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Intraspecific genetic variation matters when predicting seagrass distribution under climate change

Running Title: Intraspecific prediction of seagrass distribution

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Abstract

Seagrasses play a vital role in structuring coastal marine ecosystems, but their distributional range and genetic diversity have declined rapidly over the past decades. In order to improve conservation of seagrass species, it is important to predict how climate change may impact their ranges. Such predictions are typically made with correlative species distribution models (SDMs), which can estimate a species' potential distribution under present and future climatic scenarios given species' presence data and climatic predictor variables. However, these models are typically constructed with species-level data, and thus ignore intraspecific genetic variability, which can give rise to populations with adaptations to heterogeneous climatic conditions. Here, we explore the link between intraspecific adaptation and niche differentiation in *Thalassia hemprichii*, a seagrass broadly distributed in the tropical Indo-Pacific Ocean and a crucial provider of habitat for numerous marine species. By retrieving and re-analyzing microsatellite data published previously, we delimited two distinct phylogeographical lineages within the nominal species and found an intermediate level of differentiation in their multidimensional environmental niches, suggesting the possibility for local adaptation. We then compared projections of the species' habitat suitability under climate change scenarios using species-level and lineage-level SDMs. In the Central Tropical Indo-Pacific region, models for both levels predicted considerable range contraction in the future, but the lineage-level models predicted more severe habitat loss. Importantly, the two modelling approaches predicted opposite patterns of habitat change in the Western Tropical Indo-Pacific region. Our results highlight the necessity of conserving distinct populations and genetic pools to avoid regional extinction due to climate change and have important implications for guiding future management of seagrasses.

Keywords: climate change scenario, genetic lineage, niche conservation, range shift, species distribution model, *Thalassia hemprichii*

Introduction

Marine ecosystems worldwide are experiencing rapid shifts in environmental conditions due to climate change, the most evident of which is a steady increase in sea surface temperature (SST) (Cheung *et al.* 2013). These changes can affect marine organisms in different ways, such as by altering the structure of trophic webs (e.g., Hyndes *et al.* 2016), biasing sex ratios in species with temperature-dependent sex determination (e.g., Miyoshi *et al.* 2020), and redefining the geographical ranges of species (e.g., Pinsky *et al.* 2020). In order to guide natural resource management under this changing marine landscape, it is crucial to make future predictions of suitable habitat for target species as accurately as possible.

Species distribution models (SDMs), which estimate relationships between species' presence data and environmental predictors, have been used extensively to predict potential changes in species' distributions under climate change scenarios (Guisan *et al.* 2017). The majority of SDMs are constructed at the species-level or even higher taxonomic levels, and this is particularly true for applications to marine species (Robinson *et al.* 2011; Robinson *et al.* 2017; Chefaoui *et al.* 2018; Jayathilake & Costello 2018; Melo-Merino *et al.* 2020). One fundamental and critical assumption underlying species-level SDMs is niche conservatism, which assumes that all populations of a species have analogous environmental requirements and respond in a similar way to a changing environment (Guisan *et al.* 2017; Smith *et al.* 2019). But this assumption ignores intraspecific variation, in particular local adaptation and phenotypic plasticity (Pazzaglia *et al.* 2021), which are frequently observed especially in broadly distributed taxa (e.g., Marín-Guirao et al. 2016; Duarte *et al.* 2018; King *et al.* 2018; Benito Garzón *et al.* 2019; Peterson *et al.* 2019; Zhang *et al.* 2020b).

SDMs constructed with data for lineages below the species level can account for possible local adaptations and therefore can provide more reliable niche estimations and habitat suitability projections for species with high intraspecific variation. For instance, a species-level SDM for the threatened Japanese crayfish *Cambaroides japonicus* (De Haan 1841) predicted that this species might lose a large proportion of its suitable habitat in the future, whereas lineage-level SDMs for the same species predicted a weaker impact of climate change overall (Zhang *et al.* 2021). The importance of taxonomic units (i.e., above and below the species level) in distribution modelling has recently been recognized (Benito Garzón *et al.* 2019; Peterson *et al.* 2019; Smith *et al.* 2019; Collart *et al.* 2021), which has resulted in more SDM applications for terrestrial and freshwater species that consider intra-specific variation (e.g., Ikeda *et al.* 2017; Razgour *et al.* 2019; Zhang *et al.* 2021). Conversely, relatively few SDM studies have investigated this issue in the marine realm (but see Assis *et al.* 2018a; Cacciapaglia & van Woesik 2018; Lowen *et al.* 2019).

Seagrasses are one of the most critical habitat engineers of tropical coastal marine environments. They not only harbor rich marine biodiversity in seagrass meadows, but also provide a number of ecosystem services, such as primary productivity, habitat restoration, resources for marine life, and human recreation (Unsworth *et al.* 2018). Maintaining these services is key to achieving conservation and economic goals under global change. Yet, seagrass ecosystems are declining worldwide at an annual rate of 7% due to multiple natural and human-mediated disturbances (Orth *et al.* 2006; Waycott *et al.* 2009). It is noteworthy that climate change has received considerable attention as a major factor for the increasing loss of seagrass meadows (Jordà *et al.* 2012; Thomson *et al.* 2015; Repolho *et al.* 2017; Duarte *et al.* 2018; Smale *et al.* 2019). This is particularly true for the tropical Indo-Pacific bioregion, which supports the most seagrass diversity and a high diversity of associated flora and fauna (Short *et al.* 2007) but has suffered from striking degradation of seagrass coverage (Coles *et al.* 2011; Rasheed & Unsworth 2011; Grech *et al.* 2012; Chefaoui *et al.* 2018; Olsen *et al.* 2018; Brodie *et al.* 2020). Given the global ecological roles of seagrasses, it is imperative to make accurate forecasts of their distribution patterns in the face of climate change, but seagrasses are “among the least-studied groups” (Melo-Merino *et al.* 2020) with respect to range shift projections. The majority (if not all) of SDM studies on seagrasses have been at the species level and therefore did not incorporate potential intraspecific variation.

