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ARTICLE

Methods, Tools, and Technologies

A comparative framework to develop transferable species distribution models for animal telemetry data

Joshua A. Cullen[1] ● | Camila Domit[2] | Margaret M. Lamont[3] |
Christopher D. Marshall[4,5] | Armando J. B. Santos[1] | Christopher R. Sasso[6] |
Mehsin Al Ansi[7] | Mariana M. P. B. Fuentes[1]

[1]Department of Earth, Ocean and Atmospheric Science, Florida State University, Tallahassee, Florida, USA

[2]Laboratório de Ecologia e Conservação – Centro de Estudos Do Mar, Universidade Federal Do Paraná, Pontal Do Paraná, Paraná, Brazil

[3]U.S. Geological Survey, Wetland and Aquatic Research Center, Gainesville, Florida, USA

[4]Gulf Center for Sea Turtle Research, Texas A&M University, College Station, Texas, USA

[5]Department of Marine Biology, Texas A&M University at Galveston, Galveston, Texas, USA

[6]National Marine Fisheries Service, NOAA Southeast Fisheries Science Center, Miami, Florida, USA

[7]Department of Biological and Environmental Science, Qatar University, Doha, Qatar

Correspondence
Joshua A. Cullen
Email: joshcullen10@gmail.com

Present address
Joshua A. Cullen, Institute of Marine Sciences, , University of California Santa Cruz, , Santa Cruz, California, USA.

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Abstract

Species distribution models (SDMs) have become increasingly popular for making ecological inferences, as well as predictions to inform conservation and management. In predictive modeling, practitioners often use correlative SDMs that only evaluate a single spatial scale and do not account for differences in life stages. These modeling decisions may limit the performance of SDMs beyond the study region or sampling period. Given the increasing desire to develop transferable SDMs, a robust framework is necessary that can account for known challenges of model transferability. Here, we propose a comparative framework to develop transferable SDMs, which was tested using satellite telemetry data from green turtles (*CheloniaChelonia mydas*). This framework is characterized by a set of steps comparing among different models based on (1) model algorithm (e.g., generalized linear model vs. Gaussian process regression) and formulation (e.g., correlative model vs. hybrid model), (2) spatial scale, and (3) accounting for life stage. SDMs were fitted as resource selection functions and trained on data from the Gulf of Mexico with bathymetric depth, net primary productivity, and sea surface temperature as covariates. Independent validation datasets from Brazil and Qatar were used to assess model transferability. A correlative SDM using a hierarchical Gaussian process regression (HGPR) algorithm exhibited greater transferability than a hybrid SDM using HGPR, as well as correlative and hybrid forms of hierarchical generalized linear models. Additionally, models that evaluated habitat selection at the finest spatial scale and that did not account for life stage proved to be the most transferable in this study. The comparative framework presented here may be applied to a variety of species, ecological datasets (e.g., presence-only, presence-absence, mark-recapture), and modeling frameworks (e.g., resource selection functions, step selection functions, occupancy models) to generate transferable predictions of species–habitat associations. We expect that SDM predictions resulting from

this comparative framework will be more informative management tools and may be used to more accurately assess climate change impacts on a wide array of taxa.

KEYWORDS

correlative model, Gaussian process, generalized linear model, habitat selection, hybrid model, predictive modeling, resource selection function, scale, sea turtle, species distribution model, telemetry, transferability

INTRODUCTION

Characterizing the spatiotemporal patterns of species distributions is fundamental to ecology, especially to understand species' responses to biotic and abiotic variables (Leibold, 1995). This includes questions pertaining to community assembly patterns (Chase, 2003; Saito et al., 2021), the spread and persistence of invasive species (Latimer et al., 2009; Peterson, 2003), as well as the biophysical variables that influence a species' niche (Hutchinson, 1957; Matthiopoulos et al., 2023). Additionally, it is expected that current distributions of species will shift to satisfy energetic demands and environmental tolerances as climate change continues to directly impact the abiotic environment (e.g., changes in temperature, rainfall, salinity) on a global scale (Guo et al., 2021; Pinsky et al., 2013; Sunday et al., 2012). To evaluate current patterns and make forecasts under future scenarios, ecological models have been used to discern species–habitat relationships, as well as to predict the geographic range of a species (McHenry et al., 2019; Northrup et al., 2022; Sequeira et al., 2018). However, the performance of these models beyond the spatial or temporal bounds of the study remains unclear in many instances (Sequeira et al., 2018; Yates et al., 2018).

Transferable ecological models that provide high accuracy beyond the study domain are critical to predict responses of animals to their environment, especially under changing conditions (Wenger & Olden, 2012; Yates et al., 2018). The spatial transferability of a model refers to its capacity to make predictions outside of the study region (Randin et al., 2006). For example, spatial transferability facilitates the prediction of species distributions in locations with large data deficiencies that may otherwise preclude model development (Sequeira et al., 2018; Werkowska et al., 2017). Additionally, the temporal transferability of a model refers to its capacity to make predictions under past or future conditions (Dobrowski et al., 2011; Wenger et al., 2013), such as forecasting species distributions under future climate change scenarios (Pinsky et al., 2013; Thorson et al., 2021). However, existing methods for extrapolating relationships beyond the study domain (i.e., space and time) often exhibit poor model performance (Brodie et al., 2020; Yates et al., 2018), making it challenging to predict species distributions under changing conditions. Transferable models that provide reliable projections of species distributions irrespective of location or time period are necessary for proactive conservation and management actions, especially when assessing climate change impacts (Saavedra et al., 2020; Schliep et al., 2018; Sequeira et al., 2018).

The ability of a model to account for ontogenetic differences in resource requirements of a species may also be essential to improve model transferability over space and time (Dahlgren & Eggleston, 2000; Snover, 2008). Although the assessment of species distributions often considers species as the smallest measurement unit, much intraspecific variability remains unaccounted for across life stages (Barbeaux & Hollowed, 2018; Thorson et al., 2017). In many marine species, environmental requirements change over ontogeny and disregarding these differences may bias estimates of ecological relationships (Barbeaux & Hollowed, 2018; Fokkema et al., 2020). Specifically, predation risk, habitat complexity, and size-dependent limitations to the exploitation of resources are all common drivers of ontogenetic habitat shifts (Snover, 2008; Werner & Gilliam, 1984). Therefore, explicitly accounting for known differences across life stages is also expected to improve the biological realism and predictive performance of ecological models (Barbeaux & Hollowed, 2018; Fokkema et al., 2020; Thorson et al., 2017).

The observed patterns of species–environment relationships are strongly dependent on the spatial and temporal scales of analysis (Levin, 1992). This is essential to consider since species may perceive and respond to environmental predictors at different scales (McGarigal et al., 2016; Scales et al., 2017; Stuber & Gruber, 2020). The assessment of ecological relationships at spatial scales different from how species respond may result in improper inference of relationships that could propagate during prediction (McGarigal et al., 2016; Scales et al., 2017). Therefore, the use of a multi-scale approach to determine the characteristic scale of

spatial environmental predictors is necessary to generate informative and transferable ecological models (Chalfoun & Martin, 2007; Chandler & Hepinstall-Cymerman, 2016; Zeller et al., 2016). Moreover, the temporal scale of these predictors should also be similar to that of the observations to ensure that responses reflect the current state of the surrounding habitat, especially in dynamic environments (Mannocci et al., 2017; Scales et al., 2017). Matching the scale of the model to that of species monitoring can also benefit adaptive management plans since this is expected to facilitate clearer decision-making.

Species distribution models (SDMs) are often used to make inferences and predictions on species–habitat associations, but the manner in which they are implemented can greatly affect the generalizability of estimated relationships. Correlative SDMs are the most widely used methods to predict habitat selection since they only require species occurrence data and environmental variables (Elith & Leathwick, 2009; Guisan & Zimmermann, 2000). However, these methods have a number of limiting assumptions, such as species occurrences representing the range of all environmental conditions in which they can persist (Schurr et al., 2012), as well as not accounting for demographic processes (Keith et al., 2008; Swab et al., 2015) or established ecophysiological relationships (Kearney & Porter, 2009; Rogers et al., 2021). Alternatively, mechanistic models (e.g., individual-based models) have been developed to explicitly account for some of these biological processes, such as physiological constraints, interspecific interactions, survival, and reproduction (Buckley et al., 2010; Singer et al., 2016; Thuiller et al., 2008). Nonetheless, these models require extensive knowledge on the unique biology of a species, which may preclude the analysis of organisms with limited demographic and experimental data (Thorson, 2019; Zurell, 2017). To overcome the individual limitations of correlative and mechanistic models, the implementation of hybrid SDMs (which use key mechanisms to inform species responses to environmental predictors) may provide a biologically realistic model that simultaneously improves transferability (Ceia-Hasse et al., 2014; Dormann et al., 2012; Swab et al., 2015; Yates et al., 2018).

