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Research article

Cross-validation matters in species distribution models: a case study with goatfish species

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In an era of ongoing biodiversity, it is critical to map biodiversity patterns in space and time for better-informing conservation and management. Species distribution models (SDMs) are widely applied in various types of such biodiversity assessments. Cross-validation represents a prevalent approach to assess the discrimination capacity of a target SDM algorithm and determine its optimal parameters. Several alternative cross-validation methods exist; however, the influence of choosing a specific cross-validation method on SDM performance and predictions remains unresolved. Here, we tested the performance of random versus spatial cross-validation methods for SDM using goatfishes (Actinopteri: Syngnathiformes: Mullidae) as a case study, which are recognized as indicator species for coastal waters. Our results showed that the random versus spatial cross-validation methods resulted in different optimal model parameterizations in 57 out of 60 modeled species. Significant difference existed in predictive performance between the random and spatial cross-validation methods, and the two cross-validation methods yielded different projected present-day spatial distribution and future projection patterns of goatfishes under climate change exposure. Despite the disparity in species distributions, both approaches consistently suggested the Indo-Australian Archipelago as the hotspot of goatfish species richness and also as the most vulnerable area to climate change. Our findings highlight that the choice of cross-validation method is an overlooked source of uncertainty in SDM studies. Meanwhile, the consistency in richness predictions highlights the usefulness of SDMs in marine

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conservation. These findings emphasize that we should pay special attention to the selection of cross-validation methods in SDM studies.

Keywords: climate change, cross-validation, indicator species, species distribution model, species richness

Introduction

As biodiversity loss is accelerating (Wake and Vredenburg 2008, Ceballos et al. 2015, Urban 2015, Cowie et al. 2022), it is of great importance to assess spatial patterns of biodiversity (Rodríguez et al. 2007, Guisan et al. 2017, Araújo et al. 2019) and improve our forecast ability for their variations under climate change exposure (Pacifi et al. 2015, Urban et al. 2016, Foden et al. 2019). Species distribution models (SDMs) represent valuable tools for such assessment (Pacifi et al. 2015, Araújo et al. 2019, Dong et al. 2024). SDMs can map target species' habitat suitability by exploring relationships between distribution data and meaningful ecological predictors (Guisan and Thuiller 2005, Elith and Leathwick 2009, Guisan et al. 2017, Araújo et al. 2019, Dong et al. 2024). SDMs are routinely used in climate change biology (Thuiller et al. 2019, Hu et al. 2021), invasion biology (Liu et al. 2020, Zhang et al. 2020a), conservation biology (Marshall et al. 2014, Zhang et al. 2020b), paleoecology (Svenning et al. 2011, Wang et al. 2021, Huang et al. 2023), and more. Given this wide variety of application, researchers have proposed a set of practical guidelines to construct SDMs from sampling (Kramer-Schadt et al. 2013), through predictor calculation and selection (Dormann et al. 2013, Bede-Fazekas and Somodi 2020), to model training (Elith et al. 2008, Sillero et al. 2021, Soley-Guardia et al. 2024) and evaluation (Norberg et al. 2019). Also, best practices exist for reporting SDMs (Zurell et al. 2020, Taheri et al. 2021) and improving analytical reproducibility (Feng et al. 2019).

According to the best-practice standards (Araújo et al. 2019, Feng et al. 2019), when constructing an SDM, we should pay due attention to model settings or hyperparameters (the latter, in the case of machine-learning SDMs) of modeling algorithms in order to maximize model predictive performance. Cross-validation represents a key approach to comparing the predictive performance of competing models with different hyperparameters, hence helping to determine the optimal configuration of parameters (Araújo and Guisan 2006, Hijmans 2012, Guisan et al. 2017). Taking the widely used five-fold random cross-validation approach as an example, a randomly selected 80% of the data is used for model training and the withheld 20% for model validation, and this step is repeated five times while the validation fold is changed. To date, most SDM studies have adopted this random cross-validation strategy for model evaluation during hyperparameter optimization (i.e. optimize hyperparameter combination of target algorithms) (Guisan et al. 2017, Roberts et al. 2017). Recently, however, researchers argued that the random cross-validation approach ignores spatial autocorrelation in the training and validation datasets, especially when

data are temporally or spatially structured (Roberts et al. 2017, Valavi et al. 2019); thus, random cross-validation may affect model parameter configuration (Roberts et al. 2017, Valavi et al. 2019), often resulting in the overestimation of predictive performance which may let the modeler erroneously conclude that the model is transferable and the predictions are accurate (Veloz 2009, Guillaumot et al. 2019). To address this issue, researchers have proposed a spatial cross-validation strategy; in this approach, species distribution data are split into similar-sized square or hexagonal spatial blocks, and the blocks are assigned to several (n) folds: one fold is used for testing and $n - 1$ folds are used for training in an iterative cross-validation process. There are several approaches for block assignment; typically, they rely on iterative optimization algorithms that try to achieve a balanced separation of the presence and (pseudo)absence points among the two folds (detailed description in Roberts et al. 2017, Valavi et al. 2019). The spatial cross-validation strategy is able to split the occurrence dataset into two (i.e. train and test sets) or more (i.e. cross-validation) folds, so that the spatial dependence of the test set to the train set and the spatial autocorrelation of the test set are reduced (Merow et al. 2014, Bald et al. 2023). This approach is implemented in several R packages, such as 'blockCV' (Valavi et al. 2019) and 'ENMeval' (Kass et al. 2021), and stand-alone software, such as spatialMaxent (Bald et al. 2023).

