# Introduction

Prediction is a central tenet of ecological modeling, providing the information we need to face the imminent challenges and uncertainty arising from anthropogenic climate change [(Clark *et al.*, 2001; Houlahan *et al.*, 2017; Dietze *et al.*, 2018)](https://www.zotero.org/google-docs/?p89UbD). Species distribution shifts driven by warming temperatures are one of the most well-documented biological responses to climate change across ecosystems [(Parmesan and Yohe, 2003; Thomas, 2010; Poloczanska *et al.*, 2013; Lenoir and Svenning, 2015)](https://www.zotero.org/google-docs/?MkfOGk). Although species respond individually to changing temperatures [(Sunday *et al.*, 2012; Pacifici *et al.*, 2017b; Schuetz *et al.*, 2019)](https://www.zotero.org/google-docs/?4gwRVp), their collective responses can create novel biological communities [(Williams and Jackson, 2007; Blois *et al.*, 2013)](https://www.zotero.org/google-docs/?RuBwtZ), modify predator-prey relationships [(Pecuchet *et al.*, 2020; Goodman *et al.*, 2022)](https://www.zotero.org/google-docs/?57DJgt), and fundamentally alter ecosystem function [(Cramer *et al.*, 2001; Doney *et al.*, 2012; Grimm *et al.*, 2013; Kortsch *et al.*, 2015; Pecl *et al.*, 2017)](https://www.zotero.org/google-docs/?iJ6qQM). Understanding and predicting how these changes will influence both ecological and human communities requires information about future ecosystem states, which increases our capacity to plan for and adapt to anticipated changes rather than react to them as they unfold [(Clark *et al.*, 2001; Dietze *et al.*, 2018; Tulloch *et al.*, 2020; Link *et al.*, 2023)](https://www.zotero.org/google-docs/?Lrt7sD).

Species distribution models (SDMs) are a popular tool for predicting how species will respond to changing ecosystem conditions [(Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Araújo *et al.*, 2019)](https://www.zotero.org/google-docs/?eZ3H3k). While methodological approaches vary, correlative SDMs are united by a shared goal of relating species’ occurrence data to measured ecosystem characteristics, unmeasured (but estimatable) spatial or spatio-temporal random effects, or some combination of both [(Guisan and Thuiller, 2005; Elith and Leathwick, 2009; Anderson *et al.*, 2022; Valavi *et al.*, 2022)](https://www.zotero.org/google-docs/?kjnKny). Correlative SDMs have received criticism because they do not explicitly model mechanistic relationships or biological processes [(Pearson and Dawson, 2003; A. Lee-Yaw *et al.*, 2022; Briscoe *et al.*, 2022)](https://www.zotero.org/google-docs/?jnhqqD), but these approaches require rich datasets and sophisticated modeling techniques, making them inaccessible or infeasible for broad application. In contrast, correlative SDMs can be fit to a wide-array of data types (e.g., presence, presence-absence, abundance). Consequently, correlative SDMs remain an important and widely applied tool to understand observed species distribution patterns and predict how these may change under different environmental conditions [(Guisan *et al.*, 2013; Araújo *et al.*, 2019; Allyn *et al.*, 2020; Braun *et al.*, 2023a; Lezama-Ochoa *et al.*, 2023)](https://www.zotero.org/google-docs/?E0xkux).

Despite the rapid development of SDM techniques and the proliferation of applied use cases, we have a limited understanding of the fundamental characteristics driving predictive performance under novel environmental conditions [(but see Yates *et al.*, 2018; Muhling *et al.*, 2020; Spence and Tingley, 2020; Charney *et al.*, 2021)](https://www.zotero.org/google-docs/?dupzdm). Novel environmental conditions can emerge from sustained climate change (e.g., long-term warming) or discrete, extreme episodic events (e.g., heatwaves) that push the ecosystem into states rarely or never observed before [(Mora *et al.*, 2013; Ummenhofer and Meehl, 2017; Harris *et al.*, 2018)](https://www.zotero.org/google-docs/?kqdGjw). Although climate-driven warming has been more pronounced over land than the ocean [(IPCC, 2023)](https://www.zotero.org/google-docs/?r2N4c6), species in marine ecosystems are being pushed to keep up with a faster pace of climate change [(Parmesan and Yohe, 2003; Burrows *et al.*, 2011; Poloczanska *et al.*, 2013; Pinsky *et al.*, 2019)](https://www.zotero.org/google-docs/?TjkCee). Moreover, many marine ecosystems are already contending with novel physical or biological conditions [(Henson *et al.*, 2017; Halpern *et al.*, 2019)](https://www.zotero.org/google-docs/?thNzVJ), with nearly all of the world’s oceans expected to experience such ecological disruptions by the end of the century without immediate climate change mitigation measures [(Henson *et al.*, 2017; Lotterhos *et al.*, 2021; Mills *et al.*, 2023)](https://www.zotero.org/google-docs/?Czuplk). Consequently, a better understanding of SDM performance under novel conditions is acutely needed to help guide forward-looking conservation and management decision-making processes in marine ecosystems [(Tommasi *et al.*, 2017; Barnes *et al.*, 2022; Link *et al.*, 2023)](https://www.zotero.org/google-docs/?35PERz).