The aforementioned issues that limit the transferability of SDMs are investigated in this study using green turtles (*Chelonia mydas*) as a focal species. Green turtles are globally distributed throughout tropical and subtropical marine systems and have complex life histories (Arthur et al., 2008; Bolten, 2003), making them an appropriate species on which to develop and test SDM transferability. This study proposes a three-step comparative framework to develop transferable SDMs, where each step compares model performance based on (1) algorithm (e.g.,

generalized linear model vs. Gaussian process regression) and formulation (e.g., correlative model vs. hybrid model), (2) spatial scale of environmental covariates, and (3) influence of life stage. Specifically, three hypotheses were posited: (1) we expect a flexible algorithm will outperform a simpler algorithm, and a hybrid SDM formulation of these models will exhibit greater transferability than a correlative SDM; (2) we predict that the finest spatial scale of environmental predictors available for the marine environment will show the greatest model transferability; and (3) we hypothesize that accounting for different responses by life stage will result in a model with greater transferability. These hypotheses were tested using satellite-tagged turtles throughout the Gulf of Mexico as the training dataset, while turtles tracked in the South Atlantic and Arabian Gulf were used as independent validation datasets. Model transferability was assessed as predictive performance on these validation datasets.

MATERIALS AND METHODS

The analysis workflow for this study can generally be separated into two phases, which includes a data collection and processing step, followed by our proposed comparative framework for developing a transferable SDM. The initial phase includes the capture and tagging of green turtles from each of the study regions, processing of satellite telemetry data, behavioral state estimation to retain only non-migratory locations, as well as processing and extraction of environmental covariates. Following these preparatory steps, the second phase details the resource selection function (RSF) underpinning each of the models before covering the three-step comparative modeling framework. The procedure for model validation is further characterized for comparing measures of model transferability across all study objectives.

Capture and tagging

A total of 98 juvenile and adult green turtles were opportunistically captured over a 12-year period (2011–2022) at three distinct geographic regions, which included the Gulf of Mexico ($N = 50$), the coastline of mainland southern Brazil and an archipelago off the northern coast of Brazil (hereafter Brazil; $N = 38$), and along the coastline of Qatar (hereafter Qatar; $N = 10$) (Table 1, Figure 1; Appendix S1: Table S1). Juvenile turtles from the Gulf of Mexico, Qatar, and Brazil were opportunistically captured using the rodeo method, whereas adult turtles from the Gulf of Mexico were captured after emergence onto

TABLE 1 Summary of the raw data for the number of tagged green turtles (N_{ID}; *Chelonia mydas*), the number of tagged juveniles (N_{juv}), the number of tagged adults (N_{adult}), the total number of observations across tracks (N_{obs}), as well as the start and end years of tag transmission per study region.

Region	N_{ID}	N_{juv}	N_{adult}	N_{obs}	Start	End
		Life stage				
Gulf of Mexico	50	29	21	48,041	2011	2020
Brazil	38	19	19	74,506	2016	2022
Qatar	10	10	0	1582	2014	2015

nesting beaches, and adults from Brazil were captured by swimmers after being spotted by researchers on vessels monitoring the region. Upon capture, turtle body size was measured as curved carapace length ($\pm$0.1 cm; CCL; anterior point at the nuchal scute to the posterior tip) and Inconel flipper tags (Style 681, National Band and Tag Company, Newport, KY, USA) were attached to the trailing edge of the front flippers. Juveniles were defined as any individuals <84 cm CCL, whereas adults were defined as individuals >84 cm CCL based on the minimum size interval at maturity reported by Phillips et al. (2021) using the straight carapace length to CCL equation provided by Vander Zanden et al. (2013). After cleaning the carapace of each turtle with isopropyl alcohol, Platform Transmitter Terminals (Wildlife Computers: SPLASH10, SPOT6, MK10; Telonics: ST-14) were attached with different epoxy depending on the year and the location of the project (3M Scotch-Weld Low Odor Acrylic Adhesive DP8805NS, Devcon 5 Minute Epoxy No. 14270, Sika2 Epoxy, Superbond Epoxy, Powers Pure50+ Epoxy).

Data processing and preparation

Raw data recorded by the satellite tags resulted in 124,129 positions across all 98 individuals. These positions were filtered to remove any anomalous points and those with unknown location errors before subsequent analyses. First, observations where the Argos location quality class was missing or classified as Z (i.e., did not have reported error estimates) were removed. Observations that occurred far beyond (>200 km) the majority of positions per individual were also discarded due to exceedingly high location error. Additionally, observations that occurred before tag deployment were removed from the dataset. Due to some tags (IDs 41587, 41588, 159774, 161459) having large time gaps (>1 week) with intermittent observations at either the beginning or end of deployment, these leading/trailing observations were also removed. Any remaining

individual turtles with <30 relocations were removed due to an insufficient sample size. This resulted in the removal of one juvenile turtle (ID 161639) from the southern Brazil region and 1796 positions removed in total. Tracks were visualized over space and time to ensure no additional filtering was necessary.

A continuous-time correlated random walk state-space model (SSM) was fitted to the raw satellite telemetry data using the ANIMOTUM package (v1.1; Jonsen et al., 2023) in program R (v4.2.2; R Core Team, 2022). We accounted for location error from least-squares Argos positions using SEs associated with each of the different Argos location quality classes (Jonsen et al., 2020; Vincent et al., 2002). For location error from Kalman-filtered Argos positions, we instead used the reported semi-major axis, semi-minor error axis, and error ellipse orientation (Jonsen et al., 2020). Error associated with Fastloc-GPS positions were accounted for using a fixed variance that was 10 times smaller than the most precise Argos location class (LC 3; Jonsen et al., 2020). A speed filter of 3 m/s and a distance-angle filter to remove "spiked" trajectories (distance: 2.5–5 km; angle: 15–25°) were also applied while fitting the model to remove unlikely movements (Freitas et al., 2008; Jonsen et al., 2020, 2023). The SSM model was fitted at a regularized 4-h time step, which was slightly larger than the median observed interval from the Gulf of Mexico and Brazil regions (~1 h), while slightly smaller than the median time interval from the Qatar region (~7 h). Goodness-of-fit was visually assessed using time series, autocorrelation function, and Q–Q plots of one-step-ahead residuals. Following the fitting of the SSM, estimated locations that were interpolated within observed time gaps >3 days were removed from the dataset to reduce the likelihood of introducing relocations that were not reflective of true animal movement. One of the tracks (ID 169273) was removed entirely from the dataset after track visualization since it still appeared to exhibit highly aberrant movements even after being processed by the SSM. This resulted in 55,863 positions remaining from 96 individuals after fitting the data to the SSM (Figure 1; Appendix S1: Figure S1).

