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Niche comparison and range shifts for two *Kappaphycus* species in the Indo-Pacific Ocean under climate change

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ABSTRACT

Nowadays, eucheumatoids lead the rankings in globally cultivated seaweed production, including the seaweeds *Kappaphycus alvarezii* and *Kappaphycus striatus*. Eucheumatoids have declined in biomass over recent years, and climate change is regarded as one of the important factors. Thus, it is urgent to investigate the range dynamics of *Kappaphycus* under climate change. Considering its high practical relevance for conserving biodiversity, the niche conservatism hypothesis was tested between the two species through ecological niche modeling (ENM), ordination, and hypervolume approach which quantify the extent of niche overlap. In this study, we sifted the best-performing algorithm - Maxent and tuned parameters for fitting the distribution of both *Kappaphycus* species, compared their geographical distribution patterns, and predicted their range dynamics under climate change. All three methodological approaches indicated significant niche differences in both geographical and environmental space between the two *Kappaphycus* species. Our models predicted that range shifts mainly induced by rising sea surface temperature are likely to differ between two *Kappaphycus* species, with *K. striatus* suffering much range contraction (359,448 km^2 in 2100s RCP8.5). By the year 2100, both *Kappaphycus* species are forecast to lose suitable habitats along most of the coastline of Southeast Asia under the RCP8.5 scenario. *K. alvarezii* is predicted to expand its distributions (96,429 km^2) under the RCP2.6 scenario by the year 2100, suggesting resilience to mild global warming. Our study enhances the understanding of *Kappaphycus* aquaculture, and is conducive to the sustainable development of tropical seaweed by stressing the importance of conservation and investigation under climate change.

1. Introduction

Eucheumatoids lead the rankings in global cultivated seaweed production, which are considered as the main source of carrageenan (Dumilag et al., 2022; Porse and Rudolph, 2017). They are mainly cultivated in the Indo-Pacific Ocean, including the East Africa region (Tanzania) and Southeast Asian countries (Indonesia, the Philippines, Malaysia and Vietnam). Two species of eucheumatoids are widely cultivated and distributed in tropical regions (Kumar et al., 2020): *Kappaphycus alvarezii* and *Kappaphycus striatus*. The former accounted for 4.6% of the total global seaweed production in 2022 (FAO, 2022), the latter has been widely cultivated in tropical countries due to resistance to epiphytes and "ice-ice" infestation (Hurtado et al., 2008). However, eucheumatoid's production has declined over recent years (FAO, 2020; Mateo et al., 2021) (Table S1), this is partly attributed to climate change-associated ocean warming (Largo et al., 2017; Kumar et al., 2020), which has been recently shown to reduce the distribution range of tropical seaweed (Hu et al., 2021; Du et al., 2022). Climate change threatens seaweed aquaculture continuity, hence, the ability to meet the high global commercial demand for carrageenan in the future

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(Naylor et al., 2021). Thus, it is urgent to predict the range dynamics of *Kappaphycus* under the impact of climate change.

Ecological Niche Models (ENMs) provide a tool to predict the potential impact of climate change on distributional range shifts (Hijmans and Graham, 2006; Pearson and Dawson, 2003; Phillips and Dudík, 2008), and allows to develop conservation strategies and plans (Ali et al., 2021; Engler et al., 2004; Zhang et al., 2012). Various algorithms have been applied to construct ENMs, such as Generalized Linear Models (GLM) (Guisan et al., 2002), Generalized Additive Models (GAM) (Guisan et al., 2002) and Random Forest (RF) (Breiman, 2001). So far, consensus was lacking on the optimal choice of modelling algorithms (Lawler et al., 2006).

Phylogenetic niche conservatism (PNC) (Harvey and Pagel, 1991) is a biological term to describe the tendency for lineages to retain ancestral ecological characteristics over recent evolutionary timescales (Wiens and Graham, 2005; Peterson et al., 1999). The ecological differentiation between related species appears to be not uncommon (Pyron et al., 2015; Sexton et al., 2014). However, there has been a widespread debate about whether the ecological niche of species is conserved across space and time, different taxa seem to display diverse conclusions (Liu et al., 2020). Considering the conflicting conclusions and high practical relevance for conserving biodiversity of this hypothesis (Liu et al., 2020; Wiens et al., 2010), we think it is necessary to quantify niche differences between our target species and test the PNC hypothesis simultaneously. Accordingly, the close phylogenetic relationship between *K. striatus* and *K. alvarezii* (Dumilag et al., 2016; Lim et al., 2014) should have largely overlapped in their niche in environmental and geographical space (Warren et al., 2008). If so, both species are expected to experience similar range shifts under projected climate change, consequentially, requiring similar management and conservation. Relevant methods to test for niche conservatism include ENM (Wiens et al., 2010), ordination (Broennimann et al., 2012), hypervolume (Liu et al., 2020), and univariate techniques (Liu et al., 2020), all of which have been applied in invasive species. To quantify the niche overlap between the two *Kappaphycus* species, here we used the former three methods. Among these methods, ordination (Broennimann et al., 2012) and hypervolume (Blonder et al., 2014; 2018) are mainly based on the environmental space (Salinas-Ramos et al., 2021), while ENM projections focus on geographic space (Bosso et al., 2022).

As tropical macroalgae that mainly inhabit the intertidal zone, *Kappaphycus* species are ideal candidates to study the impact of climate change on the distribution of tropical seaweed. Based on the close phylogenetic relationship between *K. alvarezii* and *K. striatus*, they are also quite suitable to conduct a comparative study on niche and test for the phylogenetic niche conservatism hypothesis between sister species. So far, reports on ocean warming-induced distributional shifts are limited, and much literature is focused on temperate seaweed (Cayuela et al., 2009; Song and Li, 2023; Zhang et al., 2019; 2021). Studies on the comparison of their realized niche remain to be supplemented.

Through applying three techniques on niche comparison between two *Kappaphycus* species, we aimed to: 1) quantify the extent of niche overlap between the sister species of *Kappaphycus*; and 2) predict and compare range shifts between two *Kappaphycus* species under projected climate scenarios with the ultimate goal of facilitating sustainable development of eucheumtoids aquaculture. Our study proves the potential of ENMs in *Kappaphycus*' conservation and management, and provides insights in alleviating the worsening trend of eucheumatoids global production under the pressure of climate change.

