or excluded by applying causal inference methods to identify useful controls versus confounds (Pearl et al. 2016).

Highly complex and overfit models tend to perform well within the environmental space the model was trained with, but may perform poorly when projecting into future conditions (Moreno-Amat et al. 2015, Bell and Schlaepfer 2016). To limit model complexity, biological knowledge should be relied on to select the relevant environmental variables (Austin and Van Niel 2011). Preference should be to include the most proximate variables, those that have a direct physiological effect on the species being modeled, over more distal or indirect variables that are often used as proxies when proximal variables are missing (Anderson 2013, Gardner et al. 2019). Some commonly used static variables (e.g. depth and distance from shore; Bosch et al. 2018, Johnson et al. 2019) are considered proxies for other variables, such as pressure and exposure. When proxy variables are needed to represent important processes, practitioners should note that an assumption of stationarity between the proxy variable and the more direct variable it aims to represent is implicit.

Careful consideration of the causal link between each environmental variable and the focal species can simplify complex models and ensure model transferability (Barbet-Massin and Jetz 2014, Piironen and Vehtari 2017, Zangiabadi et al. 2021). In addition, collinearity between variables can make their independent influence on a species' range hard to distinguish (Bosch et al. 2018). This can be particularly problematic for temperature and depth in marine systems; although they are often highly correlated at regional scales, temperature is projected to warm while depth remains constant (Thompson et al. 2022). Projections require that SDMs have accurately estimated how these two variables shape species' ranges. A solution is to include species' data from across a broader spatial extent where latitudinal temperature gradients can break down the collinearity between temperature and depth (Thompson et al. 2023).

6. Select the SDM model

SDM models range from parametric, to semiparametric (Shelton et al. 2014), to various forms of non-parametric approaches including MaxEnt (Phillips et al. 2006) and machine- or deep-learning models (Elith et al. 2008, Christin et al. 2019). Furthermore, models of species' distribution can be purely data driven (e.g. correlative, Jarnevich et al. 2015) or built on assumed mechanisms and calibrated to data (Kearney and Porter 2009, Essington et al. 2022). Correlative models may perform well on existing data but not extrapolate well if those correlations break down (Davis et al. 1998). Mechanistic models are grounded in physiological and biological principles, and may outperform correlative models in future conditions, but are often challenging to construct (Kearney and Porter 2009, Urban 2019). Hybrid models incorporate known mechanisms in addition to phenomenological correlations, and have the potential to borrow advantages from both kinds of models (Kearney and Porter 2009). Creating ensembles by combining the outputs from several individual models using different algorithms can improve predictive ability (Araújo and New 2007, Hao et al. 2020) and can be as simple as unweighted or weighted averages (Araújo and New 2007) or as complex as super-ensembles tuned to simulated or trusted data (Anderson et al. 2017). However, an ensemble is only as good as the individual models used to build it, therefore some effort is required to choose a high-quality candidate set; using models with different covariates or structure may help identify misspecification of any single model. Practitioners seeking detailed guidance regarding different models should refer to Sofaer et al. (2019) for model development guidelines or Merow et al. (2014) for guidance on determining the appropriate model complexity.

Model choice can influence uncertainty and should therefore be guided by the objectives of the analysis, the model fit, and model evaluation. For this reason, it is critical to start with a set of candidate models that can support the objectives of the analysis. These candidate models may include different variables or differing parameterization of these variables. Second, it is necessary to evaluate candidate models for any problems in the fit itself (e.g. failure of the fitting algorithm to converge, non-sensible response curves) as well as violations of their assumptions (e.g. residual analysis, Rufener et al. 2021; posterior predictive checks, Gelman et al. 1996). Several approaches are available to compare among candidate models meeting the above criteria. Threshold-independent statistics (e.g. receiver operator curve plots) can be used to assess overall model performance and the models' discriminatory ability across species and locations; while threshold-dependent statistics (e.g. sensitivity, specificity, true skill statistic) can support accuracy assessment (Freeman and Moisen 2008, Liu et al. 2011). A more parsimonious model should in theory make better predictions (Aho et al. 2014). However, models that have good predictive power may not provide good projections (Veloz et al. 2012). Thus, model selection should be guided by ecological principles rather than selecting a model solely based on predictive power for contemporary distributions.

