



Physiology, niche characteristics and extreme events: Current and future habitat suitability of a rhodolith-forming species in the Southwestern Atlantic



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ABSTRACT

Given the ecological and biogeochemical importance of rhodolith beds, it is necessary to investigate how future environmental conditions will affect these organisms. We investigated the impacts of increased nutrient concentrations, acidification, and marine heatwaves on the performance of the rhodolith-forming species *Lithothamnion crispatum* in a short-term experiment, including the recovery of individuals after stressor removal. Furthermore, we developed an ecological niche model to establish which environmental conditions determine its current distribution along the Brazilian coast and to project responses to future climate scenarios. Although *L. crispatum* suffered a reduction in photosynthetic performance when exposed to stressors, they returned to pre-experiment values following the return of individuals to control conditions. The model showed that the most important variables in explaining the current distribution of *L. crispatum* on the Brazilian coast were maximum nitrate and temperature. In future ocean conditions, the model predicted a range expansion of habitat suitability for this species of approximately 58.5% under RCP 8.5. Physiological responses to experimental future environmental conditions corroborated model predictions of the expansion of this species' habitat suitability in the future. This study, therefore, demonstrates the benefits of applying combined approaches to examine potential species responses to climate-change drivers from multiple angles.

1. Introduction

In the southwestern (SW) Atlantic coast, the ecosystems built by free-living coralline red algae (CRA), rhodolith beds, are of particular importance. Rhodoliths harbor a great variety of living organisms, from invertebrates to important life stages of fishes, and are regarded as seed banks for many fauna, flora, and microbiota (Carvalho et al., 2020b; Fredericq et al., 2019; Simon et al., 2016). Rhodolith beds can increase local biodiversity (Foster et al., 2013). Indeed, the richness of reef fishes has been found to be higher in rhodolith beds than in adjacent fringing and pinnacle reefs in Abrolhos, the most extensive rhodolith bed in the world (Moura et al., 2021). They are also important in the global carbon cycle, storing carbon in their calcium carbonate skeletons and sediments

(Mao et al., 2020; Martin et al., 2007). However, global climate change and local stressors are expected to greatly impact and threaten these organisms and affect the functions and services they provide (Anthony et al., 2008; Diaz-Pulido et al., 2012; Schubert et al., 2019; Vásquez-Elizondo and Enríquez, 2016). Therefore, understanding the physiological, and consequent possible alterations in the geographical distribution of key rhodolith-forming species, is an important step in the conservation of these organisms and ecosystems.

Climate change manifests in a variety of forms, from the well-known increase in average temperature to the intensification of extreme weather events, amongst others (Gissi et al., 2021). In marine ecosystems, heatwaves are one of the most prevalent extreme events with widespread and profound ecological impacts (Smale et al., 2019). The

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frequency and intensity of marine heatwaves have been increasing in recent decades, and they are projected to become even more frequent and intense in the near future (IPCC, 2019; Laufkötter et al., 2020). These events are defined as periods of anomalous warming of water above the 90th percentile of the historical baseline and lasting more than 5 days (Hobday et al., 2016). The loss of benthic cover by encrusting coralline algae following events of marine heatwaves has been recorded (Short et al., 2015; Smale and Wernberg, 2013; Wernberg et al., 2013), but there are very few experimental assessments on the effects of marine heatwaves in rhodolith-forming species (Cornwall et al., 2019). Anomalous warming has also been shown to drive significant change in genetic diversity and structure in populations of marine forests, leading to a “genetic tropicalization” (Coleman et al., 2020; Gurgel et al., 2020). This indicates that marine heatwaves have wider impacts on populations and can ultimately drive directional selection and result in changes in the distribution of species (Gutschick and BassiriRad, 2003; Helmuth et al., 2014; Morán-Ordóñez et al., 2018). Another global driver of change in marine ecosystems related to the increase of atmospheric CO₂ is ocean acidification (Doney et al., 2009). Decreasing pH and changes in the carbonate chemistry severely impact species with carbonate skeletons, such as CRA (Martin and Hall-Spencer, 2017). CO₂ enrichment has impacts at the individual level, causing dissolution and weakening the calcite skeleton of coralline algae (Büdenbender et al., 2011; Kamenos et al., 2013; Mccoy and Kamenos, 2015; Ragazzola et al., 2012), and at the community level, leading coralline algal assemblages to shift towards net dissolution (Burdett et al., 2018).

However, climate change takes place concomitantly with increases in other anthropogenic impacts in marine ecosystems; the combined effects of these local and global changes can be highly detrimental to marine biota (Boyd et al., 2018; Boyd and Hutchins, 2012; Gissi et al., 2021). Besides ocean acidification driven by CO₂ emissions, local-scale variations in oceanographic and biological processes, and anthropogenic impacts, such as continental runoff, also promote acidification (Hofmann et al., 2011; Kelly et al., 2011; Rose et al., 2020). At the same time, increased continental runoff transfers substantial loads of nutrients associated with many human activities (e. g. sewage disposal, fertilizers), generating physiological damage in key species of macroalgae (Martins et al., 2012; Scherner et al., 2013). Nutrient enrichment can impact CRA directly, affecting their metabolism (Bjork et al., 1995; Schubert et al., 2019; Simkiss, 1964), or indirectly by the competition for resources with fleshy epiphytes or opportunistic algae, which benefit from eutrophic conditions (Bélanger and Gagnon, 2020; Russell et al., 2009). Thus, the possible interactions between global and local factors and their impacts in rhodoliths need to be assessed to estimate their consequences in these ecosystems (Horta et al., 2016).

Although there is a modest number of studies investigating the impacts of environmental stressors on the physiology of CRA (reviewed in Cornwall et al., 2019; Mccoy and Kamenos, 2015), fewer have explored their effects on the distribution of rhodoliths. Environmental change, including ocean acidification and nutrient enrichment, has already altered the distribution of species (range shifts; i.e. species tracking environmental conditions within their physiological limits) and led to extinctions (Berg et al., 2010; Gervais et al., 2021; Poloczanska et al., 2013; Scheffers et al., 2016). Estimating changes in the distribution of key rhodolith-forming species enables determining regions with high conservation priority, given how important the ecosystems built by these organisms are to supporting local biodiversity and connectivity (Fragkopoulou et al., 2021; Moura et al., 2021).

Considering the necessity to investigate the impacts of combined global and local drivers on the physiology of rhodolith-forming species, we tested the combined effects of marine heatwaves (MHW), increased nutrient concentration, and pCO₂ on *Lithothamnion crispatum* Hauck 1878. This species has a wide latitudinal distribution, occurring in warm temperate and tropical regions of the SW Atlantic (Amado-Filho et al., 2017), and in shallow waters to depths of 70 m (Brasileiro et al., 2016).

Lithothamnion crispatum is the most abundant species in the Abrolhos Bank, Eastern Brazil (Amado-Filho et al., 2012; Brasileiro et al., 2016), and in other rhodolith beds throughout the Brazilian coast (Amado-Filho et al., 2017; Paselli et al., 2013), and thus represents a key target for research on responses to environmental change. We observed the changes in photosynthetic yield and photosynthesis after 5 days of exposure and the recovery of individuals after the removal of stressors. Moreover, to assess the most important environmental conditions in determining the distribution of *L. crispatum* on the Brazilian coast and predict its habitat suitability into the future, we developed an ecological niche model and projected it to 2100 in two emissions scenarios; one of reduced emissions (Representative Concentration Pathway, RCP 2.6) and the worst-case scenario (RCP 8.5) (IPCC, 2014). We tested three hypotheses: i. *L. crispatum* will be negatively impacted by the exposure to the combination of global (heatwave and acidification) and local drivers (nutrient increase), unable to recover its photosynthetic yield to pre-exposure levels; ii. the current distribution of *L. crispatum* on the Brazilian coast is influenced by the past intensity of marine heatwaves, nitrate concentration and pH; and lastly, iii. Future climate conditions will reduce *L. crispatum* habitat suitability along the Brazilian coast.