Behavioral state estimation

Since we expected range-resident (i.e., not actively migrating) locations to be more reflective of preferred habitat for green turtles during regular activities (e.g., resting, feeding, exploratory movements) (Abrahms et al., 2016; Northrup et al., 2022; Vasudev et al., 2015), the mixed-membership method for movement (M4) was used to distinguish "Resident" from "Migratory"
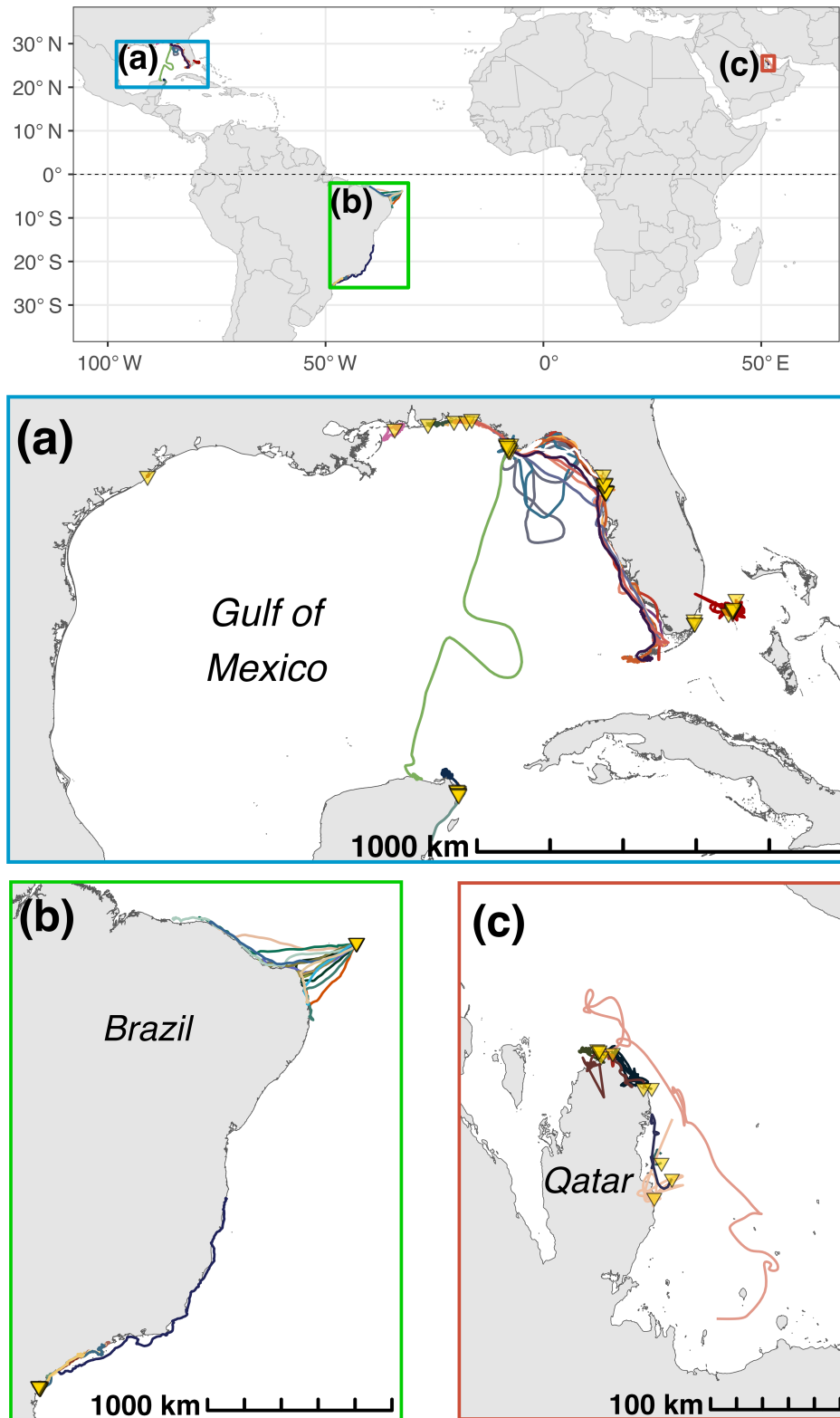
FIGURE 1 Study map showing the geographic extent for each of the green turtle (*Chelonia mydas*) datasets. Enlarged maps of turtle trajectories (*N* = 97 after processing by the state-space model) are shown for the (a) Gulf of Mexico, (b) Brazil, and (c) Qatar regions. Track colors indicate different individual turtles and gold triangles denote tagging locations.

behavioral states in green turtle tracks (Cullen et al., 2022). The Bayesian M4 method estimated behavioral states from the post-SSM regularized dataset by first segmenting the tracks and then clustering these segments into states using the BAYESMOVE R package (v0.2.3; Cullen et al., 2022). Step length and displacement were selected

as the data streams from which to estimate Resident and Migratory states since these variables were expected to largely differ between both movement modes. Since the M4 model uses a categorical distribution to estimate track segments and state-dependent distributions (Cullen et al., 2022), both data streams were first discretized into bins prior to analysis. Step lengths were discretized into five bins that were delimited at 0, 5, 10, 20, 40, and 55 km (max. step length), whereas displacement was discretized into three bins defined by limits at 0, 50, 100, and 1514 km (max. displacement) (Appendix S1: Figure S2). These bin numbers and limits were chosen to reflect the shape of the continuous distribution of each variable, while imposing a stepwise threshold indicative of migration for displacement (Cullen et al., 2022). The model tested up to four possible states and convergence on the posterior distribution was assessed during the track segmentation and clustering stages by inspecting trace plots of the log (marginal) likelihood (Appendix S1: Figure S3; see Appendix S2: Section S1 for more details). Visual inspection of the state-dependent distributions suggested that all four estimated states were biologically relevant; however, three of these states appeared to represent a Resident behavior at different displacement distances from initial tagging location (Cullen et al., 2022; Appendix S1: Figure S3). After only retaining the locations estimated to represent Resident behavior, 26,473 observations from 96 individuals remained for further analysis.

Environmental data

Both static and dynamic environmental variables were evaluated as major drivers of green turtle habitat selection. Static variables included bathymetric depth (Depth), whereas dynamic variables included net primary productivity (NPP) and sea surface temperature (SST) (Table 2; Appendix S1: Figure S4). Raster products for bathymetric depth were obtained for each of the three study regions

from the General Bathymetric Chart of Oceans (GEBCO Compilation Group, 2021). A remote sensing product for NPP was obtained from the MODIS Aqua satellite via the RERDDAPXTRACTO package (v1.1.4; Mendelssohn, 2022). Similarly, a remote sensing product for SST was accessed from the Multi-scale Ultra-high Resolution (MUR) SST Analysis global dataset (Chin et al., 2017; JPL MUR MEaSUREs Project, 2015) as an ensemble of multiple satellite products via the RERDDAPXTRACTO package. All variables needed to be evaluated at the same spatial resolution during model prediction; therefore, the depth and SST layers were coarsened to match the 5-km resolution of the NPP dataset using spatial aggregation via the TERRA package (Hijmans, 2023) in R.

Habitat selection modeling

In this study, SDMs were implemented as habitat selection analyses within a use-availability framework. To quantify habitat selection for green turtles based on depth, NPP, and SST, the data were analyzed using a RSF (Boyce & McDonald, 1999; Hooten et al., 2017). This was conducted as a down-weighted Poisson regression (DWPR):

$$\mu = \exp(\alpha + \boldsymbol{\beta}^\top \boldsymbol{x}), \quad (1)$$

$$y = \text{obs/wts}, \quad (2)$$

$$y \sim \text{Poisson}(\mu), \quad (3)$$

where μ represents the exponential of the linear predictor, α represents the intercept, $\boldsymbol{\beta}^T$ represents a transposed vector of slope coefficients, $\mathbf{x}$ is the design matrix that stores all extracted environmental values per observation, obs represents the binary indicator variable denoting whether the location was used (1) or available (0), and wts represents the weight applied to each observation

TABLE 2 Summary of environmental covariates used within the habitat selection model, including their source, spatial resolution, and temporal resolution.

Variable	Product and source	Spatial resolution	Temporal resolution
Bathymetric depth[a]	GEBCO_2021 Grid; Global	500 m	...
Net primary productivity[b]	MODIS Aqua; Global (ERDDAP)	5 km	Monthly
Sea surface temperature[c]	AMSR-E, AVHRR, MODIS, SSM/I, VIIRS, in situ; Global (ERDDAP)	1 km	Monthly

[a]https://www.gebco.net/data_and_products/gridded_bathymetry_data/#global.
[b]https://coastwatch.pfeg.noaa.gov.
[c]https://podaac.jpl.nasa.gov/dataset/MUR-JPL-L4-GLOB-v4.1.

depending on whether it was used or available (Matthiopoulos et al., 2023; Renner et al., 2015). As per Renner et al. (2015), we use the arbitrarily small weights of 1×10^{-6} for used locations and a weight of the spatial area of the study region divided by the total number of "available" locations, which results in a value of 0 for y. Additionally, these weights were also applied to each of the models to weight the likelihood estimates, which is recommended to assist model convergence on an inhomogeneous Poisson point-process (IPP) (Hooten et al., 2017; Matthiopoulos et al., 2023). Models also incorporated random effects by individual on the intercept, as well as the slopes for each of the three environmental covariates, to allow for differences in response across turtles (Muff et al., 2020). This would then result in an expression (Equation 4) similar to Equation (1):

$$\mu = \exp\left(\alpha_i + \boldsymbol{\beta}_i^\top \boldsymbol{x} + \mathbf{u}_i^\top \mathbf{z}_i\right), \qquad (4)$$

where subscript i denotes that the given term varies per individual turtle, $\mathbf{u}_i^\mathrm{T}$ represents a vector of individual-specific random slopes deviating from $\boldsymbol{\beta}^\mathrm{T}$, and $\mathbf{z}_i$ denotes a design matrix for individual i as a subset of $\mathbf{x}$. All three covariates were log-transformed prior to analysis due to highly skewed distributions for depth and NPP, as well as to ensure that all values were on the same scale to improve parameter estimation. Further model description can be found in Appendix S3.