7. Identify climate model uncertainty

GCMs use numerical methods to solve systems of equations on a three-dimensional grid. These process-based models include coupled atmosphere, ocean, and land models, representing the fundamental components of the climate system (Flato 2011). A fully coupled global system is the only way to model the global climate system because of the complex interactions between each component. When coupled to models of biogeochemical cycling, they are known as Earth system models (ESMs) and are the primary scientific tools for estimating future climate states. ESMs from major climate modeling centres participate in coordinated experiments, including the coupled model intercomparison project (CMIP), which has evolved through six discrete phases of activity over the past 30 years. The future trajectory of human activity and the associated greenhouse gas emissions are unknown, so future socio-economically based emissions scenarios are developed to illustrate the range of possible pathways. Climate models driven by these emissions scenarios produce projections of the future climate state. Each phase of CMIP contains new scenarios and updated models, and concludes with the release of open data for downstream climate change studies (Eyring et al. 2016).

Global climate projections have three sources of uncertainty: 1) internal variability; 2) model uncertainty; and 3) scenario uncertainty (Hawkins and Sutton 2009). Internal variability arises from fluctuations in climate (such as El Niño), and within a single year this fluctuation can be larger than the climate signal itself. The precise evolution of internal variability in future decades cannot be predicted. However, the range of possible outcomes resulting from internal variability can be quantified by the spread across an ensemble of realizations from the same model and scenario. Each realization starts from different initial conditions, and while they will differ in their variability, they will each experience the same overall climate change.

Climate model uncertainty results from an imperfect understanding of the climate system, and from assumptions and compromises made in representing this understanding in software-based numerical models. For example, the global scale and process complexity in ESMs and limited supercomputing capacity constrains the feasible resolution to about 100 km. Processes that are not resolved at this scale (e.g. mesoscale ocean eddies) are approximately represented by parameterizations that are imperfect and often differ between models. Climate model uncertainty can be quantified by the spread obtained when multiple independent climate models are run using the same climate scenario. Summary reports such as the IPCC Assessments normally report on the multimodel mean result (IPCC 2021), which is generally more accurate than the projections from any one model.

Regional SDMs often require information at finer spatial scales than ESMs can resolve, so the ESM outputs must be downscaled to a finer spatial resolution. Regional downscaling techniques are briefly described here and for a more complete description of the commonly used methods and their use in ecology, the reader is referred to Harris et al. (2014) and Giorgi (2019). Dynamical downscaling uses a nested modeling approach in which regional models are forced at their boundaries by ESMs to generate finer resolution projections (Peña et al. 2019, Holdsworth et al. 2021). These models directly solve the equations of motion at regional scales and are particularly effective in regions where topographic effects on wind, temperature, and precipitation are important. Regional model uncertainty can be quantified by the spread obtained when an ensemble of independent regional models is run using the same driving ESMs and climate scenario (Fig. 1C). Statistical downscaling can be used to downscale ensembles of climate models. They rely on the assumption that regional climates are driven by large-scale influences and often require a target fine-resolution simulation to train on. Both downscaling techniques inherit all the uncertainties from their parent ESMs and also introduce their own sources of uncertainty (Giorgi and Gutowski 2015). To minimize model uncertainty, bias correction methods can be applied prior to using global or regionally downscaled climate variables in SDMs; though, depending on the research question, this may add additional uncertainty to the analysis process (Maraun 2016, Xu et al. 2021).

Finally, scenario uncertainty arises because the future of human behavior, and the resulting emissions and land use changes, are unknown. Scenario uncertainty is quantified by comparing different scenarios run by the same model (or ensemble of models; Fig. 1B). CMIP6 created an ensemble of projections for a discrete range of climate scenarios. Broadly, the uncertainty is given by the range between the highest and lowest emissions scenarios (SSP585 and SSP119 in CMIP6). It has been argued, though, that the extreme high and low scenarios are less plausible and unnecessarily inflate uncertainty (Hausfather and Peters 2020). Communities of practice are forming to help inform relevant scenario selection by users (Stammer et al. 2021).

