



Future range dynamics of the red alga *Capreolia implexa* in native and invaded regions: contrasting predictions from species distribution models versus physiological knowledge

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Abstract Correlative species distribution modelling is a widely used method to predict potential species ranges but can suffer from limitations in integrating species' fundamental niches. Therefore, they might underestimate suitable ranges, but including physiological information can improve accuracy of predictions and help identify mechanisms of e.g. range limitation. However, approaches using both, results from correlative as well as physiological investigations are rare, especially in research on seaweeds. Here, we provide results from both approaches to predict the suitable habitat range of *Capreolia implexa* (Rhodophyta) in its native range (Australia and New Zealand) and invaded range (Chile) under present and future climate scenarios (year 2100, rcp 2.6 and rcp

8.5). We used the Maxent modelling technique and physiological knowledge from a temperature tolerance experiment (2–20 °C) for thermal niche estimation. Results from both approaches suggest larger suitable habitat ranges under present day conditions for both regions than currently occupied. Abiotic range limitation in the native range led to underestimation of the suitable temperature range by Maxent (here lower temperature limit = 8.3 °C). Predictions based on the laboratory temperature tolerance experiment suggest additional suitable habitat in colder regions (here lower temperature limit = 6.6 ± 0.4 °C). Under future climate conditions, both native and invaded ranges should shift southward, which will lead to an overall loss of suitable habitat in the native range. Like that, rcp 8.5 conditions should reduce the native range to 50% of the present-day extent. We demonstrate the limitation of correlative SDM modelling for species that live on continental margins and that physiological experiments can help to identify species' niches beyond correlative analyses, providing valuable information for range projections. Furthermore, we provide valuable insights relevant for both invasion management and conservation.

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Graphic abstract



Keywords Ecological niche modelling · Seaweed biogeography · Climate change · Chile · Range contraction

Introduction

Climate change is the major driving force for distributional range shifts from the equator poleward (Chen et al. 2011). This force affects terrestrial and marine species alike, regardless of taxonomic group (Harley et al. 2006; Sorte et al. 2010; Chen et al. 2011). While climate change leads to loss of species-specific biomass in lower latitudes, it may facilitate higher biomass and productivity in regions of higher latitudes (e.g. Krause-Jensen et al. 2007; Krause-Jensen et al. 2012; Bartsch et al. 2016). However, by pushing species towards continental margins, range contractions can occur, leading to an overall loss of suitable habitat or even extinction (e.g. poleward shifts in Australia and New Zealand, Wernberg et al. 2011). In contrast, expansions of species' distributional ranges are observed across the globe (e.g. Williams and Smith 2007). Here, human activity plays a major role by connecting spatially isolated places (Thuiller et al. 2005; Seebens et al. 2016), which may potentially offer new refuge areas for species under threat. However, non-indigenous species can have vast deleterious effects on recipient ecosystems, and bioinvasions are considered a major threat to biodiversity and community structure (Ruiz et al. 1997;

Casas et al. 2004; Klein and Verlaque 2008; Raffo et al. 2009).

Bioinvasions are not only of major ecological concern but also of socioeconomic interest as control and remediation costs are substantial (Pimentel et al. 2000). From an economic point of view, prevention is to be preferred over later management measures (Leung et al. 2002). Anticipation of and rapid response to invasions are important in combatting invasive species (Wotton et al. 2004). Hence, risk assessment of non-indigenous species needs thorough evaluations of invasive potential, including the identification of the suitable range within an invaded region. Correlative species distribution models (SDM) are widely applied to identify species' niches and potential habitats and can help to assess invasion risk (Thuiller et al. 2005). This method makes use of available distributional and environmental data for predictions of the suitability of other areas where the species could occur. The results can also give important information to evaluate climatic influences on species distributions under past, present and future environmental conditions and are an important tool for ecosystem management (Guisan and Thuiller 2005).

In spite of their potential power, correlative SDMs are subject to limitations which prevent them from determining the actual fundamental niche of a species. These limitations can originate from either natural causes (e.g., the restriction of a species' distributional range through the biotic and abiotic factors that define the realized niche of a given species) or technical circumstances (e.g., as lack of comprehensive data due to a regional sampling bias). Hence, correlative SDMs, projecting only the realized niche of a species, may lead to incomplete predictions of a species' suitable range and thus underestimate its potential range (Peterson 2005). Correlative models also cannot provide causal links between a predictor variable and the response, leaving it unclear if an observed response is a direct effect of an included factor or result of another collinear influence (Mac Nally 2000).

To address the above-mentioned limitation, it has been proposed to integrate physiological knowledge into predictive models (Kearney and Porter 2009). These mechanistic models do not indirectly identify a species' niche via correlative distribution analysis but instead make use of underlying physiological traits, such as temperature limits for survival, for mapping its potential range (Kearney and Porter 2009). In this

way, the fundamental niche of a species can be projected in a given region, and any discrepancies between correlative and mechanistic predictions may provide insight into underlying mechanisms which restrict a species' range (Martínez et al. 2015). Thus, a comparative approach might increase the accuracy of predictions. However, identification of physiological limits of a species demands laborious experimental investigation. Hence, studies making use of both information are still rare (but see e.g. Buckley et al. 2010; Diamond et al. 2012; Martínez et al. 2012).

