

**Patterns in thermal niche equilibria of global  
seaweed distributions**

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**Results from biogeographic studies with  
implications for invasion biology and  
forecasting of climate change effects**

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## Summary

Bioinvasions and global warming are main drivers of global biodiversity loss, and affect global seaweed populations. In this dissertation I make use of niche identification tools to address the invasive potentials of seaweeds and effects of global warming on seaweed distributions, ranging from the level of single species, to a broader Antarctica-centered and finally global perspective. I describe mechanisms of and patterns in niche restrictions and discuss them in an ecological context.

In the first research chapter, I conduct an assessment of the realized and fundamental thermal niches of the non-native South American seaweed *Capreolia implexa* (Rhodophyta). This species is native to New Zealand and Australia, and has been reported from Chile for the first time in 2014. It is so far not known how far it might be able to spread beyond its current occurrence sites. Here, the research objective is to use information on the fundamental and realized thermal niches of *C. implexa* to identify its potential suitable habitat range in South America. In this course, I also compare these two niches and estimate how well they overlap. This allows to predict effects of climate change on its distribution in its native and novel ranges and to identify potential limiting factors of its distribution. To do so, I perform a physiological growth experiment for temperature tolerance in addition to a correlative ecological niche model for *C. implexa* and use the information in a combined effort to predict the suitable habitat range of *C. implexa* in its native and novel range under present-day and future climate scenarios. It becomes clear that the fundamental niche of *C. implexa* is larger than its realized niche and that its niche is probably restricted by the absence of settling substrate south to the continental masses in the southern hemisphere. The isotherm corresponding to *C. implexa*'s tolerance limit lies in the Southern Ocean where only very limited suitable settling substrate (i.e. other coasts) exists and thus, its fundamental thermal niche is restricted by the latitudinal extent of the continental margins. Under future climatic conditions, a large contraction of the species' native distributional range is predicted, with a southward shifting northern distributional boundary and no gain at the southern edge due to the aforementioned lack of settling substrate.

As a follow-up to the first finding (restriction of the fundamental niche via continental margins), I address in the second research chapter the question whether other (especially southern hemisphere) temperate species might also have "hidden" cold-temperature tolerances beyond their realized limits. This research chapter focusses on Antarctica as a potential target region for non-native species. Species with "hidden" cold-tolerances could pose an invasion risk for Antarctica while their cold-tolerances could not be identified from their native distributional ranges via correlative niche identification approaches, analogue to the mechanisms described in research chapter one. To address this question, I investigate the realized thermal niches of twelve newly reported and supposedly non-native Antarctic seaweed species, and compare the niche extent before and after Antarctic occurrence. The results

show that the original and Antarctic niche spaces do not, or only partially, overlap, and thus that probably many temperate species do have cold-tolerances which are not discernible from their distributions. Thus, the “climate-matching” hypothesis, which states that mainly polar species pose an invasion risk for Antarctica, might not hold true for seaweeds. This is highly important, as it dramatically enlarges the pool of potential invaders for Antarctica and thus Antarctica’s risk of being invaded.

From the findings in research chapters 1 and 2 arises the question how well temperature tolerances predict the distributional patterns of seaweeds on a global scale. Therefore, in research chapter 3, I compare fundamental and realized thermal niches of 126 seaweed species. The data stem from the published literature and databases and contain physiological, environmental and distributional data. I assess to what extent experimentally determined temperature limits match with realized distributional limits. The results show that there are many species which have non-equilibrium distributions (i.e. realized thermal niches which are narrower or wider than the fundamental niches), which is surprising when considering published literature which predicted high match of thermal tolerance limits and distributional patterns. Further, it appears that cold-tolerances and sea surface temperatures and thus distributional limits are rather independent, while warm-tolerances are stronger correlated with environmental conditions. This underlines the findings of research chapters 1 and 2. In addition, the analysis showed that nearly 60% of the included species have distributional limits at or close to the thermal tolerance limits. These species will likely face increased temperature stress under climate change and range shifts are to be expected in the future.

In conclusion, I show that southern hemisphere species have a distributional barrier in the form of lack of settling substrate between Antarctica and other continents, but can still have tolerances for cold temperatures. The finding that realized and fundamental niches frequently show a mismatch in seaweeds is strengthened in the third research chapter on a global scale. Temperate species might therefore have the potential to survive polar temperature conditions, although these are not found in their native distributional ranges. Therefore, not only species from climatically matching regions but also from non-matching habitats pose an invasion risk for Antarctica. This thesis therefore contributes to the understanding and assessment of Antarctica’s invasion risk, and gives alarming results as it demonstrates that the invasion risk of this remote and pristine continent is much higher than previously assumed. Further, I give insights how thermal tolerances determine realized distributions and describe patterns in niche-fill in seaweeds on a global scale. The results are important for identification of climate change effects on seaweed distributions and forecasting of suitable ranges from a climate-change as well as bioinvasions perspective.

## Zusammenfassung

Invasive Arten und der Klimawandel sind Haupttreiber des globalen Biodiversitätsverlusts und nehmen Einfluss auf globale Großalgenverbreitungen. In dieser Dissertation nutze ich Methoden zur Ableitung von Temperaturnischen, um das Invasionspotential bestimmter Algen, sowie die Auswirkungen des Klimawandels auf Großalgenverbreitungen abzuschätzen. Dabei wird konsequent der Blickwinkel von zunächst einer Spezies, zu einer Multispezies-Antarktis-zentrierten Sicht, und abschließend auf eine globale Perspektive erweitert. Ich beschreibe Mechanismen und Muster der Nischenbegrenzungen und diskutiere sie im ökologischen Kontext.

Im ersten Forschungskapitel untersuche ich die realisierte sowie fundamentale Nische der Rotalge *Capreolia implexa*, welche als nicht-heimische Art in Chile vorkommt. Diese Spezies hat ihr angestammtes Verbreitungsgebiet in Neu-Seeland und Australien und wurde zum ersten Mal 2014 in der wissenschaftlichen Literatur für Chile nachgewiesen. Bisher ist nicht klar wie weit sie sich dort jenseits des bisher bekannten Verbreitungsgebiets weiterverbreiten könnte. In diesem Forschungskapitel nutze ich die realisierte sowie die fundamentale Temperaturnische von *C. implexa*, um das potentielle Verbreitungsgebiet der Art vorherzusagen. Dabei ermittle ich außerdem, bis zu welchem Grad beide Nischen übereinstimmen und nutze Projektionen für zukünftige Klimaverhältnisse um zu ermitteln inwieweit sich der Klimawandel auf die Artverbreitung auswirken wird. Um mein Forschungsziel zu erreichen, führe ich einen Temperaturtoleranzversuch zur Ermittlung der fundamentalen Nische durch und benutze daneben Verbreitungs- und Umweltdaten in einem Korrelationsansatz. Es wird klar, dass die fundamentale Nische der Art größer als ihre realisierte Nische ist, und, dass die Verbreitung der Art durch die Ränder der Landmassen der südlichen Hemisphäre bedingt ist, jenseits derer es kaum bis kein geeignetes Siedlungssubstrat, nämlich felsige Küsten, gibt. Für zukünftige klimatische Bedingungen wird eine Verkleinerung des ursprünglichen Verbreitungsgebiets der Art vorhergesagt, da sich die nördliche Verbreitungsgrenze weiter nach Süden verschieben wird, während es im Süden aufgrund des Mangels an geeignetem Substrat keine ausgleichende Zunahme an geeignetem Verbreitungsgebiet gibt.