The scientific community is inconclusive about which cross-validation technique is preferred generally (Roberts et al. 2017, Valavi et al. 2019, Ploton et al. 2020, Wadoux et al. 2021) and even in maximum entropy algorithm (MaxEnt)-based studies (Bald et al. 2023). For instance, Roberts et al. (2017) and Valavi et al. (2019) demonstrated that ecological data are always structured in space and time; when fitting models using structured ecological data, random cross-validation would ignore these structures and result in biases in prediction error estimation. Therefore, instead of random cross-validation, they advocated for using block cross-validation in structured data (Roberts et al. 2017, Valavi et al. 2019). However, spatial cross-validation tends to result in overly pessimistic validation measures (De Bruin et al. 2022) and it lacks a theoretical basis and should not be used according to Wadoux et al. (2021). In this study, we calibrated SDMs using two cross-validation approaches (Fig. 1). We selected goatfish species in this study for manifold reasons. First, goatfishes are marine species; evidence has shown that the geographical ranges of marine species are closely related to their thermal tolerance limits, thus distributions of marine organisms via SDMs are believed to be more accurate (Sunday et al. 2012, Stuart-Smith et al. 2017). Second, goatfish species typically inhabit coastal waters, where climatic

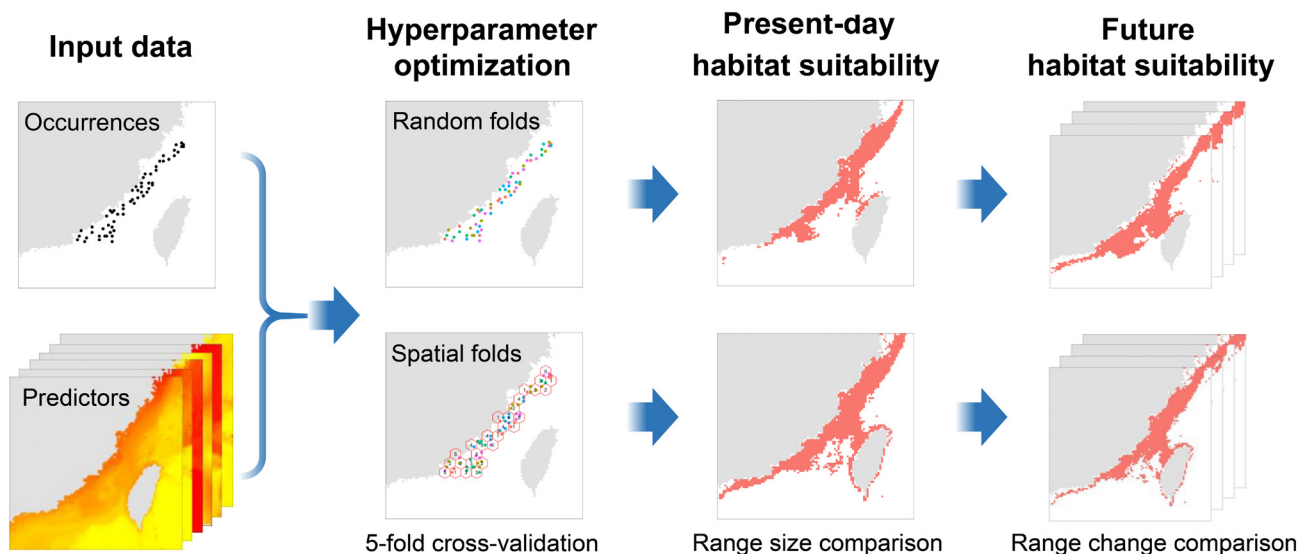


Figure 1. A conceptual diagram showing the study design. To improve figure readability, we showed the study process by simulating a virtual species along the coastal waters of China, instead of using an arbitrarily selected goatfish species.

changes in marine environmental conditions are expected to be particularly severe (Guo et al. 2022). Third, goatfishes are a species-rich group (over 100 species) (Nash et al. 2022), playing important ecological roles in coastal ecosystems (Uiblein 2007). Fourth, goatfishes are optimal study species for a global analysis due to their circum-global distribution pattern and importance as reference species for monitoring and managing the ecosystem due to their sensitivity to environmental stress (Uiblein 2007). We hypothesize that the two cross-validation strategies will result in 1) different levels of model complexity (i.e. different optimal parameter combinations of SDMs), 2) different present-day habitat suitability predictions, and 3) different future projection patterns under climate change. Our results not only highlight that the choice of cross-validation approaches represents a critical source of uncertainty in biodiversity assessments but also emphasize the urgency of conserving marine biodiversity in an era of climate change.