The relative magnitude of each source of uncertainty (internal, model, and scenario) largely depends on the spatial and temporal scales and variables of interest (Hawkins and Sutton 2009). At global averaging scales, scenario uncertainty tends to dominate, and internal variability is typically the least important, particularly in the distant future. However, at regional scales and for nearer-term time horizons (< 20 years), model variability and internal variability can be significantly larger (Frölicher et al. 2016).

Propagation of climate projection uncertainties into downstream SDM models presents a challenge. Ideally, SDM projections would be generated from all possible regional models, which had downscaled all possible ESMs, for all possible scenarios. While this approach is not practically possible, it conceptually illustrates the full cascade of uncertainty, which increases at each step of the process in moving from ESM climate projections to end-use impact studies such as species' distributions (Falloon et al. 2014). A more feasible approach to estimating these uncertainties is to generate several SDM projections from a representative range of regional models, which themselves are driven by a representative ensemble of ESMs and scenarios. Unfortunately, the necessary data for these robust uncertainty estimates are often not available. While there is some coordination under projects like the Coordinated Regional Downscaling Experiment (CORDEX; Giorgi and Gutowski 2015), there is no equivalent to the CMIP ensemble, particularly for the ocean. Regional downscaling techniques are briefly described here and for a more complete description of the commonly used methods and their use in ecology, the reader is referred to Harris et al. (2014) and Giorgi (2019). Hence, if global model projections are not sufficient, users are forced to construct these representative downscaled ensembles themselves, and to be explicit about the uncertainties that cannot be represented in their SDM projections.

8. Identify SDM uncertainty

SDMs can have at least three main sources of uncertainty (sensu Hilborn 1987). The first is from regular environmental and biological variation ('noise') that influences a species' distribution but is well observed and can be accounted for in a model and contributes to parameter uncertainty and observation error (Fig. 1A). The second source of uncertainty is the impact of extreme and unpredictable events, and their effect on species' distributions, which can be dramatic (Anderson and Ward 2019). Unanticipated events (e.g. tsunamis, disease outbreaks, extreme heat waves) not captured in the observations used to fit the SDM may only be partially accounted for in the SDM projections. For example, it may be unknown how a species will respond to extreme temperatures that are beyond observed values used to build the projections and beyond the documented temperature range for the species. Finally, there is the uncertainty stemming from ecological patterns and processes that are only partially understood, or what Hilborn (1987) calls uncertain states of nature. This can include uncertainty related to climate model outputs (guideline 7), the suitability of one environmental variable as a proxy for another, and the influence of eco-evolutionary processes (e.g. species' interactions, dispersal limitation, local adaptation; guideline 9).

Predictions from multiple SDMs can be used to characterize uncertainty arising from multiple possible structural assumptions reflecting possible states of nature (Thuiller et al. 2019, Nephin et al. 2020). Such structural assumptions could include the form with which variables act on species' distribution (e.g. linear, log-linear, quadratic, smooth, or breakpoint), whether latent variables exist (Brodie et al. 2020), and even whether covariate relationships are changing through time (Anderson et al. 2022) and/or space (Thorson et al. 2023). The range of possible projections can then be characterized, and projections combined through ensemble approaches if desired (guideline 6; Fig. 1D).

It is critical to evaluate model projection accuracy and whether projection uncertainty intervals are appropriate. Cross-validation provides a general tool to accomplish this (Hastie et al. 2009, Roberts et al. 2017, Yates et al. 2022). In cross validation, a dataset is split, and models are constructed with portions of the data while comparing predictions to the left-out portion. Common data splitting strategies include splitting by data point ('leave-one-out') or by larger folds ('k-fold') with statistical implications around such a choice (Hastie et al. 2009, Yates et al. 2022). Central to effective cross-validation is choosing an appropriate blocking scheme to characterize the uncertainty of interest – such a blocking scheme might be by time, space, phylogenetic distance, various grouping structures, or some combination thereof (Roberts et al. 2017). For example, withholding the most recent temporal block in a cross-validation can be used to evaluate an SDM's forecast ability. Projection accuracy can be quantified through scoring rules (Gneiting and Raftery 2007, Yates et al. 2022) and the scale of uncertainty intervals can be evaluated by measuring the frequency with which such intervals include the left-out observed values ('coverage'). Despite the importance of cross-validation, it is important to consider that no cross-validation strategy may fully encompass the uncertainty introduced by predicting under the novel climate conditions we face (Wenger and Olden 2012).