Aufbauend auf dem ersten Ergebnis (Begrenzung der Nischen durch Kontinentalränder), gehe ich im zweiten Forschungskapitel der Frage nach inwieweit andere Arten, insbesondere der gemäßigten südlichen Hemisphäre, Kältetoleranzen besitzen, welche nicht ihren Verbreitungsgrenzen entsprechen. Solche Arten würden aufgrund ihrer Kältetoleranz ein potentielles Invasionsrisiko für die Antarktis darstellen, wären aber als solches nicht mittels korrelativer Ansätze auf Grundlage ihrer Verbreitung erkennbar, da sie keine entsprechenden Gegenden besiedeln. Ich untersuche hier die Verbreitungsgebiete neu entdeckter, wahrscheinlich nicht-heimischer, antarktischer Großalgen und vergleiche die realisierten Temperaturnischen entsprechend ihrer ursprünglichen und ihrer Antarktis-

inklusive Verbreitungen. Die Analysen zeigen, dass die beiden Temperaturnischen nicht, oder nur teilweise, überlappen, was bedeutet, dass wahrscheinlich weitere Arten „versteckte“ Kältetoleranzen besitzen, welche sich nicht aus ihrer angestammten Verbreitung ableiten lassen. Dies bedeutet, dass die „climate-matching“-Hypothese, welche besagt, dass vor allem Arten aus anderen Gebieten mit ähnlichen klimatischen Bedingungen, also Polarregionen, ein Invasionsrisiko für die Antarktis darstellen, zu kurz greift, da auch Arten der gemäßigten Breiten über geeignete Kältetoleranzen verfügen können.

Aus den Ergebnissen der ersten beiden Kapitel ergibt sich die Frage, zu welchem Grad Temperaturtoleranzen Verbreitungsgrenzen bestimmen. Um dies zu erörtern, vergleiche ich die fundamentalen und realisierten Nischen von 126 Makroalgenarten, welche insgesamt weltweite Verbreitungen abdecken. Die Daten entstammen der publizierten wissenschaftlichen Literatur sowie Datenbanken und beinhalten physiologische als auch Verbreitungs- und Umweltdaten. Auf dieser Datengrundlage ermittle ich inwieweit tatsächliche Verbreitungsgrenzen den Temperaturtoleranzen entsprechen. Die Ergebnisse zeigen, dass eine große Zahl der untersuchten Arten „nicht-equilibrium“ Verbreitungen aufweisen (das bedeutet, dass die Verbreitungen entweder kleiner oder weiter als ihrer Toleranzgrenzen entsprechend sind). Der Grad der Abweichungen ist überraschend, da aus der wissenschaftlichen Literatur hervorgeht, dass es eine hohe Deckung zwischen Toleranzgrenzen und Verbreitungsgrenzen in marinen ektothermen Organismen gibt. Aus meinen Ergebnissen geht dagegen hervor, dass vor allem Kältetoleranzen eher unabhängig der Verbreitungsgrenzen ausgebildet sind, während Wärmetoleranzen scheinbar eher angepasst sind. Dies unterstreicht die Schlussfolgerungen aus den vorhergegangenen Kapiteln. Außerdem hat die Analyse gezeigt, dass fast 60% der untersuchten Spezies am Rand ihrer Wärmetoleranz oder sogar darüber hinaus verbreitet sind. Diese Spezies werden unter zukünftigen klimatischen Bedingungen erhöhtem Hitzestress ausgesetzt sein, was wahrscheinlich zu Habitatverlust und Verbreitungsverschiebungen führen wird.

Zusammenfassend zeige ich, dass Spezies in der Südhemisphäre durch den Südlichen Ozean in ihrer Ausbreitung eingeschränkt sind, und daher Verbreitungen aufweisen die nicht ihrer Kältetoleranz entsprechen. Dass Kältetoleranzen unabhängig von Verbreitungsgrenzen bestehen können, wird in Kapitel drei auf globaler Ebene bestätigt. Dies zeigt, dass auch nicht-polare Arten unter polaren Temperaturbedingungen überleben könnten auch wenn sich diese Kältetoleranz nicht in ihrer angestammten Verbreitung widerspiegelt. Das bedeutet, dass nicht nur Spezies aus Polarregionen, sondern ebenso aus gemäßigten Regionen ein Invasionsrisiko darstellen, und dass daher die „climate-matching“ Hypothese nicht ausreicht um das Invasionsrisiko der Antarktis abzuschätzen. Dieses Ergebnis ist alarmierend, da dadurch der Pool an potentiellen Invasoren dramatisch vergrößert wird als bisher angenommen. Darüber hinaus trägt diese Arbeit dazu bei, zu verstehen wie Temperaturtoleranzen die Verbreitung von Makroalgen bestimmen und wo es Abweichungen von

diesen Toleranzgrenzen gibt. Diese Ergebnisse sind insbesondere für die Vorhersage von Effekten klimatischer Veränderungen auf die Ausbreitungen der globalen Makroalgen von Bedeutung.



## List of abbreviations

ACC	Antarctic circumpolar current
AIC	Akaike information criterion
AUC	Area under curve
BAM-diagram	Venn-diagram describing the biotic - abiotic – movement dimensions of the ecological niche (see <sup>[1]</sup> )
ENM	Ecological niche model/ ecological niche modelling
GLM	Generalized linear model
It <sub>50</sub>	Lethal temperature 50
maxent	Maximum entropy modelling technique, <sup>[2]</sup>
OSPAR	Short for <u>O</u> slo- <u>P</u> aris Convention; commission of 15 governments and the EU
PAR	Photosynthetically active radiation
rcp	Representative concentration pathways ( <sup>[3]</sup> )
ROC	Receiver operating characteristic
SDM	Species distribution model/ species distribution modelling
SST	Sea surface temperature
WAP	Western Antarctic peninsula



## Introduction

Global warming and bioinvasions are main drivers of global biodiversity loss, and profoundly affect global species populations <sup>[4]</sup>. Due to rising temperatures, seaweed populations show poleward migrations <sup>[5-7]</sup>, which, in the southern hemisphere, leads to overall loss of suitable habitat and eventually to extinction of populations, while in the northern hemisphere, temperate species migrate poleward into colder habitats <sup>[5, 6]</sup>. At the same time, anthropogenic activities, like shipping, establishment of aquacultures, or the increase in number of floating and persistent plastic objects, leads to higher connectivity of the world's coastal ecosystems <sup>[8-10]</sup>. These activities offer opportunities for marine species to cross geographical barriers and settle new habitats. As a consequence, habitats are exposed to an immigration pressure and are facing the threat of being invaded by highly competitive species. Invasive species are a major threat to global biodiversity and can severely alter ecosystems, including seaweed communities <sup>[11-13]</sup>.

