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Hybrid Projections Improve Prediction of Distributional Shifts of Invasive and Native Seaweeds Under Climate Change

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ABSTRACT

Aim: Using correlative species distribution models (SDMs) to predict species' range shifts may have limited predictive power when extrapolating into climatic conditions outside those used to train the models. The inclusion of physiological responses to add mechanistic knowledge can increase the reliability of predictions, but it is seldom applied. The objective of this study was to demonstrate this approach with two coexisting and potentially competing macroalgae in Europe and North America—the native *Chondrus crispus* and the invasive *Grateloupia turuturu*—and discuss the implications in broader biological and ecological contexts.

Location: Worldwide.

Time Period: 2000–2014 and 2090–2100.

Major Taxa Studied: Marine macroalgae.

Methods: We (i) developed SDMs from distributional records aiming to represent the realised niche of *C. crispus* and *G. turuturu*; (ii) provided an experimental proxy of thermal fundamental niche by determining growth and survival thermal physiological thresholds (PTs), using it to project the worldwide distribution of the selected macroalgae; and (iii) combined both approaches into a hybrid one derived from the SDM habitat suitability projections post-filtered with the PTs excluding thermally unsuitable areas.

Results: Hybrid projections detected and corrected extrapolations of SDMs in areas outside the fundamental niche of thermal tolerance of species, with greater restrictions for the native *C. crispus* due to its lower upper thermal PT compared to the invasive *G. turuturu*. Both species are expected to experience future distribution changes and move towards the poles. However, because the invasive species presents a wider thermal niche unfilling state, its potential northward range shift at southern latitudes in the Northern Hemisphere will be smaller.

Main Conclusions: Habitat suitability projections were more realistic and complete with the correction of the SDMs with the PTs into hybrid projections than those obtained from the two approaches independently and could provide an early warning of the potential replacement of the native species by the invasive one at the contracting limits of distribution.

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1 | Introduction

The most common approach to projecting current biogeographical distribution patterns into the future–referred to as the potential distribution–is through the use of species distribution models (SDMs) (Guisan and Thuiller 2005). SDMs correlate current species occurrence records to the environmental factors that shape their distribution, which serves as a proxy for the realised niche when those records are complete (Araújo and Guisan 2006; Elith et al. 2010). Assessing not only the current distribution of species but also the environmental constraints that prevent them from occupying other areas can enhance the accuracy of predictions regarding future geographic shifts of both native and invasive species (e.g., Václavík and Meentemeyer 2012). However, uncertainties of SDMs increase when these models are used to extrapolate the habitat suitability of the species outside the environmental gradient where the model was trained (Araújo and Luoto 2007; Rodríguez et al. 2019). Furthermore, the modelling of invasive species presents another handicap: the niche shift (proportion of the native niche non-overlapping with the exotic niche, Guisan et al. 2014). In invaded areas, situations of niche shift are common while the invasion process is occurring, or when competitors or other biotic restrictions may preclude the alien species from occupying the realised niche of origin. Those situations have been sometimes considered as a type of niche unfilling since the conditions outside those in the native area seem to be included in the fundamental niche of tolerance of the species (sensu Petitpierre et al. 2012). Nevertheless, regarding the native distributions of species, the niche unfilling situations are in which the realised niche is narrower than the fundamental one (sensu Sunday et al. 2014). Those situations lead to the assumption that species occupy different niches in native and invaded areas when the climatic conditions are comparable, which raises the uncertainty of the SDMs' projections.

Predictions from SDMs can be improved by combining correlative modelling with mechanistic approaches to the fundamental niche, such as incorporating physiological thresholds (PTs), understood as the lethal or sub-lethal limits of a species in response to a given environmental factor (Franco et al. 2018; Martínez et al. 2015; Wilson et al. 2019). Such thresholds define the limits of a species' fundamental niche, understood as the multidimensional environmental space (hypervolume) that represents the environmental conditions within which individuals can survive and reproduce (Hutchinson 1978; Kearney and Porter 2009; Soberón and Nakamura 2009). Combining SDMs with physiological knowledge in a hybrid projection enables the identification of geographic areas that offer suitable environmental conditions beyond those found within the current distribution or native range, referring to the niche unfilling situations described above. This is a very simple methodology, applicable to other studies, that allows for the detected and corrected extrapolations of SDMs in areas outside the fundamental niche of tolerance of species. It is very similar to simpler hybrid model methodologies that consider the congruent regions between the models done separately (e.g., Ceia-Hasse et al. 2014). In fact, there are different ways to generate those hybrid models, with the most common way being using the output of a mechanistic model as a predictor for a correlative model (e.g., Enriquez-Urzelai et al. 2019; Kearney and Porter 2017). However, the use of complex Bayesian methods seems to be gaining traction in recent years, although its complexity is high since it requires more information to parameterise this type of models, and we were looking for simplicity with our hybrid projections (e.g., Talluto et al. 2016). Indeed, the use of hybrid models in marine environments is still limited (but see Rodríguez et al. 2019) and is particularly scarce for macroalgae (but see Chefaoui et al. 2019).

Biogeographical patterns of species are directly controlled by biotic interactions, abiotic conditions and species mobility (Soberón and Peterson 2005). The climatic factors determine the tolerance limits for the survival of the organisms and thus the abiotic region of the geographic space where species inhabit (Soberón and Nakamura 2009; Soberón and Peterson 2005). In general, these climatic factors have been related to temperature since it affects the metabolic processes that regulate growth and survival (Pörtner 2002; Pörtner and Farrell 2008). For this reason, temperature was traditionally considered the most relevant environmental factor shaping species distributions (e.g., Walther et al. 2002). Changes in species distributions affect both native and introduced species since the range contractions and declines of the native species open new niche opportunities for the introduced species to colonise those empty areas (Mainka and Howard 2010; Sorte et al. 2013). Regardless of whether expansion or contraction, both processes have often been associated with changes in biodiversity and community structure which, in certain cases, could produce simplification leading to a less diverse community (Galiana et al. 2014; Wernberg et al. 2011). Thus, climate change is also contributing to this community simplification since it is triggering changes in biodiversity patterns in both terrestrial and marine ecosystems (e.g., Burrows et al. 2011; Chen et al. 2011 and references therein).

Climate change is particularly relevant to invasive alien species (IAS) since their establishment in the invaded regions and their range expansion seem to be favoured by the changes, especially in aquatic systems (Mainka and Howard 2010; Sorte et al. 2013). Furthermore, the problem of introduced IAS has dramatically escalated in recent decades, due to the increased frequency and extent of human activities and global trade (Thuiller et al. 2005), becoming the second most important global threat to biodiversity (EEA 2012). It is also expected that under future environmental conditions, the frequency of entrance and impact severity will rise (Occhipinti-Ambrogi 2007; Stachowicz et al. 2002). Once established, eradicating IAS in new areas is very difficult or even impossible, which is why their introduction must be avoided at all costs (Epstein 2017; Valentine et al. 2007). So, areas that fit their fundamental niche are particularly vulnerable to invasion and therefore need to be carefully managed and protected to prevent invasion (Marcelino and Verbruggen 2015).

Here, we applied a simple hybrid methodological framework to assess how the addition of thermal tolerance as a post-filtering to traditional SDMs refines worldwide projections of range size for two marine red macroalgae present in Europe and North America, the native *Chondrus crispus* Stackhouse 1797 (Gigartinaceae, Rhodophyta) and the invasive *Grateloupia turuturu* Y. Yamada 1941 (Halymeniaceae, Rhodophyta). Thus, the general objective of this study was to predict how the distributions of the two species of red macroalgae will change if we corrected extrapolation of the standard (correlative) SDM projections in areas outside the fundamental niche of thermal

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tolerance of species using physiological experimental information. To achieve this, we first calculated PTs using the data obtained from conducting an ecophysiological experiment. We then used PTs to characterise the state of thermal niche filling or unfilling of the species in relation to the ocean warming using satellite environmental layers. Finally, we applied the newly acquired niche information as a post-filter to the SDM projections. We believe that the prediction of coastal stretches of low probability of occurrence of the native species and high values of the non-native may serve as an early warning of areas of potential invasions.