2. Methods

2.1. Study area and occurrence data

According to our research objectives and core distribution area of *Kappaphycus* species, we defined our study area between 25°E to 180°E, and between 20°S and 20°N, which covers the Central and Western Indo-Pacific Ocean (Spalding et al., 2007). Plus, we restricted study area to 100 m water depth, the maximum depth limit of *Kappaphycus* (Doty, 1987).

We obtained occurrence data for *K. alvarezii* and *K. striatus* mainly from the Global Biodiversity Information Facility (https://www.gbif.org) (GBIF, 2023), the Ocean Biogeographic Information System (https://iobis.org) (OBIS, 2023), and AquaMap database (https://www.aquamaps.org) (Kaschner, 2019). To guarantee the predictive accuracy of our *Kappaphycus* ENMs, we cleaned the presence records using the R package "CoordinateCleaner" (Zizka, 2019), and then thinned them in the environmental space through "flexsdm" package (Velazco et al., 2022) (see details in Supplementary material for Presence data filtering).

After data filtering (Fig. S1), we retained 41 occurrence records for *K. alvarezii* and 22 records for *K. striatus* (Fig. 1) (Table S2). The points are most dense along nearshore areas of the Philippines and Indonesia.

2.2. Environmental data filtering

Sea water temperature (Kumar et al., 2020), water depth (Hurtado et al., 2008), salinity (Araujo et al., 2014) and water motion (Doty, 1987; Glenn and Doty, 1992) are considered as crucial factors influencing the survival and growth of eucheumatoids. Therefore, we incorporated these factors into modelling distributions for *Kappaphycus*. According to the available data and the above-mentioned ecological requirements of *Kappaphycus* species, we pre-selected 18 environmental variables, including the annual mean, the annual maximum, the annual minimum, the annual range, the long-term average of minimum and maximum for sea surface temperature (SST), sea surface salinity (SSS) and currents velocity (CV) (Table S3) from the Bio-ORACLE database version 2.2 (https://www.bio-oracle.org) (Assis et al., 2018). Two geographical predictors: water depth and the distance to land were adopted from the Global Marine Environment Datasets (https://gmed.auckl and.ac.nz; Basher et al., 2014).

Two representative concentration pathway scenarios (RCP2.6 and RCP8.5) and the two future periods: the 2050 s (the average for 2040–2050) and the 2100 s (the average for 2090–2100) were chosen for predicting *Kappaphycus* distributions. RCP2.6 is a mitigation scenario, representing the active removal of atmospheric carbon dioxide, whereas the high-emission scenario RCP8.5 represents a failure to curb warming in the future (van Vuuren et al., 2011). We assumed that the two geographical predictors (water depth and distance to land) would remain unchanged over the next century (Zhang et al., 2020). All predictor variables were standardized to a 5 arc-minute resolution and the same extent (25°E, 180°E, 20°S, 20°N).

Since predictor collinearity could lead to model overfitting and inaccurate tests (De Marco and Nóbrega, 2018), we selected only one between a pair of highly correlated predictors via a Pearson Correlation Coefficient $|r| \geq 0.75$ (Dormann et al., 2013) (Fig. S2) for further analyses. After dealing with highly correlated predictor variables, we retained eight variables for constructing *Kappaphycus* ENMs (Table 1): distance to land (Land distance), water depth (Depth), the annual range of sea surface temperature (SST_{range}), the annual mean of sea surface temperature (SST_{mean}), the annual range of sea surface salinity (SSS_{range}), the annual mean of sea surface salinity (SSS_{mean}), the annual mean of currents velocity (CV_{mean}) and annual minimum of currents velocity (CV_{min}).

2.3. Pseudo-absence and background points sampling

We used a buffer of 100 km around the occurrences of *K. alvarezii* and *K. striatus* for delimiting the study area, and then generated pseudo-absence points randomly within the calibration area. This restricted calibration area simulates the natural dispersal limitations (Anderson and Raza, 2010). We set the number of pseudo-absence points equal to the number of occurrence points. Background points were generated

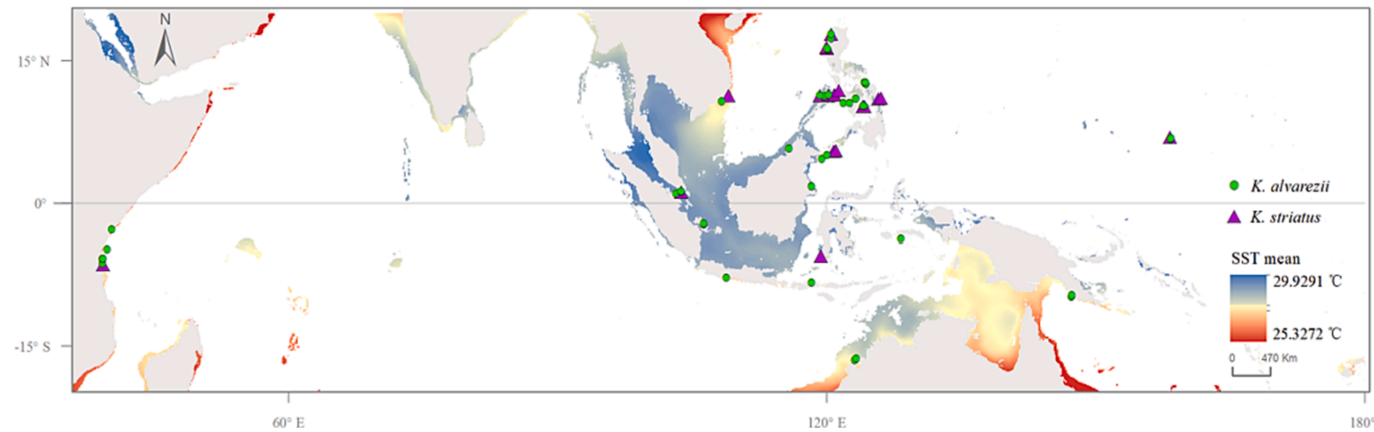

Fig. 1. Study area map and occurrence records of *K. alvarezii* and *K. striatus.* SST mean is the present annual mean of sea surface temperature. Map was constructed using ArcMap 10.4.1.

Table 1
Retained predictor variables and detailed information.