Before the data could be analyzed for each of the study objectives, locations that represented "available" habitat needed to be defined in association with each of the 49 tracked turtles from the Gulf of Mexico region, which constituted the training dataset. This was conducted by randomly sampling points within each individual's home range as calculated via kernel density estimation (see Appendix S2: Section S2.1 for more details). To maintain a consistent ratio of "used" to "available" locations, 10 available points were generated for each used point per individual, where available points were randomly assigned to a particular month-year belonging to each individual's tracking duration to capture the dynamic nature of NPP and SST. Time-matched environmental data were extracted for each point using the TERRA package. Additionally, observations for used or available points that had missing data for any of the covariates were removed prior to modeling habitat selection.

To determine the impact of both algorithm choice and whether a model accounted for physiological constraints (hybrid) or not (correlative) on predictive performance for independent validation datasets, we fitted four different RSFs. Hierarchical forms of a generalized linear model (HGLM) and Gaussian process regression (HGPR) were fit to the data, where each of these algorithms were fit as a correlative SDM and hybrid SDM (i.e., informed by green turtle temperature preference). Gaussian process regression is considered a highly flexible algorithm that estimates model responses as a distribution of flexible functions, where these functions are constrained by parameters that affect the magnitude (SD) and the correlation between function values (range or length-scale) across values of the predictor (McElreath, 2020). For this comparison, the finest available spatial resolution was used (~5 km). All models were fit using integrated nested Laplace approximation (INLA) via the INLA R package (v23.9.9; Lindgren & Rue, 2015; Rue et al., 2009).

The HGLM included quadratic effects on all three covariates (i.e., depth, NPP, SST) to capture any nonlinear relationships. For the fixed effects, we used Normal(0, 10^3) priors (similar to Muff et al., 2020). For the random effects, we used penalized complexity (PC) priors (Muff et al., 2020; Simpson et al., 2017), which enabled us to specify the probability that the SD of a Normal distribution centered at 0 would be greater (or less) than a user-specified value. Given this, we set a prior of PC(1, 0.05) on the precision (i.e., inverse of the variance) for each of the random effects of the slopes since INLA relies on the use of precision (prec) parameters. We estimated the random intercept as $\alpha_i \sim N\left(0, \sigma_\alpha^2\right)$, where σ_α^2 was set to a large, fixed value of 10^6 to avoid shrinkage that could introduce bias into the parameter estimates (Muff et al., 2020). To account for a zone of thermal preference by green turtles in the hybrid models, informative priors that reflected the average water temperature occupied by green turtles based on the literature (27°C; Lamont et al., 2015; Madrak et al., 2022; Seminoff et al., 2020) were placed on the linear and quadratic terms of the HGLM, which were Normal(6.592×30, prec $= 0.005$) and Normal(-1×30, prec $= 0.005$), respectively. A scaling factor of 30 was used on the means of the informative priors to reflect a stronger effect size, whereas a precision of 0.005 was used that was more informative than the default 0.001 value but still vague enough to allow the coefficients to vary since the actual effect size was unknown.

The correlative and hybrid formulations of the HGPR were also fit with the exact same specification for the random intercept, but assumed a 1-dimensional Gaussian random field (GRF) on each of the three covariates that included five basis functions each. These GRFs were approximated via stochastic partial differential equations (SPDE), which greatly reduced model computation time without sacrificing much accuracy (Lindgren & Rue, 2015). Similar to the HGLM, PC priors were used to estimate parameters that represented the range (or length-scale) and

SD of the Gaussian process per covariate. For the range parameter of all three covariates, we specified a PC(1, 0.05) prior that indicated there was a 5% probability the range for a given covariate was less than 1. For the SD of all covariates, we specified a PC(10, 0.05) prior that indicated there was a 5% probability the SD for a given covariate was greater than 10. The same informative priors and fixed effects for SST from the hybrid HGLM were also used in the hybrid HGPR model out of necessity since it was not possible to include the same type of informative priors on the Gaussian process.

After identifying the model algorithm and formulation (correlative vs. hybrid) that exhibited the greatest predictive performance on the independent validation datasets (i.e., greatest transferability), the effect of spatial scale on model transferability was tested. Using the finest scale environmental raster data (i.e., 5 km), covariates were aggregated at 10, 20, and 40 km spatial resolution using the TERRA package. Environmental values at each of these resolutions were then extracted for all used and available points as was done when comparing model algorithms.

Once the most predictive model algorithm and spatial scale were determined, another model was implemented that accounted for differences in habitat selection by life stage. As defined by body size (via CCL) measured for each of the captured turtles, random effects for life stage (i.e., juvenile and adult) were included on the slopes for each of the three covariates. Therefore, this final model used the most predictive algorithm and spatial scale in addition to the newly added effects by life stage. All other random effects by individual remained the same as in previous steps.

Model validation

We validated the predictive capacity of each model using two sets of independent green turtle tracks from Brazil and Qatar as a measure of transferability. The Boyce Index was selected to validate the models since this is a more appropriate metric to evaluate the predictive performance of a RSF than other common methods (e.g., AUC; Boyce et al., 2002; Northrup et al., 2022) and has been demonstrated to provide a more reliable measure of predictive performance than AUC (Cianfrani et al., 2010; Hirzel et al., 2006). Briefly, the predicted values from the RSF in each independent study region were discretized into 10 bins and the time-matched points were used to extract these values for both the Brazil and Qatar datasets (Boyce et al., 2002; Di Cola et al., 2017; Sells et al., 2022). For each time point (i.e., month-year), a Spearman rank correlation was calculated across the 10 binned values for the observed versus predicted number of turtle relocations. The Boyce Index (i.e., Spearman correlation) ranged from −1 to +1, where values near −1 represent an inverse model, values near 0 are no different from random, and values near +1 represent a highly predictive model. Due to the relatively coarse spatial resolution of the predictive map (~5 km) and the high number of observations from the small, remote island location off the northeastern coast of Brazil, we also calculated the Boyce Index for a subset of Brazil data that only evaluated the turtle locations at the mainland ($N = 15,845$) in addition to the full dataset ($N = 26,943$). This included observations from turtles that had migrated from the island to foraging grounds in coastal waters. Additionally, we evaluated environmental similarity between the training (Gulf of Mexico) and testing regions (Brazil, Qatar) to determine the extent of environmental novelty between these different study locations. This was performed using the Shape method (Velazco et al., 2024) from the FLEXSDM R package (v1.3.4; Velazco et al., 2022) where values close to zero denote high similarity and those much larger denote greater dissimilarity.