In this study we use a correlative SDM and physiological knowledge to predict the suitable range of the non-indigenous red alga *Capreolia implexa* Guiry & Womersley in Chile. *C. implexa*, first described as a species just in 1993, has an unusual biphasic life cycle that lacks the carposporophyte stage (Guiry and Womersley 1993). It was first reported from Chile from coasts between 39° 56' and 41° 45' S by Boo et al. (2014). It is likely that the species originates from Stewart Island, New Zealand and that it has been introduced either via west-wind drift or by the transport of aquaculture related material (Boo et al. 2014). Based on the finding of reproductive populations, Boo et al. (2014) considered the species to be established in several localities and expressed concerns about significant negative impacts on Chilean ecosystems. Based on the temperature range within the native distributional range of *C. implexa* in Australia and New Zealand, they suggested that it may be capable of spreading further along the coast both north- and southward. Hence, it could become a truly invasive species along Chilean coasts. *C. implexa* occupies a wide range of environments along sheltered as well as open coasts in its native range, and where it is established it forms thick, dense mats over the substrate (Nelson 2013). Possible impacts on other (seaweed) species are so far unknown, but, since *C. implexa* was perhaps introduced with aquaculture and thus has the potential to spread along Chilean coasts, it is important to predict and monitor the spread of the species to better understand the mechanisms of dispersal and possible impacts on the local Chilean flora and fauna. Due to its mat-forming growth form, it may be considered to be an ecosystem engineer, sheltering flora and fauna from stressors experienced in the intertidal (see Thiel et al. 2007) and probably preventing other species from settling (Sousa 1979; Linares et al. 2012). However, it is not clear if this

species might compete with native Chilean seaweeds or perhaps add to the diversity of native ecosystems. Indeed, little is known in general about the number and effects of introduced seaweeds in Chile, and so far only one species, *Codium fragile* subsp. *tomentosoides*, is considered a pest in aquaculture (Castilla et al. 2005). However, new introductions are reported occasionally (e.g. Kim et al. 2004; Boo et al. 2014). *C. implexa* has only been reported from Chile relatively recent and is so far not very wide-spread, and hence, offers the opportunity for close monitoring in the future.

In contrast to a potential range expansion in Chile, we propose that it might face significant contraction of its native distribution under future warming conditions, as increased water temperature will shift the thermally suitable range southward and beyond the continental margins, leading to an absolute loss of suitable habitat (see Wernberg et al. 2011 and Martínez et al. 2018 for examples). The potential spread of *C. implexa* in its non-native range and the threat of substantial habitat loss in its native range makes an intriguing contrast. Here we experimentally investigate the physiological temperature limits of *C. implexa* to project suitable potential habitats in its native as well as invaded range. This projection is then compared to a suitability prediction from the Maxent application, which uses presence-only distribution data to calculate suitability of a habitat (Phillips et al. 2016). We specifically wanted to (1) evaluate which regions in South America might be suitable for further invasions by *C. implexa*, and (2) clarify to what extent range shifts are to be expected under future climate conditions in Australia and New Zealand. We hypothesized that including the mechanistic approach will yield larger suitable habitat ranges and a comparison of both projected ranges will identify regions of contrasting suitability predictions. These regions may allow to identify possible factors which limit the realized niche of *C. implexa*.

Material and methods

Temperature tolerance experiment

We collected samples of *C. implexa* in the intertidal off Calbuco, Chile (73° 7' W, 41° 46' S) on the 15th of January 2017, transported them in darkness in a cooler

to the laboratory and confirmed their identity with available literature (Nelson 2013; Boo et al. 2014). During collection, we paid attention to sample from as many individual epilithic and epizoic patches as possible with a distance of several meters between them ($n > 20$). The samples were kept in aerated von Stosch (Grund) medium without additional iron (Andersen et al. 2005) at 18 °C with 90 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ light in green light (Leaf Green, E-Colour, Stamford CT) (18:6 L:D) until further use. Green light was used to avoid overgrowth by green algae, and streptomycin (1 mg L⁻¹; AppliChem GmbH, Darmstadt, Germany, 752 I.U./mg) added to prevent contamination with cyanobacteria. We changed the medium weekly at which time we also rinsed the specimens with fresh tap water. For our experiments, we cut off growing tips 3–4 mm in length with a sterile scalpel from different haphazardly selected tetrasporangial individuals, cleaned off epiphytes with a toothbrush under a stereomicroscope, and dragged them through 0.5% sterile agar-plates (Tatewaki and Provasoli 1964). We transferred in total 140 tips to 10 transparent 24-well culturing plates with lids to prevent evaporation of medium (3.4-mL cell volume). Experimental medium was without antibiotics and was changed and tips cleaned every 7 days.

Ten experimental temperatures were set up in insulated aquariums of 20 L volume with automatic temperature adjustment to 2–20 °C in 2 °C steps (± 0.1 °C) (Julabo F25-ME Refrigerated/Heating Circulators with external PT100 temperature sensors; JULABO GmbH, Seelbach, Germany). One sample-containing multi-well plate was used per temperature treatment and immersed in the respective aquarium to keep the samples at desired stable temperature conditions throughout the experiment. Hence, 14 individual tissue samples were used as pseudo-replicates per temperature level. Due to logistic constraints it was not possible to incubate 14 true replicates in separate experimental containers for the experiment. The experiment ran for 6 weeks. PAR (60 $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$) was provided with white light LEDs (SolarStinger SunStrip, Econlux GmbH, Köln, Germany).

For growth and survival responses, tips were photographed every week and total length was measured with Fiji software (version 1.51u). Bleached sections were treated as necrotic tissue and not measured. Growth rate was calculated as the change

in length each week ($\text{mm} \cdot \text{individual}^{-1} \cdot \text{week}^{-1}$), and specimens with negative growth rates were counted as dead specimens. Outliers were identified as outside outer fences of boxplots (fences = $Q1 - 3 \cdot \text{IQ}$ and $Q3 + 3 \cdot \text{IQ}$, respectively; Q = quartile, IQ = interquartile range) and omitted in fitting growth response curves. To identify the lethal temperature limit, a logistic regression analysis was fitted over survival rate versus temperature, and the temperature at 0.5 classification chosen as temperature threshold for survival (I_{t50}).