Code	Abbr.	Full name	Unit	Source	Original Resolution
bio02	SST. mean	Annual mean of Sea Surface Temperature	°C	Bio-ORACLE	5 arc-min (9.2 km)
bio06	SST. range	Annual range of Sea Surface Temperature	°C	Bio-ORACLE	5 arc-min (9.2 km)
bio08	SSS.mean	Annual mean of Sea Surface Salinity	PSS	Bio-ORACLE	5 arc-min (9.2 km)
bio12	SSS.range	Annual range of Sea Surface Salinity	PSS	Bio-ORACLE	5 arc-min (9.2 km)
bio14	CV.mean	Annual mean of Currents velocity	m/s	Bio-ORACLE	5 arc-min (9.2 km)
bio15	CV.min	Annual min of Currents velocity	m/s	Bio-ORACLE	5 arc-min (9.2 km)
bio89	Depth	Water depth	m	GMED	5 arc-min (9.2 km)
bio90	Land distance	Distance to land	100 km	GMED	5 arc-min (9.2 km)

with ten times the number of occurrence points for the two species, respectively (Fig. S3). Occurrence, background and pseudo-absence data were divided into 5-fold for cross-validation with 10 repetitions.

2.4. Core Modeling: Model selection, optimization and construction

Six algorithms (GLM, GAM, GBM, SVM, MaxEnt and RF) were chosen (Table S4) to construct the ENMs for the two *Kappaphycus* species. We tuned parameters for the two machine learning algorithms, MaxEnt (maximum entropy) and RF (random forest), as these could produce higher-quality outputs than employing default settings (Warren and Seifert, 2011). We set the combination of a series of hyper-parameters for the MaxEnt candidate models: the regularization parameter (RM) ranged between 0.1 and 4.0 (steps at 0.1), and three combinations of feature classes (FCs) were applied, including L (linear), LQ (linear and quadratic) and LQH (linear, quadratic and hinge). Due to the small amount of occurrence data, the two feature classes “threshold” and “product” were excluded from the construction of ENMs (Elith et al., 2011). We selected “logistic” as the output type and set the parameter “clamp = TRUE” for limiting the predictors and features to the environmental space of model training. The mtry (the number of predictors sampled for splitting at each node) values were set as 1–7 with an interval of 1 for RF candidate models. We applied a threshold that maximizes the sum of the sensitivity and specificity, also known as the threshold with the maximum true skill statistic (TSS) (Liu et al., 2016) to classify the presence and absence (Fielding and Bell, 1997) in the confusion matrix. We used the statistical indicator TSS to select the optimal combination of parameters for candidate models. In addition to the TSS metric, other four indicators were used to evaluate the model performances among different algorithms, including AUC (the area under the receiver operating characteristic curves), Continuous Boyce index (CBI), TPR (true positive rate) and TNR (true negative rate) (see details in Supplementary materials Statistical indicators).

The optimal hyper-parameters of the MaxEnt model were RM = 2.9 and FC = L for *K. alvarezii*, RM = 0.1 and FC = LQ for *K. striatus*. For RF ENMs, the optimal parameter (mtry) for *K. alvarezii* and *K. striatus* was 3 and 4, respectively. For *K. alvarezii* ENMs, three machine learning algorithms (GBM, MaxEnt and RF) showed relatively higher AUC, TSS and TNR values than other algorithms (Table S5). Other three machine learning algorithms (MaxEnt, SVM and GBM) exhibited higher Boyce values (Fig. S4; Table S5). The TSS values of GBM, MaxEnt and RF were between 0.55 and 0.7, indicating “good predictions” (de la Hoz et al., 2019). The Boyce Index values of all algorithms ranged from 0.85 to 1.0, suggesting that model predictions closely matched the presence data (Hirzel et al., 2006) (Table S5). The MaxEnt algorithm had the highest AUC, TSS, TNR and Boyce values (Fig. S4), indicating its best performance in fitting the distribution of *K. alvarezii*. The best-performing models are applied to calculate the variable importance for two *Kappaphycus* species by using the AUC indicator.

2.5. Post-modeling

The Multivariate Environmental Similarity Surfaces analysis (MESS) was used to measure the extent of similarity by comparing environmental data at reference points (here is current occurrence) with that for the model projected area which includes the whole study area in the present-day and the future (Chefaoui & Varela-Álvarez, 2018). It is also a quantitative measurement of the extent of model extrapolation risk and prediction uncertainty (Elith, 2011). MOD (most dissimilar variables) maps were plotted to reflect the predictor variable that is the most different from the training area. All the similarity calculations were conducted with R package “rmaxent” (Baumgartner and Wilson, 2021).

Buffered Minimum Convex Polygon (BMCP) was used to correct the over-predictions for the two *Kappaphycus* species (Mendes et al., 2020) using the R package “flexsdm”, which excluded the suitable pixels around the minimum convex polygon enclosing all occurrences of our target species (Kremen et al., 2008).

The corrected outputs were finally loaded into ArcGIS 10.4.1 for visualizing the *Kappaphycus* habitat suitability and binary distributions with the maximum TSS threshold (Liu et al., 2016) in the present-day and future RCP scenarios. The binary maps were then transformed into the Equal-Area Cylindrical projection for calculating range dynamics with the “Distribution changes between binary SDMs” tool in the

Python-based SDM toolbox in AcrGIS (Brown, 2014). To evaluate the degree of niche overlap with the ENM technique (Blair et al., 2013), we calculated pairwise Schoener's D index (Warren et al., 2008) using the R package "ENMeval" (Kass et al., 2021), ranging from 0 (totally different) to 1 (identical predictions).

2.6. Realized niche comparisons in environmental space

We applied ordination and hypervolume methods (Liu et al., 2020) to quantify the degree of niche overlap between the two *Kappaphycus* species in environmental space. The hypervolume method delineated the realized niche shapes and volumes (Blonder et al., 2014; 2018) with the Hutchinsonian n-dimensional hypervolumes (Hutchinson, 1957). Specifically, we first chose the Gaussian kernel density method to characterize the species' realized niches using eight environmental variables with the "hypervolume" R package (Blonder et al., 2022). The Jaccard similarity, sorensen similarity, frac_unique_1 (volume of unique component of species1 divided by volume of species1) and frac_unique_2 (volume of unique component of species2 divided by volume of species2) were then used for measuring the extent of niche overlap between two *Kappaphycus* species. The R package "BAT" (Cardoso et al., 2022) was applied to compute beta diversity, which measured the overall differentiation between kernel hypervolumes of *Kappaphycus* species. Beta diversity ranges from 0 (hypervolumes are identical) to 1 (fully dissimilar hypervolumes) (Carvalho and Cardoso, 2020; Mammola and Cardoso, 2020). Beta diversity could be split into two components: beta replacement (spatial shift between hypervolumes) and beta richness (net differences between hypervolumes) (Zhang et al., 2020).