RESULTS

Algorithm and formulation comparison

Model transferability was quite similar among each of the four algorithm–formulation combinations compared, but ultimately appeared to be greatest in the correlative HGPR model. Minimal differences in predictive performance were observed between formulations (i.e., correlative vs. hybrid) of the same model algorithm (i.e., HGLM vs. HGPR), and only slight differences when comparing across algorithms (Figures 2 and 3a). Since the low Boyce Index values for the full Brazil dataset did not appear to reflect each algorithm's predictive performance (due to the locations at the island), we only used the datasets for mainland Brazil and Qatar to evaluate model transferability. However, the full Brazil dataset was still included for comparison. The correlative and hybrid forms of the HGLM and HGPR models all exhibited high levels of transferability across both validation datasets, but the correlative HGPR model slightly outperformed the other models based on average performance for the Brazil and Qatar datasets (Figure 3a). When inspecting green turtle relationships with each of the three environmental covariates via marginal effects plots from the correlative HGPR model, it appeared there was a strong preference for shallow depths (1–10 m), low levels of NPP (0–50 g C m^{-2} day^{-1}), and increasingly warm SST (Figure 4). These relationships largely held across all four models, but differed in their magnitude of
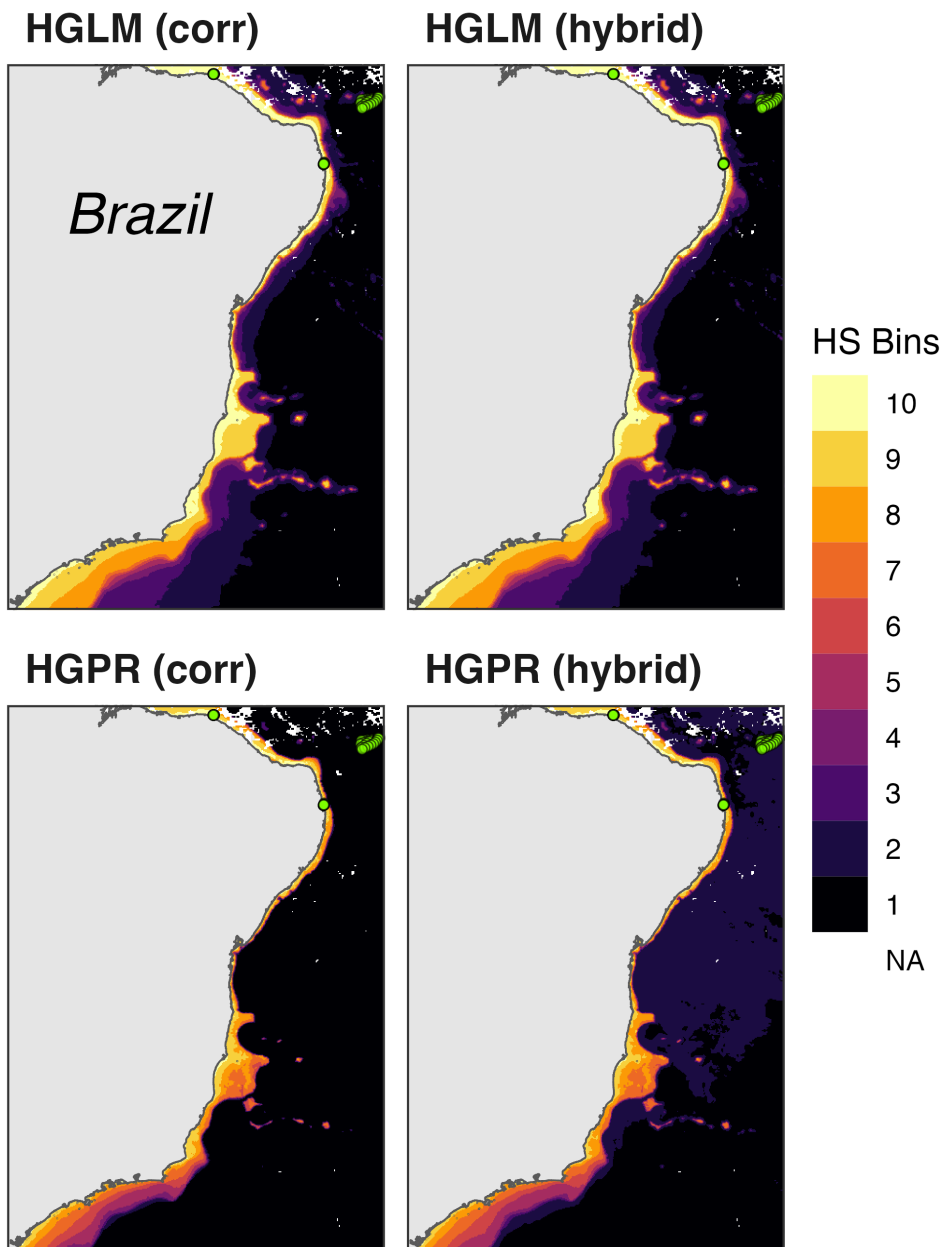
February 2022

FIGURE 2 Spatial predictions from the correlative and hybrid model forms of the hierarchical generalized linear model (HGLM) and hierarchical Gaussian process regression (HGPR) with respect to the independent observations not included in the model. Predictions are shown for the Brazil region during February 2022, where binned habitat selection (HS) values of 10 represent the greatest intensity of use and values of 1 represent the lowest intensity. Green points indicate observations during this particular month-year.

effect and flexibility in the fitted response (Appendix S1: Figure S5).

Spatial scale comparison

Although the comparison of model transferability across spatial scales (from correlative HGPR predictions) was more complicated than comparing across model algorithms, the finest spatial scale (5 km) demonstrated the greatest performance. The model that analyzed covariates at a 40-km resolution performed better than random on average for both independent validation datasets, but mapped predictions were not informative of where green turtles should be found (Figures 3b and 5). By comparison, the model analyzing covariates at a 20-km resolution
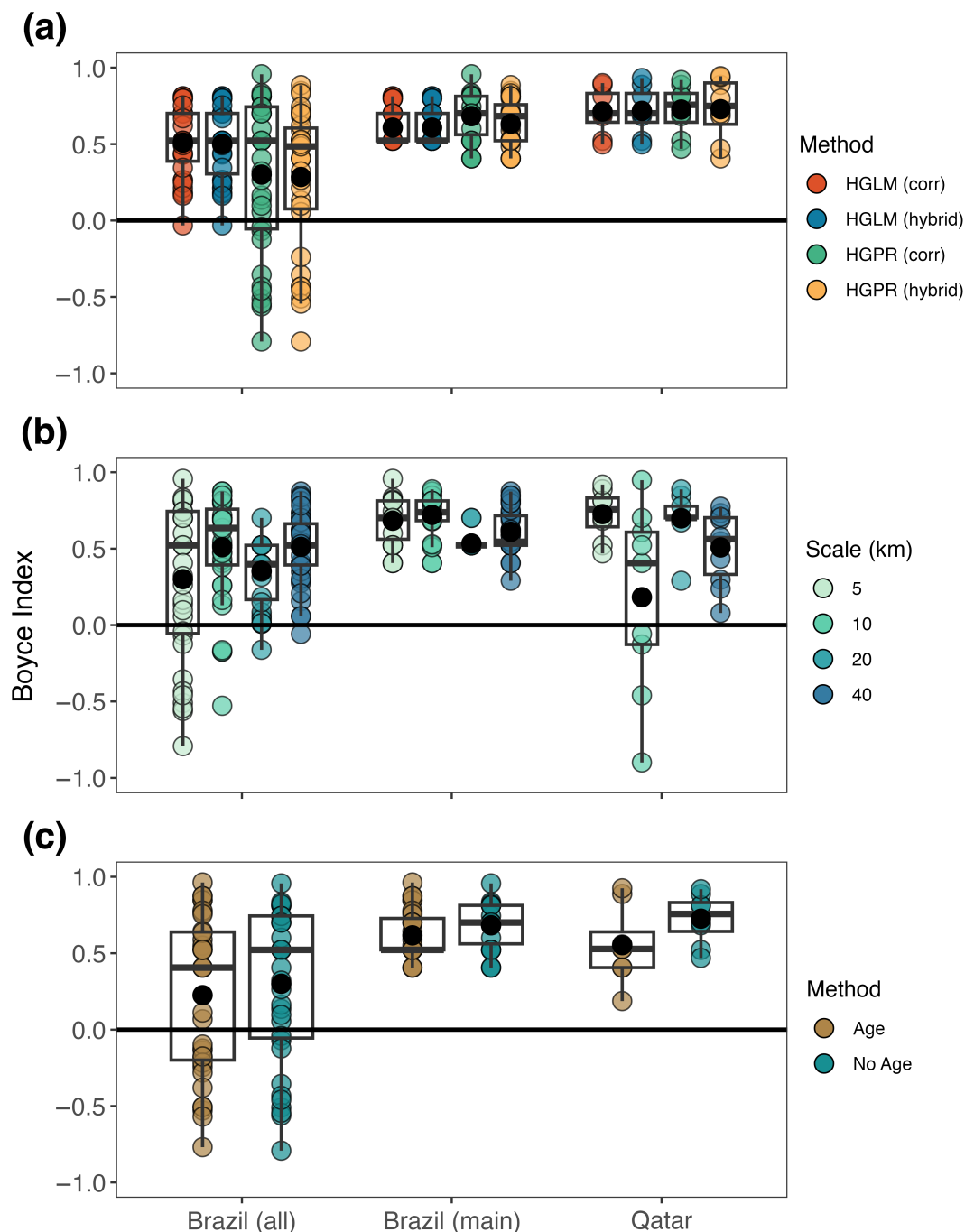
FIGURE 3 Box plots and dot plots of model validation comparison by study region for each phase of the analysis. (a) The algorithms compared were the correlative and hybrid model forms of the hierarchical generalized linear model (HGLM) and hierarchical Gaussian process regression (HGPR). (b) Spatial scales of environmental covariates were tested at 5, 10, 20, and 40 km resolution by study region. (c) Models that did or did not account for life stage by study region were also compared. The Boyce Index was calculated for each month-year of spatial predictions made for each region (colored points), where the mean values are shown as black points. The Brazil region was broken up into datasets that contain all observations ("Brazil [all]") as well as a subset that only contains observations at the mainland ("Brazil [main]"). The boxplots show the median as the midline, the lower and upper horizontal lines denote the interquartile range (IQR; 25th and 75th percentiles), and the whiskers extend no further than 1.5 × IQR.