Distributional records for SDM

Distributional data were compiled from Womersley (1994), Miller (2003), Nelson et al. (2006), Nelson (2013) and Boo et al. (2014) and expanded with data from www.gbif.org (9th of March 2018). Data from [gbif.org](http://www.gbif.org) was cleaned by excluding records from before 1993 (year of description of the species by Guiry and Womersley 1993) and only unambiguous georeferenced data used. Furthermore, duplicates were removed resulting in 82 coordinates for the SDM. To avoid spatial autocorrelation, the records were thinned in (R-Core-Team 2017) with the `spThin`-function from the R-package of the same name (Aiello-Lammens et al. 2014). Different distances were tested to find the minimum required distance between records to avoid spatial autocorrelation, resulting in a distance of 50 km, which allowed to keep 51 remaining distribution points (Fig. 1a). For a training range, Australia and New Zealand were chosen. Distributional data from South America was not included to train the model, since the introduction has been reported recently and *C. implexa* is so far only found at a few isolated sites which are characterized by comparable environmental conditions as found in its native range. Moreover, inclusion of these data in a preliminary model resulted in slightly reduced predictive power (not shown).

Environmental predictors for SDM

Environmental data layers were compiled from Bio-Oracle v2.0 (Assis et al. 2017), MerraClim (Vega et al. 2017) and WorldClim (Fick and Hijmans 2017) (Table 1). We did not include a “wave exposure” layer since this species occupies sheltered and open coasts alike (Nelson 2013). To align layers from

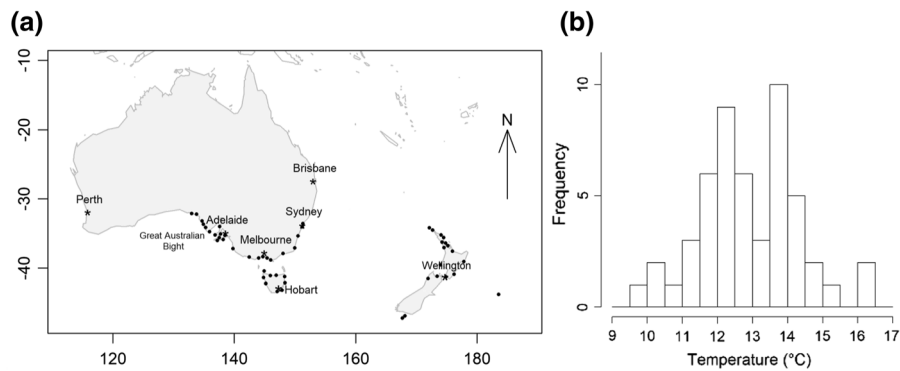


Fig. 1 **a** Occurrence data of *Capreolia implexa* around Australia and New Zealand (thinned data = black dots, cities = stars) and **b** frequency of occupied min SST conditions as sampled from the bio-oracle min SST layer from the included occurrence sites

Table 1 Predictor variables with sources

Predictor variable	Abbreviation	Unit	Range (min–max) in model training range	Origin (as specified in source)	Source	Resolution
Minimum sea surface temperature	Min SST	°C	7–25.1	Monthly averages (2000–2014)	Bio Oracle 2	5 arcmin
Maximum sea surface temperature	Max SST	°C	12.8–31.8	Monthly averages (2000–2014)	Bio Oracle 2	5 arcmin
Minimum air temperature	Min Air T	°C	– 2.5–24.8	Average monthly temperature of coldest month 2000–2010	MerraClim	5 arcmin
Maximum air temperature	Max Air T	°C	15.9–48	Average monthly temperature of warmest month 2000–2010	MerraClim	5 arcmin
Phosphate	P	mol m ⁻³	9.4×10^{-3} –1.22	DIVA Interpolation from WOD09	Bio Oracle 2	5 arcmin
Nitrate	N	Mol m ⁻³	2×10^{-6} –15.8	DIVA Interpolation from WOD09	Bio Oracle 2	5 arcmin
Cloudiness (year average) ^a	Cloud	%		Monthly averages (2005–2010)	Bio Oracle 2	5 arcmin
Maximum photosynthetically active radiation	Max PAR	E m ⁻² day ⁻¹		Monthly averages (1997–2009)	Bio Oracle 2	5 arcmin
Precipitation of driest month (February)	Min Prec	mm	0–342	Monthly average climate data (1970–2000)	WorldClim 2.0	5 arcmin
Precipitation of wettest month (June)	Max Prec	mm	6–677	Monthly average climate data (1970–2000)	WorldClim 2.0	5 arcmin
Wind speed	WS	m s ⁻¹	1.4–8.25	Monthly average climate data (1970–2000)	WorldClim 2.0	5 arcmin
Salinity	S	PSS	28.6–40.1	DIVA Interpolation from WOD09	Bio Oracle 2	5 arcmin
Substrate type	Substrate	Rock/soft		Visual identification in googleEarth	Own creation (see text for details)	5 arcmin

DIVA = Data-Interpolating Variational Analysis; WOD09 = World Ocean Database 2009

^aNo monthly data available

different sources, WorldClim and MerraClim data layers were resampled with bilinear interpolation using Bio-Oracle 2 layers as references (Phillips et al. 2006) with the resample-function from the “raster” R-package (Hijmans 2017). A layer for substratum type was created by drawing polygons around soft-bottom coastlines of ≥ 10 km length in Google Earth. These polygons were then rasterized and a layer with the binary variable rock/soft-substrate was made. Data layers were limited to coasts with the “coastline and minor islands”—polygons from www.naturalearthdata.com. For projections, only minimum sea surface temperature was used (see Results section). Future predictions were built using layers for the year 2100 under rcp 2.6 (low global warming capacity) and rcp 8.5 (high global warming capacity) scenarios as downloaded from Bio-Oracle v2.0 (Assis et al. 2017; rcp = Representative Concentration Pathways, which include greenhouse gas emissions and atmospheric concentrations, air pollutant emissions and land use, for climate projections (IPCC 2014)). All environmental layers used in this study were in 5 arcmin resolution.