The ordination approach first performed a principal component analysis (PCA) on the predictor layers through the R package "raster" (Hijmans, 2022), and then PCA scores were projected onto a grid of cells with occurrence densities of the two *Kappaphycus* species via R package "ecospat" (Broennimann et al., 2022; Di Cola et al., 2017). Schoener's D and Warren's I indicators of overlap (0–1) (Broennimann et al., 2012; Warren et al., 2008) between the two sister species were calculated to evaluate the degree of niche similarity. The closer the value is to 1, the higher is the similarity between the niches of the two species (Pack et al., 2022). Finally, a niche identity test was performed on two environmental axes to test for the niche conservatism (Di Cola et al., 2017; Warren et al., 2008) with 1,000 replications, which was used to determine whether the two entity's niches in the environmental space were equivalent (Broennimann et al., 2012).

3. Results

3.1. Model assessment

Our results show that in addition to two geographical variables (depth and distance to land), sea surface temperature, salinity and current velocity also play important role in simulating the distribution of *Kappaphycus* species (Table S6). Among the six ENM models of *K. striatus*, three machine-learning algorithms showed higher TPR and TSS values: GBM, MaxEnt and RF. According to the Boyce index (Fig. S4), GLM, GAM and SVM exhibited better performance, whereas GLM, GAM and MaxEnt performed best regarding TNR (Table S5). The MaxEnt algorithm showed the highest AUC, TSS and TPR values, indicating good performance to fit ENMs of *K. striatus*. Therefore, the outputs of MaxEnt ENMs were adopted for the following ENM analysis for *K. alvarezii* and *K. striatus* respectively.

3.2. Geographic distribution and range shifts of two Kappaphycus species

Range projections for the two *Kappaphycus* species displayed their habitats with high suitability were mainly located in the waters between latitudes 15°S and 15°N, which covered the nearshore areas of most Southeast Asian countries (Indonesia, the Philippines and Malaysia), and a small part of East Africa (Tanzania) in the current period (Fig. S5). However, *K. striatus*'s suitable habitats are larger than of *K. alvarezii* in three major eucheumatoids-producing countries, i.e. Indonesia, the Philippines, and Malaysia, by contrast, the latter is closer to the shoreline. A considerable difference between the two species in the present geographical distribution was indicated by the low value of Schoener's D index (only 0.35) (Table 2).

The binary distributions indicated no obvious change in suitable habitats for *K. alvarezii* from present to future (Fig. 2; Fig. S6a), but significant changes for *K. striatus* under two future climate scenarios (Fig. 2; Fig. S6b). The projections for the year 2100 under the RCP8.5 scenario exhibited the largest range contractions.

The suitable habitats are predicted to shrink for *K. striatus* (192,443 km^2) but expand for *K. alvarezii* (96,429 km^2) under the RCP2.6 scenario in 2100s (Table S7). By the year 2100, both *Kappaphycus* species are forecast to experience maximum range contraction under the RCP8.5 scenario (Fig. 3; Table S7 and S8). *K. alvarezii* is expected to lose habitats along the coastal areas of Malaysia and Indonesia but gain habitats along the coastal waters of the Philippines under both RCP scenarios by 2100. For *K. striatus*, most coastal areas of Southeast Asian countries (Malaysia, Indonesia, the Philippines and Vietnam) are projected to become unsuitable under both RCP scenarios until the year 2100. Under the RCP8.5 scenario, *K. striatus* displayed much larger habitat loss than *K. alvarezii.* The maximum area predicted to be lost reached 134,502 and 359,448 km^2 from the present to the year 2100 for *K. alvarezii* and *K. striatus*, respectively (Fig. 3; Table S7).

3.3. Environmental similarity analysis

According to MESS and MOD maps of *K. alvarezii*, the environmental data in the projection area for the present and future exhibited few differences from that at the current occurrence sites, except for the Sunda Shelf and parts of northern Australia presenting large environmental differences. The differences were mainly attributed to the distance to land and the annual mean of sea surface temperature (SST_{mean}) (Fig. S7a; Fig. S8a). Compared with *K. alvarezii*, environmental values at occurrence points of *K. striatus* were more similar to those in the projected region in the current and future periods except for the year 2100 under the RCP8.5 scenario, which was ascribed to the rising annual mean of SST in the nearshore areas of Southeast Asia (Fig. S7b; Fig. S8b). The ENMs of the two *Kappaphycus* species showed an overall low extrapolation risk in which sea surface temperature contributed the most. Particularly, SST_{mean} is the predictor that showed the largest difference from the current values at occurrence points (Fig. S7; Fig. S8) in the areas of predicted habitat loss (Fig. 3).

3.4. Niche comparisons between the two Kappaphycus species

The volume of the realized niche of *K. alvarezii* (80.02) was nearly 2.4 times that of *K. striatus* (32.94). Two hypervolumes could be well distinguished via a geographical variable - distance to land. *K. striatus* can distribute further from shore compared with *K. alvarezii* (Fig. 4). Niche net difference (46.6%) and niche shift (41.5%) contributed nearly equally to the overall niche differentiation (88.1%). Indicators regarding niche volumes of the two *Kappaphycus* species demonstrated a low niche overlap: Jaccard similarity (0.12), Sorensen similarity (0.21), frac_unique_ka (0.85) and frac_unique_ks (0.63) (Table 2).

The ordination approach showed that the occurrence density of *K. alvarezii* after correcting for the available environment in environment space was not similar to *K. striatus* (Fig. 5). The niche overlap metrics were 0.25 and 0.48 for Schoener's D and Warren's I, respectively (Table 2), displaying the low extent of niche similarity. The niche identity test suggested that realized niches of the two *Kappaphycus* species were significantly different ($p < 0.05$) (Fig. S9), which did not conform to the phylogenetic niche conservatism hypothesis. All methods and indicators demonstrated the low degree of niche overlap between

Table 2
Indicators of niche overlap between two *Kappaphycus* species with Ordination, ENM and Hypervolume approaches. β total = β replacement + β richness; frac_unique_ka: volume of unique component of *K. alvarezii* divided by volume of *K. alvarezii*; frac_unique_ks: volume of unique component of *K. striatus* divided by volume of *K. striatus*.