Material and methods

Species distribution data

We generated a list of 102 goatfish species following the latest taxonomy by Nash et al. (2022) and Eschmeyer's Catalog of Fishes (Fricke et al. 2018, Supporting information). We compiled a distribution database for these species by retrieving occurrence records from online repositories [such as the Global Biodiversity Information Facility (<https://www.gbif.org>) and Ocean Biodiversity Information System (<https://obis.org>)], field surveys in the South China Sea between 2016 and 2021, and an extensive literature review (including literature in English, Chinese, and Japanese) (Supporting information). Our database contains a total of 347 222 occurrence records

for 93 out of 102 goatfish species (occurrence data were not available for nine goatfish species) (Supporting information). We improved the reliability of occurrence data by excluding records outside the species' known range as described in FishBase (<https://www.fishbase.org>) and by removing records with invalid coordinates via the 'CoordinateCleaner' R package ver. 2.0.20 (Zizka et al. 2019). Besides, as with previous studies (Mammola et al. 2018, Hu et al. 2021), we reduced the possible effects of sampling bias on model fitting by keeping only one record per 5 arcmin grid cell (i.e. the resolution of our environmental predictors). Given the vital role of the sample size used for model training on the model's performance (Wisn et al. 2008), we only considered species with over five filtered records (Hernandez et al. 2006). A total of 78 species satisfied this criterion and were retained for analyses (average (\pm SD) number of filtered occurrences of 346 (\pm 478) records per species (Supporting information)).

Marine predictors

It is highly recommended that the ecologically relevant predictors are selected when building SDMs (Bosch et al. 2018, Feng et al. 2019). Evidence suggests that the geographical distribution of marine species can be influenced by different types of predictors, such as bathymetry (Colloca et al. 2003, Brown and Thatje 2014), temperature (Root et al. 2003, McHenry et al. 2019), salinity (Hall and Lewandowska 2022, Röthig et al. 2023), and ocean currents (Poloczanska et al. 2016, Wilson et al. 2016). Considering the ecological importance of marine predictors as well as the availability of data layers under climate change scenarios, we initially considered a total of 20 predictors, including 18 marine environmental predictors and two geographical predictors (Supporting information). Environmental and geographical predictors were sourced from the Bio-ORACLE v2.2 dataset (<https://>

www.bio-oracle.org) (Assis et al. 2018) and the global marine environmental dataset (<https://gmed.auckland.ac.nz>) (Basher et al. 2018), respectively. The Bio-ORACLE ver. 2.2 dataset provides both surface and benthic data layers for ecological modeling (Assis et al. 2018), given that goatfishes are benthic species primarily inhabiting sandy or muddy habitats (Kaya et al. 1999, Uiblein 2007), we selected the benthic layers for these 18 environmental predictors. We were also interested in species future projections under climate change; we considered two future time periods (2040–2050 and 2090–2100) under two representative concentration pathways (RCPs: RCP 2.6 and RCP 8.5). The Bio-ORACLE ver. 2.2 dataset produced future projections of marine environmental predictors by averaging outputs of three atmosphere–ocean general circulation models: CCSM4, HadGEM2-ES, and MIROC5 (Assis et al. 2018). We downloaded future projections of marine environmental predictors from the Bio-ORACLE ver. 2.2 dataset (Assis et al. 2018). Future projections of the geographical predictors (water depth and distance to shore) remain highly uncertain; thereby, following previous studies (Zhang et al. 2019), we hypothesized that water depth and distance to shore remain unchanged in the future. All the marine predictors had a spatial resolution of 5 arcmin.

We checked for collinearity among the 20 predictor variables across the globe by calculating pairwise Pearson's correlations (r) and excluded collinear predictors (i.e. the threshold set at $|r| > 0.7$) (Dormann et al. 2013). Based on the collinearity results and ecophysiological relevance of the predictors (Bosch et al. 2018, Araújo et al. 2019, Feng et al. 2019), we finally retained six predictors for subsequent analyses: water depth, distance to shore, maximum temperature, range of temperature, minimum salinity, and mean current velocity (Supporting information).

