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LETTER

Global estimates of suitable areas for marine algae farming

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Abstract

Marine algae, both macro and micro, have gained increasing attention for their numerous ecosystem service functions, such as food and raw materials provision and climate change mitigation. Currently, the practice of large-scale algae farming is limited to Asian waters, but significant interest has arisen from other continents. However, there is a lack of knowledge about the areas with suitable environmental conditions for expanding algae farming on a global scale. Previous studies have primarily focused on nutrient availability and thermal constraints when assessing the potential for algae culture. This study uses species distribution models based on an ensemble consensus approach to determine the extent of suitable areas and takes into account multiple environmental factors that may affect the feasibility of algae culture. Our results show that approximately 20.8 million km^2 of the ocean ($\sim$13.8% of the economic exclusive zones) is suitable for farming marine algae species, with most potential areas located near the coastline. Surprisingly, four out of the top five countries with the largest area suitable for seaweed farming, including Australia, Russia, Canada, and the US, account for 30% of the total suitable areas, yet they currently produce less than 1% of the global seaweed. Several species show promising characteristics for large-scale cultivation, but their viability for commercial production remains uncertain and subject to further assessment of economic feasibility and social acceptance. Further research on the ecological benefits of seaweed farming could also promote the development of an ecologically friendly and financially viable algae mariculture industry. This study provides a scientific basis for decision-makers to understand potential expansion areas and feasible pathways for seaweed farming, with the ultimate goal of ensuring the sustainable utilization of marine resources.

1. Introduction

With the growth and diversification of the global market for algal or macroalgal products, algae, including seaweeds (macroalgae), comprise more than 20% of total aquaculture production biomass. Algal cultivation is growing rapidly (approximately 8% per year) compared with other farmed species (Buschmann *et al* 2017, FAO 2020). In 2018, 3.2 million tons (Mt) of seaweed (dry weight) was harvested globally, an increase of 50% compared to 2010 (FAO 2020). Although most farming today occurs in the coastal areas of Asian countries, mainly China and Indonesia, technologies for offshore farming are emerging (Bak *et al* 2018, Buck *et al* 2018, Azevedo *et al* 2019, Navarrete *et al* 2021). Furthermore, there is an increasing interest in macroalgal mariculture in the Western hemisphere owing to its potential economic, social, and ecological benefits (Broch *et al* 2019).

For terrestrial environments, there is a growing recognition that natural and modified landscapes, like some agriculture systems, can provide ecosystem services that extend beyond the provision of food and raw materials (DeClerck *et al* 2010, Power 2010). The same recognition has been occurring with respect to mariculture, particularly seaweed farming (Alleway *et al* 2019). In contrast to terrestrial biomass production, seaweed farming does not require arable land or

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freshwater. Moreover, cultivated seaweed can be used for biofuel production (Milledge *et al* 2014, Michalak 2018, Sharmila *et al* 2021), animal feed (Wan *et al* 2019, Vijn *et al* 2020, Roque *et al* 2021), and bioremediation (He *et al* 2008, Huo *et al* 2011, Xiao *et al* 2017, Jiang *et al* 2020) while also providing other ecosystem services such as water quality regulation and habitat provision for wild species (Ferreira *et al* 2021). Offshore macroalgal farming has the potential to contribute to energy security and reduce greenhouse gas emissions through biofuel production, and to provide low-emission alternatives for industries as diverse as textiles, bioplastics, and fertilizers. Large-scale seaweed cultivation and sinking of the resulting biomass is also being evaluated as a strategy for ocean-based carbon sequestration (Froehlich *et al* 2019). In addition, seaweed cultivation can be implemented in eutrophic environments (Rose *et al* 2015, Xiao *et al* 2017), a condition that may cause significant environmental and economic damages (McCrackin *et al* 2017). Since seaweed mariculture can naturally abate nutrient over-enrichment in coastal systems (Kanter *et al* 2020, Xu *et al* 2023), the added value of nutrient sequestration may increase the economic viability of seaweed farming in such locations (Zollmann *et al* 2021). It is also worth noting that the infrastructure for seaweed cultivation may also provide artificial habitat for fish and other high trophic-level marine species, thus potentially contributing to marine biodiversity through indirect pathways (Corrigan *et al* 2022). While there is potential to build a thriving marine biomass industry (Duarte *et al* 2017), massive cultivation is still in its infancy and many barriers to sustainable algae development remain (Fernand *et al* 2017, Campbell *et al* 2019).

Given the significant contribution of algae farming to food security, biodiversity conservation and climate mitigation, information on areas potentially suitable for mariculture is essential for rational and coordinated planning of ocean-based activities (e.g. energy production, shipping, marine protected areas (MPAs)) (Edgar *et al* 2014, Venter *et al* 2014). Ocean-based mariculture operations generally use open facilities, meaning farmed organisms are exposed to natural environmental conditions. Therefore, the health of the local marine environment strongly affects mariculture production. Areas with suitable environmental conditions for mariculture are generally defined as areas of the ocean that can support the physical needs of farmed species for sustainable production (Tidwell and Allan 2001, Oyinlola *et al* 2018). Previous research estimated the potential for global seaweed cultivation based only on nitrogen-to-phosphorous ratio and suitable temperatures for various seaweed species (Froehlich *et al* 2019) or species-specified bio-physical thresholds which requires detailed biological parameters of given species (Cabral *et al* 2016). Species distribution models (SDMs), which consider a variety of additional environmental parameters using field data, can be used to further approximate and refine the environmental preferences of algal species and areas suitable for mariculture (Wiltshire and Tanner 2020).