For both aspects, prediction of climate change effects on global seaweed distributions, and assessment of invasiveness, knowledge of ecological niches is crucial. Different approaches exist for niche identification, either via correlative or mechanistic methods <sup>[1, 14]</sup>. In this dissertation, both approaches are applied to answer research questions which cover both invasion-related issues as well as climate-change-related ones on seaweed distributions. The geographic extents of the research chapters cover different scales which are consecutively enhanced. First, I focus on Australia, New Zealand and South America and only one single species. Second, Antarctica and globally distributed species will be added to the perspective. Third, a global perspective is taken and in total 126 species will be included. Three main issues are addressed over the research chapters. First, I apply correlative and mechanistic techniques to assess the potential geographic distributional range of the non-native red alga *Capreolia implexa* in Chile. This species was discovered in Chile in 2014 <sup>[15]</sup>, and its effects on Chilean coastal ecosystems are so far not known. Thus, my identification of suitable habitats is important to identify regions under threat of further invasion, and as a baseline to monitor to what extent *C. implexa* is a successfully spreading throughout Chile. The findings of niche restrictions in *C. implexa* deliver the basis to elaborate on the question to what extent non-polar seaweeds pose an invasion threat beyond their native habitats, in this case, for Antarctic habitats. Antarctica's isolative forces are dramatically decreasing <sup>[16]</sup> with potentially huge consequences for Antarctic biodiversity. It is an urgent matter to identify threats to Antarctica's unique and pristine habitats to implement protection matters. Antarctica has been largely isolated for millions of years and a highly specialized and endemic flora and fauna has adapted to its extreme conditions which will face dramatic changes in abiotic and biotic factors in the future. My work in the second research chapter helps to understand the invasive potential of non-polar species with respect to Antarctica as a target region. I hypothesize that next to polar species also non-polar species pose an invasion risk. This would dramatically increase the overall

invasion risk for Antarctica by increasing the number of potential successful invaders. In the third research chapter, the geographic scale is extended to a global scale and I compare realized and fundamental thermal niches of global seaweed species. By doing so, I assess how well fundamental temperature tolerance limits predict distributional limits. I investigate and describe patterns in the match between fundamental and realized niches. The results are relevant for the assessment of global warming effects on seaweed distributions as well as for the assessment of potential invaders with respect to the identification of suitable habitats. In addition, this comparison allows the estimation of the threat to global seaweed populations by increasing sea surface temperatures.

### Seaweeds as study-organisms

Seaweeds are important and dominant foundation species throughout marine coastal ecosystems worldwide (Figure 1). They provide food and shelter for associated macrofauna, epibiota and microorganisms <sup>[17, 18]</sup>, shape the underwater environment by adding three-dimensional structures with different vertical levels (comparable to terrestrial rainforests), alter environmental conditions such as incoming light <sup>[19, 20]</sup>, and influence currents and erosion along coasts <sup>[21]</sup>. Macrophyte communities are part of complex interaction webs which cover multiple trophic levels along rocky shores <sup>[22]</sup>. Kelp beds are especially impressive communities with individuals which can grow several tens of meters in height and last for many years. Macrofaunal assemblages associated with kelp beds regularly exceed 100,000 individuals per m<sup>2</sup>, and seaweed communities thus provide habitat for huge and diverse communities <sup>[17, 23]</sup>. Their effects are measurable even further away from the actual site, e.g. as particulate organic matter which is exported to the deep sea <sup>[24]</sup>, or as floating individuals which connect ecosystems via providing rafting opportunities for other organisms <sup>[25]</sup>. In addition, kelp systems are among the most productive systems on Earth, again comparable to terrestrial tropical rainforests <sup>[26]</sup>.

At the same time, seaweeds have enormous economic value and are, especially in Asian countries (e.g. China, Korea and Japan), an important food source for humans <sup>[27]</sup>. In other countries, seaweeds as a direct food source are not as prominent, but growing demand has led to the establishment of aquaculture to supplement wild-catches (see, e.g. Chile, USA, Canada; <sup>[27]</sup>, Figure 2). Further, seaweeds are cultivated and harvested for alginate and hydrocolloid (carrageenan) production, while minor uses include e.g. addition to stock feed <sup>[27]</sup>. In recent years, seaweed culture has attracted more attention as it seems to have the potential to be a building block in climate change mitigation strategies, e.g. as a source for biofuel production, as a CO<sub>2</sub> sink when exported to the deep sea (“blue carbon”), by reducing methane emission when used as a food additive for cattle, or by replacing synthetic fertilizers in agriculture <sup>[28]</sup>. However, with the establishment of more seaweed aquaculture facilities, the risk that non-native species (see below) escape from farms and establish populations in a wider geographic range is increasing, and such introductions have been observed frequently <sup>[29, 30]</sup>. Seaweeds can also

be transported and introduced unintentionally as epibionts of culture organisms, e.g. oysters <sup>[9, 31-33]</sup>. Given the extreme impacts they can have on recipient ecosystems and the necessary effort to erase them once they are established, anticipation and prevention of uncontrolled spread is very important <sup>[34]</sup>.

Global seaweed populations are heavily affected by global warming (see below) <sup>[35]</sup>. Rises in sea surface temperature (SST) lead to profound changes in abiotic conditions and cause changes in community structures and geographic distributions. While due to global warming, new habitats at high latitudes become available for establishment of populations (e.g. <sup>[36]</sup>), seaweeds are facing major extinction risks in other, low latitudinal, localities, where evasion is not possible (e.g. <sup>[6, 7]</sup>). Given the aforementioned roles of seaweeds for global coastal habitats, the consequences for these communities will be dramatic and profound effects on associated communities have to be expected <sup>[7]</sup>.



Figure 1. Kelp population, emerged during low tide, at Chiloé, Chile. Photo taken during a field trip to Chile by myself.

### Effects of climate change on seaweeds

Most of the world's ocean regions have experienced increases in sea surface temperature (SST) over the last decades, and rise in SST will continue in the future <sup>[37]</sup>. Seaweeds are highly impacted by climate change in different, potentially synergistic, ways (e.g. SST increase, acidification, wave-impact, sea-

level rise, run-off into the sea, sea-ice retreat, salinity changes, etc.)<sup>[35]</sup>. In this thesis, I focus on temperature effects. Although other abiotic drivers can influence seaweed performance in physiological ways, SST is the major predictor to explain the geographic distributions of seaweeds (<sup>[26]</sup>; see also model selection in research chapter 1). It determines growth, reproduction and survival, and species are forced to adapt to changing temperature regimes or to migrate to prevent extinction<sup>[26, 35]</sup>. Temperature affects the metabolic rates and stability of enzymes and thus basic physiological processes in seaweeds (<sup>[38]</sup>, chapter 7, and references therein). Idealized enzymes follow a curve with activity over temperature, which first increases until an optimum is reached and, with increasing temperature, decreases again. Outside the optimum range, temperature stress can occur, which will lead to decrease in overall performance and increased susceptibility to environmental stressors such as high light intensity. Both low as well as high temperatures can induce a temperature stress, and thermal niches and thus geographic ranges of seaweeds are a consequence of temperature tolerance (<sup>[38]</sup>, chapter 7, and references therein). Due to global warming, the suitable geographic ranges of seaweeds are shifting poleward, following their thermal niche preferences (see section below)<sup>[5, 6, 39]</sup>. In low latitudes, heat stress leads to loss of populations, while in the Arctic, major increases in amount of available habitat are documented and projected for future climate scenarios<sup>[5, 6, 36, 39, 40]</sup>. In addition, increase in temperature can cause increase in seaweed productivity in the Arctic, which in turn could affect community structure in polar areas<sup>[35, 36, 40, 41]</sup>. The OSPAR<sup>1</sup> commission recently recommended to implement strong measures for the protection of kelp habitats in the North-Eastern Atlantic. While they mention also other drivers, global warming was considered a major threat to all kelp species in the covered OSPAR regions, which will cause extinctions of several populations in various localities, underlining the dramatic effects of rising SST on kelp populations<sup>[7]</sup>. Heat stress will increase in the future both via increase in average as well as extreme temperature events such as heat waves<sup>[7, 42, 43]</sup> and, clearly, extinctions and large-scale distributional shifts have to be expected as a consequence. Given the important roles seaweeds play in their communities, extinctions and changes in distributional ranges, with losses and restructuring of species assemblages, will have profound effects on coastal ecosystems.