Distribution model development

We built SDMs for the 78 goatfish species via the MaxEnt, a presence–background machine learning algorithm (Phillips et al. 2006). MaxEnt is widely used to model the distribution of marine organisms (reviewed by Melo-Merino et al. 2020). We selected MaxEnt instead of other SDM algorithms or an ensemble modeling approach mainly because 1) MaxEnt shows good discrimination capacity even at a small sample size (Hernandez et al. 2006), 2) comparing different modeling algorithms is outside the scope of this study, 3) there is no particular benefit of ensemble models over individual tuned models (Hao et al. 2020), and 4) the comparison of the two selected cross-validation methods would be hindered by applying model ensembles with different model compositions. For each species, we delineated the model calibration area by establishing a 1000 km buffer around species occurrence records, which we interpret to represent the maximum dispersal capacity of goatfish. We recognize the critical role of the calibration area in SDM studies, which should reflect the accessible areas to target species over their evolutionary history (Barve et al. 2011); however, it is challenging to accurately estimate the dispersal ability of marine species

(Cowen and Sponaugle 2009, Burgess et al. 2016), especially in multi-species studies such as this one. We selected 1000 km following the work by Waldock et al. (2022). We also performed a sensitivity analysis by using a 2000 km buffer size and our main results were insensitive to the choice of buffer sizes (Supporting information). We selected 10 000 random points within the species calibration area as background data (Elith et al. 2011, Barbet-Massin et al. 2012). It has been reported that model complexity has a great impact on model performance (Morales et al. 2017, Brun et al. 2020); therefore, we optimized the hyperparameters of MaxEnt (feature class and regularization multiplier) via the 'ENMeval' R package ver. 2.0.2 (Kass et al. 2021) in two steps. First, we filtered the top 10% of the models according to their omission rates (see detailed explanation in Kass et al. 2021), then we selected the best model from these candidates based on the validation area under the receiver operating characteristic curve (AUC) (Radosavljevic and Anderson 2014, Zhang et al. 2021, Kass et al. 2022). We adopted a fivefold random cross-validation and spatial cross-validation approach to measure model predictive performance (Fig. 1). We divided species distribution data into 5×5 spatial blocks via the 'blockCV' R package ver. 3.0.0 (Valavi et al. 2019), and we assigned the blocks to five folds via 50 permutations to obtain a balanced fold assignment. Even though AUC is an acceptable goodness-of-fit measure when comparing models of the same parameters and the same dataset (Kass et al. 2022), as we did during the hyperparameter optimization, it can be misleading when evaluating models of different species (Lobo et al. 2008). Therefore, we assessed model predictive performance using the continuous Boyce index, which represents a reliable measurement for presence-only models (Hirzel et al. 2006). The continuous Boyce index varies from -1 to 1 , where positive values indicate good agreement between model prediction and species occurrences (Hirzel et al. 2006). In analogy to Engler et al. (2011), we considered models with $AUC \geq 0.7$ and continuous Boyce index ≥ 0.4 as good. We also assessed the permutation importance of each predictor in regulating species distribution, i.e. we randomly permuted the values of the predictor among the training points and measured the resulting decrease in training AUC, then rescaled the decreases to sum up to 100% (Phillips 2006, Kass et al. 2021).

We transformed the continuous habitat suitability maps into binary via a 10% presence probability threshold, which has been commonly used in presence-only distribution models (Kass et al. 2022). We acknowledge that different thresholds have been proposed to transform continuous habitat suitability predictions to binary (Liu et al. 2005). We explored the sensitivity of our results to the choice of thresholds by using an alternative threshold that maximizes the true skill statistic value (Liu et al. 2005). Our results showed that the choice of thresholds did not change our main conclusions (Supporting information). We computed the size of suitable ranges for goatfishes using spherical geometry-based area calculation of the polygonized binary suitability raster. We adopted two dispersal scenarios when predicting species future potential distribution under climate change: no

dispersal ability (species are not able to occupy newly suitable areas in the future) and unlimited dispersal ability (species are able to occupy any newly suitable areas within the calibration areas in the future) (Guisan et al. 2017, Thuiller et al. 2019). We computed the relative change in species range size (hereafter range size change) using the following formula:

Range size change (%)

$$= \frac{(\text{Size of future suitable area} - \text{size of present suitable area})}{\text{Size of present suitable area}} \times 100\%,$$

the positive value indicates net range expansion in the future, and the negative value suggests net range contraction in the future.

For each species, we used the paired Wilcoxon signed rank test (Bauer 1972) to compare the difference in the predictive performance (i.e. the continuous Boyce index) of the two cross-validation approaches. All analyses were conducted in R ver. 4.1.2 (www.r-project.org).

Results

Model discrimination abilities

SDMs for 60 out of 78 studied goatfish species showed excellent goodness-of-fit (i.e. $AUC \geq 0.7$ and continuous Boyce index ≥ 0.4) (Engler et al. 2011, Supporting information). The two cross-validation approaches resulted in different

hyperparameter optimization in 57 out of 60 (95%) goatfish species (Fig. 2a). Despite the remarkable difference in the optimization of hyperparameters, both approaches had high discrimination abilities with a mean (\pm SD) continuous Boyce index of $0.796 (\pm 0.144)$ (Fig 2b, Supporting information). The random cross-validation method (0.841 ± 0.147) had a significantly higher continuous Boyce index than the corresponding spatial cross-validation method (0.752 ± 0.128) (two-sided paired Wilcoxon signed rank test, $V=1542$, $p < 0.001$, Fig. 2b).