The capacity for SDMs to yield accurate predictions in environments that extend beyond the conditions they were trained under is complicated by multiple, interacting components [(Dormann, 2007; Williams and Jackson, 2007; Elith *et al.*, 2010)](https://www.zotero.org/google-docs/?sLlHkH). In particular, the relationship between novel conditions and SDM prediction skill is not solely driven by the degree of novelty. Rather, it will depend on how well the training data capture the species’ fundamental niche, or the range of environmentally suitable conditions [(Hutchinson, 1957; Pearman *et al.*, 2008; Veloz *et al.*, 2012)](https://www.zotero.org/google-docs/?hhmorD), and if the novel conditions create new suitable habitat areas [(Karp *et al.*, 2023)](https://www.zotero.org/google-docs/?lHxAmO). Predictions from SDMs may be particularly inaccurate when the data used to fit the model only represent a subset of the species’ fundamental niche and do not capture emerging suitable habitats under novel conditions [(Williams *et al.*, 2007)](https://www.zotero.org/google-docs/?TRUbid). Most marine SDM efforts have found that prediction skill decreases when predicting on increased environmental novelty [(Muhling *et al.*, 2020; Barnes *et al.*, 2022; Karp *et al.*, 2023)](https://www.zotero.org/google-docs/?BK7FSU)[, but with some notable exceptions](https://www.zotero.org/google-docs/?broken=NWhJRS) (e.g., [Becker *et al.*, 2019)](https://www.zotero.org/google-docs/?Gm3e8s), indicating the need for an improved understanding of SDM prediction skill across marine ecosystems and species [(Robinson *et al.*, 2011; Muhling *et al.*, 2020; Davies *et al.*, 2023)](https://www.zotero.org/google-docs/?6PeCm2).

We aimed to broaden our theoretical understanding of how ecosystem conditions and species movement characteristics influence the predictability of SDMs to novel environments. We use a simulation approach to control for the individual components influencing overall SDM prediction performance, including observation processes and the species “true” responses to environmental variables [(Hirzel *et al.*, 2001; Elith and Graham, 2009; Meynard and Kaplan, 2013)](https://www.zotero.org/google-docs/?xuieEA). Such a simulation approach also helps define the highest achievable prediction performance under known conditions (i.e., the intrinsic predictability of SDMs). This metric provides a key benchmark as the difference between the intrinsic predictability and prediction skill from real-world applications (i.e., the realized predictability) can help identify potential room for SDM improvements [(Beckage *et al.*, 2011; Pennekamp *et al.*, 2019)](https://www.zotero.org/google-docs/?wm9dtI). Finally, we synthesize our results to provide guidance to SDM practitioners as they consider disseminating model predictions to support forward-looking decision-making processes under global climate change.

# Methods

## Summary of the workflow

We simulated the distribution of two archetypal marine species and used the resulting distributions to fit SDMs and validate their predictive performance. Sea surface temperatures (SST) in two large marine ecosystems (LMEs; California Current and Northeast U.S. Shelf, Supplementary Material Appendix 1) were used as natural experiments to assess prediction performance to novel, but observed, temperatures (Fig. 1). Within a given LME, we defined the true system state (i.e., operating model) by prescribing monthly habitat suitability values for a “resident-mobile” and a “seasonally-migrating” species archetype from 1985-2020. We then fit boosted regression tree (BRT) SDMs (i.e., estimation model) using training data from 1985-2004 for each LME and species archetype (n=4 models) to data from the operating model. Fitted models were used to predict the species-specific probability of presence from 2005-2020. We compared our model predictions to the species’ true distributions, and also assessed SST novelty at each time step relative to the model training conditions. Finally, we evaluated how SDM prediction performance varied with environmental novelty between the two LMEs and species archetypes.