## Bioinvasions

Bioinvasions are one of the main drivers of global biodiversity loss, next to habitat change, climate change, overexploitation and pollution<sup>[4]</sup>. The global spread of highly competitive non-native species leads to a homogenization of communities by decreasing the abundance of locally adapted and

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<sup>1</sup> "OSPAR is the mechanism by which 15 Governments & the EU cooperate to protect the marine environment of the North-East Atlantic. ... The fifteen Governments are Belgium, Denmark, Finland, France, Germany, Iceland, Ireland, Luxembourg, The Netherlands, Norway, Portugal, Spain, Sweden, Switzerland and United Kingdom. OSPAR is so named because of the original Oslo and Paris Conventions ("OS" for Oslo and "PAR" for Paris)." (Self-definition quoted from <https://www.ospar.org/about>; March 6<sup>th</sup>, 2022)

geographically more restricted species <sup>[44]</sup>. Homogenization of global populations on genetic, taxonomic and functional levels leads to an overall loss of worldwide biotic diversity and, hence, loss of ecosystem functions <sup>[44, 45]</sup>. Non-native species pose a threat to local species communities, economy and human health <sup>[46-48]</sup>. The number and rate of global (marine) bioinvasions is ever increasing (<sup>[8]</sup> and references therein), and the removal of non-native species is a labor-intensive and costly endeavor with no guarantee of success (e.g. <sup>[49]</sup>). Thus, anticipation and prevention are to be preferred over later actions <sup>[34]</sup>.



Figure 2. Harvested *Durvillaea antarctica* left to dry on the quay in Bahía Mansa, Chile. Photo taken during a field trip to Chile by myself.

### Definition of invasive species and a note on nomenclature thereof

The definition of “invasive species” is not coherent and different definitions exist, which incoherently include or consider aspects such as “impact” or “spread” <sup>[50]</sup>. For example, species can be considered invasive if they are non-native to a region, establish populations, and spread <sup>[51]</sup>. In some definitions, the impact on the recipient ecosystem is not regarded, while other authors, like e.g. <sup>[52]</sup> and the International Union for Conservation of Nature ([www.iucn.org](http://www.iucn.org), accessed November 11<sup>th</sup> 2021), clearly do so. <sup>[50]</sup> and <sup>[51]</sup> are good references on the nomenclatural and definitive issues of the term “invasive”. The species which are treated in this dissertation have unclear status in the recipient habitats. *C. implexa* (research chapter 1), has only been discovered in Chile in 2014 by <sup>[15]</sup> and there is no definitive

information available on how this species arrived in Chile, if it spread further, or if it might have impacts on Chilean coastal ecosystems. Possible impacts are shortly discussed in research chapter 1. The species in research chapter 2 have unclear status as being “non-native” or not (see the discussion in research chapter 2). Thus, for the species treated in this dissertation, the term “non-native” is preferred over “invasive”. The term “invasive” will still be used occasionally for contextualization of results, since many cited authors used this term in their research and concept descriptions.

#### Effects of invasive seaweeds on recipient ecosystems

Non-native seaweeds can have effects on recipient community structure and species abundances<sup>[53]</sup>, they can be highly competitive and replace native species, and effects on recipient ecosystems may be direct or indirect, and on different ecosystem levels<sup>[11]</sup>. Seaweeds, as ecosystem engineers (*sensu*<sup>[54]</sup>), define the three-dimensional structure, light availability and currents in coastal ecosystems, and hence, their effects propagate into associated communities, and communities might undergo profound compositional changes<sup>[55, 56]</sup>. Thus, non-native seaweeds which affect abundances of native seaweed species can affect associated biota, even if total species richness and diversity are unaffected<sup>[53]</sup>, and references therein).

Williams and Smith<sup>[53]</sup> listed 277 invasive seaweeds and 408 introduction events worldwide in 2007, but this number is probably considerably higher as of today, as invasion events are increasing in numbers and are not always detected<sup>[8, 38]</sup>. While most introduced species are not successful in establishing populations (“tens-rule”,<sup>[57]</sup>), some can have disastrous impacts on recipient ecosystems. One of the most notorious examples of invasive seaweeds is the green alga *Caulerpa taxifolia*, which, after being released from an aquarium in Monaco, rapidly spread throughout the Mediterranean Sea and beyond, forms extensive populations and smothers other benthic species. Eradication is practically impossible once the species has established in a location<sup>[58]</sup>. As the single other marine macroalga in the list of the 100 of the world’s worst invasive species by<sup>[59]</sup>, the kelp *Undaria pinnatifida* (common name: Wakame) was included. *U. pinnatifida* is native to Asian countries (large populations in China, Japan, Korea), cultivated in large amounts, and of high economic importance<sup>[60]</sup>. But it is also a widespread and highly invasive species along American, European, and Australasian coasts<sup>[12, 60-63]</sup>. While it is difficult to clearly address impacts on recipient ecosystems<sup>[60]</sup>, negative effects on native biodiversity have been documented<sup>[12]</sup>.

For detailed descriptions of the species included in this thesis and their traits, I refer the reader to the respective chapters, and provide only a short introduction here. *C. implexa* (*Rhodophyta*; research chapter 1, Figure 3) is a species which forms very dense mats on hard substrates. Thus, it may alter its habitat by offering shelter from intertidal stressors, such as desiccation, to co-occurring flora and fauna (see<sup>[64]</sup>). In addition, it might prevent other species from settling where it has established dense mats

[65, 66] and thus directly affect intertidal communities. It was potentially introduced via aquaculture-related means and might therefore be a candidate for further spread along the Chilean coasts, where aquaculture is common and further expanding [15, 67].



Figure 3. *Capreolia implexa*, a non-native mat-forming red alga in Chile. Here near Calbuco, Chile. Photo taken during a field trip to Chile by myself.

Among the species in research chapter 2 are highly competitive and wide-spread dominant and habitat-shaping species (e.g. *Ulva* spp., *Blidingia minima*), which will probably compete with the native and highly specialized Antarctic species for substrate and resources, and may have dramatic impacts on Antarctic seaweed communities. Antarctica's coastal ecosystems are characterized by a high share of specialized and endemic species [68], but, as a consequence of global warming (see below), the Antarctic ecosystem is subject to profound physicochemical changes which will continue in the future [69]. In addition, retreat of sea-ice might offer new settling substrate to seaweeds [41]. Thus, Antarctic species will be facing a changing environment and at the same time probably be confronted with new and potentially aggressive competitors. Seaweed communities are more prone to invasions when they are disturbed [53], thus, the threat to Antarctic ecosystems via invasions is twofold, via changing climate and decreasing isolation [16, 70, 71]. It is therefore of utmost importance, to assess invasion threat for Antarctica's highly specialized ecosystems, to successfully implement mitigation strategies.