performed notably better than the 40-km scale for the Qatar dataset, but did not appear to perform as well as the other spatial resolutions for the Brazil dataset. The model evaluating 10 km resolution covariates exhibited relatively high performance in the Brazil turtles (both the subset and full dataset), but performed the worst of
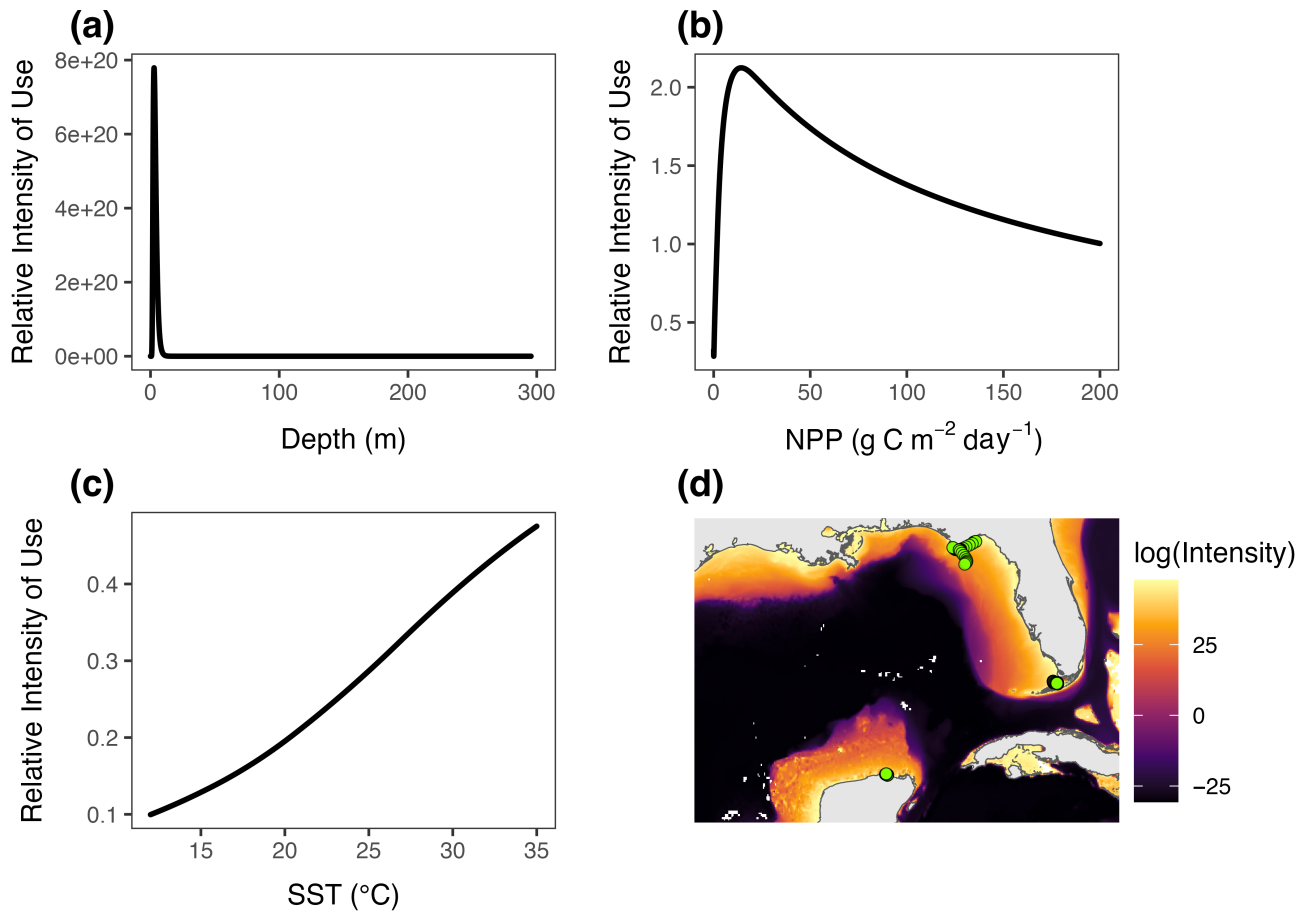
FIGURE 4 Responses of green turtles (*Chelonia mydas*) to selected environmental covariates based on the correlative hierarchical Gaussian process regression (HGPR) model trained on Gulf of Mexico data. Population-level marginal effects plots are shown for (a) bathymetric depth (Depth), (b) net primary productivity (NPP), and (c) sea surface temperature (SST). The *x*-axis for (a) depth has been reduced from its range up to 5000 m for improved clarity of the response. (d) Spatial predictions of the intensity of use for September 2020 are shown for the Gulf of Mexico on the log scale. Green points indicate time-matched observations from the training dataset.

the four spatial scales for the Qatar dataset. Lastly, the model analyzing the 5-km resolution data showed the highest transferability on average when evaluating the Qatar and mainland Brazil datasets despite not performing well when evaluating all (mainland + island) observations from Brazil (Figure 3b). As was performed for the algorithm comparison, only the mainland Brazil and Qatar datasets were used to evaluate model transferability across spatial scales. While some of the models shared similar responses to each covariate, responses were notably variable for depth and NPP across scales (Appendix S1: Figure S6).

Accounting for life stage effects

When comparing the correlative HGPR model that accounted for life stage with the model that did not, it appeared that the simpler population-level model

exhibited greater transferability. The model accounting for life stage found subtle differences in habitat selection between juvenile and adult conspecifics, where adults preferred a slightly greater range of depths and juveniles preferred areas with higher NPP (Figure 6; Appendix S1: Figure S7). When comparing the estimated transferability between models, the simpler population-level model exhibited greater predictive performance for both validation datasets (Figure 3c). As found for the prior sets of model comparisons (i.e., algorithm, spatial scale), the greatest variability and lowest Boyce Index values were calculated for the Brazil dataset that included turtle locations from the offshore island location. Alternatively, high Boyce Index values were calculated for both the Qatar dataset and the mainland Brazil dataset. As conducted for the other comparisons, only the mainland Brazil and Qatar datasets were used to assess model transferability across models.
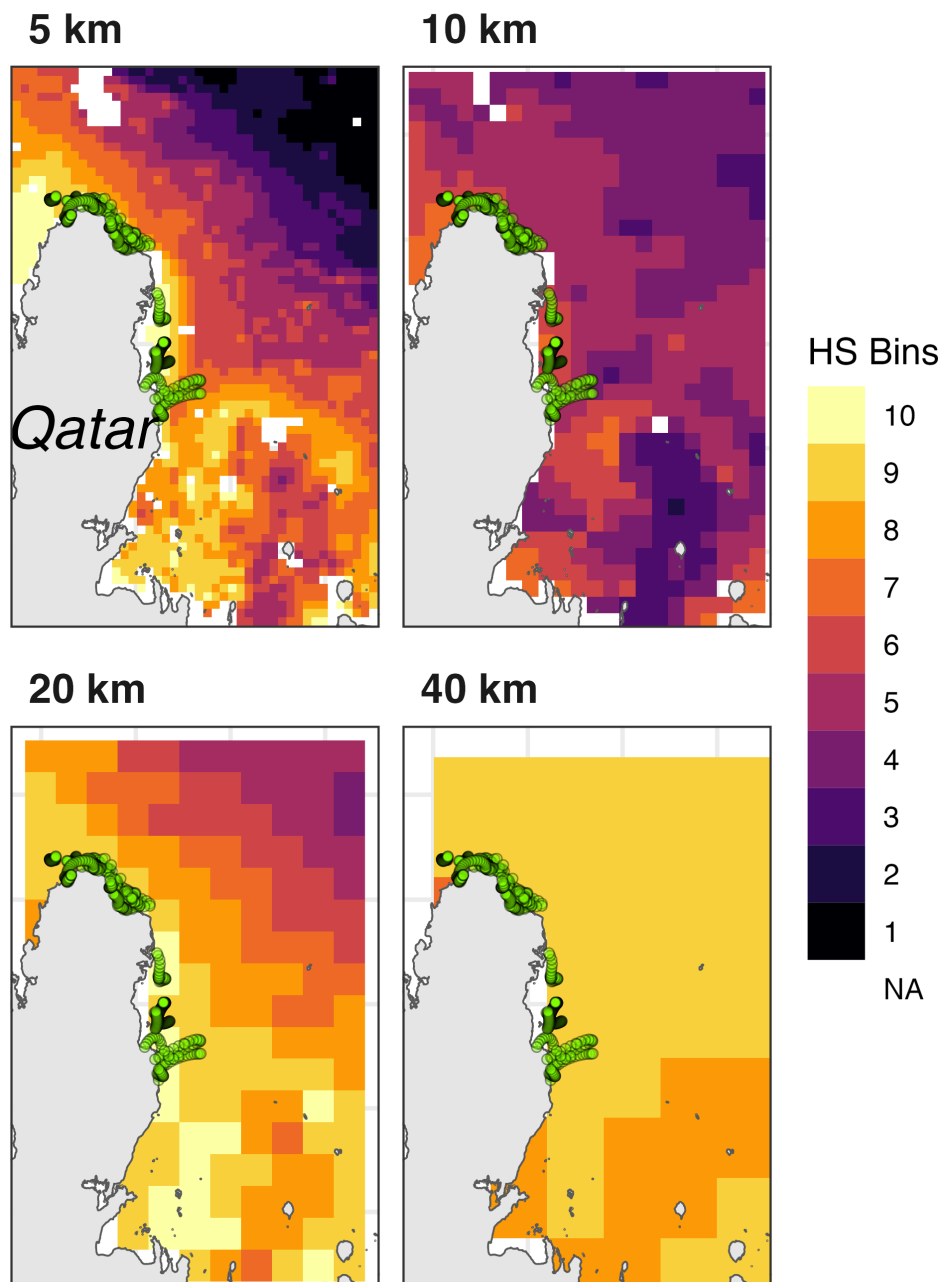
FIGURE 5 Predictions from each of the four spatial scales with respect to the independent observations not included in the model. Predictions are shown for the Qatar region during March 2014, where binned habitat selection (HS) values of 10 represent the greatest intensity of use and values of 1 represent the lowest intensity. Green points indicate observations during this particular month-year.