2. Material and methods

2.1. Experimental conditions and setup

Samples of *L. crispatum* were collected in the winter of August 2019, from rhodolith bed at Rancho Norte, within the Arvoredo Marine Biological Reserve ($-27^{\circ}16'25.8''$, $-48^{\circ}22'0.99''$), a marine protected area off the coast of Santa Catarina state, Brazil. Rhodoliths were collected from ~ 8 m depth, kept in coolers with seawater, and transported to the Phycology Laboratory at the Federal University of Santa Catarina. Samples were transferred to tanks ($V = 2\text{ L}$), with circulating seawater (salinity of 35). Afterward, rhodoliths were cleaned from epiphytes and associated fauna and acclimated for 3 months at 18°C , the temperature in the field during sample collection, and light of $34 \mu\text{mol photons m}^{-2} \text{s}^{-1}$, which was provided by fluorescent lamps in a 12-h light/dark photoperiod. This irradiance was chosen based on light levels recorded in the field (Carvalho et al., 2020b; MAARE, 2017) and based on previous experience cultivating this species in laboratory conditions. Water was exchanged every two weeks. In December 2019, samples were transferred to 20 1 L plastic containers (replicates), each with four rhodoliths of similar size. While light conditions and salinity were maintained, half of the replicates (10) were gradually ($\sim 1.5^{\circ}\text{C}$ per week) warmed to 24°C , to simulate the summer temperature of the rhodolith bed. Samples were then kept at these acclimation conditions for two weeks, at which point the experiment started. Rhodoliths are known for their difficult identification based only on morphological traits, as many species are morphologically similar and the group presents many cryptic species (Sissini et al., 2014). To avoid misidentification and help future comparisons between studies using the same taxa, we genetically identified the specimens used in the experiment; for details see Supplementary Material 1.

Our experimental design follows a scenario-based approach, or a “collapsed design”, testing the effects of multiple drivers (here, ocean acidification and increased nutrient concentration) as one factor, without loss of statistical power (Boyd et al., 2018). The experiment contained two control temperatures, simulating both mean winter (18°C) and summer (24°C) temperatures found in the studied rhodolith bed, at the sample collection depth (~ 8 m) (Sarti and Segal, 2018). These control temperatures were accompanied by natural nutrient conditions (i.e. no addition of nutrients in the seawater) and current pCO₂ concentrations ($\sim 415 \mu\text{mol mol}^{-1}$). These treatments simulated the current ocean conditions to which this population is naturally exposed to. Each treatment (winter/summer) comprised 5 aquaria ($n = 5$), each replicate with 4 rhodoliths of similar size and shape.

Measurements of physiological parameters were taken from randomly picked rhodoliths from each aquarium/treatment, resulting in one sample per aquarium. The experiment lasted for 5 days. Future ocean conditions were then simulated by the combined addition of nutrients, sudden rising water temperatures, and increasing $p\text{CO}_2$ concentration in the water. Nutrient concentrations were simulated by the addition of 70 μM of ammonium ($(\text{NH}_4)_2\text{SO}_4$), 10 μM of sodium phosphate ($\text{Na}_2\text{H}_2\text{PO}_4 \cdot 12\text{H}_2\text{O}$), and 14 μM of sodium nitrate (NaNO_3) in the seawater. Concentrations used in the experiment were based on values found by Pagliosa et al. (2006) in highly urbanized and eutrophic areas in Florianópolis, Santa Catarina. Water was exchanged daily in all treatments to ensure constant levels of nutrients. To test for recovery, after 5 days of elevated temperatures, nutrients and $p\text{CO}_2$, conditions of the future ocean conditions treatments were ceased, and replicates ($n = 5$) returned to the initial conditions and kept for 5 more days in tanks (Fig. 1).

To reproduce marine heatwaves, temperatures were increased by 6 °C in both winter and summer treatments, reaching 24 and 30 °C respectively. These temperatures were based on heatwaves recently registered in the Arvoredo's Island, which increased temperatures by 4 °C (Gouvea et al., 2017), and the prediction of increasing intensity of marine heatwaves in 2100 (Frölicher et al., 2018). To avoid pseudo-replication, as recommended by Cornwall et al. (2019), temperatures were maintained by individual heaters (Master, Brazil) in the aquaria and controlled automatically by sensors placed in the seawater inside each replicate. Temperature in all treatments was also recorded by data loggers (HOBO Pendant Temperature Data Loggers, Onset, Bourne, USA) placed randomly inside aquaria.

The concentration of $p\text{CO}_2$ chosen to simulate future ocean acidification was based on IPCC climate model predictions, where emissions of CO_2 reach up to 1000 ppm in 2100 according to RCP 8.5 (IPCC, 2014). Aeration was provided individually in tanks by a cylinder air stone, to create air bubbles and allow faster water-air equilibration (see Fig. S2 in Supplementary Material 1 for an example). In treatments of future ocean conditions, the air was pumped to each aquarium from a chamber where

CO_2 was mixed with air to reach 1000 ppm, while in treatments of current ocean conditions, the air was pumped without any injection of CO_2 . The concentration of $p\text{CO}_2$ in the air in the chamber was controlled by a Proportional-Integral-Derivative controller, which receives CO_2 readings from a built-in infrared gas analyzer and controls CO_2 injections by opening and closing an in-line solenoid valve. The controller calculates the difference between the measured CO_2 in the chamber and the programmed set point and adjusts the injection of CO_2 accordingly. Our CO_2 control system was based on Sordo et al. (2016). Measurements of pH in each aquarium were made daily using edge® Dedicated pH/ORP Meter (Hanna Technologies - HI 2002) to monitor $p\text{CO}_2$ injection.

2.1.1. Photosynthesis, respiration, and photosynthetic yield measurements

Physiological responses to the proposed future scenario were assessed by measurements of photosynthesis and respiration and photosynthetic yield. At the beginning and end of the experiment, photosynthesis and respiration rates were determined by laboratory incubations done in 150 mL sealed acrylic chambers, with circulation provided by a magnetic stirrer. First, respiration measurements were taken before the beginning of the photoperiod. Two rhodoliths were taken from each aquarium/replicate and incubated in darkness for 30 min with seawater from the respective aquarium and at the respective temperature of the treatment. Oxygen concentration was measured at the beginning, during, and at the end of the incubations with the Optical Oxygen & Temp Meter FireStingO2 (Pyro Science - FSO2-4). Afterward, incubations to determine primary production were made with the same rhodoliths at an irradiance of 1500 $\mu\text{mol photons m}^{-2} \text{s}^{-1}$ for 30 min. Control incubations without rhodoliths were also carried out to determine fluxes from biological activity in the seawater. Dark respiration (R), net primary production (NPP), and gross primary production (GPP) were estimated following equations (1) and (2) and corrected from control incubations.