## Invasibility of Antarctica and identification of potential invaders

Antarctica is considered largely isolated from other landmasses since its separation from Gondwana 40 million years ago <sup>[72, 73]</sup>. This isolation led to a high share of endemic species in the Antarctic flora and fauna <sup>[74, 75]</sup>. However, its isolative forces, i.e. extreme climatic conditions, the Antarctic Circumpolar Current (ACC) and its remoteness, are degrading due global warming and anthropogenic activities <sup>[16, 70, 71, 74, 76]</sup> (see research chapter 2). Higher connectivity via anthropogenic vectors (e.g. shipping, increase in floating litter <sup>[71, 77]</sup>) might add to the number of natural transportation vectors such as rafting kelps <sup>[16, 78]</sup> and thus lead to more intense species-exchange with non-Antarctic habitats. At the same time, global warming will challenge highly adapted Antarctic species by a changing climate and make Antarctica more suitable and accessible to non-Antarctic species.

Research on Antarctic bioinvasions largely adopts the concept of climate matching between origin and recipient sites, meaning that a focus in risk assessment of bioinvasions lay on species which might be introduced from climatically similar habitats (e.g. <sup>[70, 71, 79]</sup>). However, <sup>[80-83]</sup> reported potentially non-native species from the Western Antarctic Peninsula (WAP) which had no polar, i.e. climatically matching, distribution prior to their discovery in Antarctica. Thus, a biogeographic connection is indicated which could lead to exchange and establishment of species outside their native climatic range. This is especially relevant, as it might increase the invasion pressure for Antarctic habitats if not only species from other cold-water environments pose a threat, but also other species without such history are capable of occupying Antarctic habitats. Thus, the isolative force “extreme climate” would be weaker than assumed. This is subject to the research in research chapter 2, and, with a broader geographic and more general approach, further elaborated on in research chapter 3.

## Ecological niches

The concept of ecological niches can help to identify responses of species to a changing environment. A variety of methods has been developed to identify niches, species’ potential distributional ranges, and to predict effects on species distributions under a changing climate. The concept of the ecological niche, as well as ecological niche models (ENMs) and related species distribution models (SDMs) are introduced in the following.

### Hutchinson’s niche concept and the BAM-diagram

A niche is a multidimensional volume of ecological conditions in which a species can thrive <sup>[84]</sup> (summarized in <sup>[1]</sup>). It includes abiotic as well as biotic factors and their interactions. The basic set of suitable conditions is called the fundamental niche, while the observed niche is often restricted by a variety of factors and is called the “realized niche”. This concept is best described using the BAM diagram by <sup>[85]</sup> (Figure 4), who follow the concepts and work of <sup>[86]</sup>. The BAM-diagram is a Venn diagram to describe fundamental and realized niches in the three dimensions “biotic”, “abiotic” and

“movement” as overlapping volumes. “B” represents the suitable biotic conditions, “A” the suitable abiotic conditions, and “M” the accessible areas.

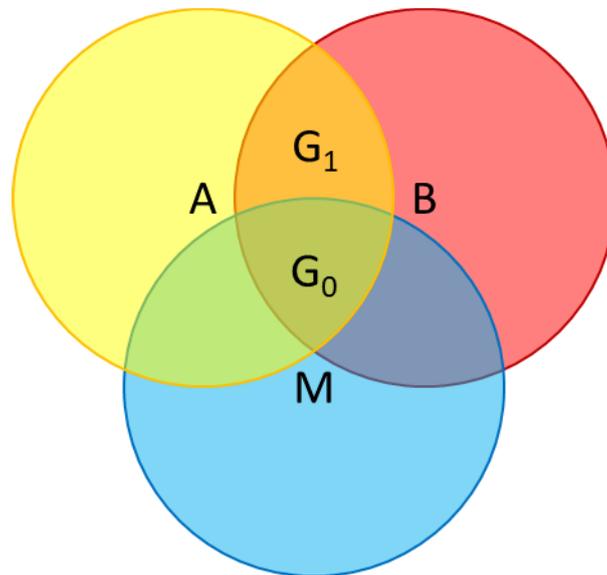


Figure 4. BAM Diagram adopted from <sup>[1]</sup>. B = biotic, A = abiotic, and M = movement factors. This Venn-diagram depicts how B, A and M factors influence a species' distribution. At the intersection of B, A and M lies the occupied distributional range of a species  $G_0$ , while the intersection of B and A represents the potential invadable area, once movement limitations are overcome,  $G_1$ .

In theory, a species can thrive only where all three circles overlap. If only two of the circles overlap, a species does not maintain populations, because a set of conditions is not met, or the area is inaccessible. In reality, of course, many exceptions exist, like e.g. sink populations which thrive under conditions which do not allow reproduction but are maintained from adjacent existing populations <sup>[87]</sup>. Another example is facilitated transport, e.g. via anthropogenic vectors, which allow to cross biogeographic barriers. Thus, identification of a niche is a complex endeavor. In this dissertation, I focus on abiotic conditions (“A”) under which a species can thrive. “M” factors, such as dispersal, or “B” factors are discussed. In ecological niche modelling (see below), a set of factors is tested for its explanatory power of a distribution, and, following the principle of parsimony, only the most important ones are retained in the final model. Most publications report ENMs with SST as the most important factor. Thus, based on literature and my own results (research chapter 2), thermal niches are analyzed in research chapters 2 and 3, while other factors play minor roles (see the respective chapters for discussions on inclusion and omission of other variables).

#### Ecological niche modelling and species distribution modelling

In the following, ecological niche models (ENMs) and species distribution models (SDMs) will be introduced very briefly. For an excellent introduction to the topic, the reader is referred to the book “Ecological Niches and Geographic Distributions” by <sup>[1]</sup>. Some background will be provided exemplarily for ENMs/SDMs on the “maxent” modelling technique by <sup>[2]</sup>, since it was used in research chapter 1.

In an ecological niche model (ENM), environmental factors are used as predictor variables, while measures such as presence/absence, abundance, etc. are used as response variables to identify the ecological niche of a species. The set of predictor variables is defined *a priori* and is ideally based on ecological knowledge of the species in question, and then used to find the most parsimonious model (i.e. including only the most important predictor variables) to explain the presence or absence of a species in a given area, or to map habitat suitability. Although the terms ENM and species distribution model (SDM) are often used interchangeably, they are, strictly speaking, not the same: The former uses knowledge of a species' presence (e.g. presence/absence, abundance) and ecological information to identify the set of suitable conditions for the response parameter (e.g. presence) in question, i.e. the niche. The latter is based on an ENM, but is explicitly used to identify a species' (potential) geographic distribution and can include e.g. dispersal capacity. The species treated in the following research chapters have extended their ranges and, evidently, mechanisms exist which allow further dispersal. Under this assumption, the terms are used interchangeably.

#### *Maxent*

The maxent ("maximum entropy") modelling technique is a machine learning approach that works with presence-only data and does not require absence-data to model a species' realized niche <sup>[2]</sup>. In very short words, "maximum entropy" means that the least informative probability distribution of an event or parameter (here: habitat suitability) is iteratively subjected to constraints which are derived from the available data. Thus, the initial probability distribution will be adjusted to fit the information contained in the distributional and related environmental data. In other words, at first, the least informative probability distribution, e.g. a uniform distribution, is applied across the entire geographic range of interest, and is then adjusted to fit the constraints of the correlation between environmental factors and a species' presence. For model verification, the data is split into one set of "training data" and one set of "testing data" (usually 70:30). That means, the model is fit to the training data and then the predictive power is tested by applying it on the testing data and calculating the sensitivity (i.e. proportion of correctly predicted presence records) and specificity (i.e. proportion of correctly predicted absences) of the model. A common index of model accuracy is the ROC (receiver operating characteristic) or AUC (area under curve) <sup>[2]</sup>. Following the concept of "reciprocal duality" <sup>[88]</sup>, the niche model can then be used to predict the habitat suitability as a function of a set of environmental parameters. Like this, it can also be applied to predict or reconstruct the habitat suitability under past, present and future conditions in the same or another geographic range. Thus, it can be a powerful tool in a variety of scenarios, like designation of conservation areas, prediction of sites susceptible to invasion, or shift of habitat suitability under changing climatic conditions. Note that the model output does not predict occurrence of a species, but habitat suitability. For an in-depth description of the method and the model, consult the original publication <sup>[2]</sup> and the website

[https://biodiversityinformatics.amnh.org/open\\_source/maxent/](https://biodiversityinformatics.amnh.org/open_source/maxent/) (last accessed: November 16<sup>th</sup>, 2021).