DISCUSSION

The comparative framework presented in this study provides guidance for other practitioners aiming to develop transferable models on other species and environments. Specifically, this study proposes that multiple modeling decisions be considered and tested during the process of building SDMs, which should ultimately result in a more transferable model than may have been developed without explicitly evaluating transferability. This framework can also be modified to implement other underlying models (such as occupancy models and a growing number of step selection functions), other datasets (e.g., presence-only occurrences, presence-absence surveys, mark-recapture), as well as even other model features such as those suggested by Yates et al. (2018)
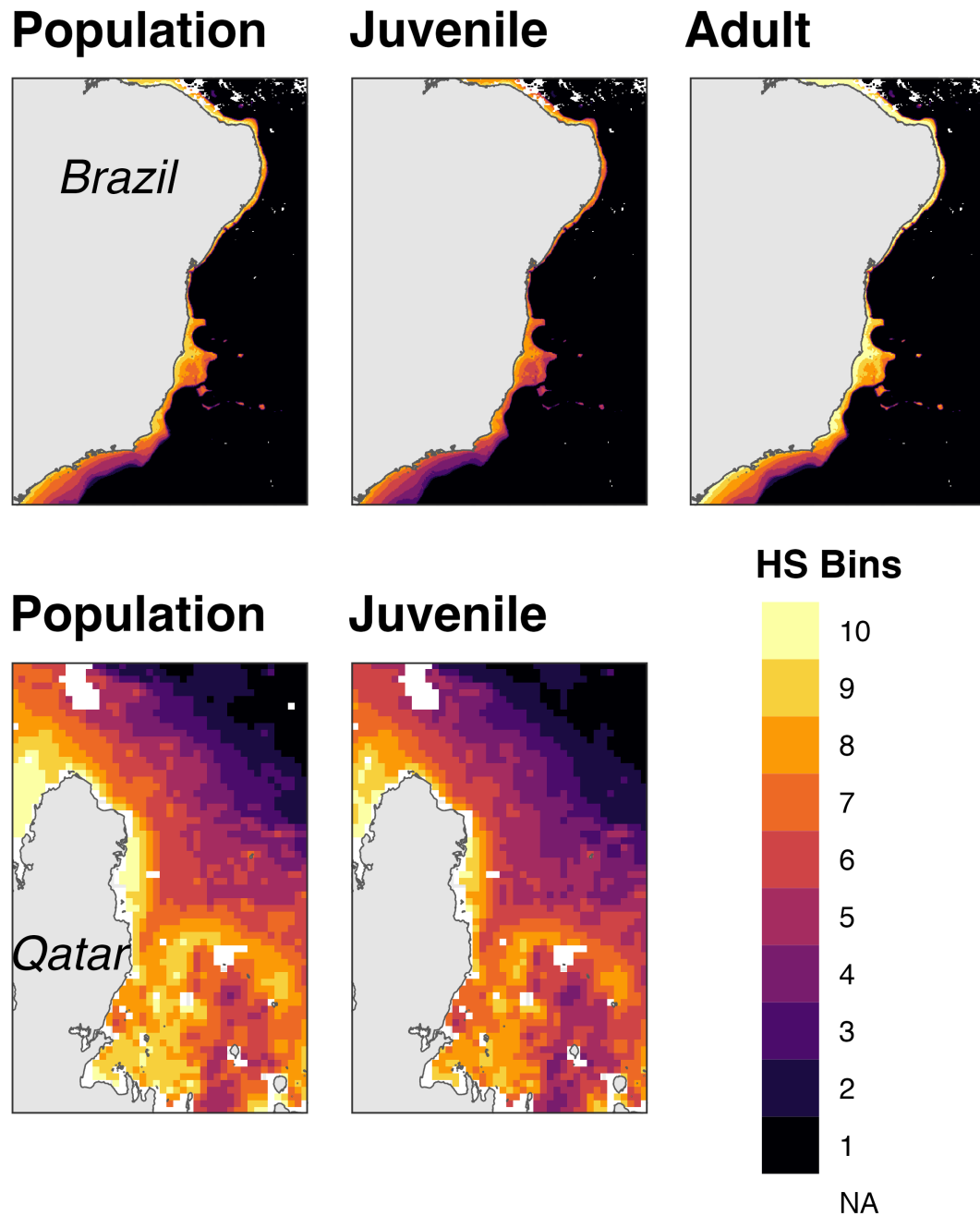
FIGURE 6 Spatial predictions from each of the two correlative hierarchical Gaussian process regression (HGPR) models that either included or did not include the effect of life stage. Predictions in the top row are shown for the Brazil region for February 2022, while predictions in the bottom row are shown for the Qatar region for March 2014. The "Population" label refers to the model that did not account for life stage, whereas "Juvenile" and "Adult" labels indicate the predictions from the model that did account for life stage. No adults were tagged in Qatar, which is why predictions for this life stage are not shown. For the predictions, binned habitat selection (HS) values of 10 represent the greatest intensity of use and values of 1 represent the lowest intensity.

or Sequeira et al. (2018). Of the three hypotheses originally posed, the first hypothesis (comparing model algorithms–formulations) was partially supported by our results, the second hypothesis (spatial scale) was fully supported by our findings, and the third hypothesis (predicting the importance of life stage effects) was not supported. Overall, the results may have been

impacted by a number of different factors, including data structure (e.g., sample size, track duration, balance of juveniles and adults) and modeling decisions (e.g., covariate selection, validation method, structure of validation data, spatial autocorrelation of covariates, spatial extent of available habitat). However, it is important to note that fitting (or training) a predictive model

on a large dataset where animals have visited a wide range of covariate values is essential to properly characterizing the response for the species of interest (Matthiopoulos et al., 2011; Schurr et al., 2012).

Model transferability by algorithm and formulation

The algorithm–formulation comparison of model transferability partly supported our hypothesis, where the HGPR algorithm displayed greater performance than the HGLM, but the correlative formulations of each algorithm performed comparably or better than that of the hybrid formulation. This suggests that the greater transferability of the HGPR algorithm was not due to the inclusion of a physiologically informed Bayesian prior (e.g., on temperature preference), but rather was reflective of the variability captured by nonlinear responses from the HGPR algorithm alone. When inspecting the marginal effect plots of the correlative HGPR model, it appeared that both depth and NPP exhibited a greater effect on green turtle habitat selection than SST (Figure 4). Therefore, adding an informative prior on SST may not have been useful for this particular dataset. The reason for this relationship may be largely due to how available habitat was defined (DeCesare et al., 2012; Holbrook et al., 2019; Northrup et al., 2013), as well as the relatively homogenous spatial field of SST in the Gulf of Mexico where temperature of available habitat was likely very similar to that of used habitat (Pinti et al., 2024). Surprisingly, the HGLM algorithm exhibited only slightly lower performance for the Qatar and mainland Brazil datasets, while showing greater performance than the HGPR algorithm for the full Brazil dataset. Despite the increasing popularity of highly flexible SDM algorithms (e.g., generalized additive models, boosted regression trees, random forests), the inclusion of quadratic polynomial terms may produce GLMs that exhibit comparable transferability while also being easier to interpret than results from machine learning algorithms.