With respect to the permutation importance of predictors, these two cross-validation approaches yielded nearly identical results (Fig. 2c). Both approaches identified maximum temperature as the most influential predictor in determining goatfish distribution, followed by distance to shore and water depth (Fig. 2c). In contrast, salinity and current velocity contributed relatively little to species distribution (Fig. 2c). Significant differences in the permutation importance of maximum temperature (two-sided paired Wilcoxon signed rank test, $V=1176$, $p < 0.01$), water depth (two-sided paired Wilcoxon signed rank test, $V=432$, $p < 0.01$), and annual mean current velocity (two-sided paired Wilcoxon signed rank test, $V=1139$, $p < 0.01$) were detected between the two types of cross-validation approaches (Fig. 2c, Supporting information).

Disparity in species richness between cross-validation methods

At the species level, regarding the habitat suitability predictions under present conditions, the spatial cross-validation ($3\,446\,035 \pm 3\,013\,058 \text{ km}^2$) predicted a significantly larger size of suitable ranges for goatfish species than that of

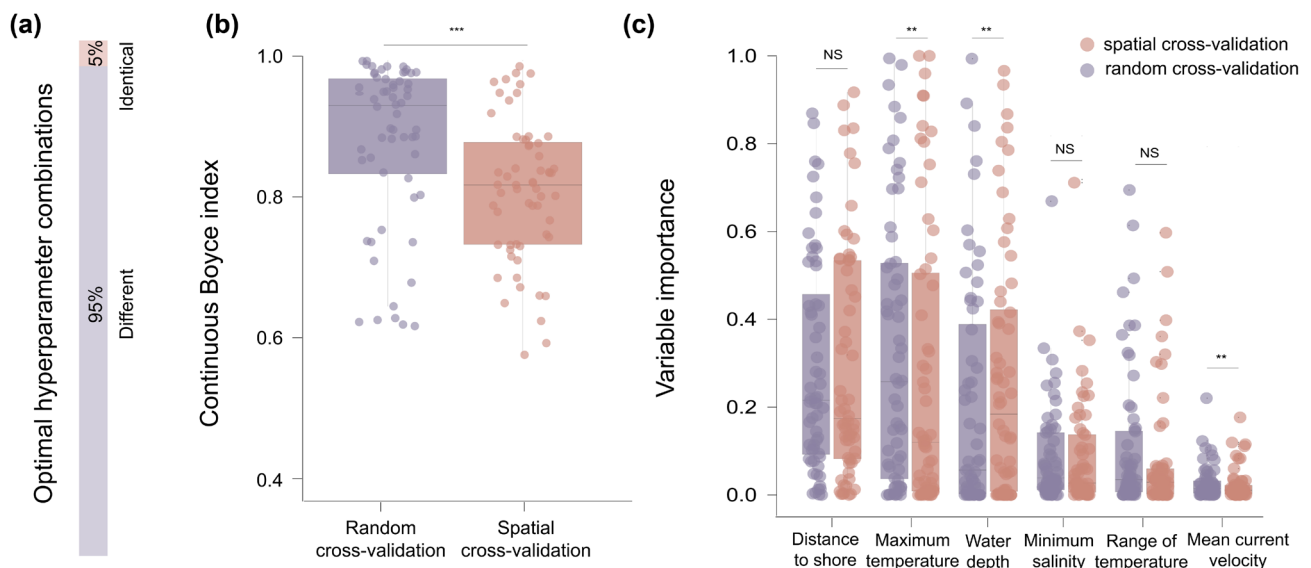


Figure 2. Discrimination abilities and variable importance of species distribution models based on random and spatial cross-validation methods. (a) Comparison of optimal parameters of MaxEnt derived from these two cross-validation methods. (b) Continuous Boyce index of these two cross-validation methods. (c) Variable importance of goatfishes derived from these two cross-validation methods. NS indicates no significant difference between these two cross-validation methods ($p > 0.05$), the asterisk (**) indicates $p < 0.01$, and asterisk (***) indicates $p < 0.001$.

the random cross-validation ($3\,147\,383 \pm 2\,763\,449\text{ km}^2$) (two-sided paired Wilcoxon signed rank test, $V=450$, $p < 0.01$; Supporting information).

Species richness patterns predicted by these two types of cross-validation methods were highly correlated ($r=0.951$, $p < 0.001$) (Supporting information); in addition, both cross-validation methods consistently suggest that the Indo-Australian Archipelago region should be the hotspot of goatfish richness (Fig. 3a–b). Despite the high level of correlation between species richness predicted by these two cross-validation methods, approximately 15.0% of study regions have different species richness values, and the percentage would increase to 53.6% if we removed from the comparison those regions that are predicted to have

zero species richness according to both cross-validation approaches (Fig. 3c).