## Simulation approach

### Operating model and species archetypes

The operating model defines all aspects of the “true” system, which we assume to know perfectly. In our operating model, the system is composed of two components: the environmental conditions and the species distribution. For the environmental conditions in each LME, we included the monthly NOAA Optimum Interpolated Sea Surface Temperature (SST, measured in ºC) data [(Reynolds *et al.*, 2007; Huang *et al.*, 2021)](https://www.zotero.org/google-docs/?SWeAzi) and water depth data from the NOAA Earth topography (ETOPO) dataset [(Amante and Eakins, 2009)](https://www.zotero.org/google-docs/?LIiFaY). SST and water depth have been an important predictor variable in many marine species distribution modeling studies, including those in the CC [(Brodie *et al.*, 2018; Liu *et al.*, 2023)](https://www.zotero.org/google-docs/?17XQyb) and the NES [(Kleisner *et al.*, 2016; Friedland *et al.*, 2023)](https://www.zotero.org/google-docs/?xwTQR5). To match the resolution of the depth data to the spatial resolution of the monthly SST data, we used bi-linear interpolation so that both habitat characteristics were available on a common 0.25o grid.

To generate the species true distribution in each LME, we simulated species presence/absence at every grid cell location (i) and monthly time step (t) from 1985-2020 using the *virtualspecies* R package [(Leroy *et al.*, 2016)](https://www.zotero.org/google-docs/?QFHIGg) and species-environment response curves that emulated the distribution of two species archetypes: a “resident-mobile” and a “seasonally-migrating” species (Supplementary Material Appendix 2). The resident-mobile species is ecologically representative of a groundfish, reef-associated fish, marine invertebrate, or forage fish species that exhibits seasonal migrations within the LME domain. The seasonally-migrating species archetype is characteristic of a highly mobile species, such as tunas, billfish or pelagic sharks, embarking on seasonal migrations within and beyond the LME domain. Alongside these ecological differences, the two species archetypes present unique SDM prediction challenges as prevalence for the resident-mobile species was relatively stable across the annual cycle (i.e., ~0.5 for all months during the year) and highly variable for the seasonally-migrating species archetype (average annual prevalence variance = 0.04 and 0.14 in the NES, and 0.19 and 0.29 in the CC LME for resident and seasonally-migrating species archetypes) (Fig. 2; Supplementary Material Appendix 2, Table 2A).

## Assessing the relationship between SDM prediction performance and environmental novelty

### Estimation models

The estimation model represents the real-world data analysis situation of building an SDM. We selected boosted regression trees (BRTs) as they have demonstrated high predictive performance in marine applications [(e.g., Muhling *et al.*, 2020; Rubbens *et al.*, 2023; Welch *et al.*, 2023)](https://www.zotero.org/google-docs/?qKS1xE) and are robust to non-linear species-environment responses and interactions among model covariates [(De’ath, 2007; Elith *et al.*, 2008)](https://www.zotero.org/google-docs/?Ga9AuU). For each ecosystem and species-archetype combination, we followed a census approach where BRTs were fit with depth, SST, and species’ presence/absence values from every grid cell and time step between 1985-2004 from the operating model. We used all the data available during the model training period to isolate the influence of novel environmental conditions on prediction performance, control for other potential sources of model prediction uncertainty, and directly leverage the recent climate-driven SST responses of each LME as natural experiments. BRT models used a tree complexity = 3, learning rate = 0.1 and bag fraction = 0.6, which ensured models were fit with the required >1000 trees [(Elith *et al.*, 2008)](https://www.zotero.org/google-docs/?RoL0mo).