To accurately project uncertainty from SDMs, models needs to be statistically valid and account for major sources of residual correlation caused by sampling schemes or spatial correlation from unmodeled covariates (Legendre and Fortin 1989). Whenever possible, SDM model uncertainty should be included in projections through error propagation methods (e.g. via hierarchical modeling or simulation–extrapolation; Stoklosa et al. 2015). Random effects provide a unified framework with which to integrate over uncertainty from latent variables and residual correlation (Shelton et al. 2014, Thorson and Minto 2014, Anderson et al. 2022). However, the omission of relevant climate variables may cause spatial or spatiotemporal random effects to absorb climate-driven variation and thereby underestimate projected impacts of climate change (guideline 5), and spatial random effects can distort the perceived contribution of covariates if the two are correlated, although approaches to maintain orthogonality exist under some modeling frameworks (Hodges and Reich 2010).

9. Identify eco-evolutionary uncertainty

Correlative SDM modeling assumes that a species' environmental niche can be estimated by correlating occurrences or abundances with environmental variation across space (Elith and Leathwick 2009, Blois et al. 2013); in other words, they assume that the current associations between species and environmental gradients across space will be predictive of the way those species respond as the climate changes through time. However, environmental conditions are only one determinant of species' distributions. Distributions are also influenced by interactions with other species, spatial patterns of dispersal, and stochasticity (i.e. random events; Vellend 2016, Thompson et al. 2020). Furthermore, SDMs also assume that all individuals of a species share the same environmental response curves (Zurell et al. 2020), but this may not be true if subpopulations are locally adapted to the conditions they experience (Aitken et al. 2008) or if environmental responses differ across life stages in an organism (Kingsolver et al. 2011). Together, eco-evolutionary processes make the relationship between species' distributions and environmental conditions context-dependent (Urban et al. 2016) which introduces three types of uncertainty when SDMs are used to project responses to future conditions: 1) uncertainty in the model parameters (Fig. 1A); 2) uncertainty in the assumption that all individuals within a species will share the same environmental responses; and 3) uncertainty in how well current species-environment relationships will reflect future species-environment relationships.

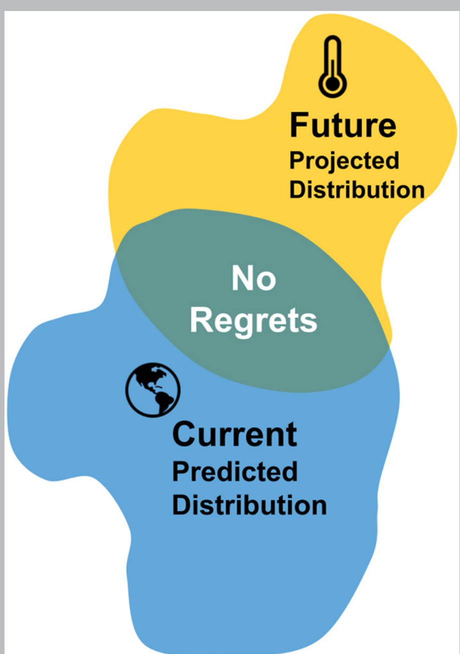
While parameter uncertainty may be partially captured in that of the fitted model (guideline 8; Fig. 1), uncertainty regarding how eco-evolutionary processes will alter species-environment relationships will not be. This uncertainty stems from eco-evolutionary processes influencing whether or not a species will shift its distribution at the same rate as the climate changes (Urban et al. 2016). If species are dispersal limited or if habitat connectivity is low, they may not be able to shift their distributions fast enough to keep pace with the changing climate (Schloss et al. 2012). Species will also only be able to establish in new habitats if there is sufficient food; if obligate mutualists are also present; and if predators, competitors, parasites, and diseases are not too abundant or prevalent (Zarnetske et al. 2012, Brown and Vellend 2014, Alexander et al. 2015, Thompson and Gonzalez 2017). The northward movement of the predatory whelk *Mexacanthina lugubris* into new habitats is an example of range expansion that is mediated by a trophic interaction (Wallingford and Sorte 2022). Alternatively, the loss of a competitor or predator may allow a species to expand its distribution to a wider range of environmental conditions than it historically occupied (Urli et al. 2016). Additionally, species that adapt – either evolutionarily or behaviorally – quickly to changing environmental conditions will not need to shift their distributions as quickly, if at all (Bell and Gonzalez 2009, Carlson et al. 2014, Thompson and Fronhofer 2019). These complex eco-evolutionary processes mean that species distributions under future climates will inevitably differ from what SDMs project based on current species' environmental associations, and thus should be communicated as hypotheses (Urban et al. 2016). Such deviations may be due to the emergence of extreme and unpredictable events (Anderson et al. 2017) such as disease outbreaks, species' interactions, invasive species, or simply from the fact that species' ranges may not perfectly track changes in climate (Wiens 2016).