The projected changes in the richness of goatfish showed similar trends across future scenarios (Fig. 4, Supporting information). We showed the projections under RCP 8.5 in 2040–2050 as an illustration. Compared with present-day baseline species richness, both cross-validation approaches projected that the central Indo-Australian Archipelago and the Red Sea will possibly experience a decline in species richness of goatfish in the future, whereas the southern Australian coastal waters might serve as refuges for goatfish against climate change (Fig. 4). Regarding the range size change of goatfishes under RCP 8.5 in 2040–2050, under no dispersal scenario, the random cross-validation approach

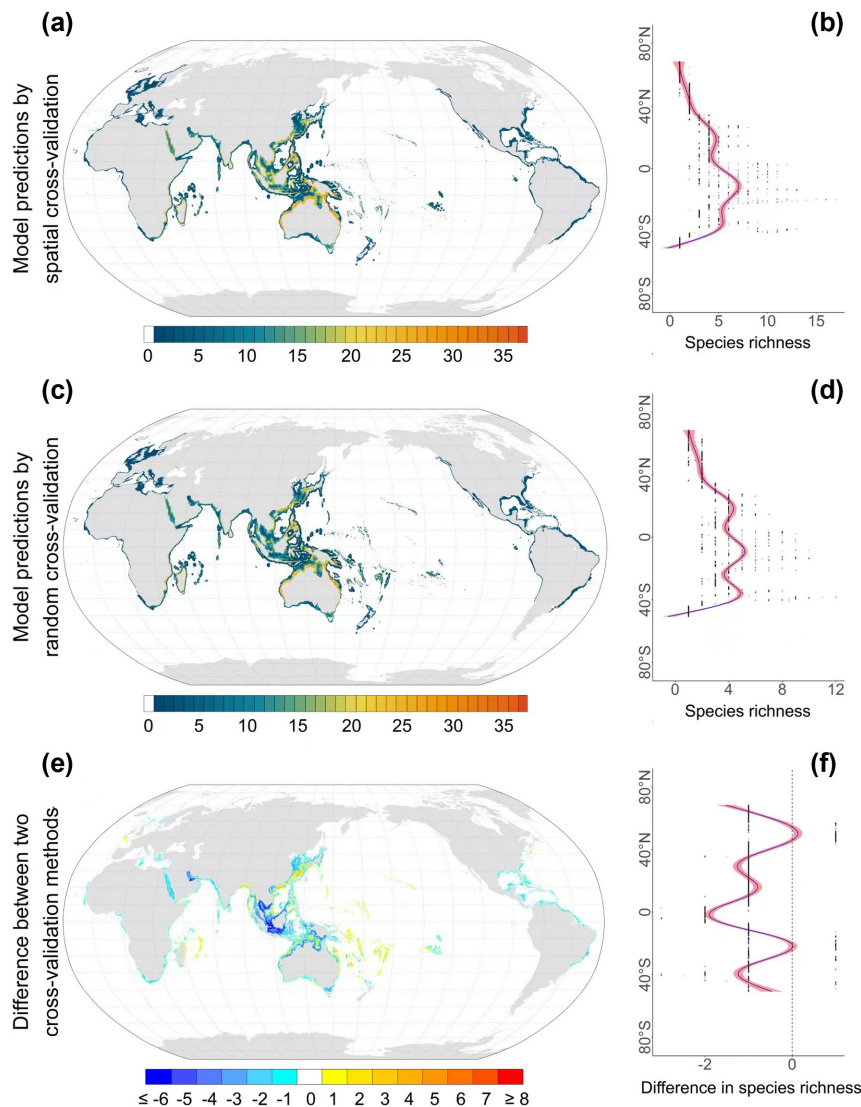


Figure 3. Spatial and latitudinal richness patterns of goatfish predicted by species distribution models based on random and spatial cross-validation under the present climate scenario. (a–b) Spatial and latitudinal richness pattern predicted by spatial cross-validation method. (c–d) Spatial and latitudinal richness pattern predicted by random cross-validation method. (e–f) Differences in species richness predicted by these two cross-validation methods (random–spatial). In panels (b), (d), and (f), the purple lines are fitted by generalized additive model and the red shaded areas represent the corresponding 95% confidence interval.