### Estimation model evaluation and predictive performance

After fitting each SDM, we then evaluated its fit to the training data and its predictive performance to the held-out, monthly 2005-2020 testing data. SDM fit was evaluated using the cross-validated deviance explained, which is calculated as the proportion of deviance explained across 10 random cross-validation folds to the overall total deviance [(Leathwick *et al.,* 2006; Elith *et al.*, 2008)](https://www.zotero.org/google-docs/?SIiMIP). We then assessed the importance of each environmental covariate using relative influence values that measure the increase in prediction error given random permutations of the covariate values [(Friedman, 2001; Elith *et al.*, 2008; Greenwell *et al.*, 2022)](https://www.zotero.org/google-docs/?DSsdmM). Finally, we summarized model prediction performance across two different dimensions: discrimination and calibration. Discrimination captures the model’s ability to correctly classify locations where a species was present from those where a species was absent, while calibration measures the true agreement between model predictions and observed values [(Pearce and Ferrier, 2000; Vaughan and Ormerod, 2005; Norberg *et al.*, 2019)](https://www.zotero.org/google-docs/?OhATBo). Consequently, discrimination metrics ignore the actual predicted values and only consider whether the habitat suitability model predictions are relatively higher at observed presence than absence locations, whereas calibration metrics quantify actual differences between predictions and observations [(Pearce and Ferrier, 2000; Vaughan and Ormerod, 2005)](https://www.zotero.org/google-docs/?9eTcZQ). As a measure of discrimination ability, we used the normalized area under the precision-recall curve (PrAUC, [Boyd *et al.*, 2013; Sofaer *et al.*, 2019)](https://www.zotero.org/google-docs/?qmvcRf). PrAUC is similar to the area under the receiver-operating curve (RocAUC, [Hanley and McNeil, 1982)](https://www.zotero.org/google-docs/?zslf08) in that it is threshold independent and calculates the confusion matrix of true/false presences and absences across all possible threshold values. However, PrAUC is more robust than RocAUC to instances when a species is rare or nearly absent from the study domain – a common situation encountered when modeling migrating species as in our seasonally-migrating warm water species archetype. Additionally, by normalizing the PrAUC measure to a minimum value for each LME and species archetype, we were able to control for the potential influence of prevalence on the PrAUC metric [(Boyd *et al.*, 2013; Sofaer *et al.*, 2019)](https://www.zotero.org/google-docs/?w7vr2J). As a measure of model calibration skill, we calculated the expected calibration error (ECE) between model predicted habitat suitability values and true presence/absence using the R package *calibratR* [(Schwarz and Heider, 2019)](https://www.zotero.org/google-docs/?T1fYFl). The ECE value indicates how well the model-predicted habitat suitabilities align with the true species’ probability of presence. The ECE is calculated as the weighted average of the difference between the mean model predicted habitat suitability values and proportion of true presences across 10 equal bins ranging from 0-1, with weights determined by the number of observations in each bin. In the context of presence/absence SDMs, ECE values range from 0-1, where a value of 0 indicates a perfectly calibrated SDM and a value of 1 indicates complete disagreement between model predictions and observations.

### Environmental Novelty

In addition to the prediction performance metrics, we summarized the monthly environmental novelty from 2005-2020 relative to the historical period of the training data (1985-2004) using Hellinger Distance [(Hellinger, 1909; Johnson and Watson, 2021; Karp *et al.*, 2023)](https://www.zotero.org/google-docs/?28MsCu). Hellinger Distance measures the difference between two normal distributions, [which we generated using](https://www.zotero.org/google-docs/?broken=MVnkaq) the mean and standard deviation of SST values during the training data period (1985-2004) and the mean and standard deviation of SST values for the prediction target month-year (2005-2020). The Hellinger Distance value ranges from 0 to 1 and quantifies how much the fitted SDM must extrapolate when making predictions, with Hellinger Distance values of 0.5 signaling when prediction conditions have differences between observation and prediction conditions that are greater than their similarities [(Johnson and Watson, 2021)](https://www.zotero.org/google-docs/?6d86Df). We then assessed the relationship between model prediction performance and Hellinger Distance for each species archetype and LME among seasons, with December/January/February = Winter, March/April/May = Spring, June/July/August = Summer and September/October/November = Fall.

# Results

## Model evaluation

BRT estimation models were well fit to the operating models across LMEs and species archetypes. For the resident-mobile species archetype, BRT model cross-validated deviance explained was 45% in the CC LE and 39% in the NES. For the seasonally-migrating warm water species, cross-validated deviance explained was slightly lower (37%) for both LMEs. Fitted BRT estimation model curves were closely aligned with the prescribed species-response curves of the operating model (Fig. 3), with only slight deviations observed in the NES for the resident-mobile species archetype at very cold temperatures, and at cold and warm temperature extremes for the seasonally-migrating warm water species.

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## Environmental novelty

Both LMEs experienced novel temperature conditions during the prediction period (2005-2020), with the degree of novelty varying considerably between the two LMEs and by season within each LME (Fig. 4). Overall, SST novelty was nearly five times higher in the NES compared to the CC across all years and seasons (mean +/- standard deviation Hellinger Distance for CC = 0.05 +/- 0.03; NES = 0.24 +/- 0.04). Both ecosystems were characterized by distinct seasonal patterns, where environmental novelty increased over time in summer and fall and then decreased over time in winter and spring. This follows expectations based on general climate warming patterns and our use of Hellinger Distance to measure environmental novelty: during warmer seasons (summer and fall), warming temperatures associated with climate change will become increasingly farther away from the overall mean temperature during the training period (1985-2004), and more novel. In contrast, novel conditions become rarer during winter and spring, as warming temperatures associated with climate change bring these seasonal temperatures closer to the training period mean temperature (Supplementary Material Appendix 4, Fig. 4A).