Models were built with Maxent (Phillips et al. 2016) and the biomod2 R-package (Thuiller et al. 2016). In Maxent we allowed linear and quadratic response curves to find the best fit. In every run, ten replicates were produced, and response curves were the average of these replications. For projections we allowed extrapolation without clamping of response curves. For the final model only predictors with model contribution of $> 20\%$ were selected. In biomod2 we built quadratic Generalized Linear Models (GLM) and identified crucial predictors based in the Akaike Information Criterion (AIC). Model evaluation was done with 70/30 (calibration/testing) partitioning in ten repetitions. Maps were binarized to suitable versus not-suitable using the “minimum training presence” threshold given by Maxent (Peterson et al. 2011).

Results

Temperature tolerance experiment and geographic projections

Stationary growth rates were measured 28 days after the start of the experiment, ranging from -1.0 mm (at 2°C) to 1.1 mm per week and individual (at 18°C)

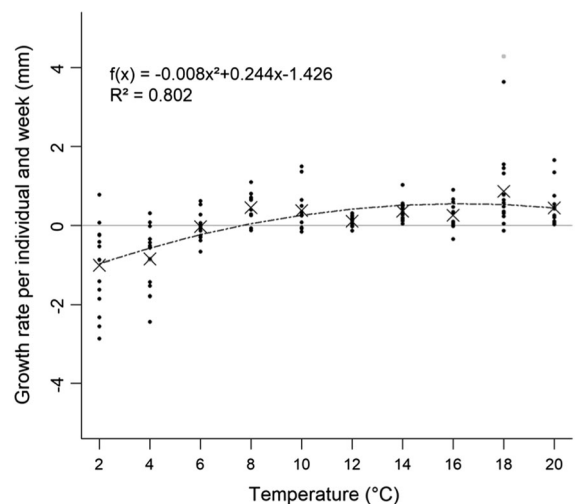


Fig. 2 Growth rates of *Capreolia implexa* per individual after 28 days of the temperature experiment. Dots represent individual replicates ($n = 140$), crosses the average per temperature level without outlier (grey), and the dashed-dotted line the 2nd order polynomial regression line. For the regression line the equation and R^2 are provided, points of intersection with the x-axis are at 7.88 and 22.66°C

(Fig. 2). A second order polynomial regression line was fitted through the average growth rates per temperature (one outlier was excluded at 18°C from mean calculation) ($f(x) = -0.008x^2 + 0.244x - 1.426$; $R^2 = 0.802$). Average zero growth was observed at 6°C , with average growth rates at lower temperatures being negative, at higher temperatures positive (Fig. 2). Growth responses to the temperature treatments after shorter exposure times are shown in Figure S1.

Lt_{50} was identified at $6.6 \pm 0.4^\circ\text{C}$ (Fig. 3). This temperature was used to project southern distribution limits for the native and novel ranges of *C. implexa* under present and future minimum Sea Surface Temperature (SST) conditions (Fig. 4). Since only the temperature range from 2 to 20°C was included in the experiment and there was no negative growth at the higher temperatures, projections were restricted to areas within this range and no shift of the northern distribution limit could be investigated. In Australia and New Zealand, the Lt_{50} was not found along the coastlines, but only south of the landmasses in the ocean. In South America the temperature limit lies south of the reported occurrences at Calbuco. Under future climate conditions, this limit shifted southward

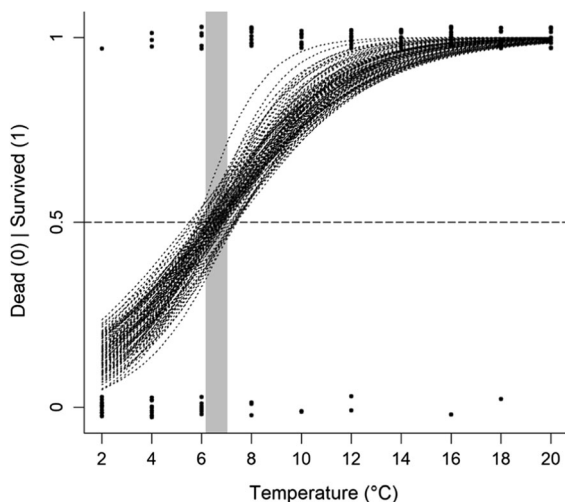


Fig. 3 Number of survived (1) versus dead (0) individuals of *C. implexa* over the experimental temperature range after 28 days. Data points are jittered for better visualization but are in fact only 1 or 0. The dotted lines display the binomial generalized linear models fitted on survival rate (100 repetitions). Lt_{50} lies at 6.6 ± 0.44 °C (grey area); AUC averaged = 0.9 ± 0.04

to the southernmost tip of the continent (year 2100 rcp 8.5, Fig. 4f).

Habitat modelling in native range

A correlation analysis revealed strong autocorrelation (> 0.85) between the Phosphate and Nitrate layers, and between Minimum SST (min SST) and Minimum Air Temperature & Maximum SST (max SST). Different combinations of uncorrelated predictors were tested to find the model with best performance while avoiding autocorrelation among explanatory variables (see Table 2). However, AUCs did not significantly differ between the combinations. Still, in all tested combinations only the SST variables had considerable explanatory power ($\geq 20\%$ in Maxent) with min SST having higher power than max SST. As a consequence, the Maxent models were reduced to only either max SST or min SST. The model with min SST had a higher overall AUC (0.782 ± 0.082) and higher model gain (0.683) than models with max SST (AUC: 0.738 ± 0.75 ; gain: 0.579). Hence, final projections were based on min SST as single predictor variable in Maxent and biomod2 (Tables 2 & 3). The response curve of habitat suitability dependent on min SST from Maxent is shown in Fig. 5. Based on the

minimum presence threshold, the predicted suitable min SST range of *C. implexa* occurs between 8.3 and 16.2 °C. In comparison, the occupied min SST range occurs between 9.7 and 16.2 °C (Fig. 1b). The occupied maximum SST in the native range lies between 14.2 and 23.9 °C (not shown).