Method	Hypervolume method							Ordination method		ENM method
Indicators	β diversity (%)			Jaccard	Sorensen	frac_unique_ka	frac_unique_ks	Schoener's D	Warren's I	Schoener's D
	β total	β replacement	β richness							
Value	88.10	41.50	46.60	0.12	0.21	0.85	0.63	0.25	0.48	0.35

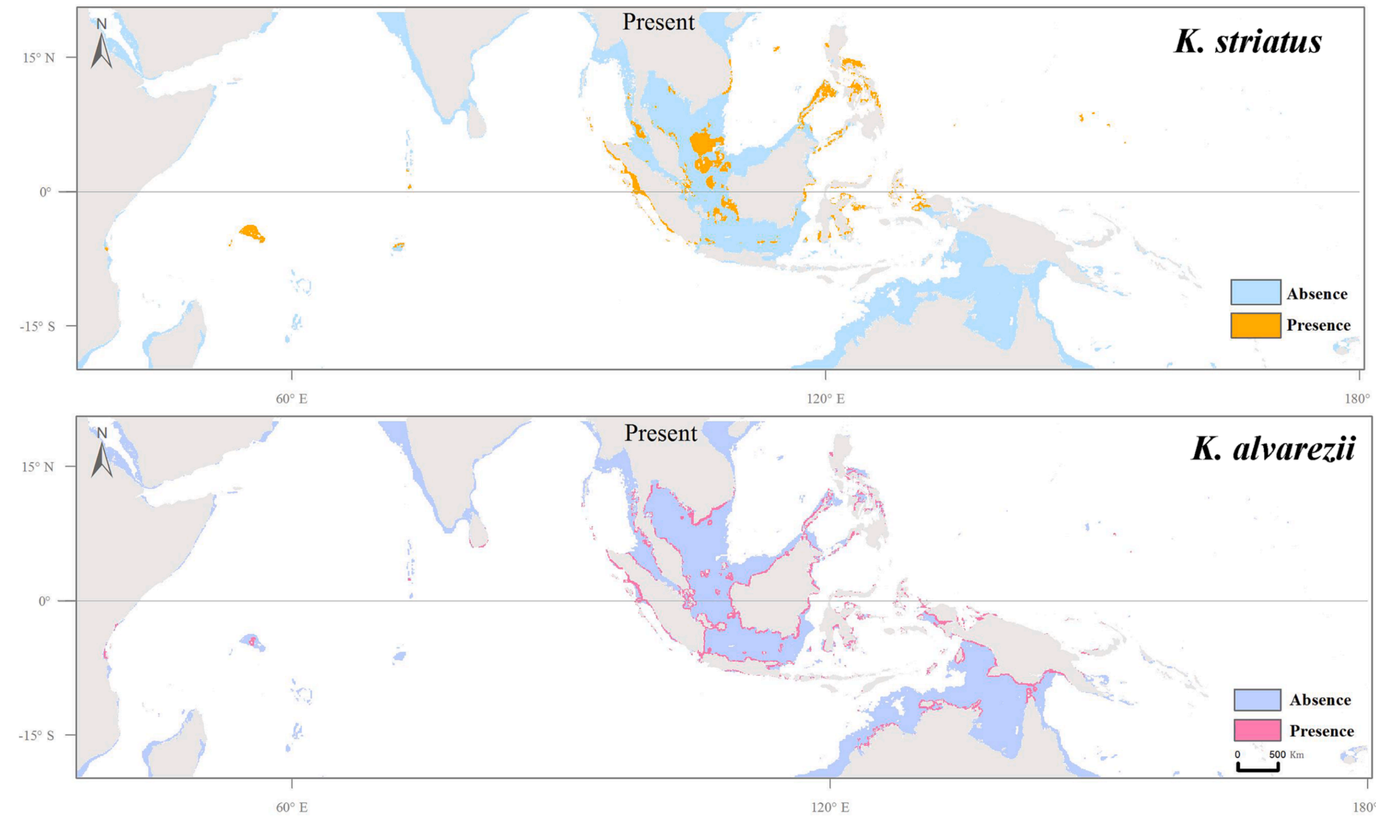

Fig. 2. Binary distribution maps of *K. striatus* and *K. alvarezii* under present-day conditions.

the two *Kappaphycus* sister species unanimously.

4. Discussion

4.1. The two Kappaphycus species show distinct niches

In our study, ecological niche modeling for the two *Kappaphycus* sister species does not conform to the PNC hypothesis, but agreed with the development of significant niche differentiation associated with speciation (Warren et al., 2008). Our present-day model projections show that two *Kappaphycus* species are widely distributed in coastal areas between latitudes 15°S and 15°N, focusing on Indonesia, the Philippines and Malaysia, which is consistent with accessible knowledge. Hayashi et al. (2010) pointed out that these areas provide the greatest potential for expanding tropical seaweed cultivation (IFC, 2003). However, according to our ENM projections, there existed considerable geographical distribution differences between the two species. The hypervolume and ordination techniques also indicated niche divergence between the two *Kappaphycus* species. *K. striatus* can distribute the further distance from shore compared with *K. alvarezii*. Hypothesis tests also implied that the niches of the sister species were rarely identical. Although extensive niche similarities were uncovered in the sister species *Lepus castroviejoi* and *Lepus corsicanus* through ENM (Acevedo et al., 2014) and across three species groups of freshwater fishes in North America (McNyset, 2009), the niche conservatism hypothesis seems to not apply to our pair of sister species. The universality of this hypothesis remains to be tested combined with more relevant studies on other sister species in the future.

Our study illustrated that the low extent of environmental niche overlap between the two *Kappaphycus* species was closely tied to that of geographical overlap (ENM technique reflected). Our results support the conclusion of Warren et al. (2008), in which niche differences allow related species to co-exist in local communities. Moreover, our results on ecological differences between *K. alvarezii* and *K. striatus* are in line with morphological differences (Roleda et al., 2021) and phylogenetic differences (Dumilag et al., 2016; Lim et al., 2014), suggesting that the two species require different management and conservation strategies (see detail in 4.3.).