## Model prediction performance and environmental novelty

SDM predictive performance did not always decline as environmental novelty increased, but rather varied among LMEs, species archetypes, and the predicted target season (Fig. 5). Predictability of the resident-mobile species, as measured by PrAUC, declined with increasing novelty for the summer and fall in both LMEs. In contrast, there was a slight positive relationship between prediction performance and novelty in the winter and spring in the CC LME only. For the seasonally-migrating warm water species archetype, both LMEs showed similar patterns: SDM predictability slightly increased and remained stable with increasing novelty during summer and fall, but decreased in winter and spring.

SDMs for both LMEs and species archetypes across all prediction target seasons were very well calibrated, resulting in small ECE values (Supplementary Material Appendix 4, Fig. 4B). ECEs were similar in the CC for both the resident-mobile and seasonally-migrating warm water species archetypes, remaining relatively stable or slightly decreasing with increasing novelty values across the four seasons. In contrast, ECEs were more variable in the NES between the two species archetypes. ECEs increased with increasing novelty in all four seasons for the resident-mobile species archetype, particularly during the winter. However, ECE values for the seasonally-migrating warm water species archetype decreased with increasing novelty across all seasons.

These results indicate an interaction between the environmental conditions that models are trained on, tested against, and the species environmental response curves (Fig. 6). Predictability decreased as novelty increased when predictions were made at the tails of the species-response curves (habitat suitability values ~<0.25) (e.g., resident-mobile species during summer and fall shown in Fig. 6A, B, and winter/spring for NES resident-mobile and seasonally-migrating NES and CC Fig. 6B, C, D). In contrast, SDM predictability increased, or was constant, under novel conditions that aligned with the center of species-response curves (habitat suitability values ~>0.75) (e.g., seasonally migrating in summer and fall in both LMEs Fig. 6C, D and winter and spring resident-mobile species in the CC Fig. 6A).

# Discussion

Identifying and understanding when, where and why ecological prediction performance varies is critical for identifying key sources of uncertainty and developing ecological models with the capacity to support forward-looking decision-making processes [(Clark *et al.*, 2001; Petchey *et al.*, 2015; Dietze, 2017; Pennekamp *et al.*, 2019)](https://www.zotero.org/google-docs/?9QoMNC). In this study, we used a simulation approach to assess the relationship between SDM predictive performance and novel environmental conditions in two contrasting LMEs. Our cross-ecosystem comparison suggests SDM prediction performance generally declines as environmental novelty increases, with important exceptions as prediction performance increased under extremely novel conditions when those conditions occurred at optimum species-response curve temperatures. This highlights the importance of both quantifying and understanding how novel future conditions influence species-response curves when developing SDMs to support decision-making processes.

## SDM predictability

### Patterns Between Large Marine Ecosystems

We identified similar relationships between SDM predictive performance and environmental novelty for both species archetypes in the CC and NES LMEs despite different dynamics and unique responses to recent climate change. The CC LME is characterized by seasonal upwelling and exhibits large inter-annual and decadal SST variability, mainly driven by the El Niño-Southern Oscillation (ENSO) and the Pacific Decadal Oscillation [(Mendelssohn *et al.*, 2003; King *et al.*, 2011)](https://www.zotero.org/google-docs/?n4dBN9). In contrast, the NES LME has lower year-to-year variability with a strong latitudinal temperature gradient resulting in subarctic ecosystem characteristics to the north and temperate characteristics to the south [(Townsend *et al.*, 2004; Thomas *et al.*, 2017)](https://www.zotero.org/google-docs/?hTM58K). Although both ecosystems have been warming in response to recent climate change, the trend in SST has been more pronounced in the NES than the CC [(Belkin, 2009; Seabra *et al.,* 2019)](https://www.zotero.org/google-docs/?VGGH4Y). In turn, SDM prediction conditions for the NES were nearly five times more novel than the CC LME (Hellinger Distance values 0-0.5 in the NES versus 0-0.2 in the CC LME). These distinct challenges influenced the variability in SDM prediction performance, with PrAUC values spanning a much greater range in the NES than the CC (~0.1 to ~1 in the NES and ~0.75 to ~1 in the CC). However, over a common novelty gradient (Hellinger Distance values 0 to ~0.2), prediction performance fell within the same general range and showed similar trends between species archetypes and among seasons, with an exception for the resident-mobile species archetype in the CC during the winter and spring seasons that had a slightly increasing trend.