The seagrass *Thalassia hemprichii* (Ehrenberg) Ascherson (Hydrocharitaceae) is a perennial climax species that is widely distributed in the tropical Indo-Pacific bioregion (Green & Short 2003), extending from Australia, the peripheral limit of its eastern range (Hernawan *et al.* 2017), to East Africa in the West Indian Ocean (Jahnke *et al.* 2019a). It reproduces sexually via seeds and asexually via vegetative growth of rhizomes. Uprooted adult plants can potentially float for months and hence colonize distant areas (Wu *et al.* 2016). In addition, this seagrass forms buoyant seeds that remain afloat for long enough to disperse a few hundreds of kilometers (Lacap *et al.* 2002). A recent survey revealed that seedlings can also disperse for over a month due to the accumulation of oxygen in the body tissue (Wu *et al.* 2016). Thus, *T. hemprichii* has excellent long-distance dispersal potential that may play a significant role in shaping population genetic structure (Lowe & Allendorf 2010). This species may be particularly vulnerable to climate change because it exhibits spatial separation of the sexes (dioecious), reinforced by physiological and morphological differentiation of each sex to variable microhabitats (Hultine *et al.* 2016). Recent genetic studies of *T. hemprichii* detected genetic lineage divisions in the East and West Indo-Pacific Ocean (Hernawan *et al.* 2017; Jahnke *et al.* 2019a), but we still do not have a clear understanding of the distribution of lineages across the entire tropical Indo-Pacific region, or whether these diverged lineages are expected to respond differentially to climate change.

In the present study, we used *T. hemprichii* as a model to: (i) examine divergence of genetic lineages in the tropical Indo-Pacific Ocean; (ii) test if phylogeographical lineages exist, and if so, quantify niche differentiation between distinct lineages; (iii) predict climate change impacts on the species' range with species-level and lineage-level SDMs. By incorporating potential intraspecific variation, our SDMs can provide more realistic predictions on how climate change will shift future distributions of a habitat-forming seagrass, thus generating valuable knowledge for guiding the long-term management of this species in the tropical Indo-Pacific coast.

Materials and methods

Datasets and intraspecific genetic clustering

We retrieved and compiled molecular datasets of two recently published regional studies of *T. hemprichii*, i.e., 17 populations in the East Indo-Pacific (Hernawan *et al.* 2017) and 11 populations in the Western Indian Ocean (Jahnke *et al.* 2019a). We used twelve microsatellites (i.e., Thh3, Thh15, Thh34, Thh41, TH07, TH34, TH37, TH43, TH52, TH66, TH73) for population structuring and lineage sorting of 1021 individuals from 28 populations across the tropical Indo-Pacific (Fig. 1a). We then estimated pairwise genetic differences among populations using the Cavalli-Sforza and Edwards chord distance and represented them in a network using the R package IGRAPH (Csardi & Nepusz 2006) with the addition of a custom script by Johansson *et al.* (2015). To visually inspect the relationships within and between the main genetic clusters inferred by STRUCTURE (Pritchard *et al.* 2000), we pruned the full network by sequentially removing edges (i.e., network pairwise links among sampling sites) of decreasing genetic distance until the point at which the main groups of tightly connected nodes still remained connected (in order to avoid the split of any large network cluster from the main network). We estimated the classification of sampling sites within network communities at each step of the pruning process with the “fastgreedy” community detection algorithm implemented in IGRAPH (Clauset *et al.* 2004, Blondel *et al.* 2008). Network analysis (Fig. 1b), Bayesian-based STRUCTURE (Fig. 1c), and molecular variation (AMOVA) (Supporting Information Table S1) revealed strong overall genetic differentiation among two distinct lineages occupying the Tropical Indo-Pacific. Based on the landscape genetic analysis of Cushman *et al.* (2014) and the definitions of global marine ecoregions (Spalding *et al.* 2007), we classified these two lineages as distinct genotypes encompassed within two biogeographic regions: the Western Tropical Indo-Pacific (WTIP) and the Central Tropical Indo-Pacific (CTIP). We then used the two lineages in subsequent ecological niche modelling.

Distribution data and marine predictors

We collected a total of 62,465 presence records of *T. hemprichii* from a recently assembled and cleaned dataset of global marine forests (Assis *et al.* 2020) and published literature (see Data availability). In SDM studies, it is critical to correct for sampling bias and remove clustered records, which may over-represent environmental conditions in better-surveyed regions (Kramer-Schadt *et al.* 2013). Therefore, presence records were filtered by: i) removing duplicated records at the resolution of our environmental predictors (i.e., keeping only one record per 5 arcmin grid cell); ii) removing records on land or with distance to land > 370 km (following other SDM studies for coastal species; e.g., Zhang *et al.* 2020a), and iii) performing spatial thinning using a distance of 20 km using the R package *spThin* (Aiello-Lammens *et al.* 2015). This distance is a reasonable approximation of the dispersal potential for this plant traveling via floating propagules (Lacap *et al.* 2002), and it can also reduce potential effects of sampling bias while retaining sufficient numbers of presence records for our analyses. As significant clustering was present in the data (particularly around Australia), these procedures removed a large proportion (up to 99%) of the presence data. Ultimately, we kept 519 records for the species-level model (hereafter "species model", records from the entire region), 479 records for the CTIP lineage-level model (hereafter "CTIP model", records within CTIP region only), and 26 records for the WTIP lineage-level model (hereafter "WTIP model", records within WTIP region only) (Fig. 1a).