The population-level responses of green turtles to the selected environmental covariates were relatively consistent across model algorithm–formulation combinations and matched known habitat use patterns to varying degrees. All models identified shallow depths as preferred by green turtles—both HGLM models found preferences ranged from 1 to 5 m, whereas both HGPR models suggested that preferences ranged from 1 to 8 m (Appendix S1: Figure S5). This is generally supported by previous studies that have found that juvenile and adult green turtles are often found in shallow coastal regions (1–10 m; Fuentes et al., 2020; Griffin et al., 2020; Hart

et al., 2013; Lamont et al., 2023). Alternatively, both HGLM models suggested a preference for very low levels of NPP, whereas the HGPR models showed relatively high preference for all but the lowest NPP values (Appendix S1: Figure S5). These differences may be attributed to the greater flexibility by the HGPR models, which still showed peaked preference at low NPP levels, but also showed only a slight drop in preference with increasing NPP that would not be possible with a quadratic polynomial for the HGLM. When evaluating responses to SST, both of the HGLM models estimated a peak thermal preference, whereas the HGPR models showed a preference for increasing SST to different degrees (Appendix S1: Figure S5). Peak SST preference was estimated to be 31°C by the correlative HGLM, whereas the hybrid HGLM estimated peak preference to be 22°C. This matches the primary range of temperatures that green turtles have been reported to inhabit (Lamont et al., 2015; Madrak et al., 2022; Seminoff et al., 2020). However, neither HGPR model estimated a temperature optimum; in addition to the similarities in SST between used and available habitat that would suggest low selection strength, this may be a result of a limited number of basis functions, the position of basis functions (on link scale) that did not capture the relationship well, or how the Gaussian process priors were defined.

Model transferability by scale

The scale of environmental covariates had a substantial impact on the spatial predictions of relative intensity of habitat use by green turtles, but this was not necessarily reflected in the model validation results. Visual inspection of the predicted intensity by scale suggests a faint similarity of spatial pattern from 5 to 20 km, but then results in an unrecognizable pattern at 40 km (Figure 5). Although it is expected that similar spatial patterns would indicate similar relationships for the underlying models, this was not necessarily the case (Appendix S1: Figure S6). So, while it is possible that the predictions from models analyzing the coarser environmental datasets (10, 20, 40 km) are not much worse than that of the finest resolution (5 km) assessed by this study, it may be possible that the Boyce Index alone was not able to substantially differentiate among these predictions. Despite finding that the finest spatial scale produced the most predictive model in this study, this is not always the case as demonstrated by Manzoor et al. (2018) where a model using 300 m resolution covariates exhibited greater transferability than the finer 50 m scale. Therefore, the spatial scale should always be evaluated as part of studies investigating animal habitat

selection or behavioral state–habitat associations (Heit et al., 2023; McGarigal et al., 2016).

With regard to study design and environmental covariates, factors such as habitat heterogeneity, data availability, data missingness, and animal movement patterns can impact inferences or predictions made from SDMs and related models (Matthiopoulos et al., 2020, 2023; O'Toole et al., 2021). In range-restricted animals that exhibit long-term site fidelity, it becomes difficult to evaluate habitat selection if they inhabit a local territory that is relatively homogeneous despite higher levels of heterogeneity across the region or landscape (Matthiopoulos et al., 2020). Additionally, the availability of high-resolution remote sensing data (<1 km) in some marine regions may be more difficult to obtain than others, resulting in the use of coarser datasets. While many remote sensing and ocean modeling products for marine systems are available at <1 km within the US Exclusive Economic Zone, datasets at this resolution were not available for the South Atlantic or Arabian Gulf on which we performed model validation. Although this does not appear to be as restrictive in terrestrial systems due to the global availability of Landsat (30 m) and Sentinel-2 (10 m) satellite imagery, data gaps still exist for marine systems. Missing data are also a pervasive problem, particularly in nearshore coastal areas, which often results in observations omitted from the analysis (Kostopoulou, 2021; Marshall et al., 2020; Ouellette & Getinet, 2016). For example, 4995 "used" and 32,981 "available" data points were removed prior to habitat selection modeling in this study, primarily due to missing environmental data along coastlines (as opposed to cloud cover). While these issues cannot be resolved easily if at all, they should be kept in mind during study design or model interpretation.

Model transferability by including life stage

Although the model that accounted for different responses by juveniles and adults did not exhibit the greatest transferability, this should not dissuade future studies from considering life stage differences. In the particular models fitted by this study, it appeared that the population-level response to depth was a compromise between the separate responses of juveniles (for slightly shallower depths) and adults (for slightly greater depths) (Appendix S1: Figure S7). These findings align with previous studies that have reported adults occupy deeper habitats more regularly than juveniles (Godley et al., 2002; Hart et al., 2017; Lamont et al., 2023; Roberts et al., 2021). Given that the Boyce Index only evaluates

observed versus predicted presences (rather than pseudo-absences), movements of juveniles in Brazil and Qatar to slightly deeper water may have reduced the predictive performance when accounting for these life stage differences. When evaluating model transferability by life stage, it appeared that the juveniles tracked in Brazil exhibited a similar Boyce Index to the population-level model, which was greater than for the adult life stage in this region (Appendix S1: Figure S8). However, this result may be due to a reduction in sample size for adults since this was the only life stage that exhibited migratory movements, which were ultimately removed prior to habitat selection modeling. Therefore, we recommend that the inclusion of responses by life stage also be evaluated in future habitat selection studies.

Study limitations and future directions

While the comparative framework presented in this study takes steps toward improving SDM transferability, there are a number of limitations that could be addressed in future work. Although the correlative HGPR model displayed high transferability for this study on green turtles, this may not necessarily reflect transferability in other untested locations or with generalist species. Our analysis of environmental similarity between the training (Gulf of Mexico) and testing regions (Brazil, Qatar) found that they were highly similar in most cases (based on depth, NPP, and SST), with the exception of pelagic regions near Brazil as well as summer months (July–September) in Qatar (Appendix S1: Figure S9). Therefore, further tests may be warranted at the edges of this species' range to evaluate model transferability under differing environmental conditions. Moreover, green turtles are considered resource specialists since they forage almost entirely on seagrass and benthic macroalgae in shallow coastal habitats from juvenile through adult life stages (Gama et al., 2016; Gillis et al., 2018; Seminoff et al., 2021). Given the limited range of potential habitats that they occupy, additional studies should evaluate whether this comparative framework is also useful for generalist species. Beyond addressing the limitations of this study, future work could extend this framework to include step selection functions, occupancy models, integrated SDMs, or the inclusion of spatial random effects. The latter could be used to capture additional variation in the model not directly accounted for by the selected covariates (Banerjee et al., 2008; Renner et al., 2015) and can be flexibly implemented in available software in R, such as the INLA or MGCV (Wood, 2011) packages.

Despite some of the abovementioned caveats, we generally recommend that future studies aiming to predict

distributions of species across broad spatial areas apply the comparative framework proposed by this study. Based on the mean prediction from the model, our findings support results from prior studies that demonstrated high predictive performance from Gaussian process models compared to other commonly used SDM algorithms (Golding & Purse, 2016; Ingram et al., 2020; Vanhatalo et al., 2012). However, the inclusion of informative priors for a hybrid SDM may be limited by both the spatial heterogeneity of the covariate, selection strength, and the range of covariate values in available habitat. The implementation of the framework presented here is expected to benefit conservation and management goals, especially as part of decision-support tools in the development of protected areas or defining priority habitat for species of concern. Wider application of transferable SDMs can therefore be used to guide proactive management decisions, whether related to the recovery of imperiled species or to prevent the establishment of invasives (Yates et al., 2018).

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Cullen et al., 2024) are available from Zenodo: https://doi.org/10.5281/zenodo.14262514.

ORCID

Joshua A. Cullen ![ORCID icon] https://orcid.org/0000-0002-6935-9340

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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