2 | Methods

2.1 | Species Distribution Models (SDMs)

2.1.1 | Distributional and Environmental Datasets

We obtained the occurrence records for constructing the SDMs for both model species, *Chondrus crispus* and *Grateloupia turuturu* (see Figure S1.1a,b in Appendix S1 of Supporting Information to see pictures of them, and Appendix S2 to read a description), both under their valid name and their synonyms, from various sources, including internet repositories and scientific literature since 1950 up to September 2024 (see Appendix S2). We cleaned the compiled datasets of repeated records using ArcMap from ArcGIS 10.8.1 software (ESRI, Redlands, CA, USA), resulting in 5474 and 1057 unique coast presences worldwide for *C. crispus* and *G. turuturu*, respectively (Figure S1.2).

We downloaded the environmental sea surface layers to perform the SDMs for the reference period (2000–2014) which represent the recent and present climate, and under the future climate change scenario Representative Concentration Pathway (RCP) 4.5 and 8.5 for the year 2090–2100 (Intergovernmental Panel on Climate Change, IPCC 2014) from the Bio-ORACLE web repository (https://www.bio-oracle.org/). Additionally, we downloaded recent (2000–2010) minimum and maximum global atmospheric temperatures from the MERRAclim dataset (Vega et al. 2017), and bathymetry values (2025) from GEBCO data set (https://www.gebco.net/). We obtained a total of 20 different variable layers for the current state and six for each of the future RCP climate scenarios for each of the two species, considering only coastal values. The extent of these layers differed between the two species because the realised niche they occupy is different, and therefore the extent was adjusted for each species following the criteria included in Zhang et al. (2024) applying a buffer of 1000 km around the distribution records and considering only the areas where species can potentially arrive by dispersal (more details in Appendix S3).

To select only relevant predictor variables with low autocorrelation among them for performing the SDMs, we used Pearson's pairwise correlation coefficients calculated with the “ENMTools” version 1.1.5 package (Warren et al. 2021) in RStudio 2024.04.1 Build 748 (Posit Team 2024), using R version 3.4.4 (R Core Team 2024). We considered only those variables with a Pearson's correlation $|r| < 0.7$ (Dormann et al. 2013) and with an ecological significance for the species distribution (Table S1.1). The final set chosen for modelling consisted of seven common predictors for both species: long-term minimum and maximum yearly records of Sea Surface Temperature (named as SSTMin and SSTMax, respectively), long-term minimum yearly records of Sea Surface Salinity (SalinMin) and Nitrate concentration (NitrMin), long-term maximum yearly records of Phosphate concentration (PhospMax), min yearly records of the Cloud cover (CloudMin), mean yearly records of the Photosynthetic Available Radiation (PARMean) and suitable depth range for the species (Bathymetry) (Table S1.1 and Figure S1.3).

2.1.2 | Modelling Techniques

We created and trained the SDMs using Maximum Entropy Modelling (MaxEnt v3.4.4, https://biodiversityinformatics.amnh.org/open_source/maxent/), a statistical approach that contrasts the actual presence records of the species with patterns of random points that reflect accessible potential sites for the species (Elith et al. 2011). It requires presence-only data and a set of environmental variables for the geographic area of interest (Phillips et al. 2006), which in this case spanned the years 2000–2014. To prevent the potential overfitting associated with the use of complex response functions of doubtful ecological meaning and low projectability (reviewed in Araújo and Guisan 2006; Austin 2002), we only selected linear, quadratic and hinge features when modelling. In addition, we modified some of the default parameters in MaxEnt when modelling, such as the replicate run type to subsample, the maximum iteration number to 1000, and the adjust sample radius to −2.

We investigated the importance of each individual environmental variable in the distribution of the species by means of the Permutation Importance coefficient and Jackknife tests of variable importance performed by MaxEnt. Given the importance of the variable selection in SDMs, we also ran Bayesian Additive Regression Trees (BARTs) and Random Forest (RFs) to see the variable selection performed with these alternative methods and if there was consensus among the methodologies despite the fact that the algorithms they use are very different (Austin and Van Niel 2011). The models were performed using the “embarcadero” version 1.2.0.1003 (Carlson 2020) and “randomForest” version 4.7–1.2 (Liaw and Wiener 2002) R packages, respectively. Since this type of model is not like MaxEnt, which only uses presences and a background but also requires absences for modelling, we had to create a dataset with pseudo-absences in R to be able to model. For this, we used the “dismo” version 1.3–16 R package (Hijmans et al. 2017), and the presence-to-pseudo-absence ratio we used was 1:2 for BARTs and 1:1 for RFs. To obtain a parsimonious final model, we selected variables with at least 20% permutation importance in MaxEnt models and those that were also selected by the other two methods used to test the variable selection (see Results).

We evaluated the model performance using the Area Under the Curve (AUC) of a Receiver Operating Characteristic (ROC) plot given in MaxEnt (Phillips et al. 2004) and also calculating the Continuous Boyce Index (CBI) using the “ecospat” version 4.1.2 R package (Di Cola et al. 2017). Such metric was calculated for the whole dataset and for datasets obtained using internal (data-splitting) validation performing 10 iterations (avoiding

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the potential bias associated with the randomisation) of a 70–30 partitioning procedure, that is, 70% of points being used for model training and the remaining 30% for testing (Fielding and Bell 1997; Guisan and Zimmermann 2000). Furthermore, model accuracy was also assessed by True Skill Statistic (TSS, comparison of the number of correct forecasts with those attributable to random guessing of a hypothetical set of perfect forecasts), Sensitivity (relative true presences), Specificity (relative true absences) and kappa coefficient calculated in R from the different models (BARTs and RFs).

2.1.3 | SDM Habitat Suitability Projections

Using only the variables selected by the previously trained SDMs, we created the SDM projections using MaxEnt and mapped the results using ArcMap. These projections were created for the reference period and for the two future climate change scenarios (RCP4.5 and 8.5 for 2090–2100) using a global extent for *G. turuturu* and including only the northern hemisphere for *C. crispus* (see Appendix S3 for more details). Besides, to test the model's classification power of the presences, we used the “10 percentile training presence” logistic threshold obtained in MaxEnt to classify the pixels with values above the threshold as suitable, or unsuitable otherwise (Liu et al. 2013; Morales and Fernández 2020).

2.2 | Physiological Thresholds (PTs)

2.2.1 | Collection Sites

We collected single gametophytes of *G. turuturu* and *C. crispus* in northern Portugal during low tides on January 2014 at Viana do Castelo (41°41′34″ N, 08°51′6.2″ W) and on February 2014 at Praia Foz Porto (41°09′32″ N, 08°41′11.33″ W), respectively. After collection, we transported the fronds to the Interdisciplinary Centre of Marine and Environmental Research (CIIMAR, Portugal) within 2 h inside a cool box. Material was briefly rinsed with freshwater to remove grazers and placed immediately into a 300 L seawater tank at the same ocean temperature at that time (14°C), where it was kept until the experiment was carried out. Because there are more than one morphologically similar species of *Grateloupia* along the Portuguese coast (Araújo et al. 2009; Bárbara and Cremades 2004), we did microscopic analysis of tissue sections to confirm the taxonomical identity of the specimens.

2.2.2 | Temperature Gradient Experiment

For the experiment, we individually tagged 240 gametophytes of each species by piercing the base of the frond with a thin nylon string bearing different colour beads. The average fresh weight of the fronds at the start of the experiment was 0.35 ± 0.01 g for *G. turuturu* and 0.43 ± 0.01 g for *C. crispus* (mean ± SE, $n = 240$).