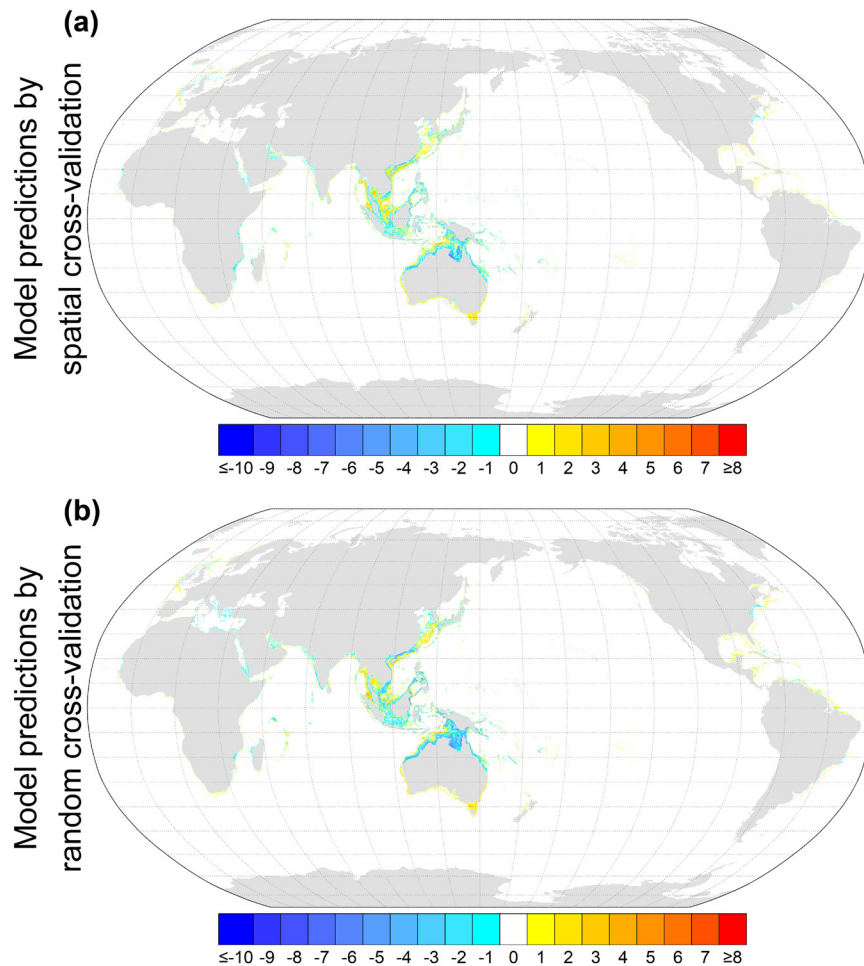


Figure 4. Projected changes in goatfish richness by species distribution models based on random and spatial cross-validation under RCP 8.5 in 2040–2050. (a) Changes in goatfish richness pattern projected by spatial cross-validation. (b) Changes in goatfish richness pattern projected by random cross-validation. Warm colors indicate increment in species richness in the future and cool colors suggest decrement. See Supporting information for other RCP and time period combinations.

($-6.0 \pm 8.7\%$) projected significantly more adverse impacts of climate change than that of the spatial cross-validation ($-5.7 \pm 10.1\%$) (two-sided paired Wilcoxon signed rank test, $V=1083$, $p < 0.01$, Supporting information). Under the unlimited dispersal scenario, no significant difference in range size change was detected between the random ($-1.4 \pm 10.9\%$) and spatial ($-1.9 \pm 12.0\%$) cross-validation approaches (two-sided paired Wilcoxon signed rank test, $V=717$, $p=0.386$; Supporting information). Results based on RCP 2.6 and/or the time period 2090–2100 are similar to the previously described RCP 8.5 \times 2040–2050 combination.

Discussion

In this study, using goatfish as a test case, we explored the effects of the choice of cross-validation approach on biodiversity predictions based on SDMs. Random and spatial cross-validation approaches yielded comparable discrimination capacities and variable importance, but they resulted in

different model optimal parameterization and different spatial distribution predictions. This suggests that we should pay due attention to the selection of cross-validation approaches.

Cross-validation: an overlooked uncertainty in biodiversity assessments

When developing an SDM, users have to make a number of subjective choices, such as on modeling algorithm(s) (Araújo and New 2007, Thuiller et al. 2019, Hao et al. 2020) and predictors (Guisan et al. 2007, Bede-Fazekas and Somodi 2020). These choices strongly influence model predictions (Araújo and New 2007, Thuiller et al. 2019). For instance, Thuiller et al. (2019) quantified the uncertainties in future biodiversity projections for 11 495 species and found that the choice of modeling algorithm represents the critical source of variability. However, the effect of cross-validation has been largely overlooked and received relatively little research attention, which is true in both terrestrial and marine realms (Guillaumot et al. 2019). Our results indicate

that the choice of cross-validation approaches has great effects on hyperparameter optimization of modeling algorithms and habitat suitability predictions of target species, which strongly highlight the uncertainties associated with selecting cross-validation strategies. On the basis of our findings, we encourage researchers to repeat their modeling using an alternative cross-validation approach to measure the uncertainty of model predictions associated with the choice of cross-validation technique.