Based on the environmental niche theory (Hutchinson 1959), SDMs consist of quantitatively describing the relationship between the observed occurrence of a species and various parameters that define its environment. Such a relationship can be developed using historical occurrence records of the species in both natural and farmed environments. SDMs can be applied to predict species distributions in the past, present, and future (Guisan and Zimmermann 2000, Elith and Leathwick 2009, Oyinlola *et al* 2022), and are considered particularly well-suited for modeling marine poikilothermic animals whose spatial distribution is closely linked to environmental conditions (Cheung *et al* 2010, Wabnitz *et al* 2018). SDMs have been widely used for estimating the potential suitable environment for not only terrestrial plants (Tshwene-Mauchaza and Aguirre-Gutiérrez 2019, McMahon *et al* 2021) but also marine plants (Jayathilake and Costello 2018, 2020). While SDMs have also been adopted for modeling the cultivation potential for farmed marine fish and bivalves (Oyinlola *et al* 2018, 2022), the use of SDMs for modeling algae farming potential has been rare.

This study aimed to predict the spatial extent of areas that are environmentally suitable for marine algae cultivation globally. We fitted SDMs to 21 currently commercially farmed seaweed species using four commonly used algorithms to quantify the environmental niche of these important farmed species. Based on current environmental conditions, we then projected a habitat suitability index (HSI) over the global ocean. The rapid development of offshore seaweed farming technologies has led us to consider not only coastal areas but also open water environments that may be suitable for seaweed farming. Observational data were resampled and fitted using a ten-fold cross-validation method to obtain results for each individual model. An ensemble model across algorithms was then generated to find suitable farming areas agreed upon across all models. Based on the predicted range of suitability, we calculated the total area of the global marine waters suitable for seaweed farming and mapped it to the exclusive economic zones (EEZs). We also discussed the implications of our results for the future development of seaweed cultivation, the reasons for its current limited scale, and strategies to realize the potential of seaweed farming.

2. Methodology

2.1. Biotic data

We obtained a list of farmed species from the Food and Agriculture Organization (FAO) database

Table 1. List of seaweed species included in this study.

ISSCAAP name	WRoMS-scientific name	N. of records
Alaria esculenta	*Alaria esculenta*	588
Capsosiphon fulvescens	*Capsosiphon fulvescens*	68
Caulerpa racemosa	*Caulerpa racemosa*	1174
Chondracanthus chamissoi	*Chondracanthus chamissoi*	9
Codium fragile	*Codium fragile*	311
Eucheuma denticulatum	*Eucheuma denticulatum*	99
Gelidium amansii	*Gelidium amansii*	51
Gracilaria gracilis	*Gracilaria gracilis*	231
Gracilaria verrucosa	*Gracilariopsis longissima*	229
Kappaphycus alvarezii	*Kappaphycus alvarezii*	34
Laminaria digitata	*Laminaria digitata*	1192
Macrocystis integrifolia	*Macrocystis pyrifera*	536
Monostroma nitidum	*Monostroma nitidum*	34
Palmaria palmata	*Palmaria palmata*	1352
Pyropia columbina	*Pyropia columbina*	17
Pyropia tenera	*Pyropia tenera*	5
Laminaria japonica	*Saccharina japonica*	478
Saccharina latissima	*Saccharina latissima*	1675
Sargassum fusiforme	*Sargassum fusiforme*	199
Enteromorpha prolifera	*Ulva prolifera*	450
Undaria pinnatifida	*Undaria pinnatifida*	591

(FAO 2022b), a nearly comprehensive dataset on the global production of capture fisheries and aquaculture, to ensure that the seaweed species included in our analysis represent those which are practically and commercially feasible for the industry. FAO records without species-level information (i.e. designated genus and species) were excluded from our analysis. Therefore, this study focused on 21 seaweed species.

To obtain a representative spatial distribution of each farmed species and quantify its environmental niche, we constructed a database combining two natural occurrence records for all 21 species from two open source databases: Ocean Biogeographic Information System (www.iobis.org/), and Global Biodiversity Information Facility (www.gbif.org/). For each species, taxonomic names were reconciled using the World Register of Marine Species (Horton *et al* 2017). Duplicate records of occurrence between databases and records for which geographic information was unavailable were removed. The final format of the species occurrence and location database was a list of presence-only points of observed locations for all species included in this study (table 1). In addition, we excluded duplicate records that belonged to the same grid cell.

2.2. Environmental data

Following general guidance on seaweed and seagrass distribution modeling (Jayathilake and Costello 2018, 2020), we collected 12 abiotic variables associated with seaweed distribution. The natural distribution of seaweed can be directly or indirectly affected by depth, distance from land, salinity, diffuse attenuation coefficient, sea surface temperature, pH, photosynthetically active radiation, wave height, dissolved oxygen, and nitrate (Jayathilake and Costello 2018, 2020). In this study, we assumed that an environment suitable for algae growth is naturally ideal for farming, while disregarding any artificial interventions (e.g. fertilization) that might alter the naturally unsuitable settings to suit the cultivation conditions. The environmental data used for modeling in this study were obtained from the Bio-oracle (version 2.2, www.bio-oracle.org/index.php) and Global Marine Environment Datasets (https://gmed.auckland.acnz) (table 2), both of which represent decades of calculated annual averages, thus indicating long-term persistent features of the environment (Tyberghein *et al* 2012, Assis *et al* 2018, Basher *et al* 2018). All environmental data layers had a 5 arc min (0.083° grid cell) resolution, approximately 9.2 km at the equator.

2.3. Model algorithms

Algorithms for SDM modeling can be classified into two main categories: (1) process-based (PB, or mechanistic) models and (2) niche-based (NB, or correlative) models (Elith and Leathwick 2009, Kearney and Porter 2009). PB models depend on physiological information about a species gained through controlled field or laboratory studies to determine the range of environmental conditions under which the species can persist. They provide the 'fundamental niche' for a species, i.e. the niche defined only by abiotic environmental variables, under which individuals of a species can live and reproduce without being constrained by any biotic interactions. NB models treat the observed distribution of a species as a function of geographically referenced

Table 2. List of environmental variables used in this study.