4.2. Effects of climate change on distributions of Kappaphycus

Future projections indicated that both *Kappaphycus* species would lose suitable habitats by the year 2100 under the RCP 8.5 scenario to a different degree. *K. striatus* is forecast to lose more habitats under two scenarios, while *K. alvarezii* could even expand its habitats under the RCP2.6 scenario until the year 2100. This suggests that *K. alvarezii* might

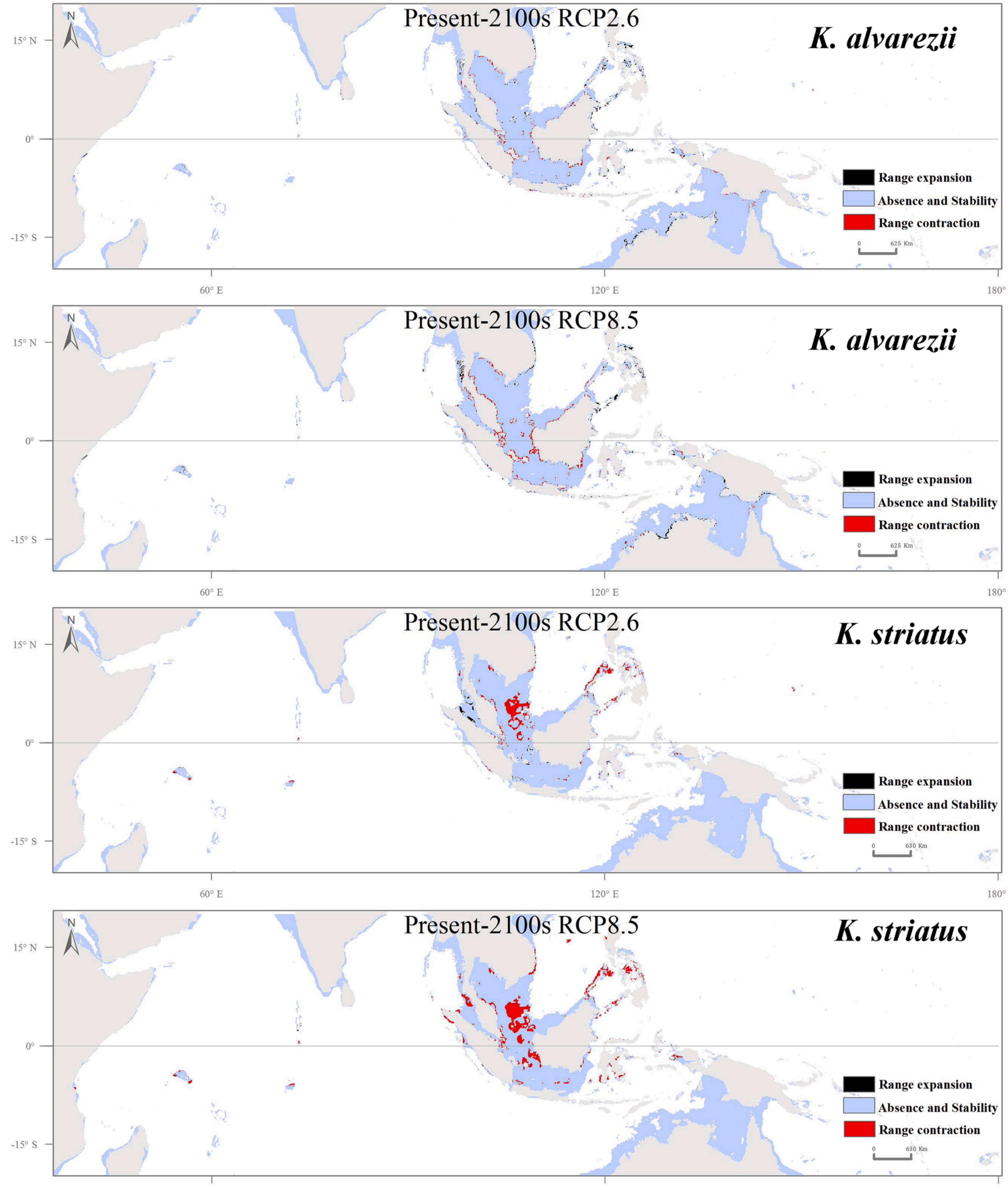

Fig. 3. Range shift maps of *K. alvarezii* and *K. striatus* under two RCP scenarios from present to the 2100 s (2090–2100). RCP: representative concentration pathway.