SDMs are often extrapolated through space (e.g. invasion biology; Liu et al. 2020, Nguyen et al. 2022) or time (Qiao et al. 2019, Santini et al. 2021) or both. Extrapolation makes the predictions prone to uncertainty (Elith et al. 2010, Mesgaran et al. 2014), which is generally hidden if the model's goodness-of-fit is evaluated (Dormann et al. 2013). The literature provides several alternative solutions to overcome this transferability issue, mainly by preventing overfitting and promoting the training of parsimonious and generalizable models (Werkowska et al. 2017, Qiao et al. 2019, Rousseau and Betts 2022, Ludwig et al. 2023). One of these approaches is spatial block cross-validation and spatial block-based training-evaluation dataset separation (Roberts et al. 2017, Valavi et al. 2019, Valavi et al. 2023). These methods typically result in SDMs with lower goodness-of-fit in exchange for better transferability (Valavi et al. 2023). Our case study of goatfishes confirmed this finding, which showed that the goodness-of-fit of spatially cross-validated models was significantly lower than those with random cross-validation. Our results highlighted previous warnings (Bede-Fazekas and Somodi 2020) on the hidden impact of the modeler's decisions if the SDMs are evaluated based only on the goodness-of-fit measures and the visual check (interpretability) of reference predictions. Despite the fact that random cross-validation approach resulted in better predictive performance than corresponding spatial cross-validation, it remains unclear which method results in overfitted or transferable models. Therefore, apart from model performance, we encourage researchers to quantify the overfitting/transferability difference between the two cross-validation approaches by applying, for example, AUC drop (Warren and Seifert 2011) or consistency measures (Somodi et al. 2024). We note, however, that independent evaluation data are required for a reliable overfitting/transferability assessment (Araújo et al. 2005, Radosavljevic and Anderson 2014), which was not available for our study.

We acknowledge that our study represents a preliminary study on the importance of the choice of cross-validation in SDMs, and future studies would be required to explore this issue further. For instance, we focused on one representative spatial blocking strategy. However, there are different methods to split distribution data into spatial folds, such as those based on latitudinal, longitudinal, or spatial blocks (details in Valavi et al. 2019). In addition, from our results, it is impossible to provide practical recommendations on selecting suitable cross-validation approaches. We encourage researchers to explore further the drivers (e.g. sample size, environmental variability, and distributional range) of differences between different cross-validation methods using the virtual species

approach (Leroy et al. 2016, Meynard et al. 2019), which hopefully will establish detailed guidelines for cross-validation selection. Moreover, different strategies have been proposed to control sampling bias in SDMs (Fithian et al. 2015, Sorbe et al. 2023). Whether the methods accounting for the sampling bias affect our findings on the cross-validation methods requires further research. In this study, we constructed SDMs using species occurrence records. Apart from opportunistic occurrences, expert range maps (Fourcade 2016, Thuiller et al. 2019) or integration of opportunistic occurrences and expert range maps (Domisch et al. 2016) have also been commonly used in SDM studies. The sensitivity of our findings to the choices of distribution data deserves further investigation.

Implications for marine conservation

Despite the differences in biodiversity predictions of goatfishes between the two types of cross-validation methods, both approaches consistently suggest that temperature is the critical predictor in determining the geographical distributions of goatfishes, and in response to climate change, goatfishes will possibly experience future range contraction irrespective of dispersal scenarios. This finding highlights the vulnerability of goatfishes to climate change. Empirical evidence shows that goatfishes are sensitive to changes in temperature and rapidly alter their distributional ranges to keep pace with changing environments (reviewed by Uiblein 2007). For instance, with increasing temperature, the striped red mullet *Mullus surmuletus* has shifted its distributional range northward (Uiblein and Heemstra 2011).

During foraging, goatfishes actively use their barbels and mouths to search for foods in the bottom sediments, which results in the uplifting of organic materials, thus attracting multiple species following goatfishes (Sazima et al. 2007, Uiblein 2007). Given the important role of goatfishes in food webs, we anticipate that the projected change in potential distribution of goatfishes under climate change might have cascading effects on associated follower fishes.

According to our model projections, goatfishes in regions like the Sunda Shelf and the Coral Triangle are projected to be extremely vulnerable to climate change. Our finding coincides with previous model predictions (Cheung et al. 2009, García Molinos et al. 2016). For instance, García Molinos et al. (2016) projected possible changes in richness patterns of marine species and highlighted the large biodiversity loss under climate change in the Coral Triangle and neighboring regions. The great sensitivity of marine species in the Sunda Shelf and the Coral Triangle to climate change might be accounted for by the rapid velocity of climate change therein (García Molinos et al. 2016). Our findings, together with previous evidence, suggests that climate change should be considered in conserving marine biodiversity and the regions like the Sunda Shelf and the Coral Triangle should have high conservation priority, especially given that financial resources for biodiversity conservation are always insufficient (Johnson et al. 2017, Xu et al. 2021).

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Author contributions

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Data availability statement

Species distribution data and R scripts are available in the Figshare Repository (<https://figshare.com/s/4f47e826f2ab0a2221cd>).

Data are available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.rr4xgxdhf> (Huang et al. 2024).

Supporting information

The Supporting information associated with this article is available with the online version.

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