Layers	Unit	Data source
Bathymetry	M	Bio-Oracle V2.2
Land distance	km $\times$ 100	GMED
Salinity (mean)	PSS	Bio-Oracle V2.2
Sea surface diffuse attenuation coefficient (mean)	m^{-1}	Bio-Oracle V2.2
Sea surface temperature (maximum)	°C	Bio-Oracle V2.2
Sea surface temperature (mean)	°C	Bio-Oracle V2.2
pH	—	Bio-Oracle V2.2
Photosynthetically active radiation (mean)	Einstein m^{-2} d^{-1}	Bio-Oracle V2.2
Wave height	M	GMED
Sea surface dissolved oxygen (mean)	ml l^{-1}	Bio-Oracle V2.2
Phosphate (mean)	ml l^{-1}	Bio-Oracle V2.2
Sea surface nitrate (mean)	μmol l^{-1}	Bio-Oracle V2.2

environmental predictor variables using multiple regression approaches. Thus, NB models provide a more realistic representation of potentially suitable seaweed cultivation areas than PB models.

In this study, we selected four different NB modeling approaches chosen from all three categories of NB techniques, including (1) profile method—BIOCLIM; (2) regression method—Genaralized Linear Model (GLM); and (3) machine learning methods—MAXENT and MAXNET. BIOCLIM is an envelope-style approach to identify sites whose environments are similar to existing observations (Elith *et al* 2006). GLMs and other regression models have been used extensively in species distribution modeling because of their statistical solid basis and ability to model ecological relationships realistically (Austin 2002). MAXENT estimates species distribution by finding the distribution of maximum entropy (i.e. closest to a uniform distribution) subject to the constraint that the expected value of each environmental variable (or its transform and/or interactions) under this estimated distribution matches its empirical mean (Phillips *et al* 2006). MAXNET is a new, alternative implementation of MAXENT (Phillips *et al* 2017), motivated by new understandings of the connection between MAXENT and Poisson point process models (Renner and Warton 2013). It uses infinitely weighted logistic regression (Fithian and Hastie 2013) to fit the MAXENT model with potentially more flexible fitted functions (via transformed features) (Valavi *et al* 2022).

2.4. Modeling process

For this study, each model for each cultivated species was generated individually, using ten cross-validated iterative runs of ten partitions with a maximum of 10 000 pseudoabsence background points randomly sampled from a pre-defined 4 km buffer area around each species' occurrence point. Thus, 100 runs for each of the four SDM algorithms were generated and then combined using a consensus ensemble approach (hereafter 'consensus approach') of each algorithm for each model (Araújo and New 2007). The consensuses of all four algorithms were combined using the consensus approach again to generate the final suitable area map of all analyzed species using a consensus threshold of 0.5. All algorithms were implemented using the default parameters provided by the software without further tuning due to the advantages specific to the consensus approach (which will be described below in the section 4).

2.5. Model testing

Model performance was assessed using the receiver operating characteristic (ROC) (Phillips *et al* 2006). The area under the curve (AUC) of ROC values between 0 and 0.5 indicates that predictions are no better than random, and a value of 1 gives the best prediction (Phillips *et al* 2006, Elith *et al* 2011). Since there are multiple runs for each model algorithm for each species, the distribution of AUC values across single runs was checked carefully to ensure that most runs for a species had an AUC value above 0.5.

2.6. Identifying potential seaweed farming areas

Our criterion for defining potential seaweed farming areas was the predicted consensus results of all algorithms. This result may be quite similar to the natural distribution of seaweed species. Ideally, the location of currently implemented farming infrastructure should be included in the biotic dataset to identify suitable farming areas (Oyinlola *et al* 2018). However, geospatial data on seaweed farming locations are lacking (Oyinlola *et al* 2018), and the rapid development of offshore seaweed farming technologies ensures that suitable environmental conditions for natural seaweed species would suit farming, so the limitations imposed by infrastructure were not considered as a problem in this study and were ignored (Froehlich *et al* 2019). Meanwhile, invasive species have always been a problem that plagues mariculture (Diana 2009, Naylor *et al* 2021). The area suitable for mariculture and the natural distribution area of a species are highly correlated (Oyinlola *et al* 2018). Based on these considerations, information on the location of seaweed mariculture was ignored under the assumption that technology improvements could make all areas environmentally suitable for growing seaweed. Finally, the richness (number of species could be farming in the area) and hotspots of seaweed mariculture were identified, providing an overall picture for global seaweed farming opportunities (Oyinlola *et al* 2018). The total area of the global marine waters suitable for seaweed farming was calculated and mapped to the EEZs.

2.7. Software used

All data processing was performed on the R computation platform (R Core Team 2022). The major SDMs modeling processes were based on the *modleR* package (Sánchez-Tapia *et al* 2020). The processing and aggregation of spatial data were based on the implementation of the *terra* package (Hijmans *et al* 2022).

3. Results

3.1. Model performance

Across all SDMs, most models had AUC values above 0.7 (figure 1(A)). For different SDMs, the BIOCLIM model performed poorly across different runs and species, while GLM, Maxent, and Maxnet models had similarly better performances. Among all species, SDMs predictions for most species performed well with high AUC values (figure 1(B)). The models were then combined using the consensus method for the prediction of suitable seaweed mariculture areas.

3.2. Predicted seaweed mariculture richness

Our results showed that approximately 20.8 million km^2 of ocean area was suitable for seaweed mariculture globally. It was estimated that nearly all coastal and nearshore areas were suitable for growing one or more seaweed species (figure 2). However, the center of the Bering Sea appeared to be suitable for farming only a few seaweed species. Hotspots for potential mariculture of seaweed occurred in temperate near-coast waters (figures 2 and S1). The coastal waters around the North Sea and the UK, Northeast Asia, Southern Australia, New Zealand, the east coast of the United States, the west coast of Canada, and coastal areas of central South America near Chile and Argentina represented the farming potential hotspots in Europe, Asia, Oceania, North America, and South America. These hotspots can allow for the cultivation of diverse seaweed species, which provide a greater range of options for local practitioners.