Predicted habitat suitability for Australia and New Zealand under present and future conditions

Projections for Australia and New Zealand for present-day climate conditions identified suitable habitat in regions without currently known presences (Fig. 6a). In Australia this was the case for large parts of the Great Australian Bight and in New Zealand mainly along the western and eastern coasts of the South Island.

The SDM including min SST was used to project habitat suitability under climate scenarios rcp 2.6 and rcp 8.5 for the year 2100 (Fig. 6b and c). Under rcp 2.6 conditions minor losses in projected suitable range are found at the southwestern coast of Australia along the Great Australian Bight and at *C. implexa*'s northern distribution limit. A small gain in suitable area is found at the eastern coast of the South Island of New Zealand. Losses in suitable habitat are much larger under rcp 8.5 scenario conditions but in the same areas as under rcp 2.6 conditions. Under rcp 8.5 conditions, loss is also predicted for the northern coasts of the North Island of New Zealand. Gain in suitable area is as described for the rcp 2.6 scenario. Overall loss of total suitable range is estimated as ~ 528 km of coastline under rcp 2.6 conditions and ~ 4226 km under rcp 8.5 conditions and gain as ~ 163 km. Gain in suitable habitat is, however, predominantly predicted for coasts with soft substrate habitats.

Predicted habitat suitability for South America under present and future conditions

Projections for South America included the reported invaded regions as suitable habitat (Fig. 7). Under present day climate conditions (Fig. 7a) suitable habitat in the non-native region is predicted for coasts between approx. 5° 10' S and 44° 55' S along the Pacific coast of South America (Peruvian coast and Chilean coast north of Chiloé island), and between 28° 28' S and 42° 58' S along the Atlantic coast (San Matías Gulf and south of the Río de la Plata in

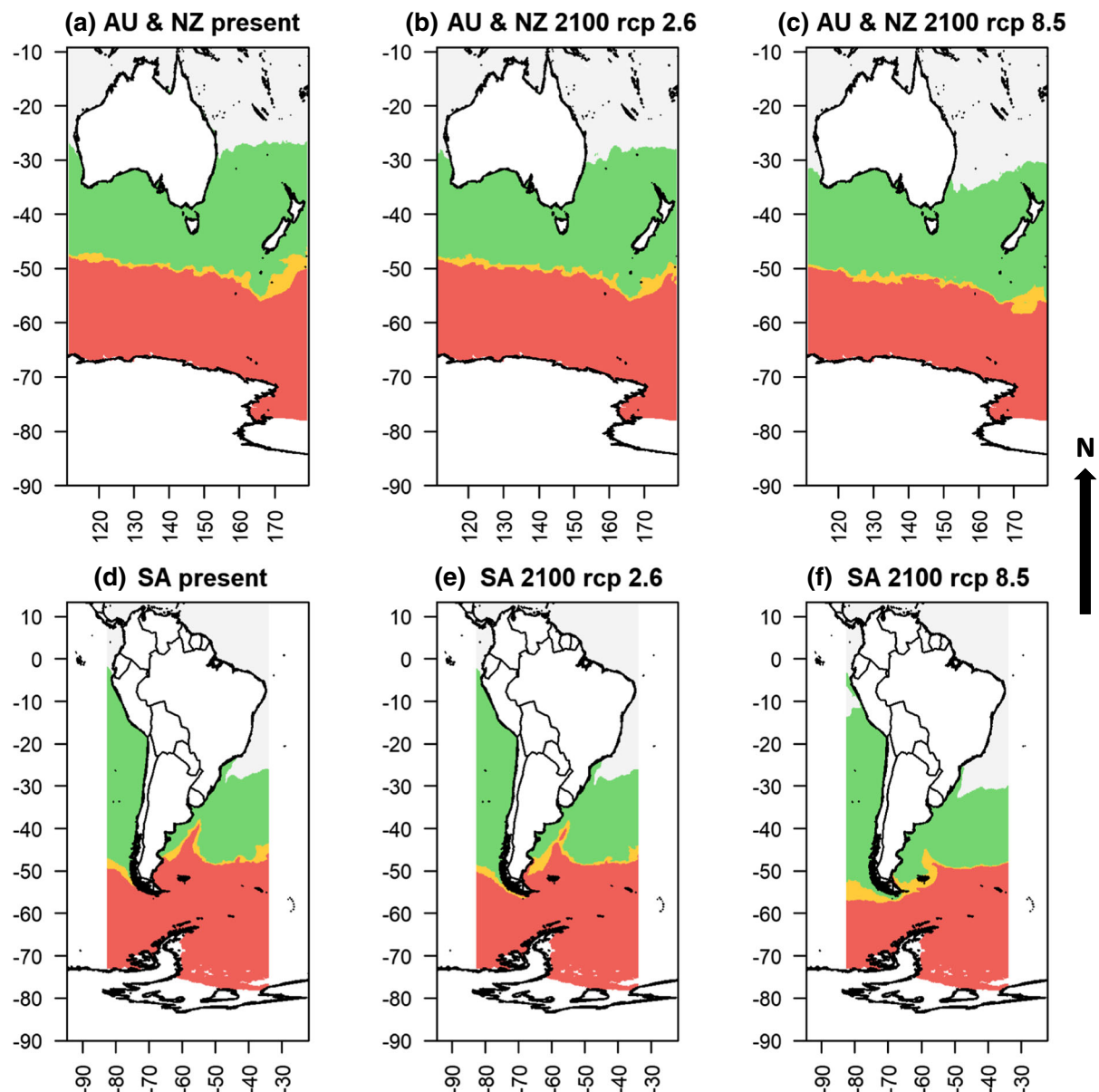


Fig. 4 Projection of the southern distributional limit of *C. implexa* in Australia, New Zealand (a–c) and South America (d–f) for present and future climate scenarios by applying the lt_{50} temperature threshold from physiological experiments.