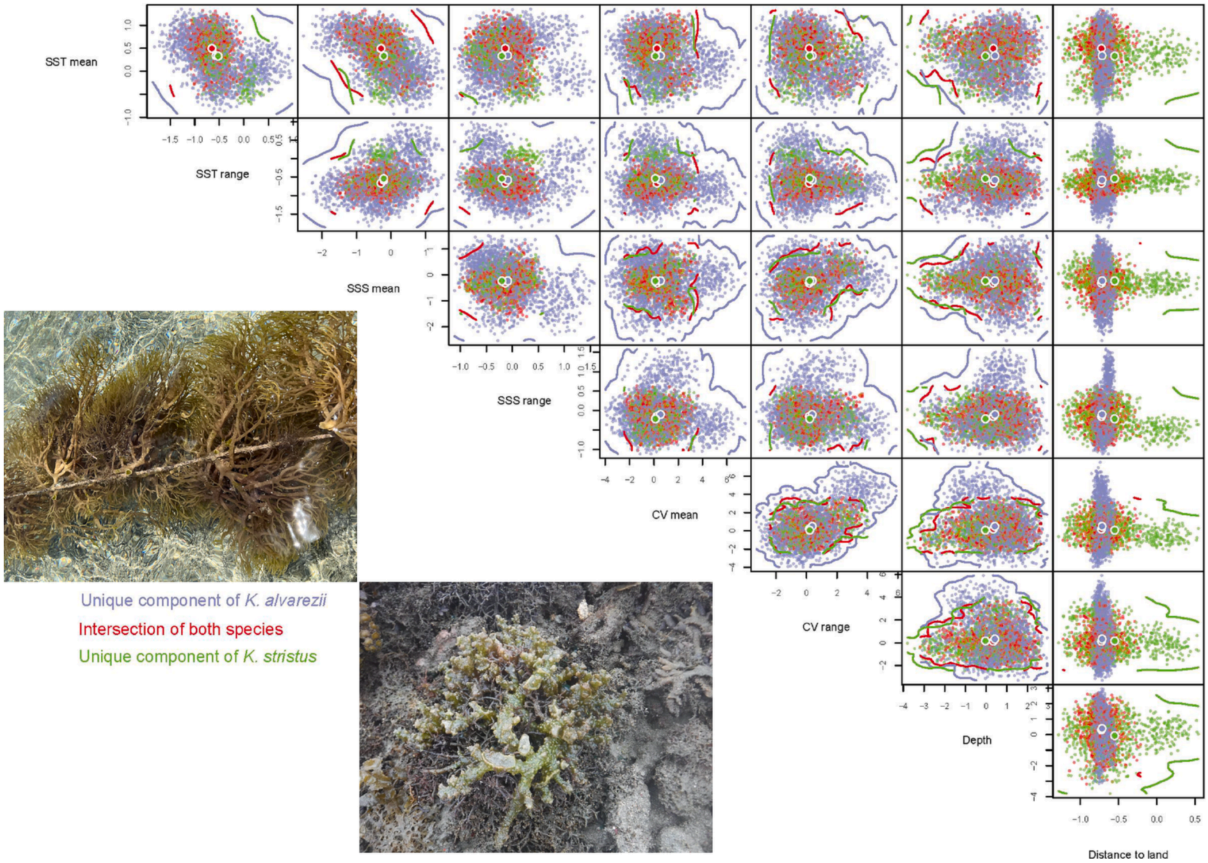

Fig. 4. The eight-dimensional hypervolumes of two *Kappaphycus* species. SST: sea surface temperature; SSS: sea surface salinity; CV: currents velocity; Depth: water depth.

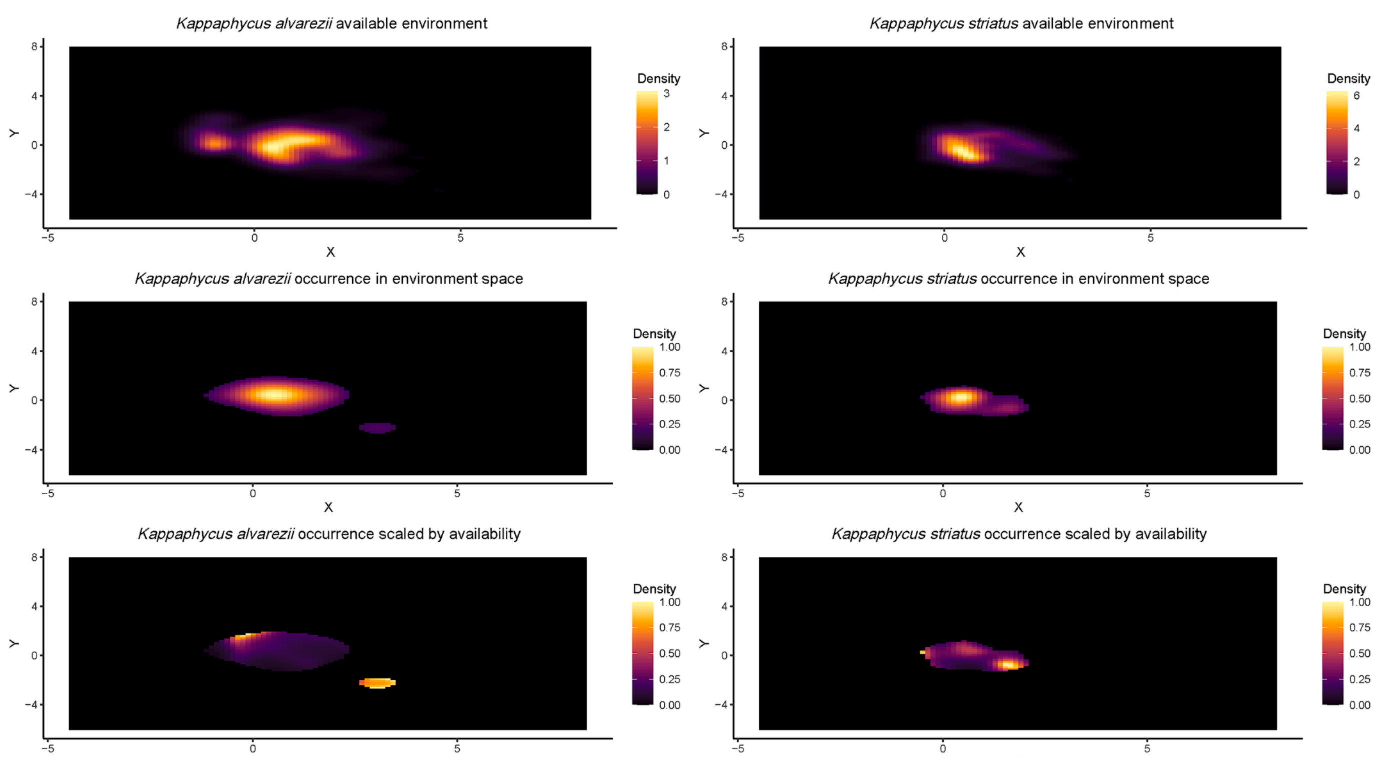

Fig. 5. Two-dimensional environmental space of the two species estimated by kernel density with R package "ecospat". The first-row two graphs indicated the density of the available environment of both *Kappaphycus*, the second-row represented the density of occurrence, and the third indicated the density of occurrence corrected by the available environment.

be more resilient to mild climate change, but remains to be investigated by combining eco-physiological experiments in the future.

Our models project that both *Kappaphycus* species will lose habitats along the coasts of Malaysia and Indonesia in the Central Indo-Pacific Ocean. Our analysis suggests that in the areas of predicted habitat loss, the annual mean of sea surface temperature (SST) is the main factor that has changed most when compared to present-day conditions. Therefore, the rising SST can be considered the main driver for the projected range shift of *Kappaphycus* species. Temperature is regarded as a crucial factor in the growth and photosynthetic performance of eucheumatoids (Kumar et al., 2020). The rising temperature due to climate change could cause eco-physiological and reproductive damage to *Kappaphycus* species and affects their metabolic processes (Bulboa et al., 2008; Largo et al., 1995; 2017; Mtolera et al., 1996). Furthermore, since *K. striatus* is better adapted to the intertidal zone than *K. alvarezii* (Pang et al., 2015), any reduction in coastal areas resulting from climate change-induced sea-level rise could lead to a substantial loss of its natural habitats. Thus, we assumed that the habitat loss could reduce *K. striatus*' production continuously if valid strategies were not taken, such as generating heat-resist strains or cultivars by priming (Jueterbock et al., 2021), gene modifications, breeding for heat-resistance, and other methods.