In addition, our model detected some suitable areas in tropical regions such as the Caribbean coasts, where seaweed farming already takes place naturally. These areas cover approximately 355 900 km^2 of the Caribbean Sea, which accounts for approximately 20% of all Caribbean countries' EEZ. However, as these areas are relatively small, they may not be clearly visible in the figure (see supplemental figure S2 for more information regarding the Caribbean coasts).

3.3. Comparison of suitable farming areas for different seaweed species

We individually examined the consensus results for all species to summarize their distinguishing features (figure S3). Most seaweed mariculture species appeared to be suitable for cultivation in most coastal oceans worldwide. In contrast, some species, such as *Capsosiphon fulvescens* and *Sargassum fusiforme*, were only suitable for farming in a specific latitudinal range. We compared the suitable areas for all analyzed species and found that *Eucheuma denticulatum* and *Caulerpa racemosa* had the largest suitable farming area (figure 3(A)). However, considering the algorithm uncertainty, *Saccharina japonica* may be the species with the largest suitable farming area, followed by *E. denticulatum* and *C. racemosa*. In addition, *Pyropia tenera* was estimated to be eligible for farming in low and mid-latitude regions with a relatively sizeable area. The estimated suitable farming area for *E. denticulatum, C. racemosa, S. japonica, M. nitidum*, and *P. tenera* varied dramatically across the different algorithms. This may indicate that these species have a wider range of ecological niches than the others. However, except for *S. japonica*, these other species are currently at very low yields (figure 3(B)). This situation also occurred for other farmable species with meaningful suitable farming areas. These results suggest species that are currently underproduced may have great potential for mariculture.

3.4. Country-level comparisons

Scientifically assessing how much of one nation's EEZ is suitable for seaweed farming can help local authorities and practitioners in their decision-making. Therefore, we calculated the proportion of each country's EEZ suitable for seaweed farming to evaluate the potential for expanding seaweed farming in each country. In general, countries along the Baltic, North Sea, and Mediterranean coasts showed a high proportion of areas suitable for seaweed farming in their EEZs (figure 4(A)). As expected, East Asian countries had a relatively high proportion of EEZs suitable for seaweed farming. Australia, Indonesia, Russia, Canada, and the United States had a larger absolute area suitable for seaweed farming than other countries. Among them, Australia had the largest absolute area suitable for seaweed farming with over 2 million km^2 (figure 4(B)).

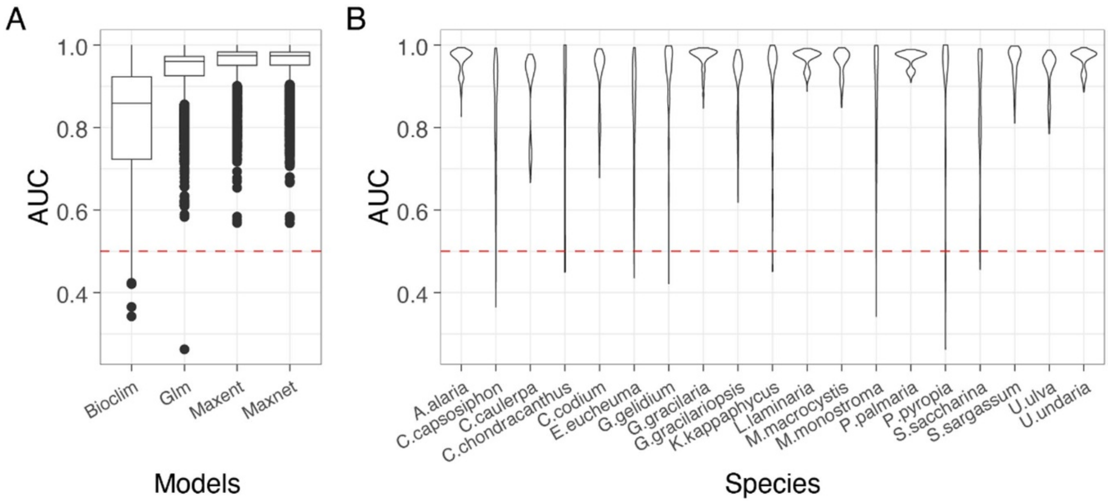

Figure 1. Prediction evaluation of each species distribution model (SDM) used in the analysis. (A) Areas under the curve (AUC) for different SDM algorithms, regardless of seaweed species; (B) AUC for different seaweed species, regardless of algorithms. AUC values above 0.5 indicate fair predictions.