Our results suggest consistent relationships between SDM prediction performance and environmental novelty, indicating there could be general novelty thresholds beyond which SDM predictions are no longer useful. These thresholds, or forecast horizons in a true forecasting context, delineate the distance in time, geographic, or environmental space when predictions are no longer proficient given some validation metric or combination of metrics [(Petchey *et al.*, 2015; Yates *et al.,* 2018)](https://www.zotero.org/google-docs/?b0z4CD). If we apply a cutoff value of 0.7 to the PrAUC metric, which is a value commonly used with RocAUC as a benchmark for models with acceptable discrimination ability [(Swets 1988; Hosmer and Lemeshow 2000; Hijmans 2012; Muhling *et al.*, 2020)](https://www.zotero.org/google-docs/?W75UsR), this horizon occurred when environmental conditions yielded a Hellinger Distance value of ~0.3 for the resident-mobile species archetype and ~0.1 for the seasonally-migrating warm water species during the winter and spring seasons. These Hellinger Distance values are lower than the 0.5 value when environments become more dissimilar than similar [(Johnson and Watson, 2021)](https://www.zotero.org/google-docs/?7pxcbh). Karp et al. (2023) documented SDM performance declines around the 0.5 threshold, though there was some evidence for a change in the strength of the relationship between SDM prediction performance and environmental novelty at lower Hellinger Distance values of ~0.35 (Fig. S16 in [Karp *et al.*, 2023)](https://www.zotero.org/google-docs/?yyt88H). Together, this suggests that novel environmental conditions can pose significant challenges to SDM prediction performance before training and testing conditions are entirely distinguishable from another and highlights the need to assess these relationships on a continuous gradient rather than applying a binary cutoff to delineate similar/novel or analogue/non-analogue conditions. Future work could investigate the occurrence and variability of this novelty forecast horizon by including other LMEs or introducing uncertainty from different SDM components (e.g., moving from a census to smaller monthly sample sizes or including driver uncertainty in SDM predictions) or SDM algorithms (e.g., spatio-temporal mixed effects models). With further exploration of SDM performance and forecast horizons, we could progress from using environmental novelty metrics to map SDM prediction uncertainties [(Owens *et al.*, 2013; Mesgaran *et al.*, 2014; Velazco *et al.*, 2023)](https://www.zotero.org/google-docs/?tHPtzj) or applying thresholds to mask predicted values (e.g., [Zurell *et al.*, 2012; Rose *et al.*, 2023)](https://www.zotero.org/google-docs/?4jXG7b),to leveraging continuous extrapolation values as SDM prediction weights to reflect more or less certainty when predictions are made to temporal, geographic, or environmental spaces that approach forecast horizons.

### Patterns Between Species Archetypes

Alongside the cross ecosystem comparison, we also compared SDM prediction performance for two contrasting species archetypes in each LME. The patterns we observed cannot be simply explained by documented relationships between SDM prediction performance and the degree of environmental novelty or species archetype characteristics and related challenges in estimating accurate species-response curves. Although our results generally agreed with previous work documenting declined SDM prediction performance with increased environmental novelty [(Barnes *et al.*, 2022; Brodie *et al.*, 2022; Karp *et al.*, 2023)](https://www.zotero.org/google-docs/?1sUR6O), SDM prediction performance increased over similar degrees of environmental novelty for the seasonally-migrating species in the summer and fall in both LMEs. Additionally, SDM predictive performance has been found to be poorer for migratory or generalist species with broad environmental tolerances, where sampling the fundamental niche (e.g., [Yates *et al.*, 2018; Muhling *et al.*, 2020; Brodie *et al.*, 2022)](https://www.zotero.org/google-docs/?wxr44O) and characterizing the true species-environment response curves is more challenging [(Williams and Jackson, 2007; Albert *et al.*, 2010)](https://www.zotero.org/google-docs/?HdOwcy). However, using a census of all available training data, estimation model species-response curves for both species archetypes in both LMEs mirrored the operating model species-response curves (Fig. 3). Moreover, the only potential species-response curve truncation occurred for the seasonally-migrating warm water species archetype in the NES at warm temperatures during the summer and fall (Fig. 3), which manifested in *increased* prediction performance even though similarly novel conditions resulted in *decreased* prediction performance during the winter and spring (Fig. 5).