Over the last several years some SDMs incorporate more biological realism. A recent advance is the move from single-species' models to multi-species models known as joint species distribution models (JSDMs; Warton et al. 2015). For example, JSDMs have been used to understand the joint influence of ongoing environmental change and fishing pressure on groundfish species' richness in Canada's Pacific waters (Thompson et al. 2022). The flexible hierarchical structure makes it possible to account for correlation among species and provide more robust uncertainty estimates, and allows relevant biological information (e.g. functional trait and phylogenetic information) to be added to the model. While species' correlations from JSDMs do not necessarily represent species' interactions (Pollock et al. 2014, Dormann et al. 2018), they can be used to understand when there is substantial statistical correlation between species in their shared response to the environment (as represented in the model) or residual correlation (not explained by the model). Finally, there are models for different taxonomic and spatial scales (e.g. for alpha, beta, and gamma diversity; summarized in Pollock et al. 2020) that may be appropriate depending on specific objectives. For example, if an objective can be evaluated with species' diversity or aggregate biomass rather than information from individual species, then macroecological models may provide sufficient results with fewer input data than species-specific models. However, it is important to consider that although these strategies will produce a better estimate of environmental response curves they may not necessarily resolve all eco-evolutionary uncertainty.

Eco-evolutionary uncertainty is distinct from uncertainty associated with statistical model fitting (guideline 8) and from climate model uncertainty (guideline 7). In cases where evidence of local adaptation or phenotypic plasticity to climate variation is available, this information can be incorporated into SDMs (Benito Garzón et al. 2011, Homburg et al. 2014, Valladares et al. 2014, Lowen et al. 2019); however, for most species, this information is lacking. One signal of local adaptation is that SDM parameter coefficients may vary across the species' range. In addition, practitioners can account for eco-evolutionary uncertainty in the interpretation and communication of the results (guideline 10). Much of the uncertainty associated with eco-evolutionary processes stems from whether species will successfully establish in new locations, and whether they will be lost in areas where conditions are projected to become unsuitable. Researchers can be reasonably certain of areas where species are projected to persist in future climates, but less certain of areas where species are projected to shift, and this can be highlighted when communicating SDM results (Fig. 1E, Box 1). Where species are expected to shift, either as a range retraction or an expansion, monitoring programs can help to understand species' range dynamics and provide data to refine model(s) over time.

Box 1: No regrets strategy

No regrets strategies for climate change adaptation are based on present day actions that can be undertaken without understanding all dimensions and impacts of climate change (Circles of Social Life 1996, IPCC 1996). Focusing spatial planning effort on areas that are projected to remain suitable for a focal species (e.g. Fig. 1E) offers a no regrets (sensu Heltberg et al. 2009, Hoegh-Guldberg and Bruno John 2010) strategy for dealing with much of the uncertainty associated with SDM projections. While practitioners can aim to reduce uncertainty in the modeling process, they can also present model outputs in ways that have the highest confidence. Where predicted and projected probabilities of suitable habitat overlap, there is greater certainty that the species' presence will not change, and a greater likelihood that such space will meet resource management operational goals (Kujala et al. 2013a, b). In these areas, conservation will benefit the species now, and focuses attention on areas of the species' projected range where SDM models have the highest certainty. An evidence-based no regrets strategy can inform risk management and decision making processes (Makino et al. 2015).