We set an outdoor experimental culturing facility that consisted of 24 tanks of 20 L at 11 different temperatures: 7.2°C ± 0.03°C, 10.1°C ± 0.02°C, 11.7°C ± 0.01°C, 13.7°C ± 0.01°C, 15.8°C ± 0.01°C, 17.8°C ± 0.01°C, 19.8°C ± 0.01°C, 21.9°C ± 0.01°C, 24.0°C ± 0.01°C, 25.8°C ± 0.01°C and 27.8°C ± 0.01°C (mean ± SE, $n \geq 2190$ during the entire experiment). Four experimental tanks for the lowest temperature and two tanks for all other temperatures were set. Each experimental tank contained a plastic frame with nylon lines, on which 10 replicates of each species were attached. After the fronds were moved to the experimental tanks filled with water at ambient temperature, the gradient was created by modifying the temperature of each tank approximately 2°C every 2 h until the target temperature was reached to avoid any temperature shock. We then ran the experiment for 30 days, and the temperatures were controlled using titanium heaters and individual temperature probes regulated by digital controllers (Aqua Medic AT Control System, GmbH, Bissendorf, Germany) with a programmed error of 0.1°C. To buffer against changes in ambient temperature, the experimental tanks were submerged into three water-baths (eight tanks per water-bath), set at 7°C, 14°C and 22°C for the tanks at low (7°C to 12°C), medium (14°C to 20°C) and high temperatures (22°C to 28°C), respectively (Figure S1.1c,d). We checked daily the temperature and salinity using a Hach HQ40d Portable Meter with IntelliCAL CDC401 Standard Conductivity Probe provided with a temperature sensor (Hach Company, Loveland, CO, USA). AT Control temperature records were also regularly downloaded to monitor sensor readings, ensuring rapid response in case of temperature fluctuations.

We maintained salinity constant at 35 PSU by refilling the tanks with fresh seawater, compensating for the evaporation. To avoid nutrient limitation, inorganic N and P were added every two days for a final concentration of 50 and 5 μM, respectively. Due to the occurrence of a green algae bloom around day 10 of the experiment, the seawater was immediately completely exchanged in all tanks and the addition of nutrients was halved afterwards to prevent further blooms. The seawater was constantly aerated and agitated by bubbling air pump systems. During the whole experiment, tanks were covered with transparent Plexiglas lids to avoid excessive ultraviolet radiation, and were exposed to natural sunlight with an average daily peak of photosynthetically active radiation (PAR) around 1600 μE m^{-2} s^{-1}.

2.2.3 | Estimate of Growth and Survival Thresholds

We weighted each frond to the nearest 0.01 g prior to the experiment and then after 10, 20 and 30 days. The difference between these measurements was used to calculate growth or shrinkage. Survival was assessed by classifying fronds as dead or alive. Death was revealed by obvious tissue depigmentation and decay, missing fragments, absence of marginal proliferations accompanied by excess weight loss (more than 40% of theinitial weight of the frond). In addition, fronds missing from the tank were deemed as decomposed and scored as dead.

We plotted growth and survival against experimental temperatures to detect PTs. Prior to statistical analysis, data were checked for homogeneity of variance using Cochran's test (Underwood 1997) and visually inspected for detecting outliers that were then omitted in the analysis. When the growth response reached a stationary-constant state (last 10 days of the experiment), the highest temperature at which at least 50% of individuals showed growth was chosen as the best proxy

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for the upper growth threshold (UGT_{50}) (similar to Martínez et al. 2015).

We analysed the relationship between survival and temperature using logistic regressions. The temperature corresponding to the survival probability of 0.5 or upper survival threshold (UST_{50}) was calculated, and as in growth, the value obtained after 30 days of experiment was taken as a proxy of the UST_{50} (Bischoff and Wiencke 1995; Hernández et al. 2023). We compared both upper thresholds and if they were different, the lower one was selected as the final upper physiological thermal threshold (UPT), following the most conservative criterion to establish the limit at which the populations are viable to grow and survive with at least 50% of the individuals alive, named as UPT_{50}. That threshold served us as a proxy of the thermal fundamental niche since with our experiments we explored the right side of the species' thermal tolerance curve, that is, the tolerance and responses to the heat (Anderson 2013). Analyses were done using STATISTICA 7.0 software (StatSoft Inc., Tulsa, OK, USA) and RStudio 1.4 with R version 4.0.5 (Posit Team 2024; R Core Team 2024).

2.3 | Hybrid Habitat Suitability Projections

To combine the mechanistic approach (ecophysiological experiments) with the correlative approach (SDMs), we first applied the UPT_{50} values obtained in the experiment for both species to the SSTMax environmental layers (for the reference period and for the two RCPs). Thus, we classified all map cells for possible presences or absences, that is, cells containing values below the thresholds were considered as suitable sites, or otherwise unsuitable. Secondly, to combine both projections into a "hybrid" one, we used these layers as a threshold to mask and post-filter the ones derived from SDMs. Therefore, only the suitable pixels according to the ecophysiology, that is, those below the UPTs, were included in the final projections showing the values for habitat suitability based on the MaxEnt algorithm, representing the congruence between methods. All hybrid projection analyses were conducted in ArcMap.

3 | Results

3.1 | SDMs

Species distribution models revealed a high dependence of the geographical distribution of both species on SSTs. The three tested models, that is, MaxEnt, BART and RF, agreed on the selection of at least one of the two variables related to the averaged minimum and maximum temperature, that is, SSTMin and SSTMax. According to our model results, these variables appeared to have the strongest influence on species distributions (Table 1, Figure S1.4), agreeing with the traditional models of seaweed biogeography (reviewed in Lüning 1990). In the case of the invasive species, the minimum values of salinity were also determinant in defining its distribution together with SSTMin (Table 1, Figure S1.4). Furthermore, models were valid according to the MaxEnt and BART AUC values (between 0.83 and 0.98; see Swets 1988) and also according to the CBI MaxEnt values (between 0.93 and 1.00; see Hirzel et al. 2006); and to the accuracy estimates given by the BARTs (TSS values between 0.85 and 0.89; see Allouche et al. 2006) and by RFs (sensitivity values between 0.93 and 0.95, specificity values between 0.94 and 0.96 and kappa between 0.87 and 0.90; see Landis and Koch 1977) (Table 1).

3.1.1 | Recent-Present SDM Habitat Suitability Projections

The resulting present habitat suitability maps based on the final-reduced MaxEnt models, using only the two selected variables per species (SSTMin and SSTMax for *C. crispus* and SSTMin and SalinMin for *G. turuturu*), showed that only at latitudes between 28° and 70° N for *C. crispus*, and between 2° and 79° N, but not in all coastlines and in a patchy way, and 5° and 56° S for *G. turuturu*, the habitat suitability was higher than 0.10. Applying the 10 percentile training presence logistic threshold (0.293 for both species), we observed that the current distribution of both species was almost perfectly captured by the SDMs (Figure 1a,d). Only 239 of the 5474 total distributional records (4.37%) of *C. crispus* were wrongly classified, as was expected with a 0.95 value of sensitivity in the models (Figure 1a). In the case of *G. turuturu* (Figure 1d), with a 0.93 value of sensitivity, such discordances accounted for 5.30% of the total distributional records (56 of the 1057) for this species.

3.1.2 | Future SDM Habitat Suitability Projections

The future SDM projections created for the RCP4.5 (2090–2100) climate change scenario for *C. crispus* forecasted that according to the presence/absence MaxEnt logistic threshold, 18.6% of populations from the Iberian Peninsula will be affected since the suitable habitat will be reduced in ~487 km of the coastline in that area (Figure 1b). Similarly, 2.03% of the populations from the East coast of the USA would be affected (15 out of 740) by the reduction in habitat favourability in ~54 km of coastline and 16.33% (8 out of 49) on the West coast by the reduction in ~134 km (Figure 1b). Under the RCP8.5 (2090–2100) climate change projections, 20.54% (152 out of 740) of populations from the East coast of the USA (disappearance of the favourable values of habitat suitability in ~352 km of the coastline), 44.90% (22 out of 49) from the West EEUU coast (~585 km), all the Iberian Peninsula populations, and almost all French populations from the Biscay Bay (~663 km) will be under the risk of disappearance since the habitat will become unsuitable (Figure 1c). Under both climate change scenarios, a range shift of the habitat suitability towards the poles was noticeable, being more pronounced under the RCP8.5 (Figure 1b,c).

