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# Misconception of model transferability precludes estimates of seagrass community reorganization in a changing climate

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ARISING FROM B. H. Daru and B. M. Rock *Nature Plants* https://doi.org/10.1038/s41477-023-01445-6 (2023)

Daru and Rock[1] used species distribution modelling (SDM) to project widespread reductions in seagrass species' range sizes and increased endemism under end-of-century climate change. These shifts in alpha diversity were found to be similar across four Representative Concentration Pathway (RCP) scenarios. Global beta-diversity patterns would become more heterogeneous. From their models, Daru and Rock conclude that the redistribution of seagrasses would cause present-day marine protected areas to be ineffective, calling for the prioritization of new conservation areas. However, conceptual and methodological shortfalls in their implementation of SDM undermine accurate estimates of seagrass community reorganization in a changing climate.

SDM[2] is a statistical approach aimed at providing insights into the ecological requirements of species and projecting their distributions across space and time. Model transferability is a fundamental and transversal principle in statistical modelling, which refers to the ability of a model to accurately predict beyond the data it was originally trained on, often involving extrapolation[3,4]. In SDM, elementary statistical protocols for model transferability[2,5,6] involve developing a model fitting observed species occurrence data against relevant climate variables for the corresponding period. To project changes in distribution, the same model is then applied directly to new climate data representing scenarios of future climate conditions. This approach ensures that the model captures the species' ecological relationships with climate variables and that it produces projections of future distributions that are comparable with predictions made for the baseline. Daru and Rock[1] misconceived the principle of model transferability when estimating seagrass community reorganization in a changing climate. Daru and Rock correctly developed models fitting seagrass occurrence records against present-day climate data. However, they did not apply these models to future RCP climate data. Instead, they developed entirely new models, attempting to explain present-day seagrass distributions with climate conditions from the future. Their models consequently do not capture the effect of climate change on the distribution of seagrasses, which is highly concerning when results are used to guide critical conservation decisions regarding marine protected areas. Their shortfall is evident in the code provided by Daru and Rock in the paper's supplementary information[1], where they use the sdm function of the R package phyloregion, which is not designed for transferability. Their incorrect implementation of SDM resulted in minor distribution changes under future climates and little sensitivity to different emission scenarios, which is highly unexpected.

To demonstrate the consequences of Daru and Rock's[1] conceptual and methodological shortfalls, we developed SDM for the same species (Fig. 1) using their original set of predictor variables (Bio-ORACLE v.2.0 (ref. 7): long-term average and range of temperature, salinity and current velocity, for both surface and benthic realms). We adapted their code[1] by critically modifying the sdm function for model transferability and adding extensive comments for clarity. We further enhanced the transferability potential of the model by implementing key decision steps regarding input data and parameter settings[8]. Daru and Rock modelled and projected seagrasses across whole exclusive economic zones, which may extend up to 200 nautical miles offshore into areas of thousands of metres of depth where seagrass does not occur. We therefore restricted model fitting to coastal regions with a maximum depth of 30 m to bring realism to the model, as this accounts for the light-dependent nature and typical depth distribution of seagrass communities[9]. Additionally, the MaxEnt algorithm used by Daru and Rock can build very complex, nonlinear species–climate relationships highly prone to overfitting—that is, models that are too complex and fit noise or data idiosyncrasies rather than capturing the general underlying patterns[10,11]. To overcome this, we removed highly correlated predictor variables (specifically, average sea surface and benthic current velocity, and average sea surface salinity