$$\text{NPP and } R = \Delta o_2 * V / \Delta t * FW \quad (1)$$

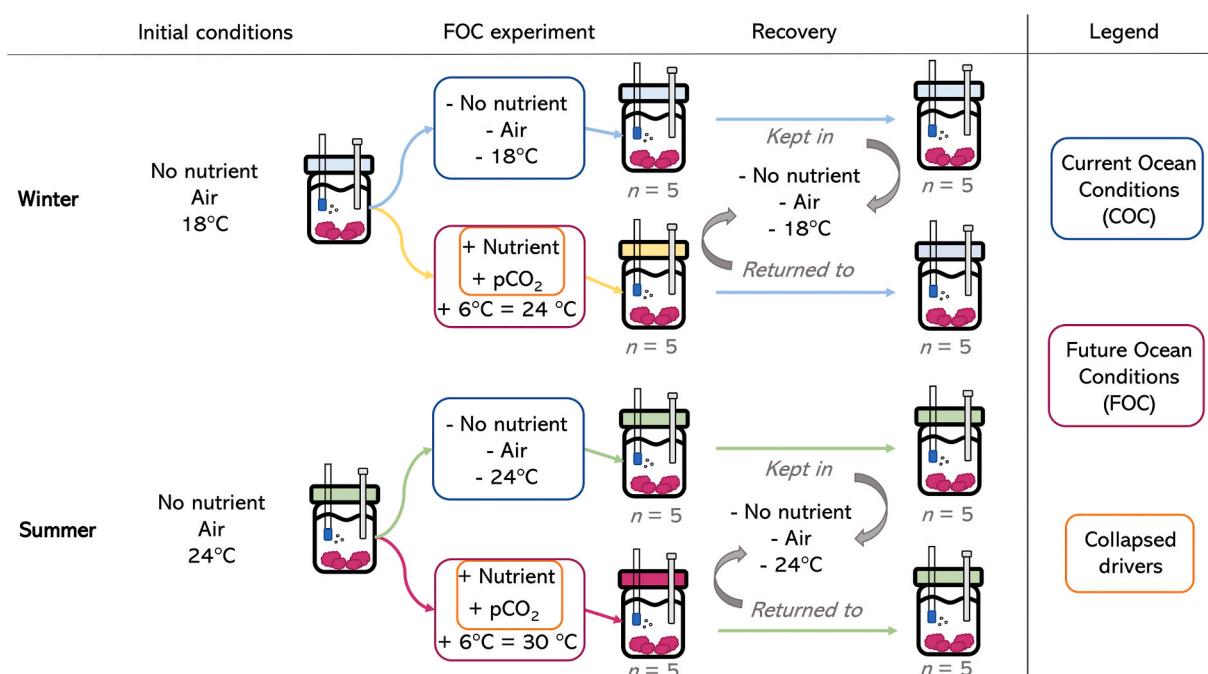


Fig. 1. Schematic representation of the experimental design describing the initial conditions, the experiment with heatwave, increased nutrient conditions and $p\text{CO}_2$, and the recovery period, where replicates were returned to initial conditions. Conditions circled in blue represent the Current Ocean Conditions (COC) of each season, while dark pink represents the Future Ocean Conditions (FOC). Circled in orange are the collapsed drivers, two factors that vary together, and as such, their effects are measured jointly in the statistical analyses. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

$$GPP = NPP + R \quad (2)$$

Where V is the volume of the incubation chamber (L), FW is the fresh weight of the algae (g), Δt is the incubation time (h) and ΔO₂ is the final minus initial concentrations of O₂ (μmol O₂ L⁻¹).

Photosynthetic yield was measured in the first, third, fifth (days with future ocean conditions), seventh, ninth, and eleventh (recovery) days of the experiment. Measurements of effective quantum yield (Fv/Fm), estimated by the *in vivo* chlorophyll *a* fluorescence of photosystem II, were made before the beginning of the photoperiod. Three measurements were taken from one rhodolith in each aquarium replicate, picked randomly, of different parts of the thallus, with a pulse-amplitude modulated chlorophyll *a* fluorometer (Junior PAM – Walz Germany). The measurement of fluorescence in the dark allows the estimation of the basal fluorescence (F₀), and after the application of a saturating pulse, maximum fluorescence (F) is estimated (Schreiber et al., 1986).

2.1.2. Statistical analyses

We tested the data (GPP and Fv/Fm) for homogeneity of variances using the Bartlett test, and the absence of this condition led us to run non-parametric analyses. To test if variations observed in GGP were caused by experimental conditions, we performed a Permutational Analysis of Variance (PERMANOVA), where explanatory variables comprised the different temperatures among treatments (18, 24, and 30 °C), time (beginning and end of the experiment), and the collapsed conditions of nutrients (addition/no addition of nutrients) and pCO₂ (addition/no addition of pCO₂), named as Nutrients + pCO₂. To test if there was a recovery of the photosynthetic apparatus (Fv/Fm) after treatments were ceased and conditions returned to initial values, we ran PERMANOVA with the following explanatory variables: temperature, nutrients + pCO₂, and time (days 1, 3, 5, 7, 9, and 11). All analyses were run on R 4.0.2 (R Core Team, 2020) using the R package “vegan” (Oksanen et al., 2019), and the dissimilarity matrix used in both analyses was Bray-Curtis. We considered $\alpha = 0.05$ as statistically significant in our results.

2.2. Ecological niche model

We extracted bottom-of-the-ocean environmental predictors (Table 1) from Bio-ORACLE v2.0 (Assis et al., 2018) and from the R packages “SCC26” and “SCC85” (Chih-Lin, 2020a, 2020b), which have historical bottom data and climate change projections (RCP 2.6 and 8.5) from CMIP5 (Taylor et al., 2012). To test whether events of extreme temperatures contribute to determining the distribution of *L. crispatum*, a layer of the MHW median intensity (the sea surface temperature anomaly associated with a heatwave event) from 1982 to 2019 was developed in MATLAB R2015a following the methodology and data

Table 1

Predictors used in the model, their units, and sources. “Future prediction” lists variables that have been predicted to the future scenarios RCP 2.6 and 8.5 and used in the future projections in this study.

Predictor	Unit	Source	Future prediction
Long-term max. nitrate at min. depth	μmol L ⁻¹	Assis et al. (2018)	No
Long-term max. salinity at min. depth	PSS	Assis et al. (2018)	Yes
Long-term max. temperature at min. depth	Celsius	Assis et al. (2018)	Yes
Minimum depth of the seafloor (bathymetry)	Meters	Assis et al. (2018)	No
Calcite saturation state	–	(Chih-Lin, 2020a, 2020b)	Yes
Mean pH at the seafloor	–	(Chih-Lin, 2020a, 2020b)	Yes
Median heatwave intensity	Celsius	Jacox et al. (2020)	No

used by Jacox et al. (2020), which calculates MHW from monthly sea surface temperature anomalies. We defined MHWs as periods with anomalous warming of the surface of the ocean above a seasonally varying 90th-percentile threshold, following the definition of Hobday et al. (2016). For further explanation regarding methodology and analysis, refer to Jacox et al. (2020). To match the resolution of the Bio-ORACLE layers (9.2 km, or c. 0.08° at the Equator), CIMP5 and heatwave layers were interpolated bilinearly using the function *disaggregate* of the R package “raster” (Hijmans, 2020). Multicollinearity between predictors was tested via Variance Inflation Factor (VIF), using the R function *vifstep* of the R package “usdm” (Naimi et al., 2014). A VIF greater than 10 indicates a collinearity problem between the variables (Chatterjee and Hadi, 2006; Naimi et al., 2014), and as such, we used this function to exclude variables with VIF > 10. Environmental predictors used in the final model were selected based on biological relevance, on the amount of contribution of each variable to the model (variables kept when contribution was >5%; Elith et al., 2008), and in combination with experimental settings (temperature, nutrients and pH), and are described in Table 1.

To build the Ecological Niche Models (ENMs), occurrence data of *L. crispatum* was downloaded from the Global Biodiversity Information Facility (GBIF, 2020), and published literature (Supplementary Material 2), using the keyword “*Lithothamnion crispatum*”. Occurrence data was cleaned of duplicates, and locations were corrected manually in QGIS 3.6 when the description of sampling sites did not match the coordinates depicted. The correction of coordinates was curated by a specialist in Brazilian rhodoliths, M.N. Sissini. To reduce sampling bias, occurrences were filtered using the R function envSamp (<https://github.com/SaraVarela/envSample>). While geographically cleaned occurrences can have similar environmental information, by cleaning occurrences in the environmental space, close occurrences with very different and important environmental information are kept (Varela et al., 2014). The filters for this selection were maximum temperature and maximum nitrate, described by Carvalho et al. (2019) as the variables most important for explaining the distribution and abundance of Brazilian rhodolith beds. This step removed 7 occurrences out of the 27 raw occurrences for *L. crispatum*, maintaining 20 occurrences to be used in the model.