For *G. turuturu*, projections under the RCP4.5 (2090–2100) climate change scenario predicted a worldwide poleward range shift that will impact two of the Mediterranean French populations in Europe, almost half of the Tasmanian populations (47.50%) and 4 out of 211 (1.90%) populations from New Zealand (Figure 1e). Under the RCP8.5 (2090–2100) climate change scenario, the habitat suitability in the western USA, South Africa, Tasmania and New Zealand appeared to decrease, presenting values below the logistic threshold which impossibilities the sustenance of some current populations and consequently driving

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TABLE 1 | The upper part of the table shows the permutation importance of each environmental variable using linear, quadratic and hinge features gave by MaxEnt.

	Chondrus crispus	Grateloupia turuturu
Environmental predictor	**Permutation importance**	**Permutation importance**
SSTMin	**26.1**	**20.0**
SSTMax	**21.7**	15.1
SalinMin	12.2	**20.3**
NitrMin	2.8	2.8
PhospMax	15.4	2.6
CloudMin	7.8	12.3
PARMean	2.7	19.2
Bathymetry	11.3	7.6
AUC full model MaxEnt	0.904[a]	0.922[a]
CBI full model MaxEnt	1.000[a]	0.976[a]
AUC 70% training data MaxEnt	0.920[a]	0.911[a]
CBI 70% training data MaxEnt	0.994[a]	0.979[a]
AUC final model MaxEnt	0.847[b]	0.834[b]
CBI final model MaxEnt	0.988[a]	0.927[a]
AUC BART	0.984[a]	0.975[a]
TSS BART	0.887[a]	0.853[a]
Sensitivity RF	0.947	0.932
Specificity RF	0.957	0.942
Kappa RF	0.904[a]	0.874[a]

Note: The bottom part of the table shows a summary of the performance metrics (AUCs and CBIs) used to evaluate the different models calibrated on all data, on the test datasets generated after cross-validation (mean value after 10-fold cross-validation using 70–30 partitioning) and on the final models calculated with MaxEnt, and also calculated in BART models; and of the accuracy metrics (TSS, sensitivity, specificity and kappa) of the different models performed in R (BART and RFs). Common selected variables by all approaches that were used for the final models in MaxEnt are marked in bold. AUC: [a]good (0.85–1.00), [b]fair (0.70–0.85), [c]poor (0.55–0.70), [d]fail (0.00–0.55) (Swets 1988). CBI: [a]excellent (>0.70), [b]good (0.50–0.70), [c]weak (<0.30) (Hirzel et al. 2006). TSS and Kappa: [a]good (0.60–1.00), [b]fair (0.20–0.60), [c]poor (0.00–0.02), [d]fail (≤ 0.0) (Allouche et al. 2006; Landis and Koch 1977).

their extinction (Figure 1f). This decline is expected along a large stretch of these coastlines, where the range shift towards the poles will also be more noticeable. As a result, a great part of the native coastline range (~5159 km) will become unsuitable for this species (Figure 1f).

3.2 | Physiological Thresholds to Water Temperature

The native species, *C. crispus*, showed steady growth during the whole experiment and in all temperatures except for the two highest ones, 26°C and 28°C (Figure 2a,c,e). At 30 days, the upper growth threshold (UGT_{50}) was 24°C (Figure 2e), and the upper survival threshold (UST_{50}), which decreased with time, was 25.85°C (Table S1.2, Figure S1.5). Following the most conservative criterion, the final UPT_{50} selected was 24°C.

The invasive *G. turuturu* grew at all temperatures up to the 10th day of the experiment, but evident loss of biomass above 18°C from 20 days onward was observed, except at the highest temperature of the experiment (28°C) at which half of the individuals showed growth (Figure 2b,d,f). For that reason, and after confirming with literature that survival was reported at that temperature (Simon et al. 1999, 2001), 28°C was considered viable for the *G. turuturu* population and selected as the UGT_{50} (Figure 2f). The anomalous mortality at intermediate temperatures (see Figure 2d,f) avoided a proper logistic regression for the survival analysis. Thus, the final UPT_{50} selected was 28°C.

3.3 | Hybrid Projections

3.3.1 | Present Hybrid Habitat Suitability Projections

Maps obtained by applying the UPTs (24°C and 28°C for *C. crispus* and *G. turuturu*, respectively) as classification thresholds for post-filtering the MaxEnt results into the hybrid projections revealed that the maximum SST values at latitudes from the Equator to 20°–30° N (Mauritania and Florida, respectively) and to 12°–25° S (Angola and Madagascar, respectively) were higher than the UPTs for both species (Figure S1.6a), explaining their

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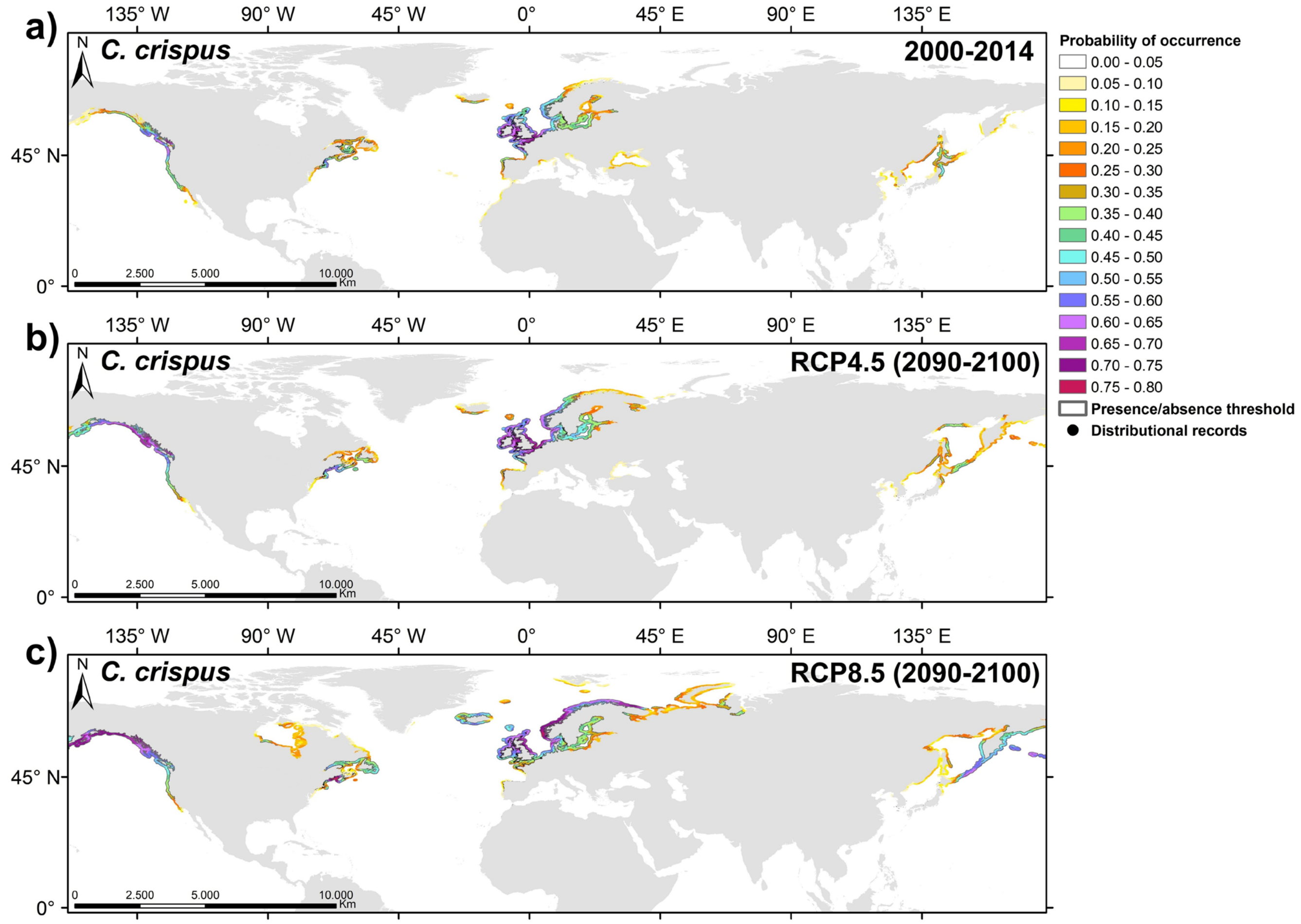