It is important to properly select the extent of the study area used to sample background records when constructing presence-background SDMs for target species (Barve *et al.* 2011; Vale *et al.* 2014). For coastal marine species, it is common practice to develop SDMs within the Exclusive Economic Zone (i.e., within 370 km from the coast) (e.g., Lins *et al.* 2018; Stephenson *et al.* 2020; Zhang *et al.* 2020a). Besides, given the distributional range and records of *T. hemprichii* from online repositories and literature (Fig. 1a), we restricted our study to the areas within 370 km of land between 25°E and 180°E, and between 50°S and 40°N. Please note that our study extent includes southern Australia and New Zealand, where this species does not naturally occur. It is always challenging to estimate an appropriate study extent for a species (Barve *et al.* 2011), but the extent we selected should represent the plausible accessible areas to *T. hemprichii* over evolutionary time. We subsetted this main study extent to create separate study extents for the WTIP and CTIP lineages (Fig. 1a) based on our molecular results (see details in the Lineage genetic diversity in the Results section).

A number of marine predictors have been demonstrated to influence the geographical distribution of marine species (Bosch *et al.* 2018). Based on previous studies (including seagrasses; e.g., Jayathilake & Costello 2018; Zhang *et al.* 2020a), we initially considered twenty such predictors for modeling, including two geographical predictors (water depth and distance to land) from the Global Marine Environment Datasets (http://gmed.auckland.ac.nz; Basher *et al.* 2018) and eighteen environmental predictors (including annual mean, maximum, minimum, range, average of the minimum records per year, and average of the maximum records per year) for SST, sea surface salinity, and sea surface current velocity from the Bio-ORACLE database v2.1 (https://www.bio-oracle.org; Assis *et al.* 2018b). In SDM studies, highly collinear predictors can lead to spurious interpretations of variable importance and unexpected predictions if correlations change in different projection scenarios (Dormann *et al.* 2013). Hence, we checked collinearity by calculating the pairwise Pearson's correlation coefficients (r) among the twenty predictors (Supporting Information Fig. S1) and selected one among highly correlated predictors ($|r| > 0.7$) (Dormann *et al.* 2013) based on present-day and future data availability, biological importance, and previous findings on important variables for estimating seagrass distribution (Jayathilake & Costello 2018). In the end, we retained the two geographical predictors and six environmental predictors: annual mean current velocity, minimum current velocity, annual mean sea surface salinity, annual range of sea surface salinity, annual mean SST, and annual range of SST.

To project future habitat suitability of *T. hemprichii*, we considered four representative concentration pathway (RCP) scenarios (i.e., RCP 2.6, RCP 4.5, RCP 6.0, and RCP 8.5), and two time periods (i.e., 2050s: the average for 2040–2050s, and 2100s: the average for 2090–2100). We obtained the corresponding projections of future marine environmental layers from the Bio-ORACLE database v2.1. We assumed that the two geographical predictors would remain unchanged for future projections (Zhang *et al.* 2020a).

Niche differentiation estimation

To estimate whether the two lineages of *T. hemprichii* occupy different niche spaces, we characterized their realized niches using Hutchinsonian *n*-dimensional hypervolumes (Hutchinson 1957) *sensu* Blonder *et al.* (2018). We quantified the realized niches of the WTIP and CTIP lineages using the eight selected marine predictor variables (see previous section). In short, we extracted and standardized (i.e., zero means and unit variance) marine predictor values associated with the presence records for the two lineages. We then determined the volumes and shapes of the realized niches with the R package *hypervolume* using the Gaussian method (Blonder 2019). We measured the extent of niche differentiation between the two lineages with the *kernel.beta* function (Mammola & Cardoso 2020) in the R package *BAT* (Cardoso *et al.* 2015, 2020). Following Carvalho & Cardoso (2020), niche differentiation between hypervolumes was partitioned into the following two processes: niche shift (replacement of space between hypervolumes) and niche contraction/expansion (net difference between hypervolumes). The niche differentiation index ranges from 0 (niches overlap entirely) to 1 (niches are fully dissimilar) (Carvalho & Cardoso 2020; Mammola & Cardoso 2020). In addition, to ascertain whether the realized niches of the two lineages were still different after considering the environmental space available, we conducted a niche similarity test (Broennimann *et al.* 2012) using the R package *ecospat* (Di Cola *et al.* 2017). This test compares the empirical realized environmental niche of CTIP with random niches permuted for WTIP over its available environmental space.

Species distribution modelling

We built SDMs using Maxent 3.4.4, a presence-background machine learning algorithm with two main complexity tuning parameters: regularization multiplier, which penalizes complexity by removing predictors with low predictive ability, and feature class, which allows for increasing complexity of the model response (Phillips *et al.* 2017). For each model (species model, WTIP model, and CTIP model), we randomly generated 10,000 background points within the corresponding study region. As Maxent's default settings for the main tuning parameters can result in overfit models (Radosavljevic & Anderson 2014), we used a version of the R package *ENMeval* under expansion (1.9.0; https://github.com/jamiemkass/ENMeval) to tune our Maxent models over ranges of each parameter and chose models with optimal complexity based on performance metrics calculated on withheld data (Muscarella *et al.* 2014). In brief, we considered a total of 32 candidate models with different combinations of regularization multipliers (RM; ranging from 0.5 to 4.0, at 0.5 interval), which penalize complexity more with higher values, and feature classes (linear, quadratic, hinge), which allow responses with differing flexibility. Rather than using conventional random cross-validation to judge model performance, we used a spatial block cross-validation approach, which typically results in evaluations that better reflect the model's ability to transfer to non-analog conditions (Roberts *et al.* 2017; Valavi *et al.* 2019). Briefly, each study region was divided into four spatial blocks containing an equal number of presence records, three blocks were used for model training and the remaining block for validation, then this procedure was repeated until every block was used for model validation. As with previous studies (e.g., Radosavljevic & Anderson 2014; Kass *et al.* 2020), the optimal model was selected by sequentially considering a 10% omission rate (i.e., the percentage of validation presences with habitat suitability predictions lower than that of the 10th quantile of training predictions), followed by the area under the receiver operating characteristics curve (AUC) calculated on the validation data (i.e., the model's ability to discriminate between presence and background records) to break ties. We acknowledge that AUC is a poor measure for the absolute performance of presence-background models (e.g., Jiménez-Valverde 2012), but nonetheless this metric can be used to make relative comparisons of candidate models fitted with the same data (Lobo *et al.* 2008).