#### *Limitations of correlative ENMs and physiological information as alternative*

Correlative ENMs, as described above, can underestimate an ecological niche for different reasons. The most basic limitation is that only little data are available in the literature or in databases, and these data do not encompass the whole occupied geographic extent of a species <sup>[1, 89]</sup>. There might be habitats which are not easily accessible (e.g. polar areas) but provide suitable habitat for a species in question. Due to lack of presence data, such regions could then erroneously be classified as unsuitable. Contrary, other habitats might be oversampled, indicating high abundances while the data in fact just represents sampling effort. A simple example is that there are more reported occurrences along roads or close to cities than further away from infrastructure <sup>[1, 90]</sup>. But also comprehensive database such as [www.gbif.org](http://www.gbif.org) suffer from bias in data, by uneven sampling effort and funding across countries and regions <sup>[91]</sup>.

Other limitations can occur from the species' distribution itself, even if it is well sampled over the entire geographic extent: A species distributional extent might be restricted to a subset of environmental conditions by impassable geographic barriers or via excluding biotic interactions. Thus, it would not be "in equilibrium" with its suitable space <sup>[1]</sup> or show an underfilling or overfilling of its fundamental niche. Overcoming of geographic barriers is especially relevant in invasion biology and projections based on incomplete niche estimates can lead to underestimations of suitable ranges (see <sup>[92]</sup> and <sup>[93]</sup>). Human activities offer a variety of vectors to cross geographic barriers. In the marine realm, shipping activities connect disjunct habitats and allow species to travel to novel geographic regions where they might encounter suitable habitats and might become invasive <sup>[8]</sup>. Another drastic example is the opening of the Suez Canal, which allows species migrations into the Mediterranean Sea (see <sup>[94]</sup>). Both phenomena led to numerous species migrations with in part profound effects on the affected flora and fauna compositions. The disappearance of dispersal barriers can thus lead to dramatic alterations of the realized niches and it is not always possible to anticipate distribution patterns in newly available habitats.

<sup>[14]</sup> proposed to include mechanistic data to overcome data limitations in correlative modelling, i.e. to include physiological experimental data in predictions of suitable ranges, such as information on temperature tolerances. However, a purely mechanistic approach can lead to overestimations of the suitable range under real-world conditions as it ignores other factors which restrict the distribution and can thus be oversimplistic. Therefore, both approaches have to be critically assessed and compared <sup>[95]</sup>. Comparisons of predictions based on experimental information and distributional data, can yield insights into the mechanisms which restrict the geographic distribution <sup>[95]</sup>.

In this thesis, I apply different niche identification methods, namely maxent and physiological, mechanistic, knowledge (research chapter 1), and climate envelope identification (research chapters 2 and 3). Climate envelopes describe the extent of the temperature range in which the species find suitable conditions and are derived from known distributions and environmental data.

## Thesis outline

### Research questions and hypotheses

As elaborated above, global seaweed populations are facing major challenges as consequences of global warming and enhances connectivity between separated regions. At the poles, warming will lead to distributional shifts towards the poles where the amount of suitable habitat is finite. At the warm edges of their distributions, warming will lead to heat stress and potentially to range contractions. Thus, species will have conflicts at both edges of their distributional ranges, facing both competition between non-native and native species and facing extinction risk at their trailing edge. Migrations are further facilitated via transportation across large geographical extents and thus pressure on established populations is increased. Especially the pristine Antarctic ecosystems are of major concern as they are treated as the last frontier for bioinvasions <sup>[71]</sup>. In the following research chapters, I apply the niche concept to assess the suitable range the non-native red alga of *C. implexa* in Chile, the invasion risk for Antarctica, and identify patterns in niche-equilibrium on a global scale. The latter gives also an estimation of the global threat of increasing SSTs to seaweed populations.

The research objectives of chapters two and three are direct follow-ups to the findings of the respective preceding chapters, and gradually increase the geographic scope and generality of the applied methods and findings.

### Research objective of research chapter 1

In research chapter 1, the realized niche and the fundamental lower temperature limit of *C. implexa* are identified experimentally and the results will be used to project its potential distributional limits in its native and novel range under present-day and future climatic conditions.

I hypothesize that the fundamental niche is wider than the realized niche and that the potential suitable range of *C. implexa* has been underestimated in a previous publication by <sup>[15]</sup>. The comparison of the results should allow to identify mechanisms which restrict the fundamental niche and potential geographic range of *C. implexa*.

### Research objective research chapter 2

In the second research chapter, the finding of research chapter 1 is applied with a focus on Antarctica as a recipient ecosystem for species introductions. I hypothesize that especially species in the southern hemisphere might have truncated realized niches by the lack of settling substrate between Antarctica and other landmasses in the southern hemisphere (i.e. “non-equilibrium” distributions <sup>[1]</sup>). This means

that species in South America, Australia, New Zealand, Southern Africa and other isolated temperate regions would have cold-tolerances which are not discernable from their current distributions. As a consequence, I predict that the invasion risk of Antarctica is highly underestimated as long as it is assumed that only species from climatically matching source regions are considered as potential invaders, and that also non-polar species pose an invasion risk.

#### *Research objective of research chapter 3*

In research chapter 3, I further elaborate on the comparison of realized and fundamental niches. I assess how widespread non-equilibrium distributions are and how well fundamental temperature tolerances predict seaweed distributions. Based on the findings from research chapter 2, I hypothesize that cold-tolerances are wide-spread even if the respective species are not distributed in cold environments, i.e. that cold-tolerances are independent of environmental conditions. <sup>[96, 97]</sup> evaluated the predictability of species via thermal tolerances and found a close match between thermal tolerance and distributional limits, and thus a good predictability of climate change effects via SDMs. However, their study focused on other organisms than seaweeds. Seaweeds are limited in dispersal capabilities and thus, responses of seaweeds to thermal conditions might differ from other, mobile, organisms. Therefore, I further hypothesize that there will be deviations from the fundamental thermal niches in realized distributions in seaweeds which has implications for the predictability of seaweed distributions based on information on thermal tolerances. The results are also important in the context of research chapter 2 (i.e. detection of cold-tolerance in seaweeds) and for the assessment of climate change effects on seaweed distributions.

#### *Applied methods*

In research chapter 1, I conduct a physiological experiment for the lower temperature tolerance with *C. implexa* specimens, collected from the field in Chile. In addition, a correlative SDM (maxent), is used. I use the results from both approaches to identify the suitable habitat of *C. implexa* under current and future climatic conditions.