Red $> lt_{50}$, green $< lt_{50}$, yellow = 6.6 ± 0.44 °C. Limits are projected onto minimum SST layers. Temperatures above 20 °C are excluded (light grey), white areas near Antarctica are due to lack of data

Argentina, most of Uruguay and parts of Brazil). Under future conditions (Fig. 7b and c) southward expansion of invadable habitat is predicted for both the rcp 2.6 as well as the rcp 8.5 scenario with much larger shifts under rcp 8.5 conditions. Under the latter conditions northern limits are predicted at approximately $24^{\circ} 58' S$ on the Pacific coast and $29^{\circ} 12'$ on the

Atlantic coast. Southern limits are predicted at approximately $51^{\circ} 48' S$ in Chile and $47^{\circ} S$ in Argentina. As such, the northern and southern limits of predicted suitable habitat along the Pacific coast would be shifted approximately 2160 km and 770 km to the south, respectively. The Peruvian coast as well as the northern Chilean coast become

Table 2 Model contributions of predictor variables and model performances of different predictor combinations

Predictor variable	Model 1	Model 2	Model 3	Model 4	Model 5
Minimum sea surface temperature (Min SST)	76.6 (0.68)*	–	79 (0.68)*	–	51.8 (0.68)*
Maximum sea surface temperature (Max SST)	–	70.1 (0.57)*	–	72.3 (0.57)*	27.5 (0.57)*
Minimum air temperature (Min Air T)	–	0.1	–	0.1	0.2
Maximum air temperature (Max Air T)	0.2	0	0.2	0.1	0.3
Phosphate	6	6.5	–	–	0
Nitrate	–	–	7.6	8.3	8.8
Cloudiness (year average)	0.3	0.2	0.1	0.2	0.1
Maximum Photosynthetically Active Radiation	1.1	1.9	1	1.6	0.8
Precipitation of driest month	10.7	17.1	7.5	14	6.9
Precipitation of wettest month	2.1	1.2	1.6	0.9	1
Wind speed	1.1	0.3	1.4	0.3	1
Salinity	0.2	1.5	0	1.3	0.2
Substrate (rock/soft) Australia and New Zealand	1.7	1.1	1.7	1	1.4
AUC of the model	0.74 ± 0.055	0.738 ± 0.054	0.744 ± 0.053	0.74 ± 0.056	0.73 ± 0.053
Test gain of the model	0.517	0.534	0.518	0.531	0.49

The combinations here include only predictors with correlation coefficients among them < 0.85. Test gain of individual predictor variables in brackets (only predictors with model contribution of ≥ 20%, bold letters). Asterisks mark predictors with contribution > 20% to the models

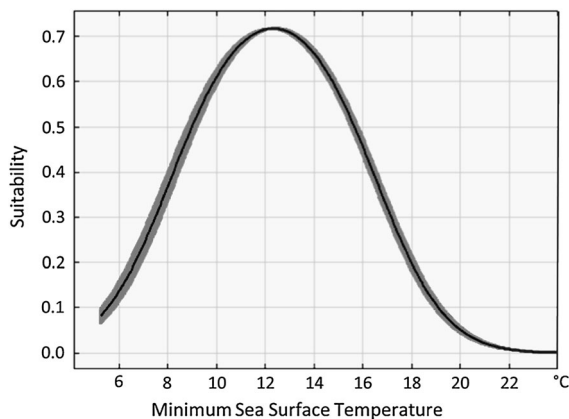


Fig. 5 Maxent response curve of *Capreolia implexa*, showing the predicted habitat suitability dependent on min SST. Black line is the average of 10 replicated runs ± SD (grey area)

unsuitable. In the south suitable habitat becomes available as south as the Chilean Magallanes region. On the Atlantic coast shifts would not be as pronounced. However, northern and southern limits are still predicted to shift approximately 90 km and 490 km, respectively, i.e., a minor loss of suitable habitat in the northern region with greater gains for more southern coasts.

Discussion

The experimental investigation of the lower temperature survival threshold of *C. implexa* suggests that this species, native to Australia and New Zealand and recently found in few localities in southern Chile, may be able to establish new populations on a much broader geographical extent than presently expected. Present-day minimum ocean temperatures seem warm enough for the expansion of the species along Chilean and other South American coasts (including the Atlantic coast, should it become established there), with current thermal conditions being within its fundamental thermal niche. A previous assumption of the invasive potential of *C. implexa* based on the known occupied temperature range in its native habitat hence resulted in a too narrow expected range for Chile (Boo et al. 2014). We have shown that the correlative model approach alone is not suitable to detect the whole temperature range of the investigated species. Furthermore, we predict that under future climate warming *C. implexa* will likely lose suitable habitat in its native range due to a shift of suitable temperature conditions further southward.