Predictive performances of the three best-performing Maxent models were further assessed using the continuous Boyce index, a reliable evaluation measure of presence-only algorithms (Hirzel *et al.* 2006). The continuous Boyce index ranges from −1 to 1, where positive values suggest that model predictions match well with the presence data, and negative values suggest a poor match (Hirzel *et al.* 2006). Variable importance for each model was determined using permutation importance calculated by Maxent. For this method, presence and background data values for each predictor variable in turn were randomly permuted and training AUC recalculated—a large drop in AUC indicates higher importance (Phillips 2017). In addition, we estimated the marginal response curves of important predictors (i.e., curves representing habitat suitability along a range of the values of one predictor variable while keeping the other predictors constant). We converted continuous habitat suitability predictions for *T. hemprichii* to binary values using the same 10% omission thresholds that we used for model evaluation (Radosavljevic & Anderson 2014). We then transformed the binary habitat suitability projections to the Lambert Cylindrical Equal Area projection at a resolution of 10 km and calculated areas of potential distribution (Zhang *et al.* 2020a).

It is of great importance to consider species dispersal ability into SDMs when estimating climate change impacts (Araújo *et al.* 2006; Guisan *et al.* 2017). Given that species move across trans-regional across barriers in marine environments (Robinson *et al.* 2011; Pearman *et al.* 2020), and the relatively high dispersal ability of *T. hemprichii* (Lacap *et al.* 2002), we estimated range size change under an unlimited dispersal scenario, which assumes that species have unrestricted dispersal ability and can disperse to any suitable area (Araújo *et al.* 2006; Zhang *et al.* 2020c). Range size change was calculated as follows:

$$\text{range size change} = \frac{futuresuitablearea - presentsuitablearea}{presentsuitablearea} \times 100\%,$$

where negative and positive values represent range contraction and expansion, respectively.

We used the optimal species- and lineage-level models to make projections of future potential distribution based on the different RCP scenarios for the two future time periods. Making projections using SDMs into novel environmental space (i.e., outside the range of training data) results in some degree of extrapolations, which should be quantified to determine levels of uncertainty (Elith *et al.* 2010). Therefore, we measured the similarity between present-day and future environmental conditions using multivariate environmental similarity surfaces (MESS) (Elith *et al.* 2010). In practice, we calculated the MESS with the R package *rmaxent* (Baumgartner & Wilson 2021) for each model using the top three most important predictors via permutation importance: positive MESS values indicate conditions more similar to the training data, while negative values indicate conditions more different (i.e., novel).

Results

Lineage genetic diversity

We found significant genetic divergence between the populations of *T. hemprichii* in the Western Tropical Indo-Pacific and Central Tropical Indo-Pacific regions. The genetic data for the two lineages that we used for this analysis originated from disparate sources, and we found some minor discrepancies (see Data availability) between the two datasets after carefully inspecting the calibrated fragment lengths of the microsatellites (Hernawan *et al.* 2017; Jahnke *et al.* 2019a). Regardless, even after deleting a few microsatellites (e.g., Thh41, TH07 and TH37), two genetic lineages in *T. hemprichii* remained significantly diverged (i.e., CTIP and WTIP) across the

Tropical Indo-Pacific (Fig. 1b, 1c). Genetic variation among lineages accounted for 43.42% of the total genetic variation ($\Phi_{CT} = 0.43$, $p < 0.0001$; Supporting Information Table S1). Very limited genetic admixture was observed between the CTIP and WTIP lineages. The CTIP lineage harbored strikingly rich genetic diversity, with three times more alleles and allelic richness, and eight times fewer private alleles than the WTIP lineage (Supporting Information Table S2).

Niche differentiation between hypervolumes

The size of the realized niche of the CTIP lineage was one order of magnitude greater than that of the WTIP lineage (CTIP lineage: 17295.6; WTIP lineage: 2273.2) (Fig. 2). Niche differentiation between the two hypervolumes (0.97) was mainly due to variation in niche size (0.79), whereas niche shift contributed only marginally (0.18). Difference in realized niches was easily distinguished via water depth and distance to land, with the WTIP lineage selecting a narrow range of water depth and distance to land (Fig. 2). The two lineages also exhibited niche differentiation with respect to annual mean sea surface salinity. In addition, the CTIP lineage niche was broader with respect to annual mean SST and annual range SST, whereas that of the WTIP lineage was broader for annual mean current velocity, minimum current velocity, and annual range of sea surface salinity (Fig. 2). Niche differentiation between the two hypervolumes was also high (0.86) when we considered only marine environmental predictors (i.e., excluding water depth and distance to land) (Supporting Information Fig. S2). Regarding the niche similarity analysis, after 1000 iterations the resulting *p*-values were above 0.05 for both overlap metrics available in the *ecospat* package (0.10 for Schoener's D and 0.07 for Warren's I; Supporting Information Fig. S3). This demonstrates that the realized environmental niche occupied by WTIP is less similar to the niche occupied by CTIP when compared to random permutations over the full environmental space of WTIP.