FIGURE 1 | Habitat suitability projection maps obtained by the final MaxEnt models showing the presence probability of *Chondrus crispus* from (a) to (c) and of *Grateloupia turuturu* from (d) to (f) for the reference period (2000–2014) (a and d), for the RCP4.5 (2090–2100) warming scenario (b and e), and for the RCP8.5 (2090–2100) warming scenario (c and f). The presence/absence MaxEnt logistic threshold is included as a grey line, and current distribution is superimposed by black dots for both species. The projected system used for the maps was the World Geodetic System 1984 (WGS84).

anti-equatorial distribution, that is, absence in tropical areas. In the case of *C. crispus*, also, the current African, Japanese and Korean populations seemed to be at risk of disappearance due to thermal stress and thermal niche filling, since the SSTMax in those regions was higher than the species' UPT$_{50}$ (Figure S1.6a). A similar thermal niche filling situation seemed to be occurring with the African and Caribbean populations of *G. turuturu* (Figure S1.6a). Conversely, in other parts of the globe, current populations seemed to experience a thermal niche unfilling with respect to the UPT$_{50}$; in Asia and the Mediterranean Sea, however, the thermal safety margins are minimal (Figure S1.6a).

The present hybrid habitat suitability maps for *C. crispus*, which included thermal restrictions as a post-filter, showed that the lower habitat suitability values derived from the MaxEnt (below 0.15) at lower latitudes were thermally unsuitable, which is in concordance also with the presence/absence threshold applied (Figure 3a). In the case of *G. turuturu*, including the PT restriction did eliminate higher habitat favourability values that, according to the presence/absence threshold, were suitable for the species in Africa, Asia, the interior of the Persian Gulf and the eastern USA (~2562 km in total), although it does not affect any of the current populations of the species (Figure 3d).

3.3.2 | Future Hybrid Habitat Suitability Projections

For the RCP4.5 (2090–2100) future climate scenario, the UPT$_{50}$ of *G. turuturu* will be exceeded in the Mediterranean and in half of its native range in Asia, affecting the populations located in these regions (Figure S1.6b). The hybrid habitat suitability maps were more restrictive than the SDMs alone for both studied species, although more drastically in the case of the invasive species (Figure 3b,e). Thus, the inclusion of UPT$_{50}$ thermal restrictions in *C. crispus*' projection only meant that ~60 km of coastline in Japan, which were suitable according to the MaxEnt threshold, were removed from the map (Figure 3b). However, in the case of *G. turuturu*, the number of kilometres reached a total of ~6924 km, affecting some of the current populations of the species in Asia (51 out of 224, i.e., 22.77%) and the Mediterranean Sea (6 out of 14, 42.86%) (Figure 3e).

Finally, for the RCP8.5 (2090–2100) future climate change scenario, the 24°C UPT$_{50}$ of *C. crispus* will be exceeded along a large stretch of the Atlantic coast of the United States and at the inner part of Biscay Bay (Figure S1.6c). Nevertheless, only a small part of the Massachusetts coast in the USA (~112 km) that was considered as presence according to the MaxEnt

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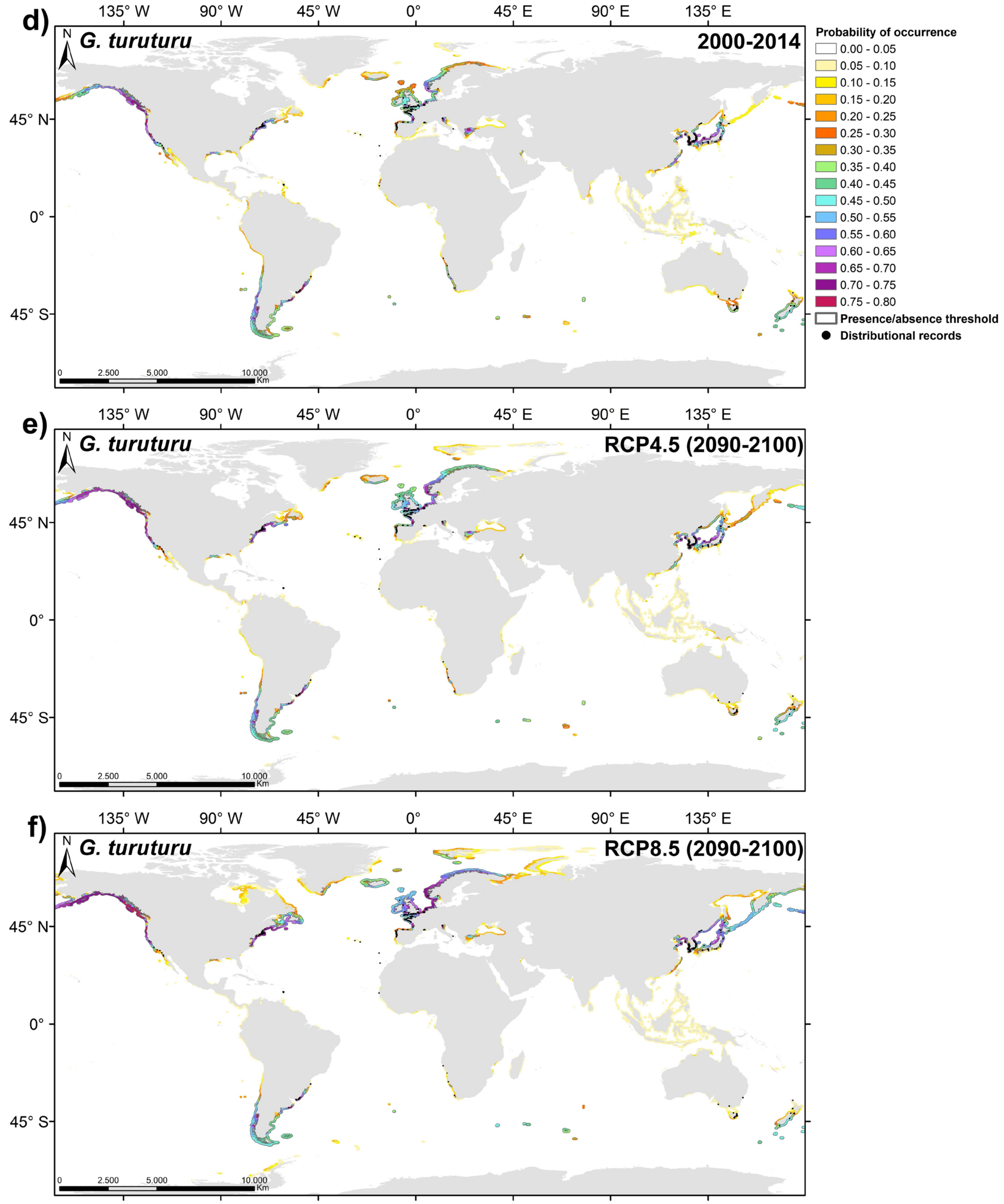

FIGURE 1 | (Continued)

threshold would become thermally unsuitable according to the UPT_{50} since the rest of the coast had already been classified as unfavourable according to the SDM threshold (Figure 3c). For its part, the 28°C UPT_{50} of *G. turuturu* will be exceeded in almost all its native range and in the entire Mediterranean Sea (Figure S1.6c), in addition to the ones that were also unsuitable in the other two previous scenarios such as in Africa or America (Figure S1.6a–c). In some of these areas the MaxEnt projection (Figure 1f) classified the coastline as suitable, so in this case, the hybrid approach was also more restrictive than both approaches