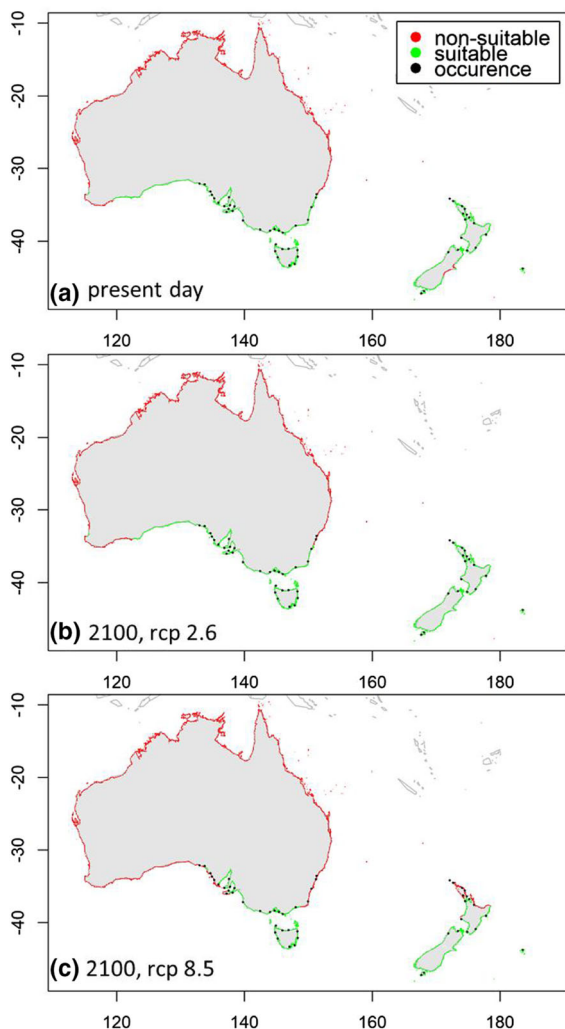


Fig. 6 Binary habitat suitability predictions for Australia and New Zealand based on correlative SDMs for **a** present, **b** 2100 rcp 2.6 and **c** 2100 rcp 8.5 climate scenarios

Our Maxent model correctly identified the currently occupied Chilean coasts as suitable areas and with an AUC of 0.782 ± 0.082 can be evaluated as “good” (Swets 1988; Duan et al. 2014). However, it predicted

a wider suitable range in Australia and New Zealand than currently known to be colonized. In particular, the Great Australian Bight as well as along the western and eastern coasts of the South Island of New Zealand large stretches of (sandy) coastline are unoccupied although predicted as suitable. In our model, substrate availability had no influence on the prediction. During our field sampling in Chile we saw that rocky structures on sandy beaches were colonized by *C. implexa*, which probably lead to the rejection of substrate as a predictor at this resolution. The shore of the Great Australian Bight is characterized by steep cliffs, making it difficult to access. Therefore, the lack of occurrence in this part of the species’ range may simply be the result of a sampling bias, i.e., a lack of survey in this region.

Compared to the correlative SDM, the prediction based on temperature tolerance resulted in different habitat suitability maps for South America, with greater extensions of the southern limits. Hence, we assume an unfilled-niche situation in the native range with respect to tolerated lower minimum SST conditions. Although the Maxent response curve is already extrapolated to lower temperatures than occupied in the native range (8.33°C vs. 9.96°C), it was not able to identify the physiological lower limit of $6.6 \pm 0.4^\circ\text{C}$. This shortcoming is likely due to the fact that *C. implexa* does not experience this low temperature in its native range, as the coasts of Australia and New Zealand do not reach into such cold waters. Hence, here the fundamental niche is truncated at its lower end by the absence of suitable substrata (i.e., rocky intertidal shores) in colder waters, leading to a too narrow Maxent response curve. The logistic regression curve, derived from our experiments, yields a lower temperature limit in colder temperatures than the Maxent response curve. This highlights the assumption that correlative response curves do not necessarily exhibit the same shape as mechanistic

Table 3 Model parameters of the glm with min SST as single predictor variable

Model	AUC	Df	Residual deviance	AIC	Coefficient	Intercept	ROC	Sensitivity	Specificity
Min SST	0.782 ± 0.08					− 20.43	0.74	92.55	56.48
<i>Null</i>		100	140	142					
$(\text{Min SST})^2$		99	110.96	114.96	− 0.12				
<i>Min SST</i>		98	101.87	107.87	+ 3.19				

AUC Area Under Curve, Df degrees of freedom, AIC Akaike Information Criterion, ROC Receiver Operating Characteristic

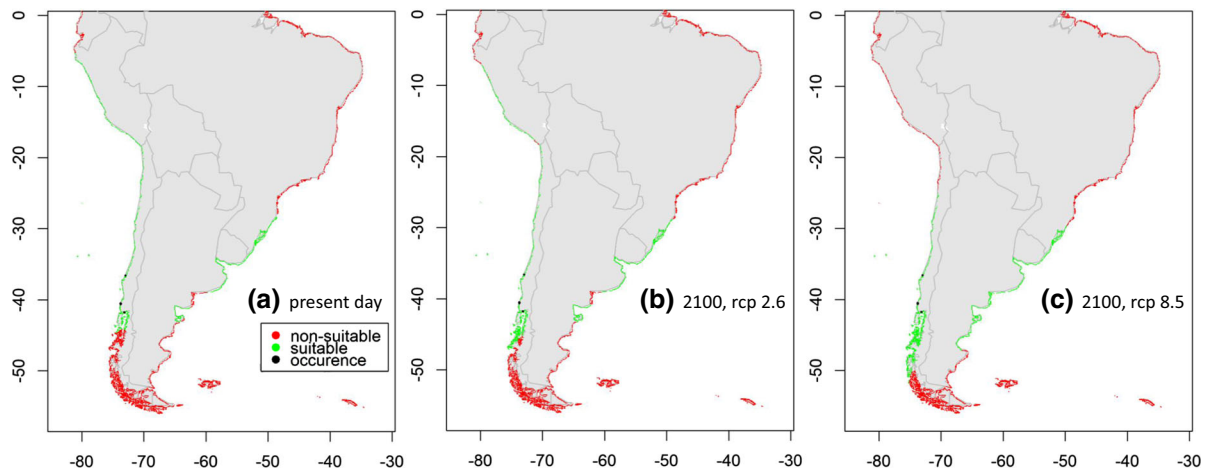


Fig. 7 Binary (suitable vs. non-suitable) habitat suitability predictions for South America from Maxent. Model trained on native area (Australia & New Zealand) and projected to the invaded area under **a** present, **b** 2100 rcp 2.6 and **c** 2100 rcp 8.5 climate scenarios