Our results revealed an important interaction between environmental novelty and species archetypes through their species-response curves, which can generate contrasting SDM prediction performance patterns over similar environmental novelty gradients. This highlights the need to both quantify and understand the relationship between environmental novelty and species-specific responses. Univariate and multivariate environmental novelty or extrapolation metrics (e.g., Hellinger Distance used here, *dsmextra* Extrapolation Detection tool - [Bouchet *et al.*, 2020](https://www.zotero.org/google-docs/?TJVYoc), Multivariate Environmental Similarity Surface - [Elith *et al.*, 2010)](https://www.zotero.org/google-docs/?9vnPxp) consider the difference from observed conditions to the prediction, or forecasting conditions. While these values may then translate into SDM prediction uncertainty, our work shows that this relationship will depend on where those conditions map onto species-response curves. In particular, prediction performance suffered only when novel conditions occurred at the tails of the species-response curves, whereas performance increased despite novel conditions when they overlapped optimum environmental ranges. Additionally, our results highlight that better or more training data may not always translate into increased SDM prediction performance [(Brodie *et al.*, 2022)](https://www.zotero.org/google-docs/?WFQGZ0). By design, our simulation experiment resulted in SDMs with an excellent fit to the training data. However, because of the degree of novelty in the NES, SDMs for both species archetypes still had poor predictions during certain seasons. Along with being a precautionary example of how limited SDM predictions can be even under ideal conditions, considering this result in an applied context, it emphasizes the need for iterative SDM forecasting (e.g., [Clark *et al.*, 2001; Dietze *et al.*, 2018)](https://www.zotero.org/google-docs/?NJydOe). Iterative forecasts with updated models integrating recent observations and environmental conditions will increase our understanding of SDM prediction performance.

### Patterns Between Prediction Performance Metrics

We focused on discrimination ability as a measure of SDM prediction performance and one important attribute of SDM prediction skill. Discrimination metrics (e.g., PrAUC or RocAUC) measure the model’s ability to correctly classify occupied and unoccupied locations without considering the actual differences between model predictions and observations, which is measured by calibration metrics (e.g., RMSE, MAE) [(Pearce and Ferrier, 2000; Vaughan and Ormerod, 2005)](https://www.zotero.org/google-docs/?Be3JZJ). These prediction attributes are complementary and their relative importance will depend on the modeling objective; model discrimination ability may be most helpful when SDM predictions will be used to prioritize sites, while model calibration ability will be more important when precision of true probability of presence is tantamount [(Lawson *et al.*, 2014; Norberg *et al.*, 2019)](https://www.zotero.org/google-docs/?3oobLE).

We did not detect a consistent relationship between SDM discrimination and calibration performance between LMEs and species archetypes. Focusing on the NES LME, discrimination and calibration errors for the resident-mobile species archetype followed expectations as both discrimination and calibration performance decreased with increased novelty (Fig. 5 and Supplementary Material Appendix 4, Fig. 4B). Unexpectedly, calibration performance increased under increasingly novel conditions for the seasonally-migrating warm water species archetype and these calibration performance gains only translated into increased discrimination performance during the summer and fall seasons. Similar disconnects between SDM prediction metric patterns have been discussed and observed in other studies and remain difficult to explain (e.g., [Zimmermann *et al.,* 2009](https://www.zotero.org/google-docs/?Szzk30); Brodie *et al.,* 2020; [Warren *et al.*, 2020)](https://www.zotero.org/google-docs/?0yedYa). In this study, it is possible that SDM predictions for the seasonally-migrating species in the NES were a closer approximation of the true probability of presence, which during the spring and winter would be nearly zero given extremely cold temperatures. However, model predictions under these novel conditions were still biased high enough to generate false presences, which then decreased SDM classification ability. Overall, future work is still needed to build a more nuanced understanding of the relationship between SDM discrimination and calibration performance.