Model performance

The tuning parameter settings with optimal complexity for the species-level and lineage-level models ranged from relatively simple to complex. The optimal species-level model was the most complex (hinge features and 0.5 RM), while those for the lineage-level models were simpler (CTIP: linear/quadratic/hinge features and 2.5 RM; WTIP: linear/quadratic features and 0.5 RM) (Table 1). The average 10% omission rate was considerably lower for the WTIP lineage-level model (3.57%) than for the other models (CTIP: 26.69%; species: 17.93%, Table 1) — as this was lower than the expectation of average 10% omission for the metric, it indicates that the optimal settings results in models that may over-predict to some extent for WTIP. Although omission rate was used primarily for model selection, the average validation AUC scores used to break ties were very high for all optimal models (Table 1); we think this is due to the fact that a majority of presence data are in near-shore waters (Fig. 1a), which likely inflated the model's ability to discriminate between these presences and background records in deeper water. In addition, all three optimal models had relatively high continuous Boyce index scores (over 0.90; Table 1), indicating that final model predictions matched the presence data well. The eight predictors had different levels of importance in the three models, but water depth and distance to land consistently played important roles (Table 2). In particular, these two predictors accounted for more than 95% of permutation importance in the WTIP model (Table 2). For the CTIP and species models, annual mean SST also had a high permutation importance (~29% and ~24%, respectively) (Table 2). Response curves for water depth and distance to land suggest that shallow coastal waters are more suitable for *T. hemprichii* (Supporting Information Fig. S4, Table S3).

Present-day habitat suitability projections

Under present-day conditions, species and lineage models projected similar but not identical habitat suitability patterns, with a large part of the East African coast and the Pacific region as suitable habitat for this species (Fig. 3). Compared with the species model, the CTIP model predicted more southern distribution in Australia (Fig. 3c, 3d). In particular, the CTIP model predicted suitable conditions in the Spencer Gulf, Southern Australia, where the species does not naturally occur (Fig. 3a, 3c). The species model did not capture this pattern (Fig. 3b, 3d). Moreover, the WTIP model identified more suitable habitat in the Red Sea than the species-level model (Fig. 3c, 3d). Overall, species- and lineage-level models predicted comparable suitable areas for *T. hemprichii* in the WTIP region (species model: 302,800 square km; WTIP model: 315,000 square km), while the species model predicted broader suitable area for the CTIP region (species model: 1,873,800 square km; CTIP model: 1,757,900 square km).

Climate change impacts on habitat suitability

Species- and lineage-level models resulted in different future habitat suitability projections in the CTIP region, with the lineage-level model resulting in predictions of more loss of suitable areas (Table 3, Fig. 4). Both species- and lineage-level models predict considerable future loss of suitable area in the CTIP region, especially on the Sunda Shelf (i.e., Indonesia and Malaysia) (Table 3, Fig. 4). Compared with the species model, the CTIP model projected more extensive range loss under all climatic scenarios (Table 3). Interestingly, both models predicted that the species will shift slightly southwards in Australia.

Species-level and lineage-level models predicted different impacts of climate change on habitat suitability for *T. hemprichii* in the WTIP region (Table 3). The WTIP model predicted range expansion (except under the RCP 2.6 scenario for the 2050s), whereas the species model consistently indicated range contraction (Table 3). Overall, both species- and lineage-level models predicted that future climate change marginally affects habitat suitability in the WTIP region and that changes in range size were mostly < 15%, with the exception of a higher value (~24%) for the species model in the 2100s for the RCP 8.5 scenario (Table 3). The WTIP model predicted that habitat suitability of *T. hemprichii* in the WTIP region will remain stable in the future, while the species model predicted range contraction in the Red Sea and expansion in southern Madagascar and South Africa (Fig. 4).

Both species and CTIP models consistently showed that MESS values in the Sunda Shelf were slightly negative, which demonstrates small differences in climatic conditions between the present-day and future scenarios for this region (Supporting Information Fig. S5). For the WTIP region, the lineage and species model showed high environmental similarity except slight environmental dissimilarity in the Red Sea between present-day and future scenarios (Supporting Information Fig. S5). These results indicate a low degree of extrapolation in our model predictions.

Discussion

This study identified two diverged genetic lineages (WTIP and CTIP) in the seagrass *T. hemprichii* across the tropical Indo-Pacific. The observed niche differentiation between the two lineages suggests a violation of the niche conservatism assumption for species-level SDMs, and our lineage-level predictions of present and future range importantly avoid this assumption. Despite differences between the habitat suitability predictions of the lineage-level and species-level SDMs, they consistently predict that the CTIP lineage is at greater risk of range contraction in the future. Although genetic or genomic data that can be used to construct lineage-level SDMs are not always available, our study emphasizes how incorporating information about phylogeographical structure when modelling the impacts of climate change provides more realistic predictions to better understand future range shifts (Smith *et al.* 2019; Zhang *et al.* 2021).