As the performance of modeling algorithms varies widely based on the particularities of the target species, we tested the predictive ability of a suite of algorithms with our data to select the ones more fit to our species, as recommended by Qiao et al. (2015) and Escobar et al. (2018). In total, 7 algorithms were tested (Gradient Boosting Machines, Random Forests, Artificial Neural Networks, Generalized Linear Model, Classification Tree Analysis, Flexible Discriminant Analysis, and Multiple Adaptive Regression Splines), and the results of model performance can be found in the Supplementary Material 1 (Fig. S3). The models with the better performance on the metrics used in this study (further explained below) were three machine learning (ML) algorithms: Gradient Boosting Machines (GBM, also known as Boosted Regression Trees – BRT), Artificial Neural Networks (ANN), and Random Forests (RF). Pseudo-absence selection has a great influence on model performance and accuracy, and as such, we followed the recommendations of Barbet-Massin et al. (2012) for the generation of pseudo-absences. For ML algorithms, a number of pseudo-absences equal to the number of presences yields better predictive accuracy, and when the number of pseudo-absences is different from the number of presences, model predictive quality is better when giving an equal weight for presences and absences (Barbet-Massin et al., 2012). For this reason, we generated 60 pseudo-absences (three times the number of presences, 20), and weighted absences equally to the presences. Considering the low number of pseudo-absences, 10 datasets of pseudo-absences were generated and used for 10 different runs of each model, to reduce the influence of pseudo-absence selection. Barbet-Massin et al. (2012) also recommend selecting pseudo-absences with a geographical exclusion (2° apart from each presence) when there are few presences, yielding significantly better models. As our model has very few presences, we generated the

pseudo-absences within 20 and 25 km around the presences, approximately 2° of distance at the Equator.

To project the current and future habitat suitability for *L. crispatum* along the Brazilian coast, an ensemble modeling approach was applied. All models and pseudo-absences were generated using the “biomod2” R package, as were model evaluations (Thuiller et al., 2020). Individual runs of each presence-absence algorithm (ANN, GBM, and RF) were made with 10 iterations in each of the 10 pseudo-absence datasets, resulting in 300 models. For each run, the data was split between a calibration and a validation set (70%/30%, respectively). Model parameters were selected according to the recommendations of Elith et al. (2008) for GBM, of Breiman (2002) for RF, and for ANN, default parameters were used. Model performance was accessed via the receiver operating characteristic (ROC) curve (AUC; Fielding and Bell, 1997), and true skill statistics (TSS, Allouche et al., 2006). The ensemble model comprised only models that obtained TSS values above the 0.8 threshold. Three ensemble algorithms were run: committee averaging (CA, average of binary predictions), the weighted mean of probabilities (WMean, the weighted sum by the selected evaluation method scores), and coefficient of variation of probabilities (CV, coefficient of variation of the probabilities over selected models, a measure of uncertainty of the prediction). For further information regarding ensemble algorithms, refer to Thuiller et al. (2020). The final model was then projected current and future conditions, in two scenarios of emissions: RCP 2.6 and RCP 8.5. For variables that did not have projections for the future (Table 1), their layers from the present were used.

Variable importance was calculated through a randomization procedure that uses Pearson's correlation between the predictions of the model and predictions where a given variable has been randomly permuted (Thuiller et al., 2020). The variable importance technique in Biomod2 is similar to the principle of variable importance calculation in RF and varies between 0 and 1, where the highest values represent the highest influence of the variable in the model (Thuiller et al., 2020). However, this technique does not account for interactions between variables, and therefore, does not sum to one. Three iterations were run to determine variables' importance, and this result is presented in percentage (variable studied * 100/sum of all variables' importance) to facilitate interpretation. Response curves generated are based on the Evaluation Strip method (Elith et al., 2005), where n-1 variables are set to a fixed value (in our case, the mean), and only the studied variable varies across the whole data range, where variations calculated show the sensibility of the model to the studied variable (Thuiller et al., 2020).

3. Results

3.1. Aquarium experiment

The permutational analysis of variance showed no significant

Table 2

PERMANOVA results between GPP and Time, Temperature, and Nutrient + pCO₂. SS: Sum of squares, MS: Mean of Squares, Pseudo-F: Pseudo-F statistics, R²: partial R-squared values, and P: P values, based on 999 permutations and Bray-Curtis dissimilarity. Significant interactions are shown in bold.

Source of variation	Df	SS	MS	Pseudo-F	R ²	p
Day	1	0.443	0.443	15.437	0.216	0.001
Temperature	1	0.130	0.130	4.541	0.064	0.009
Nutrient + pCO ₂	1	0.181	0.181	6.296	0.088	0.004
Time: Temperature	1	0.178	0.178	6.201	0.087	0.001
Time: Nutrient + pCO ₂	1	0.146	0.146	5.082	0.071	0.010
Temperature: Nutrient + pCO ₂	1	0.026	0.026	0.893	0.012	0.381
Time: Temperature: Nutrient + pCO ₂	1	0.026	0.026	0.893	0.012	0.388
Residuals	32	0.919	0.029	–	0.448	–
Total	39	2.050	–	–	1.000	–

interaction ($p = 0.388$, Table 2) between the effects of temperature, time, and nutrients + pCO₂ on the gross primary production (GPP) of *L. crispatum*. However, there was a significant interaction between temperature and time, and the collapsed conditions of nutrients + pCO₂ ($p = 0.001$ and $p = 0.01$, respectively; Table 2), demonstrating that there was a significant difference between the response of algae in current and future ocean conditions (Fig. 2). PERMANOVA also showed no significant interaction ($p = 0.251$, Table 3) between the effects of temperature, time, and nutrients + pCO₂ on the photosynthetic yield (Fv/Fm) of *L. crispatum* in the 10 days of experiment (future ocean conditions plus recovery, Fig. 3), and only the effects of temperature and nutrients + pCO₂ individually had significant effects ($p = 0.001$ for both; Table 3).

3.2. Ecological niche model

The ensemble models presented high validation scores, with TSS = 0.987 and ROC = 0.998 for the CA ensemble model, and TSS = 0.968 and ROC = 0.996 for the WMean model (evaluations based on the testing data). The coefficient of variation is small in coastal areas, demonstrating that model projections on the coast have low uncertainty (Fig. S4 in Supplementary Material 1). To facilitate interpretation, we chose to show here only the results of the CA ensemble model, which reached better evaluation metrics; Kappa, TSS, and ROC statistics of each model run are available in Supplementary Material 1 (Fig. S5).