In research chapter 2, an envelope approach is used to identify suitable combinations of minimum and maximum (i.e. winter and summer) SSTs, which allow the species to thrive. Here, minimum volume ellipses are drawn around the two-dimensional environmental data (minimum and maximum SST) as sampled from the known distributions. These ellipses can be treated as representations of the realized thermal niches of the species. The ellipses are then contrasted with the conditions at the Antarctic sites from where the species have been reported, and the overlaps between both geographic ranges (pre-Antarctic and Antarctica-inclusive range) are calculated. To do so, I use the functions provided via the “dynRB”-package (“dynRB” = “Dynamic Range Boxes”) by <sup>[98]</sup> for niche overlap estimation. In this

way, I assess to what extent the addition of Antarctic habitats increases the realized thermal niche sizes and to what extent the climatic conditions from the original and the Antarctic sites match.

In research chapter 3, a comparable but simpler approach is used. Here, only minimum and maximum realized and fundamental thermal limits are compared, without taking combinations of minimum and maximum SST into account. I examine to what extent realized and fundamental niches coincide and how well temperature tolerances predict distributions. To do so, I compare thermal tolerance limits of 126 seaweed species with their distributional thermal limits (i.e. realized thermal niches) and analyze distributional limits as a function of thermal tolerance limits and the degree of non-equilibrium as a function of latitudinal range via linear (mixed) effects models. The thermal tolerance limits are taken from the published scientific literature and the realized limits are based on distributional data.

## List of publications and declaration of contributions

This thesis consists of three individual research chapters. The first two are published in international peer-reviewed scientific journals, the third is in preparation for submission. My contributions to the respective chapters are as follows:

<b>Title</b>	<b>Future range dynamics of the red alga <i>Capreolia implexa</i> in native and invaded regions: contrasting predictions from species distribution models versus physiological knowledge</b>
<b>Authors</b>	Philipp Laeseke, Brezo Martínez, Andrés Mansilla, Kai Bischof
<b>Published in</b>	Biological Invasions, 22(4), 1339-1352
<b>doi</b>	10.1007/s10530-019-02186-4

<b>Task</b>	<b>Contribution of the Candidate in %</b>
Experimental Concept and Design:	80
Experimental work and/or acquisition of (experimental) data:	80
Data analysis and interpretation:	90
Preparation of Figures and Tables:	100
Drafting of the manuscript:	90

<b>Title</b>	<b>Invaders in waiting? – Non-equilibrium in Southern Hemisphere seaweed distributions may lead to underestimation of Antarctic invasion potential</b>
<b>Authors</b>	Philipp Laeseke, Brezo Martínez, Andrés Mansilla, Kai Bischof
<b>Published in</b>	Frontiers of Biogeography 13-4
<b>doi</b>	10.21425/F5FBG50879

<b>Task</b>	<b>Contribution of the Candidate in %</b>
Experimental Concept and Design:	95
Experimental work and/or acquisition of (experimental) data:	100
Data analysis and interpretation:	95
Preparation of Figures and Tables:	100
Drafting of the manuscript:	90

<b>Title</b>	<b>Patterns in thermal niche equilibrium in global seaweed distributions</b>
<b>Authors</b>	Philipp Laeseke, Brezo Martínez, Kai Bischof
<b>Published in</b>	<i>In preparation</i>
<b>doi</b>	<i>In preparation</i>

<b>Task</b>	<b>Contribution of the Candidate in %</b>
Experimental Concept and Design:	90
Experimental work and/or acquisition of (experimental) data:	60
Data analysis and interpretation:	95
Preparation of Figures and Tables:	100
Drafting of the manuscript:	90



## Research chapter 1 – publication 1

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

Authors: Philipp Laeseke<sup>1</sup>, Brezo Martínez<sup>2</sup>, Andrés Mansilla<sup>3</sup>, Kai Bischof<sup>1</sup>

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Published in: *Biological Invasions*, 22(4), 1339-1352. doi: <https://doi.org/10.1007/s10530-019-02186-4>. Date of Publication: 1<sup>st</sup> of January 2020.

### 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.

### Introduction

Climate change is the major driving force for distributional range shifts from the equator poleward <sup>[99]</sup>. This force affects terrestrial and marine species alike, regardless of taxonomic group <sup>[99-101]</sup>. 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. <sup>[102-104]</sup>). 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, <sup>[6]</sup>). In contrast, expansions of species' distributional ranges are observed across the globe (e.g. <sup>[53]</sup>). Here, human activity plays a major role by connecting spatially isolated places (<sup>[105,106]</sup>), 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 <sup>[11-13, 107]</sup>. Bioinvasions are not only of major ecological concern but also of socioeconomic interest as control and remediation costs are substantial <sup>[46]</sup>. From an economic point of view, prevention is to be preferred over later management measures <sup>[34]</sup>. Anticipation of and rapid response to invasions are important in combatting invasive species <sup>[49]</sup>. 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 <sup>[105]</sup>. 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 <sup>[108]</sup>.

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 <sup>[93]</sup>. 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 <sup>[109]</sup>.

To address the above-mentioned limitation, it has been proposed to integrate physiological knowledge into predictive models <sup>[14]</sup>. 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 <sup>[14]</sup>. 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 <sup>[95]</sup>. 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. <sup>[110-112]</sup>).

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 <sup>[113]</sup>. It was first reported from Chile from coasts between 39° 56' and 41° 45' S by <sup>[15]</sup>. 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 <sup>[15]</sup>. Based on the finding of reproductive populations, <sup>[15]</sup> 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 <sup>[114]</sup>. 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 <sup>[64]</sup>) and probably preventing other species from settling <sup>[65, 66]</sup>. 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 <sup>[115]</sup>. However, new introductions are reported occasionally (e.g. <sup>[15, 116]</sup>). *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 <sup>[6, 39]</sup> 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 <sup>[117]</sup>. We specifically wanted to (1) evaluate <sup>[117]</sup> 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 15<sup>th</sup> of January 2017, transported them in darkness in a cooler to the laboratory and confirmed their identity with available literature [15, 114]. During collection, we paid attention to sample from as many individual epilithic and epizoid 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 [118] 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<sup>-1</sup>; 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 [119]. 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 ( $\pm 0.1$  °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 =  $Q1 - 3 \cdot IQ$  and  $Q3 + 3 \cdot IQ$ , 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 ( $It_{50}$ ).

#### Distributional records for SDM

Distributional data were compiled from [114, 120-122] and [15] and expanded with data from www.gbif.org (9th of March 2018). Data from gbif.org was cleaned by excluding records from before 1993 (year of description of the species by [113]) 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 [123] with the spThin-function from the R-package of the same name [124]. 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 (Figure 5a). 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).