response curves (Martínez et al. 2015). Modelling ecological niches based on unfilled niches results in predictions of a too narrow spatial extent and can lead to underestimation of species' potential ranges (Peterson 2005). Boo et al. (2014) also used known occupied temperatures by *C. implexa* in its native range to estimate its invasion potential in Chile and assumed a suitable range between Valparaíso in the north and Golfo de Penas in the south. By assuming a temperature limit of around 10 °C instead of the physiological limit of 6.6 ± 0.4 °C, the southern limit of predicted suitable range is shifted approximately 14° to the north along Chilean coasts. Given the highly structured coastline of Chile with its irregular coastline and fjords, this results in an extremely large difference in predicted potential habitat (but see below).

In contrast, the northern range limit might be overestimated and subject to complex climatic interactions. In northern Chile the distributional range of seaweeds is restricted by upper survival temperatures of the most sensitive life-cycle stages and occasionally dramatically reduced via elevated temperatures during El Niño events (Peters and Breeman 1993). Hence, the distributional range might be limited by much lower than the highest occupied SST in the native range. Peters and Breeman (1993) found that most of their investigated species exhibited a “safety margin” of 6–10 °C between their upper survival temperature and the highest temperatures at their northern distribution limits. Therefore, the predicted northern distribution

limit might be subject to El Niño events and hence lie further south. Unfortunately, we were not able to identify the upper survival limit of *C. implexa* in our experiments and identification of its potential niche needs therefore further investigation.

The Humboldt-current-system along Pacific South American coasts is characterized by heterogeneous environmental conditions (e.g. latitudinal differences in upwelling or freshwater influences) and several biogeographically distinct zones exist along the Chilean coasts (i.e., breaks in species composition), with a prominent break around 30° S (see e.g. Thiel et al. 2007; Camus 2001; Haye et al. 2014; Koch et al. 2015). It is hitherto unknown what factors define this biogeographic break, but Haye et al. (2014) identified low dispersal capacity as a main predictor for phylogeographic structure across this break. Guiry and Womersley (1993) described *C. implexa* as a “creeping” species, making it probably dependent on other transportation means for further spread along the coastline. The region around Calbuco is characterized by extensive aquaculture facilities, and Boo et al. (2014) assumed related trade and transport as possible dispersal vectors. Connected ports along the coast may therefore be primary sites for further invasion by *C. implexa*, whereas more remote regions may be under lower invasion risk (Seebens et al. 2016). In its native range this species occupies a variety of hard substrata such as mussels and rock surfaces in sheltered as well as open coasts (Nelson 2013) and has also been found on wooden structures and even fallen tree trunks (Boo

et al. 2014), making it potentially a successful invader if transportation means are available.

To give a holistic estimation of the invasion potential of *C. implexa* further studies will have to be carried out to investigate factors limiting the fundamental niche (i.e., defining the realized niche). Purely mechanistic approaches tend to overestimate the suitable range by disregarding complex interactions of influencing factors (Mac Nally 2000). Moreover, *C. implexa* has a biphasic life cycle and different life-history stages might have different temperature tolerances (e.g., Wiencke et al. 2006) and reproduction may depend on certain temperature and/or light-regimes (Lüning 1985). Studies on biotic interactions with other species (e.g. competition with native species) as well as potential synergistic negative effects of abiotic parameters, especially at the margins of the tolerated temperature range, are necessary to allow more elaborate predictions of the invasion potential of *C. implexa* (Fernández et al. 2015; Mellin et al. 2016). This is especially intriguing with regard to the heterogeneous environments along the Chilean coast.

In its native range, warming of SST is predicted to lead to a substantial loss of total suitable area as it will be restricted by a southward shifting northern limit and the edges of the landmasses. Especially under rcp 8.5 conditions, the range shift would be large with approximately 50% of the predicted current range in mainland Australia and large parts along New Zealand's North Island becoming unsuitable. Gain in suitable habitat in the native range is negligible in comparison. This prediction is in accordance with Wernberg et al. (2011) and Martínez et al. (2018), who reported a significant loss in suitable habitat for Australian and New Zealand seaweeds under climate change. Shifts in seaweed distribution under climate change are a phenomenon observed and predicted worldwide and are of tremendous extent and consequences (Wernberg et al. 2011; Assis et al. 2018; Martínez et al. 2018). Effects can be dramatic as these shifts affect ecosystem engineers such as large kelps, which can provide habitat for large numbers of associated organisms (Christie et al. 2003). *C. implexa* may be a smaller species and shifts of its distributional range may therefore not have such obvious consequences for its environment, but as a mat-forming species that covers rocky surfaces with thick interconnected layers, it provides a refuge from desiccation

during low tide for smaller organisms and probably influences settlement of other species (Sousa 1979). For South America we predicted a shift of the southern distributional limit making more southern coasts suitable. Southern species in retreat from global warming will leave space available for southward migrating species and will also face enhanced competition at their northern distributional limits, probably decreasing survival (Poloczanska et al. 2008). Like this, while facing loss of habitat in its native range, *C. implexa* might exploit newly available coasts in South America as refuges.

In this study we showed that *C. implexa* has a wider tolerated temperature range than can be conducted from distributional records alone. In this way, we have demonstrated that physiological knowledge is necessary to accurately estimate a species' fundamental niche, especially when physical factors (e.g. barriers) limit the realized niche. Furthermore, we have shown that *C. implexa* will, as for many other seaweeds, probably face significant loss of habitat in its native region due to warming. In contrast, coasts of South America might provide habitat even under warming conditions.

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Compliance with ethical standards

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