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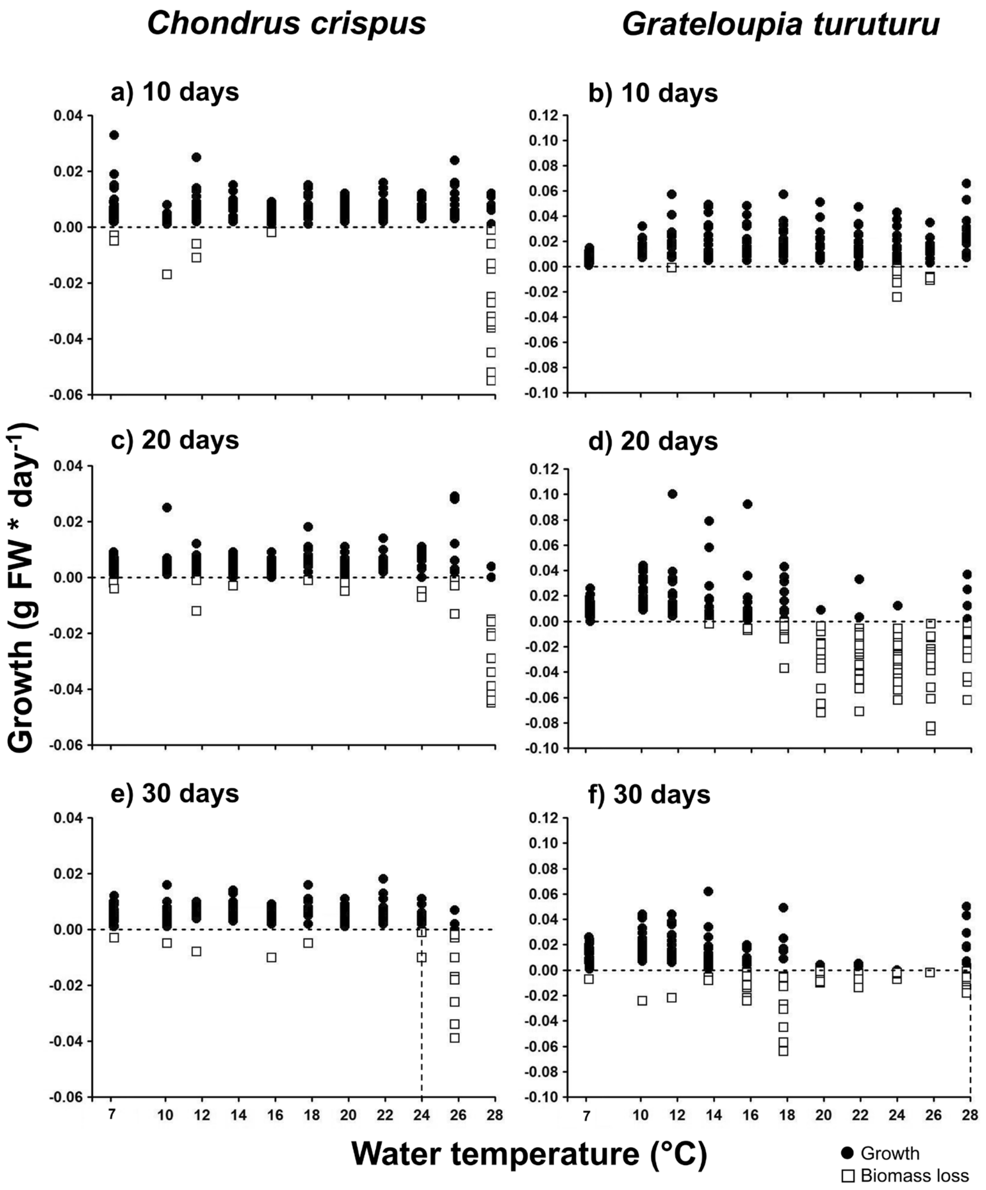

FIGURE 2 | Growth responses to seawater temperature after 10 (a, b), 20 (c, d), and 30 days (e, f) of the experiment for *C. crispus* (left) and *G. turuturu* (right). Filled circles indicate growth (expressed in grams fresh weight (FW) per day) and open squares represent biomass loss of individual replicates. Vertical dotted lines at 30 days of experiment indicate the temperature selected as best proxy of upper growth thresholds. Note that the ordinate axis values are different for each species.

independently (Figure 3f). Thus, the hybrid approach restricted ~1386 km in the East USA coast, ~2503 km in the Mediterranean Sea affecting 42.86% of the populations of this sea, ~6670 km in the Asian native coast affecting 79.92% of the current populations there (179 out of 224) (Figure 3f).

4 | Discussion

Habitat suitability projections of *G. turuturu* and *C. crispus* were made more realistic by correcting flawed projections by SDMs, eliminating those areas where the SDMs projections extrapolated and that were above the PT of species, that is, SDMs predicted as suitable some areas that were not thermally suitable for the studied species. Thus, SDMs projections were refined by including thermal restrictions established by the UPTs obtained experimentally, thus obtaining a hybrid projection. Both approaches independently were congruent in predicting a poleward shift of species due to climate change. However, in thermally unfavourable areas where the correlative approach tended to overpredict species presence, even if only at low suitability values, the inclusion of mechanistic knowledge improved the ecological plausibility of the projections. Because physiological information was applied as a post-filter rather than incorporated during model calibration, this improvement cannot be quantified using confusion-matrix-based accuracy metrics, which assess model performance under historical conditions rather than the realism of future projections (Santini et al. 2021; Zhang et al. 2024). Although laboratory-derived thermal limits are obtained under controlled conditions and from specific populations (Feng et al. 2020), they nonetheless provide biologically meaningful constraints that refine habitat suitability patterns

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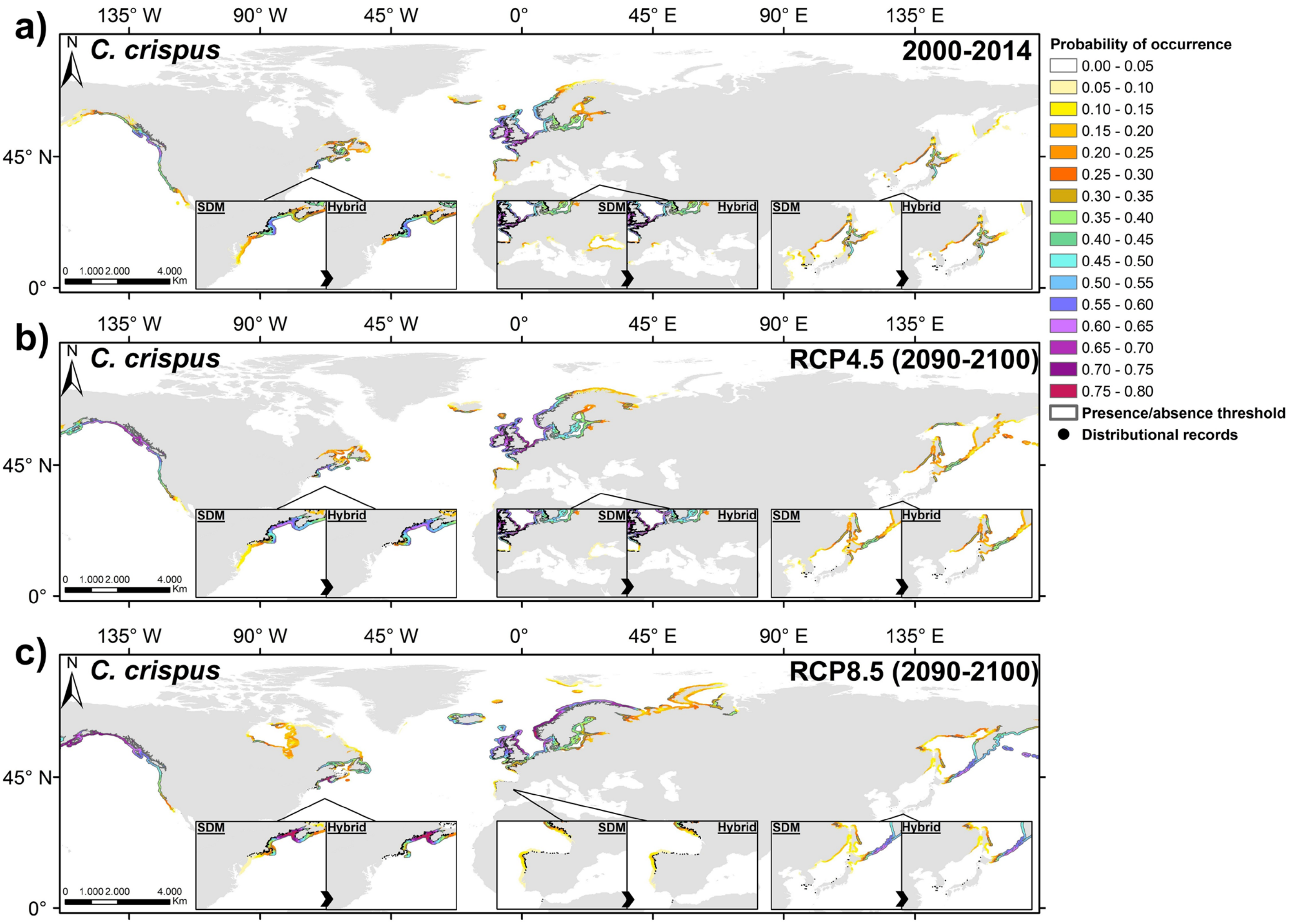