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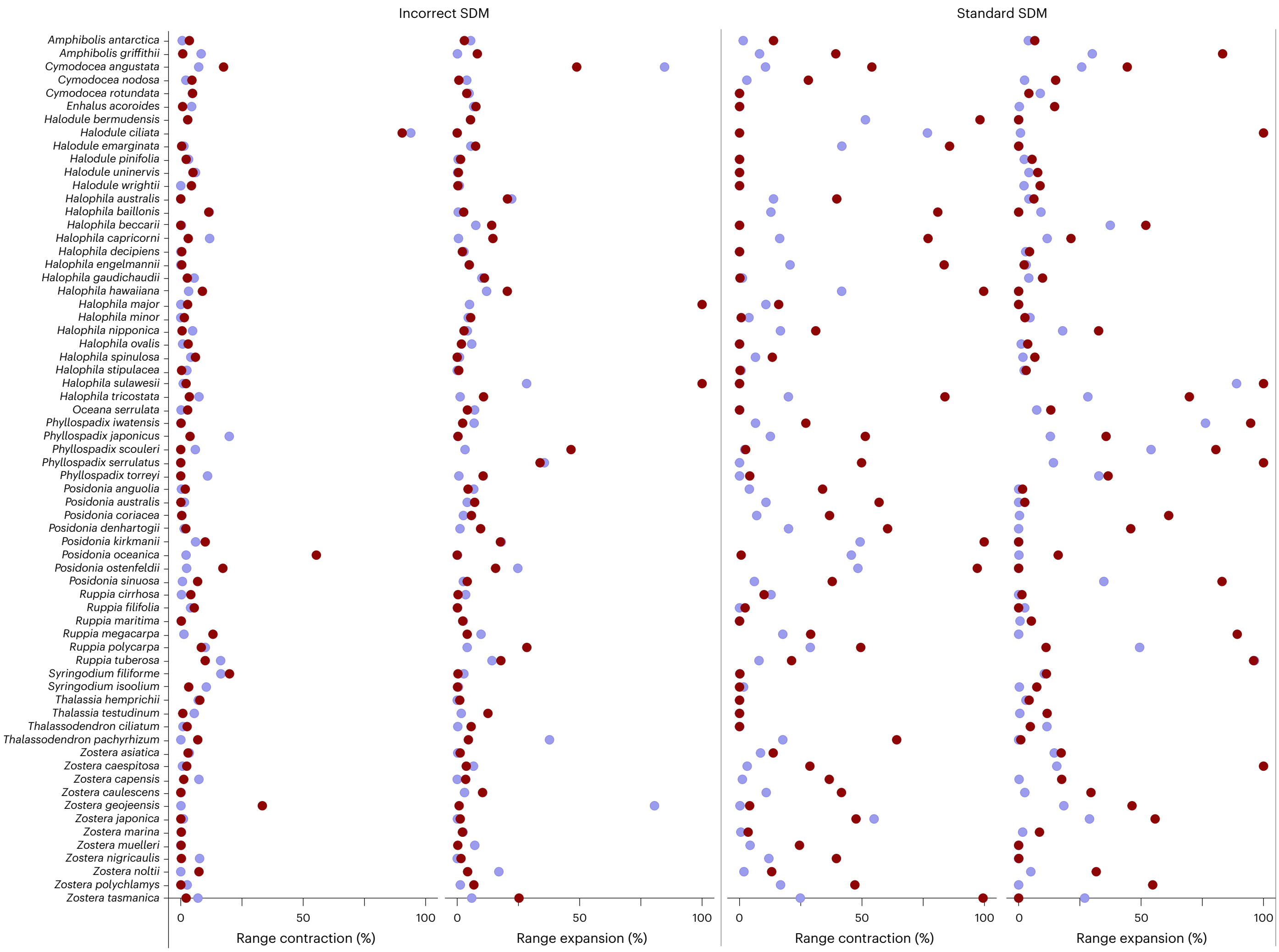


**Fig. 1 | Seagrass species range contraction and expansion projected using incorrect and standard SDM approaches.** Seagrass species range contraction and expansion under the most contrasting end-of-century RCP scenarios of climate change projected with the incorrect SDM approach[1] and a standard SDM version with proper integration of model transferability and decision steps regarding input data and parameter settings. The red circles depict changes under RCP 8.5 (highest emissions), and the blue circles depict changes under RCP 2.6 (lowest emissions).