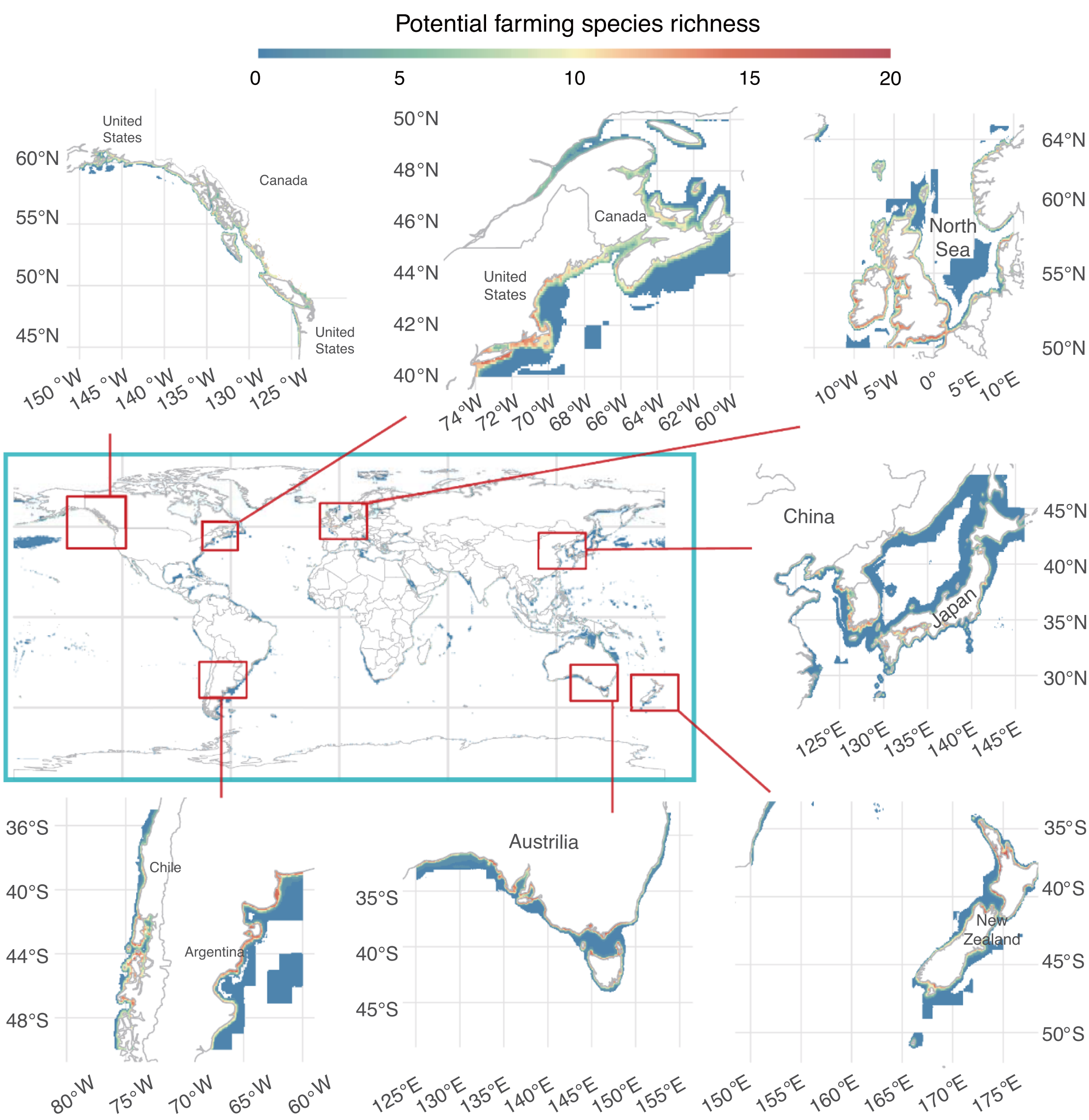

Figure 2. Predicted global farming species richness potential and farming potential hotspots (in red rectangular).

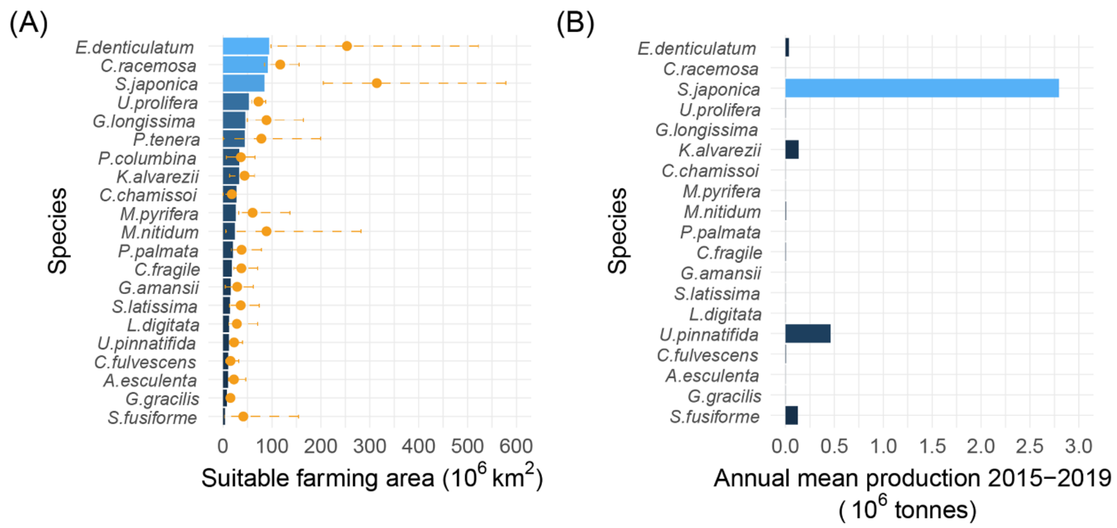

Figure 3. Estimated suitable farming areas by species (A) and current production corresponding to each species (B). Consensus results are shown as bars, while the average areas of the different algorithms are shown as orange dots. The orange dashed error bars represent the maximum and minimum estimated areas for the different algorithms.