The binary map of current habitat suitability for *L. crispatum* matches the occurrences found for this species (Fig. 4), and shows suitability in the southeastern and northeastern regions of Brazil, with a few other locations in the south and north. The variable with the highest relative importance was maximum nitrate (0.202), followed by maximum temperature (0.048), maximum salinity (0.025), bathymetry (0.021), and calcite saturation (0.010). Median heatwave intensity and pH had low importance for the ensemble model (Fig. 5, values in percentage). The highest probabilities of occurrence are from 0 to 5 µmol L⁻¹ maximum nitrate, 20 to 28.5 °C for maximum temperature, 35 to 37 for maximum salinity, and 1 to 4 for calcite saturation (Fig. 6, Fig. S6). Under future

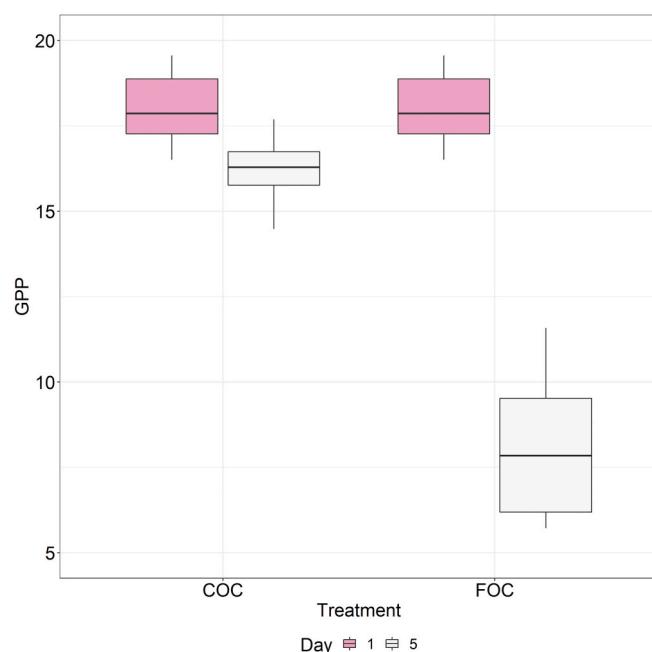


Fig. 2. Boxplots of gross primary production (GPP) values in each treatment and each day (beginning and end of experiment). Center lines in boxplots represent the median, the lower and upper ends of the box represent the 25th and 75th percentiles, and whiskers show the maximum and minimum values. COC – Current Ocean Conditions; FOC – Future Ocean Conditions: increased temperature (+6 °C), nutrients and pCO₂.

Table 3

PERMANOVA results between Fv/Fm and Time, Temperature, and Nutrient + $p\text{CO}_2$. SS: Sum of squares, MS: Mean of Squares, Pseudo-F: Pseudo-F statistics, R^2 : partial R-squared values, and P: P values, based on 999 permutations and Bray-Curtis dissimilarity. Significant interactions are shown in bold.

Source of variation	Df	SS	MS	F	R^2	p
Day	1	0.009	0.009	0.647	0.001	0.446
Temperature	1	1.938	1.938	14.511	0.249	0.001
Nutrient + $p\text{CO}_2$	1	0.898	0.898	65.073	0.115	0.001
Time: Temperature	1	0.014	0.014	1.009	0.002	0.296
Time: Nutrient + $p\text{CO}_2$	1	0.009	0.009	0.665	0.001	0.445
Temperature: Nutrient + $p\text{CO}_2$	1	0.052	0.052	3.782	0.007	0.059
Time: Temperature: Nutrient + $p\text{CO}_2$	1	0.016	0.016	1.192	0.002	0.251
Residuals	352	4.856	0.014	–	0.623	–
Total	359	7.793	–	–	1.000	–

climate scenarios, there are predicted shifts in the distribution of *L. crispatum* in both RCP 2.6 and RCP 8.5, mostly to the southern and northern coasts of Brazil (Fig. 7). Under RCP 2.6, the predicted loss of suitable habitats is of 1.24% (i.e., the percentage of pixels with predicted

habitat suitability in the present that in the future prediction are now unsuitable), while the gain is of 43.12%. Under RCP 8.5, the predicted loss is of 4.76%, with a 58.49% of gain of suitable habitats.

4. Discussion

By combining laboratory experiments and statistical modeling of species ecological niches, our study revealed that extreme warming events have likely played little role in determining the distribution of *L. crispatum* in the SW Atlantic Ocean, reflecting their ability to withstand such conditions. Although the combination of a heatwave, nutrient enrichment and CO_2 enrichment reduced the photosynthetic yield and photosynthesis of *L. crispatum* in both winter and summer conditions in the short term, it was insufficient to preclude the recovery of individuals after the removal of stressors. This result is in accordance with model results, which showed the low importance of heatwaves and pH in determining the current habitat suitability of this species on the Brazilian coast. Moreover, future climate conditions in both emissions scenarios demonstrate that *L. crispatum* may not be strongly affected by altered environmental conditions based on our data. This is the first study that we are aware of to model the current and future habitat

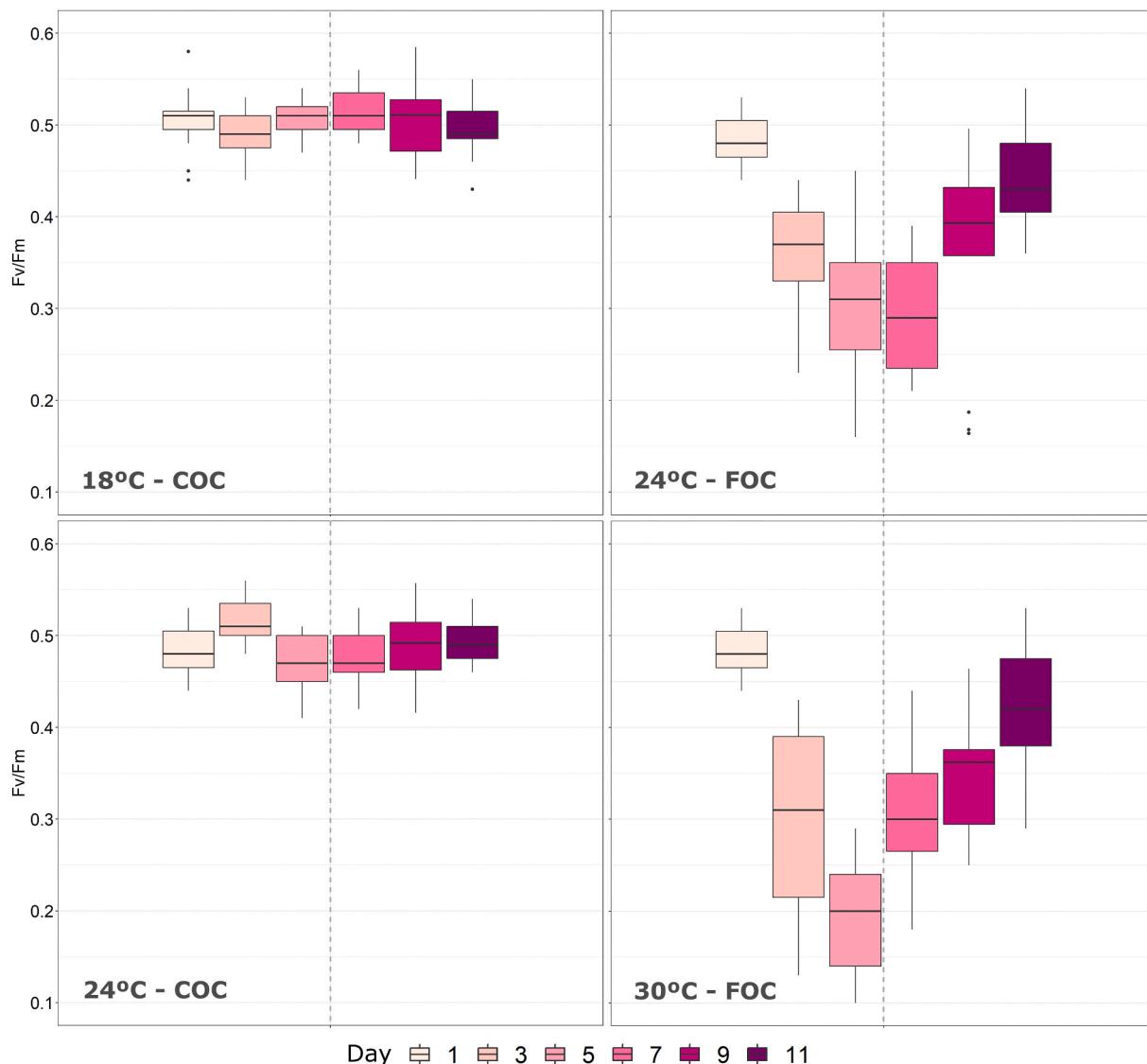


Fig. 3. Boxplots of Fv/Fm values in each treatment and each day. Center lines in boxplots represent the median, dots represent outliers, the lower and upper ends of the box represent the 25th and 75th percentiles, and whiskers show the maximum and minimum values. The vertical dotted line divides the data of the FOC experiment (days 1, 3 and 5) from the recovery period (days 7, 9, and 11). COC – Current Ocean Conditions; FOC – Future Ocean Conditions.