(variance inflation factor > 5)), considered simple response functions (linear, threshold and hinge) and carefully tuned regularization with L1-penalization by testing a set of beta multiplier parameter values (2, 5, 10, 15 and 20) under a fivefold cross-validation framework[10,11]. We executed the code until the climate change projection stage, the critical step where Daru and Rock[1] deviated from established statistical protocols. We compared the incorrect SDM approach[1] with the standard SDM version considering proper implementation of model transferability and well-established practices, focusing on species-by-species range shifts and species richness estimates projected for the most contrasting end-of-century RCP scenarios of climate change (RCPs 8.5 and 2.6, representing the highest and lowest emissions, respectively)[1].

The two modelling approaches yield fundamentally different results. The incorrect SDM approach[1] failed to project the expected differences in species distribution ranges under the most contrasting RCP scenarios (Fig. 1). The inappropriate model transferability resulted in near-identical projections: average range expansions of 8.23% and 10.59% and contractions of 5.19% and 6.32% under the two RCP scenarios. These projections contrast with the standard SDM approach results, which align with expectations: increased expansion (from 12.42% to 26.98%) and contraction (from 12.07% to 30.01%) rates correlate with higher emissions. This difference in range change between RCP scenarios is in line with numerous SDM applications for different marine taxa[12], including seagrasses[9], and is supported by the temperature anomalies estimated in the climate models used, varying up to 4.45 °C and 10.98 °C, depending on the scenario[7,13]. Accordingly, the incorrect SDM approach projected minimal geographic range changes in species richness between scenarios, and without a clear latitudinal pattern, which is unexpected for marine range shifts[14]. Notably, changes were evident only in offshore regions, along the borders of exclusive economic zones, where seagrasses do not occur (Fig. 2). A latitudinal pattern, however, was clear in the standard SDM approach, which projected generalized poleward range shifts coupled with losses at lower latitudes, depending on the RCP scenario (Fig. 2). Such range-shifting patterns are consistent with observations from recent decades[14] and projections elsewhere[9,15]. The outcomes of the incorrect SDM approach[1] deviated even from present-day distributions, as shown in their predicted range maps. The models failed to realistically map geographic patterns of seagrasses, overpredicting distributions across whole exclusive economic zones (Fig. 2) and down to a maximum predicted depth of 6,396 m, in contrast with the 30 m constraint imposed in the standard version.

In summary, by misinterpreting the concept of model transferability and not considering well-established standards of SDM, Daru and Rock[1] developed inaccurate and misleading projections of seagrass species richness changes under end-of-century RCP scenarios.