Critical marine predictor variables for seagrasses

Both the lineage-level and species-level SDMs showed that distance to land, water depth, and annual mean SST represent the most essential factors in explaining the distributional patterns of *T. hemprichii*. The importance of these three predictors has been emphasized in previous studies of

Thalassia species (e.g., Duarte 1991; Lapointe *et al.* 1994; Fourqurean & Zieman 2002; Zhang *et al.* 2014) and other seagrasses (e.g., Baumstark *et al.* 2016; Jayathilake & Costello 2018). Further, water depth and distance to land play significant roles in other efforts to map seagrass using WorldView-2 satellite imagery (Baumstark *et al.* 2016). Water depth correlates with the amount of sunlight irradiance that reaches the seagrass, and with the rate of respiration of rhizomes and shoot density, thereby constraining the extension of seagrass meadows and primary productivity to shallower areas (Duarte 1991). SST affects the photosynthesis, growth, and mortality of seagrass, as demonstrated by field measurements and experimental manipulations of *T. hemprichii* (Collier & Waycott 2014; Pedersen *et al.* 2016; Rasmusson *et al.* 2020). In general, the total nitrogen and phosphorus concentrations of the water column decrease with increasing distance from land, despite a gradient of decreasing P limitation but increasing N limitation (Lapointe *et al.* 1994). Nutrient inputs thus interact with changing temperatures to produce impacts on seagrass shoot densities, areal production rates, and biomass (Lapointe *et al.* 1994; Yamakita *et al.* 2011). The predominant roles of the two geographical predictors and the negligible roles of marine environmental predictors in the WTIP lineage-level model (Table 2) may partially explain the marginal impacts of climate change predicted for this region.

Due to data availability, we used marine predictors at a spatial resolution of 5 arcmin (about 9.2 km at the equator). Within each grid cell, predictors such as temperature and salinity might be homogeneous, but water depth can vary considerably. Seagrasses mainly inhabit shallow waters (Duarte 1991) and it would be reasonable to define study extent using water depth. We found that when limiting the study region using water depth, our main conclusions regarding the change in range size still held, but the predictive ability of the SDMs decreased (Supporting Information Tables S4-S5). Given the limitations of the water depth layer and the decreased model performance upon its inclusion, we decided to delineate the study region using distance to land.

To increase the reliability of marine SDMs, future efforts should be made to develop more high-resolution marine predictors.

Incorporating intraspecific variation into SDMs for seagrasses

Seagrasses provide vital ecological services in marine ecosystems and SDMs have been applied to this taxonomic group for multiple purposes (see reviews by Robinson *et al.* 2011; Robinson *et al.* 2017; Melo-Merino *et al.* 2020). Nonetheless, all previously reported SDMs on seagrasses were built at the species level and thus have not considered possible intraspecific variation. For instance, Chefaoui *et al.* (2018) developed species-level SDMs for two seagrasses (*Posidonia oceanica* and *Cymodocea nodosa*) in the Mediterranean Sea and predicted that the two species are likely to experience dramatic habitat loss in the future. We fully agree that species-level SDMs are by definition informative, but given the high prevalence of intraspecific variation in marine macrophytes (e.g., King *et al.* 2018), and the significance of intraspecific variation in SDMs (Benito Garzón *et al.* 2019; Smith *et al.* 2019; Zhang *et al.* 2021; Collart *et al.* 2021), incorporating intraspecific genetic variation into forecasts of seagrass distribution should result in more realistic scenarios of the potential consequences of climate change, providing that adaptive intraspecific variation can be distinguished from clonal variation for seagrass populations under changing conditions.

The importance of taxonomic resolution in SDMs has been addressed in several terrestrial and freshwater species, but much more sparsely for marine species (see review by Smith *et al.* 2019; Collart *et al.* 2021). Species-level SDMs that disregard existing intraspecific variation can either over- or under-estimate climate change impact on distributional change. For instance, species-level models for the lodgepole pine *Pinus contorta* consistently predicted more extreme habitat loss than subspecies-level models (Oney *et al.* 2013). As another example, although a species-level model for the reef-building coral *Porites lobata* predicted over 5% habitat expansion, when modelling this species as five genetically isolated subpopulations the prediction was ca. 50% habitat loss (Cacciapaglia & van Woesik 2018). In the present study, the species model consistently predicted low impacts of climate change in the CTIP region in comparison to the lineage model (e.g., the habitat loss vs. stability in the Sunda Shelf in Fig. 4c vs. Fig. 4d). As for the WTIP region, we found the opposite pattern. Here, the lineage model predicted stable future habitats in the southern Red Sea (Fig. 4c), whereas the species model predicted habitat loss, including to the north of Mauritius (Fig. 4d). In addition, both species and lineage models predict a southward range expansion in the southern CTIP, but only the species model clearly predicts this in the WTIP. Southern expansion is likely correlated with future temperature increases in areas which are now too cold (Supporting Information Fig. S6). We should note that MESS values in the equatorial regions were slightly negative, which indicates novel future environmental conditions. This is due in part to higher future SST values for this region than those used by the present-day SDM (Supporting Information Fig. S7)—thus, SDM projections in this region should be associated with more uncertainty.

That the difference between the future projections for the two lineages could be attributed to the large difference in sample size (479 records for CTIP and 26 records for WTIP) is unlikely, because. i) compared with other algorithms, Maxent is less sensitive to sample size and has better performance for small sample sizes (e.g., Hernandez *et al.* 2006; Wisz *et al.* 2008); ii) models for both lineages had similarly high predictive abilities when using cross-validation with spatial partitioning, which results in lower performance metrics for overfit models than conventional random partitioning (Roberts *et al.* 2017). Further, as the range of WTIP is much larger than that of CTIP, it is reasonable that less occurrence data would be necessary to properly characterize the occupied environments for CTIP. However, SDMs were developed in this study without considering physiological information of the species, and traits related to dispersal and resilience to climate change. Such considerations in a mechanistic SDM could result in different future range projections *as compared with the results obtained with our approach*. Further studies involving both field investigations and associated data updates and methodological developments for models [e.g., developing ensembles of small models (Breiner *et al.* 2018) or changing the study extent] would further improve our predictions for climate change impacts on *T. hemprichii* in the Tropical Indo-Pacific.