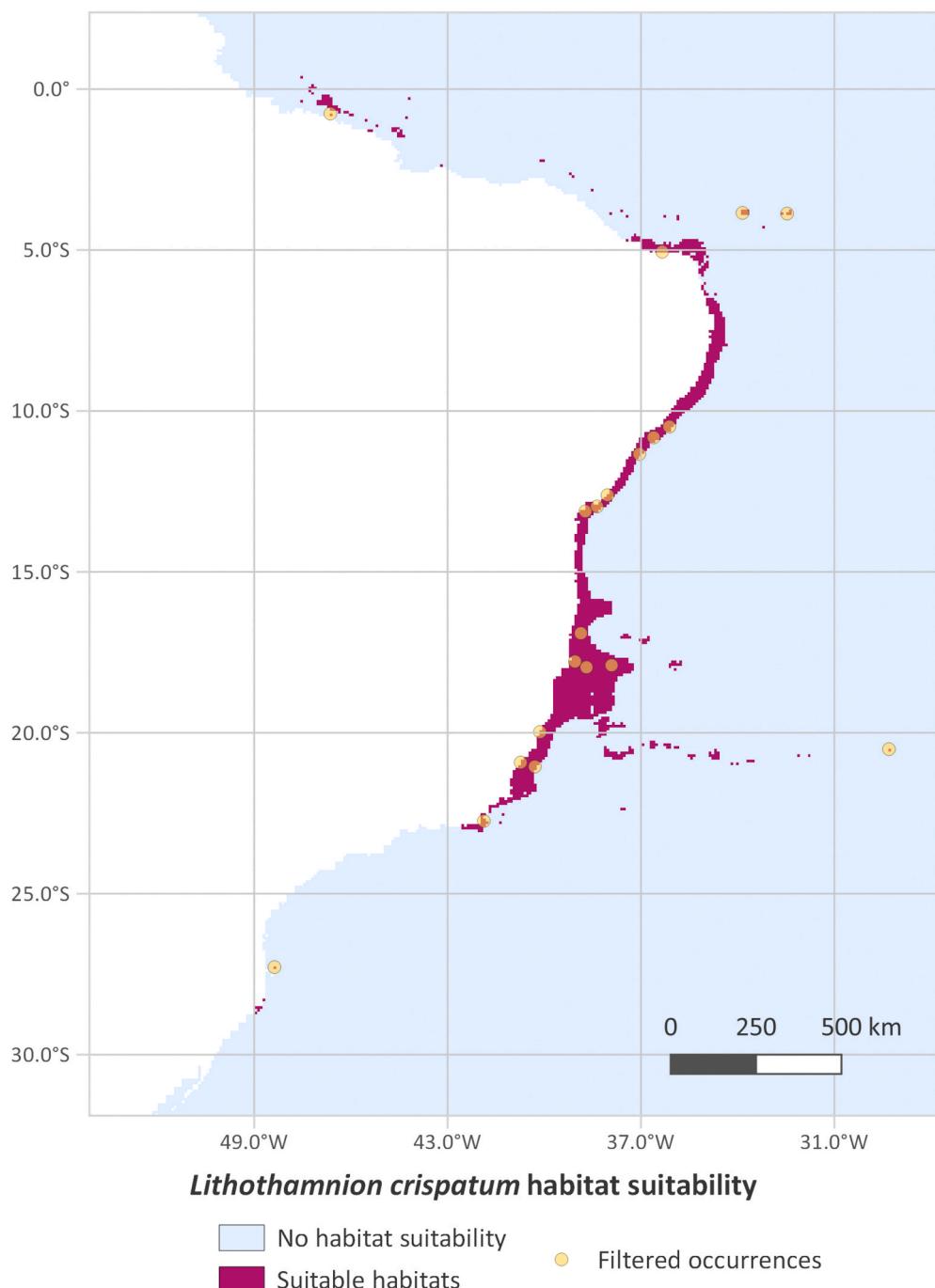


Fig. 4. Binary map of *L. crispatum* habitat suitability under current conditions from CA ensemble model. Regions in dark pink represent suitable habitats, while light blue represent regions without suitable conditions. Occurrences used in the model are presented in yellow circles. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

suitability of an individual rhodolith-forming species. Previous studies have focused on creating models of many rhodolith-forming species in Brazil or elsewhere (Carvalho et al., 2020a; Fragkopoulou et al., 2021), of mäerl species in the Mediterranean (Martin et al., 2014), and of multiple species forming coralline algal beds in Scottish waters (Simon-Nutbrown et al., 2020). By looking at a single species, we can achieve better inferences of the factors influencing the current and future distribution of these organisms, and raise key points regarding the ecology and resilience of rhodoliths that need to be addressed in future studies.

According to our results, marine heatwaves contributed little in determining the current distribution of *L. crispatum*. Although we did not

use a layer with heatwave intensity projection for the future as it had very little contribution to the overall model, the data suggest it is unlikely that this would have changed the prediction of future habitat suitability for *L. crispatum*. However, as these events are predicted to get more severe, long-lasting, and frequent (IPCC, 2019), this trend may change, and indeed affect the distribution of this species to some unknown extent. We tested the effects of such extreme events for five days, and the survival of rhodoliths to longer events is likely different than what we observed in our experiment. Longer experiments (from months to years) have demonstrated conflicting responses of CRA to altered pH and/or temperature conditions. Some studies have observed resistance of rhodolith species to lower pH, but with impairment to its carbonate

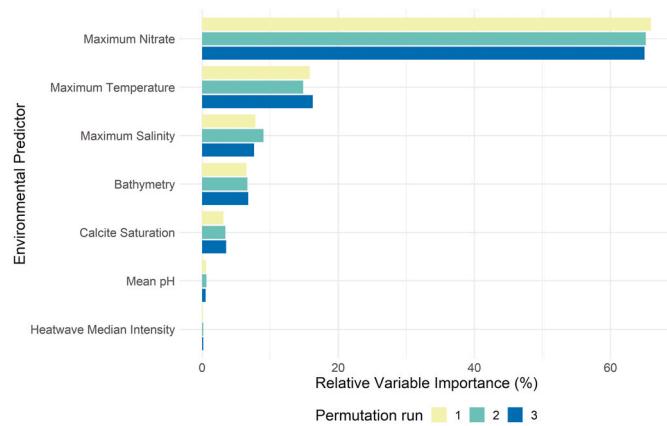


Fig. 5. Relative importance of variables used in the CA ensemble model represented in percentage. Each bar represents one iteration run, where the variable was randomly shuffled and its importance calculated through the difference between the correlation value of the predictions of model fitted with the variable shuffled, and the model formed with the same original dataset. The higher the value, the more influence the variable has on the model.

skeleton or other physiological processes (Kamenos et al., 2013; Martin et al., 2013; Qui-Minet et al., 2019; Sordo et al., 2016), while other showed decreasing photosynthetic rates and even mortality of algae in high CO₂ and elevated temperatures (Martin and Gattuso, 2009). The observed resistance to altered environmental conditions can be regarded as gained tolerance to the new conditions (Cornwall et al., 2020; Moore et al., 2021), or energetic trade-offs (McCoy and Kamenos, 2015). However, Sordo et al. (2018) showed that although individuals of *Phymatolithon lusitanicum* had an overall positive response during the first eleven months of exposure to high CO₂ conditions, after 20 months, the pattern was reversed. This indicates that resistance to changed

conditions may be short-lived, and further long-term studies investigating the performance of rhodoliths under changed environmental conditions are necessary to understand the different patterns.