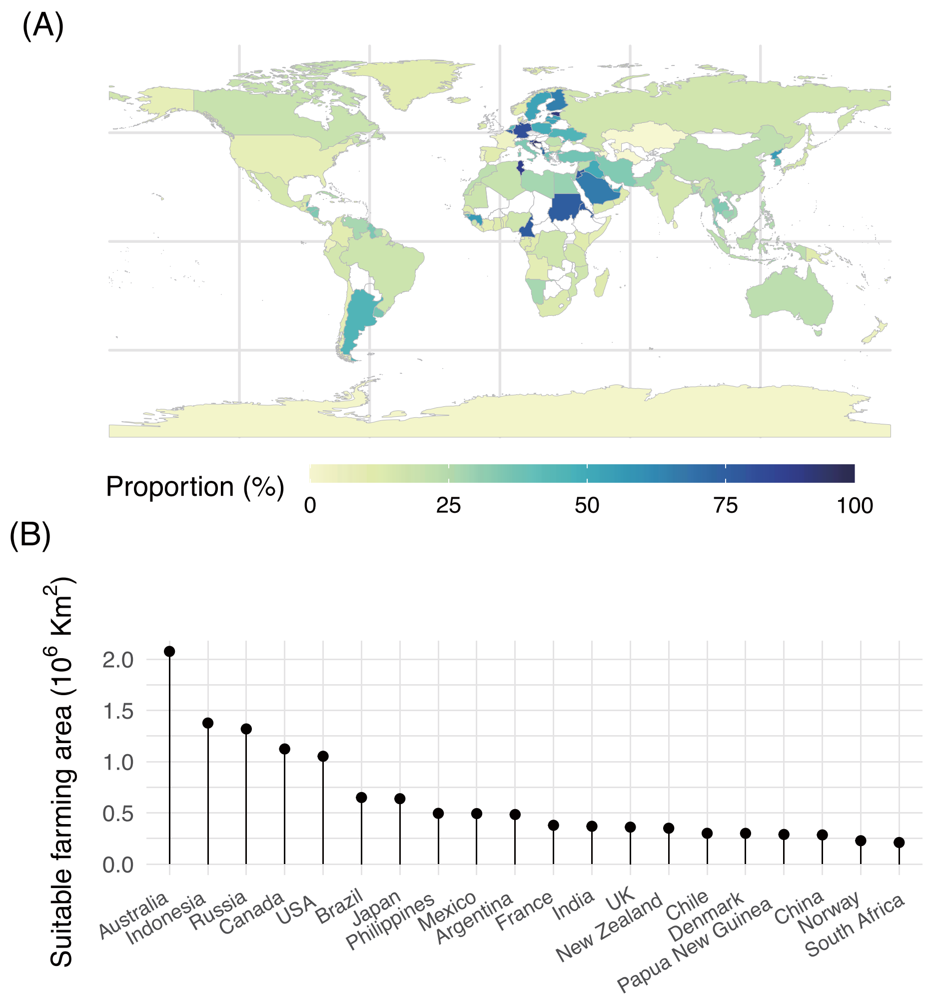

Figure 4. Comparison of estimated suitable seaweed farming areas at the national level. (A) Proportion of EEZs in each country; (B) top 20 countries with the largest absolute suitable farming areas.

4. Discussion

4.1. Model selection and performance

Understanding current trends and predicting future distributions of species is pivotal for the implementation of biodiversity conservation measures, and the same considerations are also essential for estimating mariculture potential. Often, knowing the ecological niche of the species of interest is the core method for both workflows. The term 'ecological niche' was initially vaguely defined and used to describe the ecological position, habitat, and requirements of a species (Takola and Schielzeth 2022). Hutchinson proposed the most popular and widely cited definition of ecological niche as an abstract n-dimensional environmental space that allows a population to persist indefinitely (Hutchinson 1957, 1978). Based on this theory, SDMs have been further developed as a method to map suitable locations for species occurrence. They generate a model to represent the 'ecological niche' of the species, which can be implemented under current or future environmental conditions to estimate the environmental suitability of species occurrence (Wiens *et al* 2009). Due to the dependency of fish and bivalves on the local marine environment, SDMs have already been used to identify areas suitable for farming these animals. For marine algae, the areas suitable for farming have only been estimated using the thermal tolerance and nutrient limitations of the species (Froehlich *et al* 2019). To fill this gap, this study used SDMs with a comprehensive set of limiting factors to provide a more realistic estimate of potential seaweed farming areas.

Regardless of the modeling approach chosen, the results and accuracy of SDMs may vary across different datasets and algorithms. To avoid these natural limitations, we implemented an ensemble-consensus modeling workflow. Introduced to statistical mechanics by Gibbs in 1878, an ensemble is an idealized, one-time consideration consisting of a large number (possibly infinite) of copies of a system, each representing a possible state that the natural system might be in at a particular time (Araújo and New 2007). This study implemented an ensemble approach based on ten-fold cross-validation to avoid variability between different input sample datasets. Each algorithm fitted ten realizations of initial samples (by ten-fold cross-validation) to obtain the final ensemble predictions (Prasad *et al* 2006). Instead of selecting the 'best' model from an ensemble or carefully tuning hyperparameters, a more promising approach is to explore the resulting range of projections (Araújo and New 2007). Due to the limitation of the relatively small dataset and ensemble size, we chose to define a 'bounding box' with a HSI greater than 0.5, estimated from the ensemble of each algorithm. This approach provided a conservative prediction of the areas suitable for seaweed farming.

This ensemble consensus workflow can avoid one of the significant problems in the species distribution assessment, namely that the true results are not precisely known (Elith *et al* 2006). The consensus input datasets and algorithms in this study provided a conservative result for habitats suitable for farming of a particular species, which can be interpreted as the area most similar to the environment in which the species naturally occurs. Although the true presence/absence of the species in this suitable area is challenging to prove, mariculture potential still exists in this area, as the species could be introduced by humans rather than naturally.

Our estimated global areas suitable for seaweed farming and hotspots occurred mainly nearshore, which was in line with current knowledge. However, potential does not mean the same thing as productivity. Our ensemble consensus approach provided a conservative estimate. Still, the production or yield potential of seaweed farming should be evaluated not only by spatial analysis but also by models that consider seaweed growth mechanisms. The main goal of this study was to demonstrate that future work on seaweed farming potential should consider not only nutrient supply but also other natural environmental factors that may limit seaweed growth. We were also fully aware that seaweed farming in offshore waters is only feasible through advances in farming technology. In this study, we capped ourselves to finding natural habitats suitable for seaweed farming, ignoring human intervention and species currently farmed but not recorded to contain their exact scientific names. The results obtained by our approach were relatively conservative but may inspire future studies.

4.2. Expansion of seaweed farming

Our results revealed that Australia has the greatest area suitable for seaweed farming, followed by Indonesia, Russia, Canada, and the United States. However, for the seaweed species we studied, China had the most outstanding production, followed by the Philippines, Korea, Malaysia, and Japan (figure 5). It is a paradox that countries with the largest area suitable for seaweed farming are not currently producing much seaweed. Australia, Russia, Canada, and the US, together account for 30% of the total suitable areas, yet they currently produce less than 1% of the global seaweed. The implementation of commercial seaweed cultivation in these countries is limited, not only because of the lack of farming traditions and underdeveloped markets, but also because of questionable economic viability (Radulovich *et al* 2015). This situation is unlikely to change in the short term, posing a challenge to the future expansion of seaweed farming.