FIGURE 3 | Final hybrid habitat suitability projections for *C. crispus* from (a) to (c) and for *G. turuturu* from (d) to (f) at the reference period (2000–2014) (a and d), at the RCP4.5 (2090–2100) warming scenario (b and e), and at the RCP8.5 (2090–2100) warming scenario (c and f). The presence/absence MaxEnt logistic threshold is included as a grey line, and the current distribution is superimposed by black dots for both species. Inset maps highlight areas where SDMs and hybrid projections diverged. The projected system used for the maps was WGS84.

and reduce ecologically implausible predictions. This is in concordance with previous studies that compared different models and suggested that the hybrid projections and models provide more accurate predictions than the correlative and mechanistic models independently (e.g., Caetano et al. 2020; Enriquez-Urzelai et al. 2019). This improvement has been observed in different types of hybrid modelling, including the approach used here although it was not a hybrid model indeed, where the hybrid projection arises from the congruence between the models, thus considering only the appropriate regions according to all modelling approaches combined (e.g., Ceia-Hasse et al. 2014; Franco et al. 2018; Martínez et al. 2015). To date, however, only few studies have been conducted for macroalgae (Chefaoui et al. 2019; Franco et al. 2018; Martínez et al. 2015).

The physiological thresholds obtained here by conducting the ecophysiological experiments using gametophytes of each species, that is, mechanistic approach showed that the invasive species, *Grateloupia turuturu*, was more thermally tolerant (4°C greater) than the native species, *Chondrus crispus*. Due to that thermal tolerance difference and according to the models, it seems that *G. turuturu* is more likely to persist than *C. crispus* at the southern distribution range which they both share. In addition to its higher thermal tolerance of 4°C, which agreed with previous studies that tested short-term effects of temperature and salinity in photosynthesis (Rodrigo and Robaina 1997; Simon et al. 1999, 2001), our experiments showed that *G. turuturu* was characterised with a higher growth potential than *C. crispus*. Furthermore, when we selected our physiological thresholds as a proxy of the thermal fundamental niche of the species, we followed the most conservative criterion considering that viable populations require survival of at least 50% of individuals. Moreover, the phase of the species life cycle is also a very determining factor: it has been reported that juveniles are more resistant to thermal stress than adults (Bhattacharya 1985; Hughes and Otto 1999; Mathieson and Burns 1975). By using adults (gametophytes) in our study, we are considering the most sensitive life stage to heat and the first one to be affected by it.

When we applied the UPT$_{50}$ as a threshold to classify the SSTMax pixels, a current situation of thermal niche unfilling around the whole globe was revealed, except for some of the Asiatic populations of *C. crispus*. Thus, according to the maximum temperature that these species can endure, the fundamental thermal niche is wider than the realised niche they currently occupy (Sunday et al. 2014). However, we observed that the degree of unfilling was different around the globe; for example, it was very reduced in the *G. turuturu*'s native area where the

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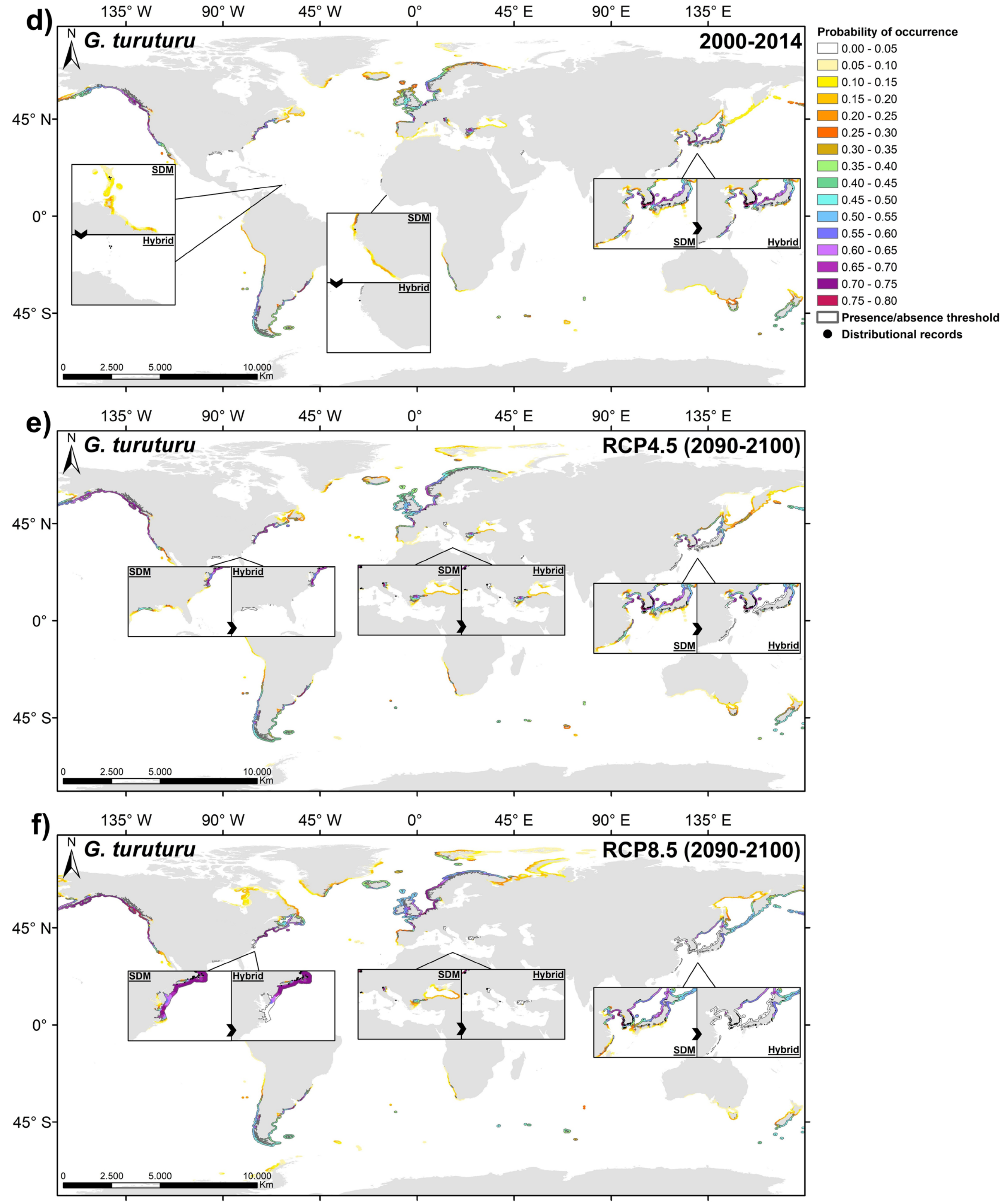

FIGURE 3 | (Continued)

SDMs also reported an almost complete disappearance of its populations. Furthermore, according to the SSTMax projection layers for the different RCPs studied here, the increase of the SST will be greater at the Asian native range than in the invaded area, so if *G. turuturu* does not have a wider thermal resistance there, it will face a massive extinction of its current native populations. For this reason, it will be advisable to study its thermal tolerance and genetics in its native area to see if thermal ecotypes are present in this species, as has been demonstrated in other macroalgae species (Bischoff and Wiencke 1995; King

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et al. 2019). We know this is not the case for the native European species, that is, *C. crispus*, since previous studies have shown that the threshold obtained here agrees with the literature and that there is no ecotypic variation in thermal tolerance thresholds across its European distribution (Hernández et al. 2023). Therefore, although our study did not test the PTs across the full geographic range of either species, we believe it is a good proxy for this thermal threshold.