Our observations of *L. crispatum* recovery after the removal of stressors, in both summer and winter simulations, may reflect its phenotypic plasticity to changes in environmental conditions (Fox et al., 2019), represented by its current distribution on the Brazilian coast. This species is found from shallow waters to mesophotic zones, and its latitudinal range stretches from the Amazon's mouth to southern Brazil, and as such is one of the most abundant species on the Brazilian coast (Amado-Filho et al., 2017). This widespread distribution reflects the ability of *L. crispatum* to withstand a wide range of temperatures, as observed in our study with a tolerance to 30 °C. Natural fluctuations in the ocean's pH (Hofmann et al., 2011) can also help to explain the plasticity of *L. crispatum* in more acidic conditions. Additionally, CRA have been demonstrated to somewhat control the pH in their boundary layer to sustain calcification, even in simulated scenarios of ocean acidification (Hofmann et al., 2016; McNicholl et al., 2019, 2020), a strategy that likely comes from the exposure of this group of organisms to past ocean acidification and warming (Bergstrom et al., 2020). Future research focusing on *L. crispatum* will benefit from investigating the different strategies used by this species to cope with decreased pH and elevated temperatures.

Our experiment results corroborate model predictions of greater potential habitat suitability of *L. crispatum* under future scenarios. These adaptations to future conditions can be better understood by looking at the evolutionary history of this and related species, and previous experimental evaluations. CRA have a great presence in the geological record, which shows that this group likely thrived under a wide range of temperatures, light, and nutrient levels, and are theorized to have peaked in mid-Miocene substituting coral reefs due to enhanced trophic resources (Halfar and Mutti, 2005). More specifically, Hapalidiales, the order to which the genus *Lithothamnion* belongs, diverged ca. 65–117 My

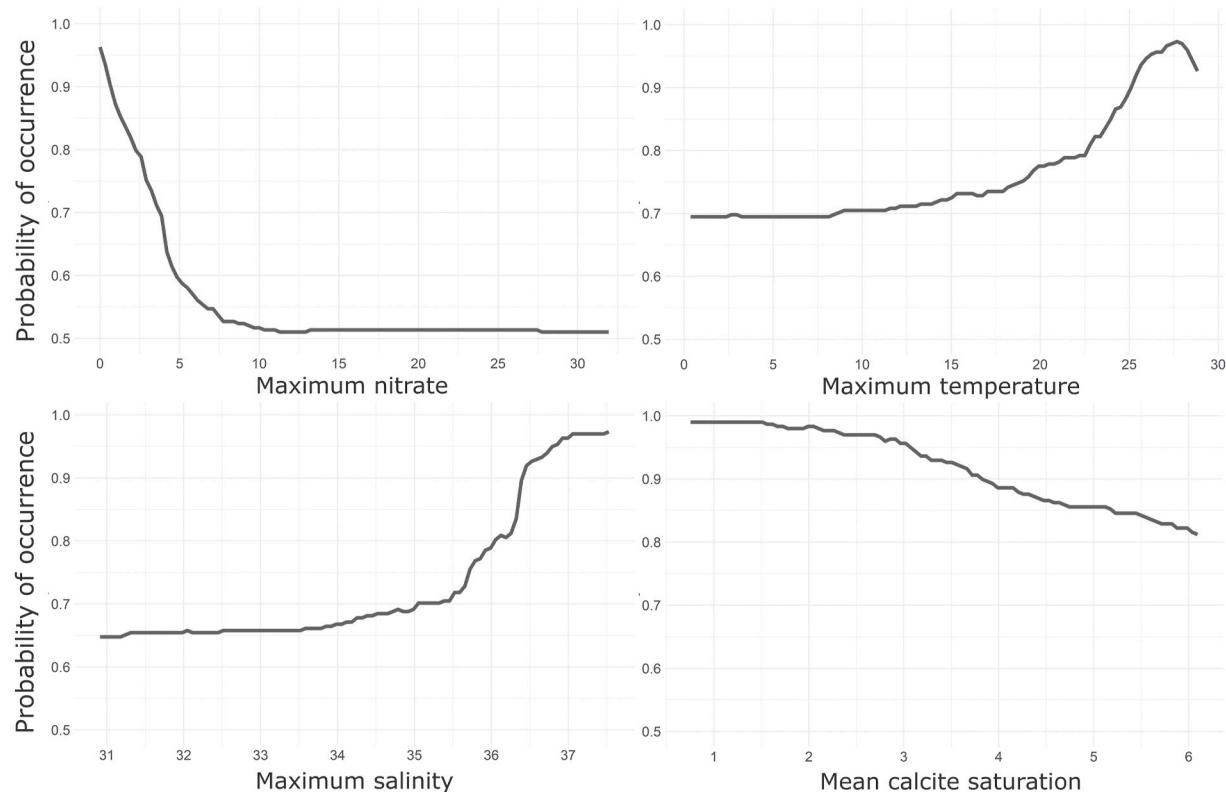


Fig. 6. Response curves of maximum nitrate, maximum temperature, maximum salinity and mean calcite saturation showing *L. crispatum* probability of occurrence according to the variation of each variable. The variations in each curve show the sensibility of the ensemble model to the variable varying across its whole range.

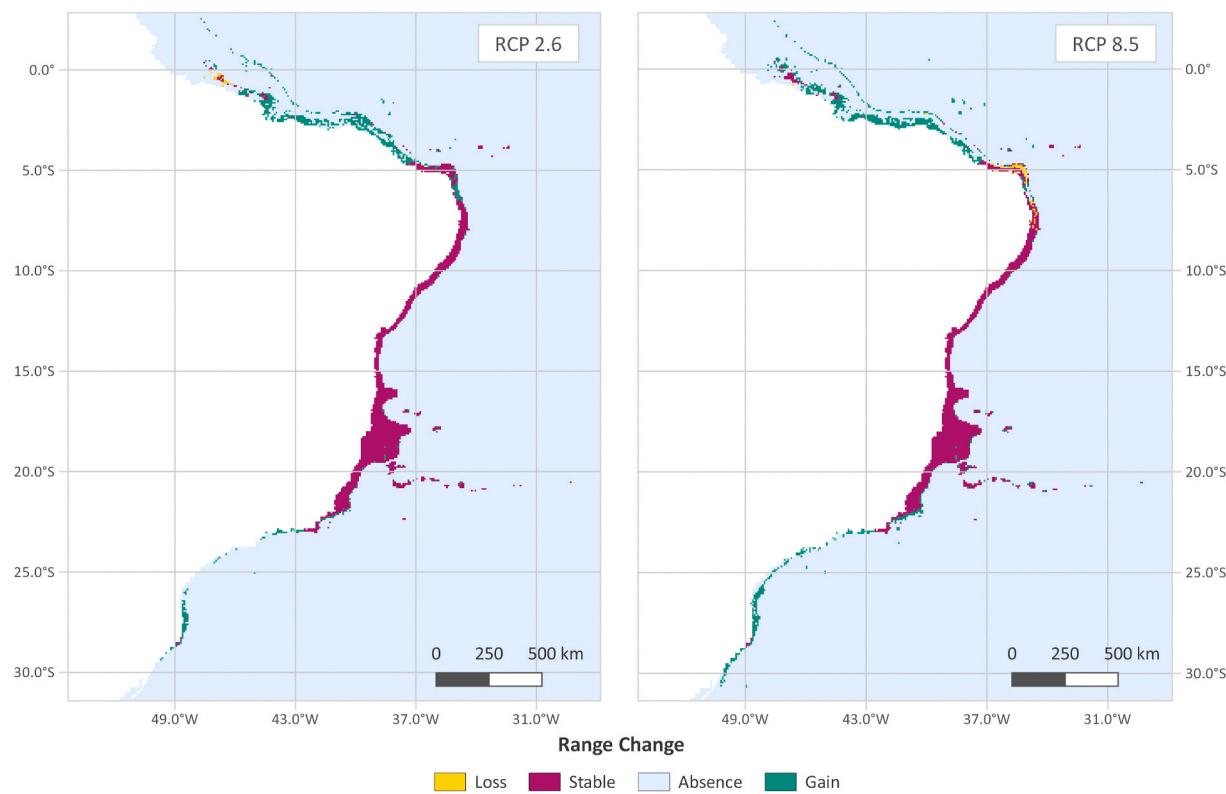


Fig. 7. Future projections of *L. crispatum* under the scenarios of RCP 2.6 and 8.5. Expected range changes are partitioned in loss of current suitable habitat (orange), gain of future areas with suitable habitats (green), presence in current and future conditions (stable habitat suitability – dark pink), and absence in current and future conditions (light blue). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