### Accounting for other sources of uncertainty

A primary goal of our simulation approach was to isolate the effect of environmental novelty on SDM prediction performance by controlling for as many sources of prediction uncertainty as possible. For SDM predictions at either short-term (i.e., daily to annual forecasts) or longer-term time scales (i.e., decadal to century-scale projections), there are a number of different sources of uncertainty, including uncertainty in initial conditions, future covariate values, and uncertainty from the fitted SDM [(Dietze *et al.*, 2018; Reum *et al.*, 2020; Tittensor *et al.*, 2021; Brodie *et al.*, 2022)](https://www.zotero.org/google-docs/?3BYAEn). We limited potential uncertainty from the initial conditions and the fitted SDM using a census of all available data within each LME to train the BRT estimation models. The census data also guaranteed that we accurately represented the temperature conditions within each LME, where a random collection of sample locations and temperatures might not correlate with the overall temperature patterns within the LME. Next, we included the true SST values when predicting the held-out test conditions. This is inherently different from forecasting applications that would need to use forecast SST values, which have large uncertainties that increase with forecast lead time [(Stock *et al.*, 2015; Hervieux *et al.*, 2019; Jacox *et al.*, 2020)](https://www.zotero.org/google-docs/?n86ltM). Finally, multiple environmental variables and biological processes influence observed species occurrence patterns. Our focus on a single dynamic environmental variable and archetype species movement and seasonal migration patterns represents a simplification of real ecosystem dynamics. Therefore, our findings about the relationships between prediction performance and environmental novelty should be interpreted as the “best-case” scenario, setting goal posts and quantifying expectations about just how accurate we can expect SDMs to be when making predictions over relatively near-term time scales.

Our simulation approach establishes a “best-case” scenario by characterizing the intrinsic predictability of species distributions or the maximum prediction skill we can expect using a correctly and fully specified model, while removing all potential sources of prediction uncertainty [(Beckage *et al.*, 2011; Pennekamp *et al.*, 2019)](https://www.zotero.org/google-docs/?gn06W2). Although this skill level is not achievable using real data, the difference between the intrinsic predictability and realized prediction skill values for typical SDM efforts informs and guides SDM model improvement efforts [(Beckage *et al.*, 2011; Pennekamp *et al.*, 2019)](https://www.zotero.org/google-docs/?fSksiq). Notably, over a similar range of novel environmental conditions, and despite very different underlying system dynamics, the intrinsic predictability was relatively high for both the CC and NES LME. However, the NES experienced potential future conditions that were an order of magnitude more novel than those in the CC where intrinsic predictability experienced the greatest declines across all seasons for the resident-mobile species and during the winter and spring for the seasonally-migrating species (Fig. 5). Given such challenges, changing the spatial or temporal scale of the predictions could be one potential way of improving performance [(Seo *et al.*, 2009; Beckage *et al.*, 2011; Tommasi *et al.*, 2017)](https://www.zotero.org/google-docs/?5ojuZM). Ongoing efforts to investigate how predictability changes across management-relevant space or time scales will also further elucidate intrinsic predictability of SDMs [(Brodie *et al.*, 2021, 2022)](https://www.zotero.org/google-docs/?JdGSqq).

## Implications for SDM practice and applications

The need for expanded and improved SDM practice and application will intensify with ongoing climate variability and change. Here, we identified key factors that influenced SDM prediction performance to novel environmental conditions between two ecosystems with different underlying dynamics and responses to recent climate change. Our simulation framework identified unexpected shifts in SDM prediction performance as a function of environmental novelty, indicating the importance of understanding both the magnitude of novel conditions and how these novel conditions relate to the species-environment response. These results provide valuable guidance for SDM practitioners in real-world applications. While extremely novel environmental conditions may always pose challenges for SDMs even with a correctly specified species-response curve, practitioners should continue to try to maximize data quantity and quality to fully characterize a species’ fundamental niche to limit additional declines in prediction performance (e.g., [Brodie *et al.*, 2022; Davies *et al.*, 2023)](https://www.zotero.org/google-docs/?Ihjchn). Notably, mixed effects or hierarchical species distribution modeling algorithms are well positioned to support practitioners in this effort as they can readily accommodate data from different sampling platforms or modalities [(Pacifici *et al.*, 2017a; Grüss and Thorson, 2019; Strebel *et al.*, 2022; Braun *et al.*, 2023b)](https://www.zotero.org/google-docs/?KiDFUE). Our model validation process demonstrates the value of exploratory plots that display the environmental novelty of prediction conditions relative to the estimated species-response curves across the gradient of environmental variable values. Noting when prediction target conditions overlap with extreme environmental values in the species-response curve can guide our expectations of SDM predictive performance. Finally, these results echo calls to continue communicating model uncertainties, particularly as they relate to novel or extrapolated environmental conditions (e.g., [Brodie *et al.*, 2022; Davies *et al.*, 2023)](https://www.zotero.org/google-docs/?aR3HMb). Communicating confidence in model predictions will not only open opportunities for model improvement, but it will also support the capacity for stakeholders to better understand model predictions and leverage model output to support decision-making processes.

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