While many seaweed species seemed suitable for farming globally, yields may be more difficult to predict. *S. japonica* has demonstrated remarkable productivity, while the farming of other species is still

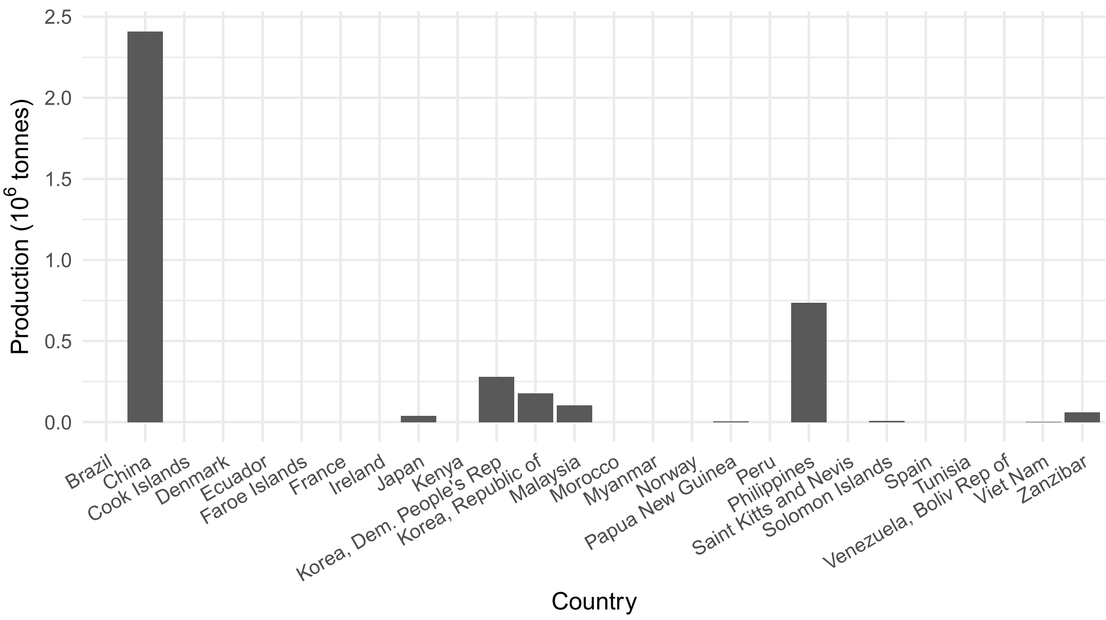

Figure 5. Annual average production of seaweed by country. Note that countries with very low production are difficult to be shown.

in the initial development stage. Our study suggests that *E. denticulatum* has the greatest farming potential spatially, but its yield is currently not comparable to its potential. *E. denticulatum* is widely used as a raw material for Iota-type carrageenan (Krstonošić *et al* 2021). Additional market and feasibility studies are needed to realize its farming potential in practice.

Despite the estimated large number of suitable areas around the world and the vast potential for aquaculture, seaweed farming remains concentrated in a few Asian countries. According to FAO, major seaweed farming countries include China, Indonesia, South Korea, Philippines, North Korea, and Japan, accounting for approximately 97% of global production. Of these, only a few countries including China, South Korea, Japan, Indonesia, and the Philippines consume seaweed or seaweed products directly as human food or food ingredients (FAO 2022a) (table S1), while many others use seaweed primarily for non-food purposes (Tiwari and Troy 2015). Outside of Asia, the U.S. state of Hawaii has a long tradition of eating seaweeds and poke restaurants serving seaweed along with seaweed salads and nori-based sushi (Abbott 1978, Soegiarto and Sulustijo 1990, Montaño 2002). In the EU, seaweed is primarily utilized for the commercial production of food and non-food additives, such as alginates (Tiwari and Troy 2015). In addition, the trade volume of major seaweed producers is not commensurate with its vast production quantity. For example, China is the largest importer of seaweed, while Indonesia is the largest exporter of seaweed. In 2019, China imported only 0.27 mmt and Indonesia only exported 0.18 mmt of seaweed, but their production was 17.7 and 9.8 million metric tons, respectively. The above facts reveal that the market for seaweed in these large producing countries is limited to domestic use. In contrast, according to our analysis, Australia has the largest ideally suitable seaweed farming area, but its seaweed production accounts for only 15.6% of its domestic use (all for non-food purposes), and its seaweed demand is mainly met through trade. Barriers to realizing the full potential of seaweed farming in high-potential countries like Australia include: (1) technical challenges in offshore seaweed cultivation; (2) negative perceptions of mariculture that ignore the environmental benefits of seaweed aquaculture; (3) hurdles to obtaining licenses or permits for seaweed farming; (4) disconnect between production, research and innovation; and (5) lack of market incentives and monetary compensation for the ecosystem benefits of seaweed farming (Duarte *et al* 2022). Overcoming these barriers requires extensive cooperation between academia, industry, market operators and entrepreneurs, communicators, authorities, and decision-makers. Expanding the use of seaweed in energy and other sectors (e.g. using red seaweed to make high-quality paper products) will also help incentivize seaweed farming and enhance economic profitability (Goh and Lee 2010, Seo *et al* 2010). Further, the potential ecological benefits of seaweed will be a throttle to realize their farming potential, for example, by promoting seaweed farming as a nature-based solution to climate change or eutrophication problems.