ago (Aguirre et al., 2010; Peña et al., 2020), when $p\text{CO}_2$ values (Hönisch et al., 2012) and temperature (Hansen et al., 2013) were higher than those found today [$< 600 \text{ ppm}$ and $< 8^\circ\text{C}$ warmer than present day, Royer et al. (2004)]. Thus, CRA likely evolved calcification strategies that enabled persistence during past ocean acidification and warming oscillations, and potentially in future ocean conditions (Bergstrom et al., 2020), as demonstrated in our model projections. Moreover, previous experimental studies with different CRA species have shown that some species do tolerate higher $p\text{CO}_2$, temperatures, and nutrient concentrations (Cornwall et al., 2020; Johnson and Carpenter, 2018; Schubert et al., 2019; Sordo et al., 2019). Our experiment results corroborate the ability of *L. crispatum* to survive in such conditions and may indicate conservatism of the traits that allowed the group to cope with past ocean conditions, but further phylogenetic and physiological studies are needed to corroborate this hypothesis.

Based on future projections of habitat suitability, our model predicts greater suitability in 2100, in both RCP 2.6 and 8.5 scenarios, than in the present. Assessing the accuracy of ENM projections in the future is challenging, as climate change brings non-analog environmental conditions (conditions that do not exist in the present), and predicting how species will respond to these conditions is complex (Fitzpatrick and Hargrove, 2009; Refsgaard et al., 2014). Given nitrate was the environmental variable that contributed most to our model, our predictions may change based on future predictions of nitrate. Although future prediction layers for nitrate were not available, changes in concentrations and the spatial distribution of nitrate in coastal zones worldwide are expected (Galloway et al., 2004; Van Der Struijk and Kroese, 2010). However, higher nutrient levels in the past (11–16 My ago) favored the expansion of rhodophytes to the detriment of other reef-building organisms, indicating that CRA may still be resistant to a greater availability of nutrients and in fact thrive in such scenarios (Halpern and Mutti, 2005). Maximum temperature, which was also important in the model, helps explain the range expansion to southern areas of Brazil,

where future warming is expected and is indeed already being observed (Vergés et al., 2014). Increases in salinity, together with temperature, also led to the prediction of increased habitat suitability, as the response curves for both these variables in the model show high probability of occurrence in higher values. This is an extrapolation of the model as these new conditions are outside of the calibration range (Hirzel and Le Lay, 2008), and consequently, our results should be considered as a preliminary attempt to predict the future of *L. crispatum* distribution.

It is important to note that we lack important information about *L. crispatum* (and CRA in general), which would allow the characterization of its true distribution, and as such, our results should be read carefully. Although our model was able to correctly predict habitat suitability for the existing occurrences of *L. crispatum*, the low number of occurrences makes it unlikely that we have described the full climatic niche of the species here (Barbet-Massin et al., 2012). Moreover, dispersal is highly important in shaping species' geographical distribution, as limited dispersal can restrict the occupation of suitable habitats by the species (Peterson et al., 2012). Information about CRA's dispersal capability is still largely undescribed (Rindi et al., 2019), and assessing the importance of dispersal in determining the distribution of CRA is not possible at the moment. Another important factor shaping species distributions and their niche is their interactions with other species, and changes in interactions caused by environmental changes will also play an important part in determining the fate of a species (Ockendon et al., 2014; Strona and Bradshaw, 2018; Vergés et al., 2016). Marine heatwaves have already resulted in increased turf cover in calcification accretion units placed in shallow coral reefs at Abrolhos in Brazil (Reis et al., 2016), and increased nutrient conditions and ocean acidification also favor the growth of fleshy algae (Legrand et al., 2017; Scherner et al., 2013). Trophic interactions will also suffer changes under climate change, such as herbivorous fish interactions that are predicted to decrease in the tropics and expand poleward, exercising more pressure in algal communities in middle latitudes (Inagaki et al., 2020).

Moreover, grazers control CRA cover by epiphytes and the competition with other groups of algae, but in conditions of increased pCO₂ levels, increased grazing activity by sea urchins and gastropods was shown to weaken the structural integrity of the thalli, making CRA more susceptible to ocean acidification (Legrand et al., 2019; Rich et al., 2018). Therefore, many other factors need to be considered to create more precise predictions of the future of rhodolith-forming species.

Having raised some of the caveats in our model, future predictions, and experiment, it is also necessary to consider the importance of studies investigating the future habitat suitability of key species. Predictions of future species ranges are inherently uncertain, more so when hampered by data deficiencies for either species or environmental conditions. However, conservation actions need information rapidly to attempt to mitigate some of the impacts of climate change, and studies like these are important to, at least, bring this discussion to the table of decision-makers (Rilov et al., 2019). The importance of rhodolith beds in both the past and present is clear, given their importance for the life stages of many other species. Their ability to withstand extreme events and future global environmental change may make them critical species for maintaining and restoring marine communities into the future. If our study is any indication, *L. crispatum* may be one of those species, and its higher habitat suitability in the future in matching regions where important fishes are predicted to shift their biotic interactions and distributions (Inagaki et al., 2020) can perhaps create the opportunity of these species to survive to novel environmental conditions. Of course, many other studies are required to confirm this hypothesis, investigating how the presence of rhodoliths beds influences the distribution of important fauna, and if *L. crispatum* has the dispersal ability necessary to colonize new regions. But considering the higher sensitivity of reef-building coral species to climate change (Anthony et al., 2011; Roth et al., 2020), rhodolith beds formed by tolerant species may increase in importance in the future ocean. Nevertheless, there are distinct functional properties between reef fish assemblages from reefs and rhodolith beds (Moura et al., 2021), indicating that a change to an ecosystem based solely on rhodoliths will result in changes in the biodiversity and functioning of ecosystems (Roth et al., 2020).

Despite the recognition of rhodolith beds' key role in healthy ecosystem function, in Brazil they are nearly entirely unprotected, even after the recent increase of Marine Protected Areas to 26% of the Ecological-Economic Zone (Soares and Lucas, 2018). Although some rhodolith beds are found within Marine Protected Areas in Brazil, existing protected areas only cover small portions of these habitats, especially in Abrolhos Bank (Amado-Filho et al., 2017; Moura et al., 2013). Rhodolith beds have been proposed as high priority areas for conservation as they represent an important dispersal pathway in the Brazilian coast (Magris et al., 2020), and our study further emphasizes the importance of conserving these ecosystems. By exploring the physiological response of *L. crispatum* to future environmental conditions, and its following recovery, this study demonstrated, and corroborated, model predictions of the expansion of this species' habitat suitability in the future. The apparent ability of *L. crispatum* to survive extreme conditions suggests this species can be a potential target for conservation, especially considering that climate refugia of this species are correlated with high priority areas for conservation delineated by Magris et al. (2020).

Declaration of competing interest

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

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2021.105394>.

CRediT author statement

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