Intraspecific variation and local adaptation in seagrass

Differences in response to thermal changes related to intraspecific variation, whether eco-physiological or evolutionary, are well-documented in seagrasses (King *et al.* 2018). This variation, partly based on phenotypic plasticity or local adaptation, ultimately might permit seagrasses to acclimatize and adapt to changes in climate (Duarte *et al.* 2018). The marine predictor variables that played a predominant role in our SDMs (e.g., annual mean SST and water depth) could be responsible for both long- and short-term local adaptation of *T. hemprichii* to a changing climate (King *et al.* 2018; Jahnke *et al.* 2019b). In support of this, common-garden experiments have revealed a clear local adaptation to increased temperatures in *Zostera marina* (Franssen *et al.* 2011; 2014), and to a depth gradient in *Posidonia oceanica* (Marín-Guirao *et al.* 2016; Jahnke *et al.* 2019b). Further, parallel adaptation of *Z. marina* to thermal clines along the American and European coasts was demonstrated using a space-for-time substitution design and gene expression profiling (Jueterbock *et al.* 2016). Such adaptive local differentiation induced by divergent environmental forces (e.g., light, depth and temperature) has led to structured populations and lineages in seagrasses at various spatial scales (Dattolo *et al.* 2014; Jueterbock *et al.* 2016; Jahnke *et al.* 2019b), suggesting that adaptation to local conditions is a key mechanism for seagrasses to face global climate change.

Although we identified high genetic differentiation between the WTIP and CTIP lineages (Supporting Information Table S2), which may represent an extreme case of intraspecific genetic divergence, we were not able to ascertain the adaptive components of divergence across a common landscape within the tropical Indo-Pacific. In *T. hemprichii*, natural selection imposed by environmental heterogeneity might have resulted in the evolution of locally adapted populations with considerable variation in productivity, growth rate and competitive interactions (Martins & Bandeira 2001; Lyimo *et al.* 2006; Larkum *et al.* 2018). Low genetic difference between lineages with associated environments that are very different is likely the result of admixture between geographically distant populations over evolutionary time, resulting in the species having a wide range and a broad fundamental niche. In this case, lineage-level SDMs would not be appropriate and a full-species SDM should be used because the populations are distant spatially but not genetically.

Future studies should focus on distinguishing neutral genetic differentiation from local adaptation using reciprocal transplant trials (e.g., common gardens and provenance trials; see Joyce & Rehfeldt 2013; Ralph *et al.* 2018). Also, it is most important to mechanistically assess the sub-lethal susceptibility of *T. hemprichii* to thermal stress, including the effects of heat and hypoxia on photosynthesis, respiration, and primary productivity (Pedersen *et al.* 2016; Rasmusson *et al.* 2020), before the strongest impacts of future climate change are sustained. Intraspecific genetic diversity across populations can increase a species' adaptive capacity and result in cascading effects to the entire ecosystem (Evans *et al.* 2017). It is thus important to identify the most temperature-tolerant genotypes from the WTIP and CTIP lineages, perhaps by manipulating temperature to quantify the performance of individual genotypes of *T. hemprichii* across thermal gradients. It is also essential to clarify whether genotype complementarity or dominance enhance the adaptive capacity in a population (Hughes & Stachowicz 2011).

Conservation implications

The challenge of designing effective actions for seagrass conservation in the Indo-Pacific exists in the gap between science, policy, and practice (Fortes 2018). In this study, the separation in geographic distribution and high niche differentiation between the CTIP and WTIP lineages suggest that *T. hemprichii* populations may be locally adapted (Merilä & Hendry 2014). For species with significant intraspecific genetic diversity, it is crucial to help maintain the species' potential for adaptive responses to climate change by conserving this diversity (D'Amen *et al.* 2013). In particular, lineage differentiation can be explained by recruitment rate (Lyimo *et al.* 2006; Sherman *et al.* 2018), nutrient resorption (Martins & Bandeira 2001), dispersal barriers (Melroy *et al.* 2017), and evolutionary history from the origin center to the distributional margins (Mukai 1993). Dramatic future habitat loss in the CTIP was predicted by both the species- and lineage-level models (Fig. 4), stressing the urgency to develop monitoring programs to rescue evolutionary and/or ecologically important units in *T. hemprichii*, particularly the populations and gene pools that have persisted through past long-term climate change because of local adaptation (Bell 2017; Hernawan *et al.* 2017). Furthermore, the recognition of high niche differentiation between the WTIP and CTIP lineages may help to establish coherent principles and regulating practices by which the different areas that *T. hemprichii* inhabits can be protected efficiently.

The biomass, abundance, and productivity of seagrasses are highly correlated with both habitat suitability (Martins & Bandeira 2001; Saunders *et al.* 2013) and epiphytic species biodiversity (Lyimo *et al.* 2008). Optimizing productivity of *T. hemprichii* in a given site or population can help to increase associated community diversity (Eklöf *et al.* 2006; Lyimo *et al.* 2008). Thus, it is necessary to explore how community diversity and structure correlate with the genetic composition and structure of the foundational species *T. hemprichii*. Such research can help validate the results of SDMs in this study and quantify the relationship between *T. hemprichii* and its relevant community components (Ikeda *et al.* 2017). Since populations in each of the CTIP and WTIP lineages are locally adapted, policymakers and stakeholders are encouraged to use local seed sources of *T. hemprichii* to ensure management strategies for successful restoration and conservation purposes. To this end, mechanistic studies underlying thermal adaptation by linking ecology to genetics should be done to better understand how *T. hemprichii* will adapt to climate change (Duarte *et al.* 2018; Hu *et al.* 2020).

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Data availability

Environmental layers can be downloaded from the Global Marine Environment Datasets (http://gmed.auckland.ac.nz) and the Bio-ORACLE database v2.1 (https://www.bio-oracle.org). Microsatellite datasets and presence records of *Thalassia hemprichii* have be deposited in Dryad entry https://doi.org/10.5061/dryad.vhhmgqnsh.