4.3. Opportunities and potential risks of seaweed farming

Modified and natural landscapes offer ecosystem services beyond providing food and raw materials, with novel applications presenting opportunities for seaweed farming to expand for ecosystem functions and surpass conventional economic considerations. The inorganic nutrient removal effect of red seaweed has been proved in an *in-situ* trial in China (He *et al* 2008). Regional programs have identified seaweed aquaculture as a natural absorber of over-enriched nutrients and a method for eutrophication mitigation to abate nutrient over-enrichment in coastal ecosystems (Kanter *et al* 2020) (e.g. the Mediterranean Action Plan). Other studies suggest that although the climate mitigation effect of seaweed farming may not offset all human activities, seaweed farming remains a viable option for regional and local climate mitigation plans (Froehlich *et al* 2019). This evidence indicates that the expansion potential of seaweed farming should be evaluated not only based on the economic benefits but also from an ecological perspective. Scientific and feasibility assessments of algae culture from an ecological point of view can help achieve the goal of ecological civilization that benefits humanity.

Criteria such as conflicts with MPAs and the strength of existing mariculture infrastructure were traditionally considered when estimating potential farming areas (Oyinlola *et al* 2018). However, stable ocean environments and valuable ecosystem services may render these criteria less important. Stable ocean environments facilitate infrastructure deployment, and seaweed farming's ecosystem values could enable farming activities in multi-purpose MPAs. Despite the growing importance of seaweed farming for food, feed, cosmetics, pharmaceuticals, and increasing global production (7% annual increase in harvested biomass between 2000 and 2016) (Aldridge *et al* 2021), mariculture currently represents only 0.4% of the total macroalgae carbon capture. Therefore, seaweed mariculture has significant untapped potential for carbon sequestration, nutrient mitigation, and providing habitat services to wild species (Chopin *et al* 2001, Fei 2004, He *et al* 2008, Sanderson *et al* 2012, Wang *et al* 2014, Fossberg *et al* 2018, Alleway *et al* 2019). A comprehensive assessment methodology is needed to evaluate seaweed farming's economic, social, and environmental viability to further assess the potential of seaweed farming in multi-purpose MPAs.

While seaweed mariculture has the potential to provide numerous ecosystem services and benefits, it should acknowledge that large-scale expansion of seaweed aquaculture can pose significant risks to marine biodiversity and critical habitats, as evidenced by the threats already observed in certain parts of the world (Bhuyan 2023). In places such as the coasts of several Caribbean countries and off the coast of Hawaii, the production of native marine macroalgae is already a threat to biodiversity, tourism, and navigation due to anthropogenic eutrophication. The increase in sea temperature and excess of nutrients could further amplify this threat, especially in vulnerable environments such as coral reefs. Placing seaweed farms above reefs or seagrass beds can also alter the physiochemical and biological factors of the local ecosystem, causing undesired changes (Kelly *et al* 2020).

Moreover, the potential risk of invasive species must be considered when evaluating potential farmable species. Invasive seaweed cultivation has been shown to cause competition, suffocation, and death of reef-building corals, highlighting the need to avoid introducing non-native species (Edwards 2015, Neilson *et al* 2018). While some evidence suggests that mariculture of native seaweed has had little to no impact on wild macroalgae populations (Spillias *et al* 2023), the infrastructure of seaweed farms can provide a unique environment for invasive species to grow (Taormina *et al* 2018, Barbier *et al* 2020). In some cases, seaweed farms may inhibit bloom-forming microalgae (Yang *et al* 2015, Jiang *et al* 2020), but poor management of seaweed farms can facilitate the growth of harmful macro-algae species (Liu *et al* 2009, 2010, 2013, Zhang *et al* 2011, 2017, Huo *et al* 2015, 2016, Spillias *et al* 2023).

Therefore, it is vital to ensure that seaweed mariculture expansion is carried out sustainably and responsibly, taking into consideration the potential risks and impacts on marine ecosystems (Campbell *et al* 2019). This can be achieved through careful selection of sites and farming species, reduction of chemical use, and regular monitoring and mitigation of environmental impacts. By balancing the expansion of seaweed aquaculture with marine conservation, we can ensure a more sustainable and resilient future for our oceans.

4.4. Limitations and future research focus

Our study evaluated the expansion potential of seaweed farming globally, but it had some limitations. We only included 21 out of 30 currently farmed seaweed species recorded by FAO in our analysis, excluding those recorded either with the abbreviation '*spp.*' or other ISSCAAP names that do not correspond to any species in the biological records. The species we excluded consist not only of species farmed on a small scale but also species with substantial production, such as *Eucheuma spp.* and *Gracilaria spp.* Thus, our results may have underestimated the potential of seaweed farming. Although our ensemble-concensus approach provided a conservative spatial estimate of suitable seaweed farming areas, our results were still useful in identifying global opportunities for seaweed farming expansion. Future studies may focus on analyzing these excluded species to provide a more comprehensive and refined analysis.

Additionally, our model did not identify biologically or ecologically significant habitats that provide critical ecosystem services including supporting biodiversity, such as coral reefs or seagrass. It is crucial to carefully consider the potential impacts of seaweed farming on these sensitive ecosystems and to take appropriate measures to mitigate any negative effects. This requires incorporating detailed information on the distribution and extent of coral reefs and seagrass beds into models of seaweed mariculture suitability, in order to identify areas where seaweed farming may pose the greatest risks to these habitats. Incorporating this information will help ensure that seaweed aquaculture expansion is properly planned and effectively managed in these vulnerable areas, minimizing negative impacts on marine biodiversity and habitats. It will also help to identify areas where seaweed farming can provide ecosystem services, such as nutrient removal or artificial habitat creation, while avoiding areas where it may cause harm.

Furthermore, our study only evaluated the environmental suitability of seaweed mariculture and overlooked the social and economic factors which can greatly affect its success. The social acceptability of seaweed farming can vary greatly among different cultures and communities. Various factors such as the availability of capital, labor, and market demand can significantly influence the economic viability of seaweed farms. It is important to consider the social context and economic barriers. Therefore, future studies should incorporate social and economic factors into the evaluation of seaweed mariculture expansion to ensure the sustainability and long-term viability of seaweed farming.

Data availability statement

The data that support the findings of this study are openly available at the following URL/DOI: https://github.com/DanileLiu/seaweed_suit_area. Data will be available from 01 June 2023.

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