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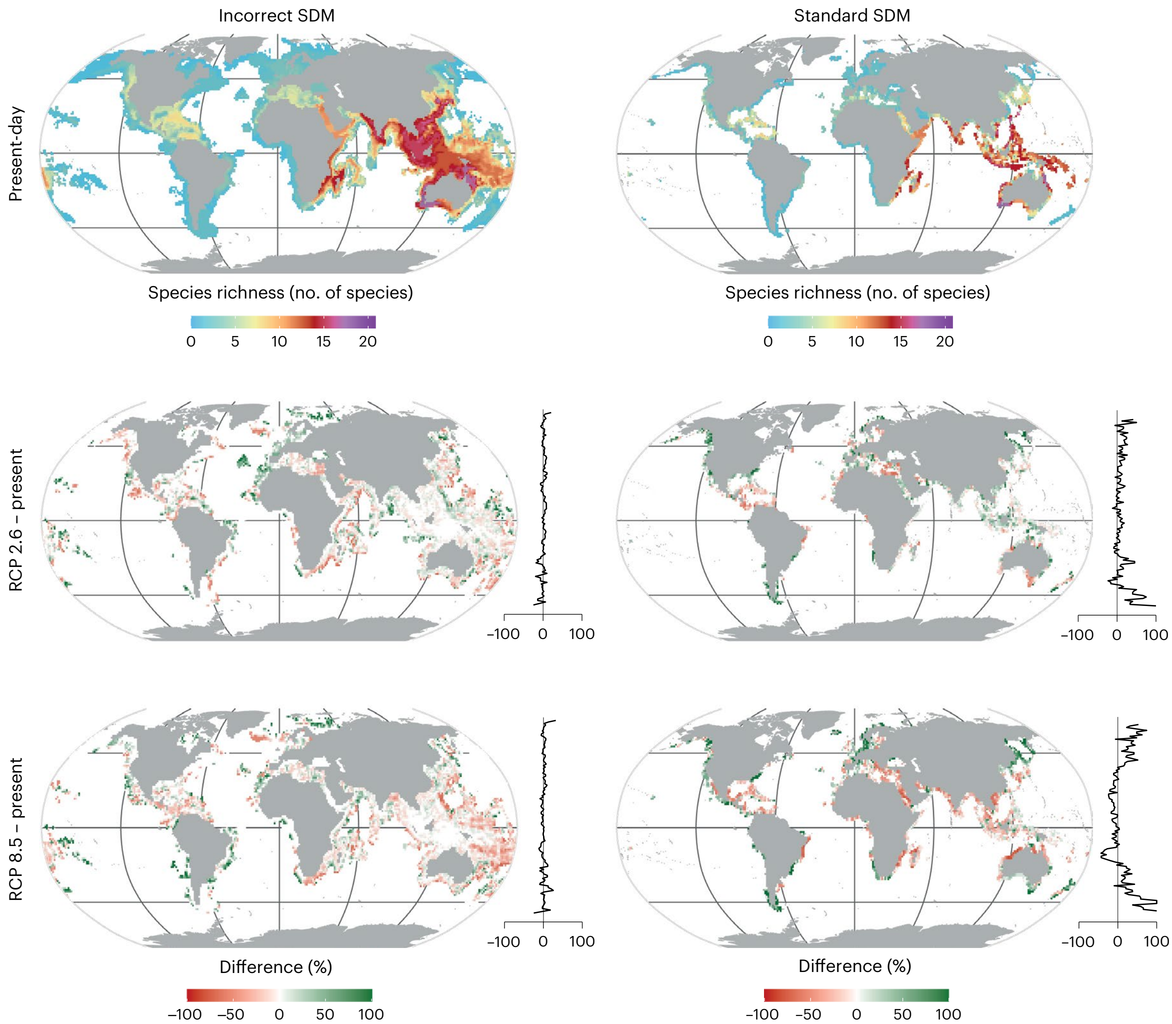


**Fig. 2 | Geographic patterns of seagrass species richness projected using incorrect and standard SDM approaches.** Geographic patterns of seagrass species richness predicted for present-day conditions and projected under the most contrasting end-of-century RCP (8.5 and 2.6 for the highest and lowest emissions, respectively) scenarios of climate change with the incorrect SDM approach[1] and a standard SDM version with proper integration of model transferability and decision steps regarding input data and parameter settings. Positive values in RCP projections indicate increasing seagrass species richness, and negative values indicate decreasing species richness. The latitudinal plots depict the average change in species richness across 1° latitudinal bins.

These flawed estimates propagated into additional analyses focused on endemism (weighted and phylogenetic) and beta-diversity patterns, thereby providing a biased overall view of seagrass community reorganization in a changing climate. By reproducing the study of Daru and Rock[1] to assess the consequences of their methodological errors, we demonstrate the consequences of conceptual and methodological shortfalls, invalidating the major conclusions of this study and highlighting the need for a valid assessment of the consequences of climate change for seagrass species diversity across the world.

## Data availability

The layers used for SDM are openly available via Figshare at https://doi.org/10.6084/m9.figshare.23800401.v3 (ref. 16).

## Code availability

The code used for SDM is openly available via Figshare at https://doi.org/10.6084/m9.figshare.23800401.v3 (ref. 16).

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## Author contributions

J.A. and M.B.A. conceived the study. J.A., L.G., T.L. and E.F. produced the models. J.A., E.A.S. and M.B.A. wrote the paper. All authors reviewed the paper.

## Competing interests

The authors declare no competing interests.

## Additional information

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