4.3. Implications for eucheumatoids farming

Our comparative analyses show both *Kappaphycus* species don't overlap their niche in environmental and geographical space. Moreover, they respond differently to environmental change, *K. striatus* is predicted to experience more severe habitat loss than *K. alvarezii* under climate change, suggesting that the two species may require different management strategies. Complementary farming approaches could be considered. For example, the realized niche of *K. striatus* suggests that it could be cultivated further offshore, while *K. alvarezii* is the opposite. In this way, the sea resources can be used effectively. Furthermore, to guarantee the development of eucheumatoids aquaculture, future sea surface temperature changes need to be closely monitored especially at cultivation sites of *K. striatus*, and corresponding mitigation strategies need to be established.

Considering the effect of ocean warming on the distribution of eucheumatoids, planting *K. striatus* in a little deeper water depth could be also regarded as an alternative way to escape the future rising SST. In addition, we suggest that cultivation sites could be moved to higher latitudes in the future. It is necessary to conduct further evaluation and field surveys for ascertaining which area is suitable for *Kappaphycus* in higher-latitude areas. As a tried-and-trusted species in tropical areas (Porse and Rudolph, 2017), *K. striatus* had rare invasive records (Ask et al., 2003; Hurtado et al., 2016). The introduction of *Kappaphycus* strains and cultivars outside its natural range will be a reasonable measure for maintaining the sustainable industry (Hurtado et al., 2019), but policymakers should consider the biological invasion risks. Our study allows us to foresee management changes that are necessary to keep the sustainable and healthy development of eucheumatoids aquaculture in coastal communities and countries.

Our predictions showed a small area of suitable habitats in northern Australia for *K. alvarezii*, but few distribution records have been documented there so far. For future cultivation of *Kappaphycus* in this area, we must conduct fine-scale distribution investigations, and evaluate the habitat availability in these areas. Our predictions demonstrated that under the RCP2.6 scenario, *K. alvarezii* would experience range expansion in the coastal waters of the Philippines, indicating if the carbon dioxide emission gets alleviated effectively in the future, it will expand potential cultivation areas along the coasts of this country for *K. alvarezii*.

Our model predicted the larger suitable natural habitats for *K. striatus* in three major eucheumatoids-producing countries, Indonesia, the Philippines, and Malaysia, in agreement with the situation that *K. striatus* could be farmed much more widely in Southeast countries. Other factors, such as adaptability to seasonal environmental changes and disease resistance, should also be taken into account in the future. Previous studies have shown that *K. striatus* is more resilient to physical and chemical changes, such as UV radiation, high photosynthetically active radiation, desiccation, and salinity fluctuations, as well as the "ice-ice" disease (Pang et al., 2015), which could encourage seaweed farmers to focus on cultivating this species. For instance, observation in Lombok Island and Indonesia revealed that seaweed farmers practice rotational seaweed culture during the peak of dry and wet seasons, in which the elevated seawater temperature and decreasing salinity are more likely to cause "ice-ice" outbreaks (Ward et al., 2021). During this time, *K. striatus* or *Eucheuma spinosum* are more cultivated instead of the susceptible *K. alvarezii*. The same preference of farmers towards *K. striatus* was also reported in the Philippines due to its better resistance to epiphytes and "ice-ice" infestation (Hurtado et al., 2008). Therefore, to achieve more accurate predictions regarding the implications of climate change for eucheumatoids farming, models that incorporate aquaculture-related variables should be developed.

4.4. Model insufficiencies

While the Maxent algorithm remained robust with small sample sizes in our study, the small sampling sizes cause model variability and reduced accuracy (Wisz et al., 2008), which may explain why our models did not reach "excellent" performance. To fully realize ENMs' potential, we have to increase data quality and availability by increasing collection efforts in the future (Cayuela et al., 2009). Furthermore, eucheumatoids' growth is usually affected by various biological factors. For example, other macroalgae (*Ulva pertusa*, *Cladophora*, *Sargassum*, etc.) attach to the *Kappaphycus* thalli, where they compete for light and nutrients (Largo et al., 2017). Besides, some aquatic animals such as sea urchins, sea stars, and surgeon fish bite the fresh eucheumatoid tissues, causing tissues wounds and consequently the prevalence of the "ice-ice" disease (Mateo et al., 2021; Largo et al., 1995). Incorporating such biological interactions in model projections would increase the reliability of predicted habitat shifts.

5. Conclusions

Our study indicated the feasibility of MaxEnt algorithm in modeling the distribution of eucheumatoid, providing a reference to apply this technique to other tropical macroalgae. We uncovered significant niche differences in the geographical and environmental space between the two *Kappaphycus* species by applying a series of methodologies and indicators. Our predictions demonstrated that both *Kappaphycus* species would lose suitable habitats under the RCP 8.5 scenario by the year 2100, attributing to the rising sea surface temperature. *K. striatus* is projected to experience more severe habitat loss than *K. alvarezii*. Whether both *Kappaphycus* species with niche divergence hold distinct adaptive capacities under climate change, requires physiological tests next. Based on our predicted responses to climate change, the two *Kappaphycus* species are likely to require different management and conservation strategies. We proposed measurements to improve ecological niche modeling for cultivated species under the context of climate change, which remain to be conducted next. Our study proved the potential of ENMs to estimate suitable habitats for tropic seaweed and forecast the impact of climate change on their geographical distribution. Our work can provide reference to formulate conservation and management strategies, and insights into the sustainable development of tropical seaweed aquaculture.

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CRediT authorship contribution statement

Yu-Qun Du: Conceptualization, Methodology, Software, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, Visualization. **Alexander Jueterbock:** Writing – review & editing, Visualization, Formal analysis. **Muhammad Firdaus:** Writing – review & editing. **Anicia Q. Hurtado:** Writing – review & editing. **Delin Duan:** Conceptualization, Project administration, Funding acquisition, Supervision, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Data availability statement

Environmental layers can be downloaded from the Global Marine Environment Data sets (http://gmed.auckland.ac.nz) and the Bio-ORACLE database version 2.1 (https://www.bio-oracle.org). Occurrence records of *K. alvarezii* and *K. striatus* are available from online repositories, including the Global Biodiversity Information Facility (http://www.gbif.org), Ocean Biodiversity Information System (https://obis.org), and AquaMap database (https://www.aquamaps.org).

GBIF Occurrence Download 10.15468/dl.sbtrgb Accessed from R via rgbif (https://github.com/ropensci/rgbif) on 2023-02-19.

GBIF Occurrence Download 10.15468/dl.zw9a24 Accessed from R via rgbif (https://github.com/ropensci/rgbif) on 2023-02-18.

Appendix A. Supplementary data

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