Author contributions

Z.-M.H. and Z.Z. conceived the project. Z.-M.H. and J.Z. collected molecular data, J.Z. and P.F. performed genetic analyses, Z.Z. collected species distribution data and conducted ecological niche analyses with critical suggestions from J.M.K. and S.M. Z.-M.H., Z.Z., S.M., J.M.K., Z.-Q.Z., S.D., J.A., and A.J. interpreted and discussed the results, wrote and/or revised the manuscript. All authors approved the final version of the manuscript.

Tables

Table 1. Maxent parameters, performance metrics on spatially withheld data (validation AUC and omission rate) and the full dataset (continuous Boyce index), and 10th percentile presence thresholds of the two lineage-level models and the species-level model. Validation AUC and 10% omission rate results are expressed as means ± standard deviation across spatial partitions.

Model	RM[1]	Feature class[2]	Average validation AUC	Average 10% omission rate (%)	10% omission threshold	Continuous Boyce index
WTIP[3]	0.5	LQ	0.99(± 0.01)	3.57(± 7.14)	0.12	0.92
CTIP[4]	2.5	LQH	0.96(± 0.03)	26.69(± 37.42)	0.37	0.99
Species	0.5	H	0.96(± 0.02)	17.93(± 17.62)	0.30	0.99

[1] RM: regularization multiplier.

[2] Feature Class: L (linear), Q (quadratic), and H (hinge) were considered.

[3] WTIP: the Western Tropical Indo-Pacific lineage-level model

[4] CTIP: the Central Tropical Indo-Pacific lineage-level model

Table 2. Permutation importance (%) of marine predictors in each Maxent model. Values in bold showed important predictors.

Predictors	WTIP[1]	CTIP[2]	Species
Water depth [m]	**14.10**	**51.05**	**46.91**
Distance to land [km]	**81.87**	**11.58**	**9.30**
Minimum current velocity [m/s]	0.46	0.00	0.03
Annual mean current velocity [m/s]	0.15	0.04	0.27
Annual mean sea surface salinity [PSS]	0.80	2.49	1.92
Annual range of sea surface salinity [PSS]	0.93	4.96	**13.38**
Annual mean sea surface temperature [°C]	0.83	**28.68**	**23.47**
Annual range of sea surface temperature [°C]	0.87	1.20	4.73

[1] WTIP: Western Tropical Indo-Pacific lineage-level model

[2] CTIP: Central Tropical Indo-Pacific lineage-level model

Table 3. Range size change (%) of *Thalassia hemprichii* under future climate scenarios. Values in parentheses indicate range size change predicted by the species-level model.

RCP[1]	WTIP[2]		CTIP[3]	
	2050s	2100s	2050s	2100s
RCP 2.6	–0.2 (–2.5)	4.4 (–3.8)	–40.6 (–29.3)	–34.5 (–27.8)
RCP 4.5	1.3 (–6.3)	4.2 (–6.3)	–49.7 (–26.1)	–55.7 (–26.4)
RCP 6.0	3.4 (–0.4)	7.5 (–15.0)	–43.8 (–30.3)	–63.7 (–23.2)
RCP 8.5	4.0 (–10.9)	13.2 (–23.7)	–53.7 (–27.4)	–72.1 (–25.8)

[1] RCP: representative concentration pathway.

[2] WTIP: Western Tropical Indo-Pacific lineage-level model

[3] CTIP: Central Tropical Indo-Pacific lineage-level model

Figure Legends

Figure 1. (a) Map of study regions and presence records used in this study. Blue and red points represent sample collection locations for molecular analyses in the Western Tropical Indo-Pacific (WTIP) and the Central Tropical Indo-Pacific (CTIP). Gray crosses show presence records used for the species distribution models. (b) Network of microsatellite genetic differentiation (Cavalli-Sforza and Edwards chord distances). The topology results from pruning the network for pairwise genetic distances <0.534. The smallest chord distance (0.499) between the WTIP and CTIP lineages is shown. (c) Genetic lineage division over space based on STRUCTURE clustering (k = 2). Population abbreviations are the same as in Hernawan *et al.* (2017) and Jahnke *et al.* (2019a), and their classification to network analysis is in agreement with that of STRUCTURE (Fig. 1c).

Figure 2. The realized niches for the two lineages of *Thalassia hemprichii* quantified via eight-dimensional hypervolumes. The axes represent unitless values as the predictors were standardized before analyses. Circles with white rims indicate hypervolume centroids. Boundaries and shapes of hypervolumes were delineated by 10,000 points randomly sampled within each hypervolume. The photograph depicts *T. hemprichii*.

Figure 3. Present-day continuous (a, b) and binary (c, d) habitat suitability predictions for *Thalassia hemprichii* by lineage-level (a, c) and species-level (b, d) Maxent models. Dashed lines represent the equator. To improve the legibility of the binary predictions, we increased the pixel size by downscaling the spatial resolution to 30 arcmin. High-resolution predictions can be downloaded from Dryad (https://doi.org/10.5061/dryad.vhhmgqnsh).

Figure 4. Changes in continuous (a, b) and binary (c, d) habitat suitability for *Thalassia hemprichii* projected by lineage-level (a, c) and species-level (b, d) Maxent models under the RCP 8.5 scenario in the 2050s. Dashed lines indicate the equator. The category "stable" represents areas predicted to be suitable under both present-day and future climatic conditions, "loss" indicates areas predicted to be suitable under present-day conditions but unsuitable in the future, and "gain" indicates areas predicted to be unsuitable under present-day conditions but suitable in the future. To improve the legibility of the binary predictions, we increased the pixel size by downscaling the spatial resolution to 30 arcmin. High-resolution predictions can be downloaded from Dryad (https://doi.org/10.5061/dryad.vhhmgqnsh).

Supporting Information

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