10. Communicate the results and uncertainties

For SDM projections to be used appropriately in science-based decision making, it is imperative that the results and associated uncertainty are communicated effectively to both technical and non-technical audiences (Baron 2010, Raimi et al. 2017, Corner et al. 2018). In the context of the changing ocean, where ideal marine management decisions achieve objectives both now and in the future, the clear communication of results aids in identifying data deficiencies and reducing misinterpretation or dismissal of important findings (Brodie et al. 2022, Jansen et al. 2022). Meaningful maps of uncertainty across the study area are indispensable for interpreting results by identifying areas of certainty (Fig. 1). Specifically, they can be used to visualize which areas within a projection will have suitable environmental conditions for the species of interest and a low level of uncertainty in the model components and outputs. However, a recent literature search of species' distribution modeling papers published in 2020 found that 96% of papers did not include uncertainty maps (Jansen et al. 2022).

Communication with the end users should consider their knowledge, expertise, and values (Raimi et al. 2017). Use of common and non-technical language to state the intent, spatial, and temporal context of the projection will clarify to end users how the SDM can support operational needs. For example, the 'And, But, Therefore' approach described in Olson (2015) can be implemented to create a story containing three distinct components, by introducing a specific issue ('And'), identifying a conflict ('But'), and providing a resolution ('Therefore'). This storyline can help researchers clarify important decisions made during the analysis process. Where possible, the narrative should communicate results for time scales relevant to management. Managers often seek advice for operational needs over the next five years, while climate change models project over a 50–100-year time scale. While this is a time scale mismatch, researchers can use projections into the future to illustrate the implications for decision making in the present day. Involving end users throughout the development of SDM projections will ensure that researchers are aware of the values held by end users in the decision context, while end users understand the scope, proper interpretation, and limitations of model outputs (Dietz 2013, Guillera-Arroita et al. 2015, Villero et al. 2017). When communicating results the narrative should lead first with all the information that is known or more certain, followed by the process of discussing uncertainties and strategies to address them (Corner et al. 2018). It is important to acknowledge that uncertainties, both quantifiable and unquantifiable, exist in the modeling process and cannot be fully eliminated. Study caveats, and the potential for major assumption violations during the analytical process, should be transparently communicated (US National Research Council 2008). Communication strategies for quantifiable uncertainties should include using standardized descriptions for statements of uncertainty; for example the IPCC has developed seven verbal descriptions of uncertainty, such as 'unlikely' and 'very likely' to convey the probability of a projected outcome

(Table 1 in Budescu et al. 2012, IPCC 2021). A certainty-focused approach can help reduce uncertainty paralysis and improve objectives-based risk management associated with climate-mediated change (Duplisea et al. 2021, Roux et al. 2022).

Conclusion

Based on recommendations of an international workshop of SDM experts, we have outlined potential sources of uncertainty linked to the various stages of analysis needed to complete an SDM projection into future climates (Table 1). This begins with the need to identify sources of uncertainty during goal setting and at the onset of an analysis (guidelines 1 and 2), while selecting relevant data sources (guidelines 3–5), throughout model building and evaluation (guideline 6), right through uncertainty estimation and the interpretation of results (guidelines 7–9) and, finally, during the communication of results (guideline 10).

Through the application of SDM outputs, researchers and end users may identify important data gaps or other elements that need to be reassessed for clarity; this feedback can lead to iterative improvement of both the analytical process and resulting outputs. The need to build a community of practice that includes a diversity of perspectives and skills for projecting marine species' distributions is a challenge and a gap. Partnerships between scientists, practitioners, and managers are necessary to evaluate approaches that can lead to clear and consistent standards and science advice to support a variety of marine spatial planning decisions now and in the years to come.

Many ecosystems have species and environmental data shortfalls that will limit a modeler's ability to minimize some sources of uncertainty in SDM projections. For example, there are currently few datasets available of downscaled, high-resolution climate variables for marine regions and no coordinated global effort to develop them. However, even in the absence of such data, these guidelines provide practical steps for identifying the relevant sources of uncertainty, quantifying their magnitude (if possible), and communicating their effects. Following these guidelines will help practitioners to identify areas of higher confidence where species' distributions are not expected to change. SDM projections may represent the best available knowledge to inform management strategies; thus, it is essential to acknowledge and report on uncertainty to avoid poor management decisions. By following the guidelines laid out in this review and communicating the decisions that were made throughout the analysis process, SDM projections can be informative to researchers, managers, and policy makers interested in planning for a changing and uncertain future climate.

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Data availability statement

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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