The correlative models used here, SDMs, pointed out that SST was the environmental variable that influenced the distribution of both species the most. This has been also reported in the literature since isotherms are considered a good proxy to establish marine species distribution limits (van den Hoek 1982; Lüning 1990). The future projections revealed poleward range shifts for both species, being more pronounced for *C. crispus*, especially in areas where both species occur (Europe and North America). However, this does not mean that, even if the conditions towards higher latitudes will become favourable, the species will be able to colonise these regions, because successful colonisation depends on many other factors and also dispersal capacity in this species is low (e.g., Collén et al. 2014; Hruby and Norton 1979). Furthermore, as SSTs are increasing rapidly due to climate change, the rate of increase could be underestimated in the applied environmental layers since these are average layers from 2000 to 2014. Moreover, species seem not to have the necessary rapid capacity to adapt their physiology and compensate for the thermal increases they are currently experiencing (e.g., Hernández et al. 2023), and the PTs are therefore not expected to evolve at the same speed as the thermal increase is occurring (Harvey et al. 2014; Somero 2010, 2012). Invasive species are not usually in equilibrium with the environment in the areas where they invade considering that the time elapsed since their appearance is not long enough to have already achieved it, as seems to be the case of *G. turuturu* in this study (Petrocelli et al. 2020). Because SDMs are based on the current distributions of species including the recently invaded areas that are not yet in niche equilibrium, the inclusion of physiological information refined the projections. In this respect, it is worth noting that the invasive species *G. turuturu* is widely distributed outside its native range, primarily due to maritime transport (e.g., Mathieson et al. 2008). Hence the importance of considering the global scale in models and projections in this case.

The hybrid approach has the advantage of including the best characteristics of each kind of model, that is, the physiological information that seems to determine the macroalgae survival without excluding the information provided by other key environmental variables included in the SDMs. Thus, the SDMs tend to overestimate habitat suitability at lower latitudes; however, the inclusion of physiological information into hybrid predictions restricted overestimations in thermally unsuitable areas (Kearney et al. 2010). In our study, hybrid projections constrained overestimations that were common to both species in areas such as the eastern USA, the Mediterranean Sea or the Asian coast. In Europe, where both species coexist, our projections showed that *C. crispus* will see populations in its southern limit in the Iberian Peninsula and France diminish while *G. turuturu* will be able to persist and would therefore be the "winner" there. A similar situation occurred in the rest of the globe since according to our projections at warmer limits in the North Hemisphere the invasive *G. turuturu* would persist at lower latitudes than the native *C. crispus*. In fact, on the Portuguese coast, *C. crispus* was already reported to be declining in its southern limit, suffering a range shift of 180 km from the 1960s until 2000–2006 (Lima et al. 2007). The invasive species could occupy the empty niches that the native is leaving, which can lead to an ecological change if the role of the native species is not supplied by the invasive that is replacing it (Galiana et al. 2014; Wernberg et al. 2011).

In conclusion, this study confirms that the combination of mechanistic and correlative approaches into a hybrid projection is a step further to predict species distributions since PTs provided valuable information to add to the SDMs projections not captured by this correlative approach otherwise. Using the mechanistic approach, we observed that gametophytes of *C. crispus* and *G. turuturu* exhibited UPT_{50} of 24°C and 28°C, respectively. SDMs and hybrid habitat suitability projections coincided in showing that both species appeared to suffer potential range contractions under the RCPs scenarios for 2090–2100. The degree of disappearance at the contracting limits will be more pronounced for the native species than for the invasive one that could persist in areas where *C. crispus* will disappear. We demonstrated, as previously suggested by Sorte et al. (2013), that climate change may provide favourable conditions for invasive species, such as *G. turuturu* in our study, to expand and thrive. This might become especially true when native species, such as *C. crispus*, are thermally stressed and unable to maintain and/or expand their ranges and, in concert, invasive species can tolerate warmer temperatures.

Author Contributions

F.A. and I.H. designed the experiment, and F.A. provided the experimental facilities. F.A., I.H. and S.H. participated in the experiment execution. I.H., L.R. and F.C. elaborated a first draft of the manuscript. S.H. performed the final statistical analyses and together with B.D.C.M. led the writing of the manuscript and its revision. All authors participated in the revision of the drafts, giving their final approval for publication.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.7d7wm382k.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section. **Appendix S1:** jbi70152-sup-0001-AppendixS1.docx. **Table S1.1**. Relevant environmental predictors included in the models, their units, corresponding period of time, data source and main patterns. **Table S1:2** Results of the binomial GLM models done to explore the survival responses of *Chondrus crispus* against temperatures during the different periods of study (10, 20 and 30 days). The pseudo-R^2s are the McKelvey and Zavoine (1975) ones. Graph showing the logistic curves is shown in Figure S1.5. **Figure S1:1** Photos of the studied species where (a) is *Chondrus crispus* and (b) is *Grateloupia turuturu* and (c) and (d) show the experimental setup. **Figure S1:2** Worldwide current distributions of *Chondrus crispus* (blue circles) and *Grateloupia turuturu* (orange triangles). The projected system used for the map was the World Geodetic System 1984 (WGS84). **Figure S1:3**. Worldwide geographical pattern of the environmental variables included in the models, where (a) corresponds to the long-term minimal sea surface temperature (SSTMin), (b) long-term maximal sea surface temperature (SSTMax), (c) long-term minimal sea surface salinity (SalinMin), (d) long-term minimal nitrate concentration (NitrMin), (e) long-term maximal phosphate concentration (PhospMax), (f) minimal cloud cover (CloudMin), (g) mean Photosynthetic Available Radiation (PARMean) and (h) values of bathymetry considered to create the binomial layers to exclude unsuitable depths for each species (Bathymetry). The projected system used for the maps was the WGS84. **Figure S1:4** Jackknifes ("leave one out") of test gain for the MaxEnt models done, where (a) corresponds to *Chondrus crispus* model and (b) to *Grateloupia turuturu* model. **Figure S1:5** Survival responses to seawater temperature of *Chondrus crispus* after 10 (black solid line), 20 (black dashed line) and 30 days (black dotted line) of experiment. Results of the binomial GLM models done to get the curves are shown in Table S1.2. The intersections of the logistic regressions with the dotted horizontal line at 0.5 value survival probability indicate the UST_{50} for each given time interval and the boxed value represents the UST_{50} selected as the best proxy of the upper thermal survival threshold. **Figure S1:6** Global habitat suitability maps based on the UPT_{50} obtained by means of the ecophysiological experiments for (a) reference period (2000–2014), (b) RCP4.5 2090–2100 climate change scenario and (c) RCP8.5 2090–2100 climate change scenario. In grey are shown the coastline areas outside of our experiment temperatures (below 12°C), in blue the thermal suitable areas for both species, in orange the thermal suitable areas just for *G. turuturu* and in pink the unsuitable areas for both species. Current distribution is superimposed by dark blue circles for *C. crispus* and by black triangles for *G. turuturu*. The projected system used for the maps was WGS84. **Appendix S2:** Study Species and Distribution Records **Appendix S3:** Environmental Dataset

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