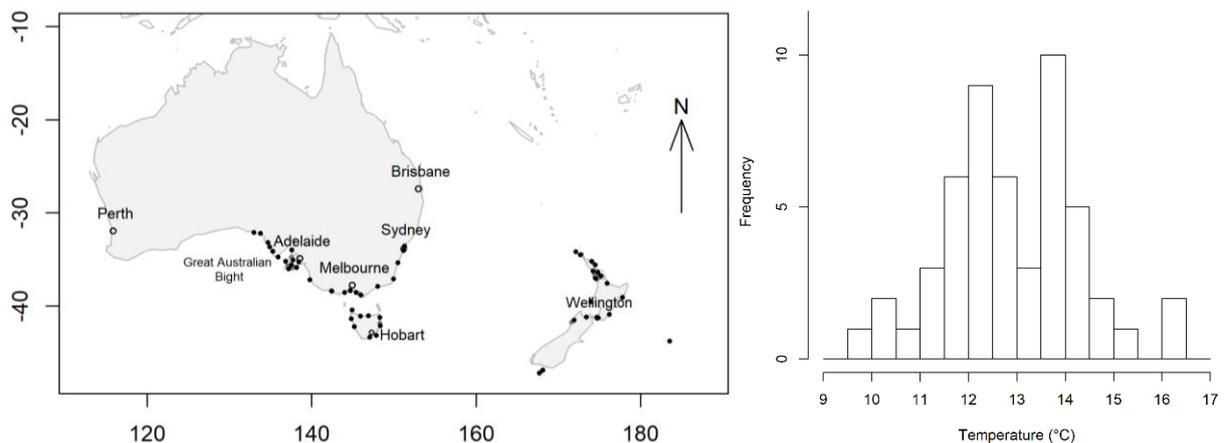


Figure 5. a) Occurrence data of *Capreolia implexa* around Australia and New Zealand (thinned data = black dots, cities = stars) and b) frequency of occupied min SST conditions as sampled from the bio-oracle min SST layer from the included occurrence sites.

#### Environmental predictors for SDM

Environmental data layers were compiled from Bio-Oracle v2.0 [125], MerraClim [126] and WorldClim [127] (Table 1). We did not include a “wave exposure” layer since this species occupies sheltered and open coasts alike [114]. To align layers from different sources, WorldClim and MerraClim data layers were resampled with bilinear interpolation using Bio-Oracle 2 layers as references [2] with the resample-

function from the “raster” R-package <sup>[128]</sup>. A layer for substratum type was created by drawing polygons around soft-bottom coastlines of  $\geq 10$  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](http://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 <sup>[125]</sup> ; rcp = Representative Concentration Pathways, which include greenhouse gas emissions and atmospheric concentrations, air pollutant emissions and land use, for climate projections <sup>[3]</sup>. All environmental layers used in this study were in 5 arcmin resolution.

Table 1. Predictor variables with sources. <sup>1</sup>no monthly data available; DIVA=Data-Interpolating Variational Analysis; WOD09=World Ocean Database 2009.

Predictor variable	Abbreviation	Unit	Range (min – max)	Origin	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 <sup>-3</sup>	9.4*10 <sup>-3</sup> – 1.22	DIVA Interpolation from WOD09	Bio Oracle 2	5 arcmin
Nitrate	N	Mol m <sup>-3</sup>	2*10 <sup>-6</sup> – 15.8	DIVA Interpolation from WOD09	Bio Oracle 2	5 arcmin
Cloudiness (year average) <sup>1</sup>	Cloud	%		Monthly averages (2005 – 2010)	Bio Oracle 2	5 arcmin
Maximum Photosynthetically Active Radiation	Max PAR	E m <sup>-2</sup> day <sup>-1</sup>		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 <sup>-1</sup>	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	Self-made (see text for details)	5 arcmin

Models were built with Maxent<sup>[117]</sup> and the biomod2 R-package<sup>[129]</sup>. 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<sup>[1]</sup>.

## 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) (Figure 6). 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 (Figure 6). Growth responses to the temperature treatments after shorter exposure times are shown in Figure S1-1.

Lt<sub>50</sub> was identified at  $6.6 \pm 0.4$  °C (Figure 7). 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 (Figure 8). 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<sub>50</sub> 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 to the southernmost tip of the continent (year 2100 rcp 8.5, Figure 8f).

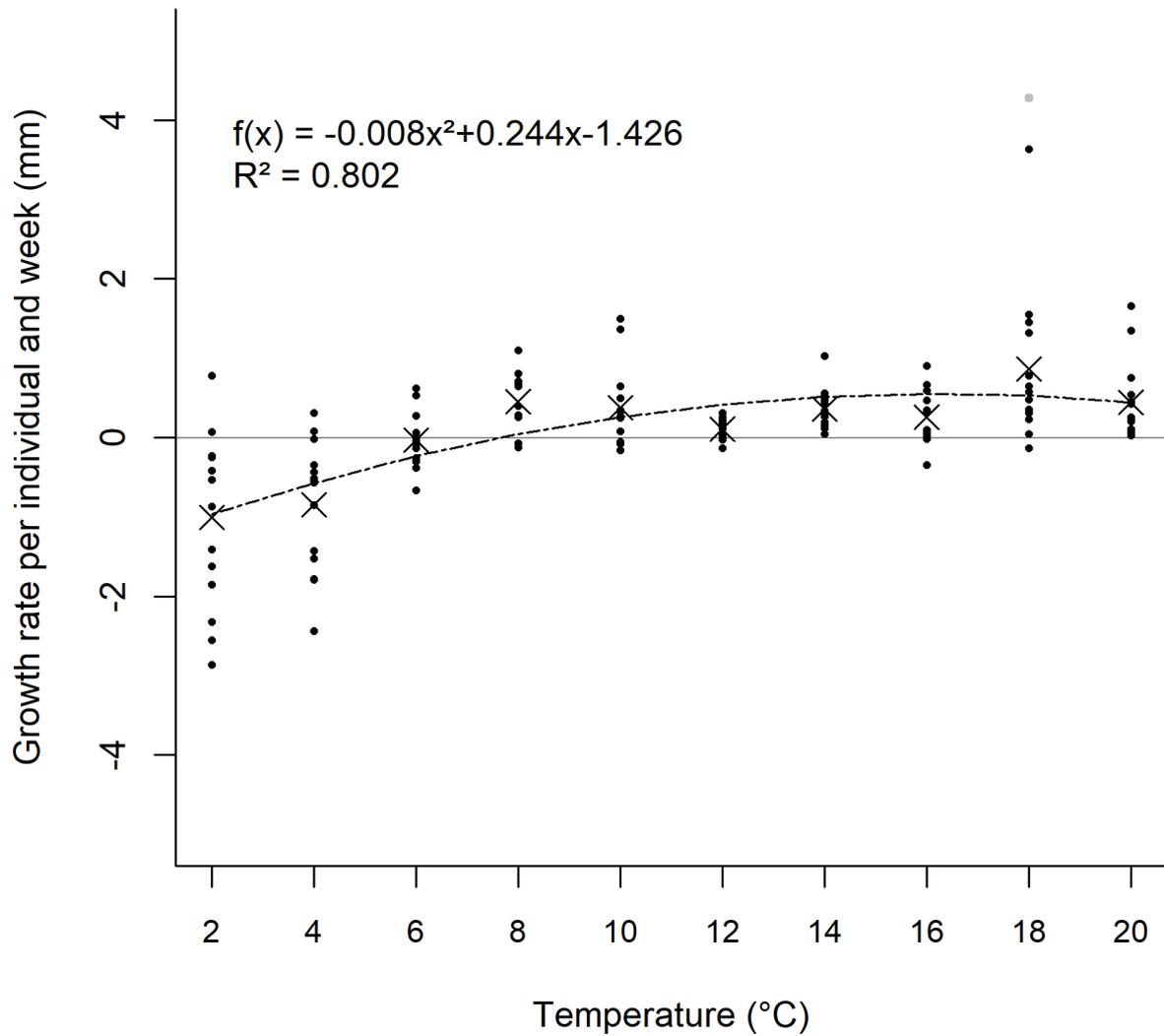


Figure 6. Growth rates of *Capreolia implexa* per individual after 28 days of the temperature experiment. Dots represent individual replicates ( $n = 140$ ), crosses the average per temperature level without outlier (grey), and the dashed-dotted line the 2<sup>nd</sup> order polynomial regression line. 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.

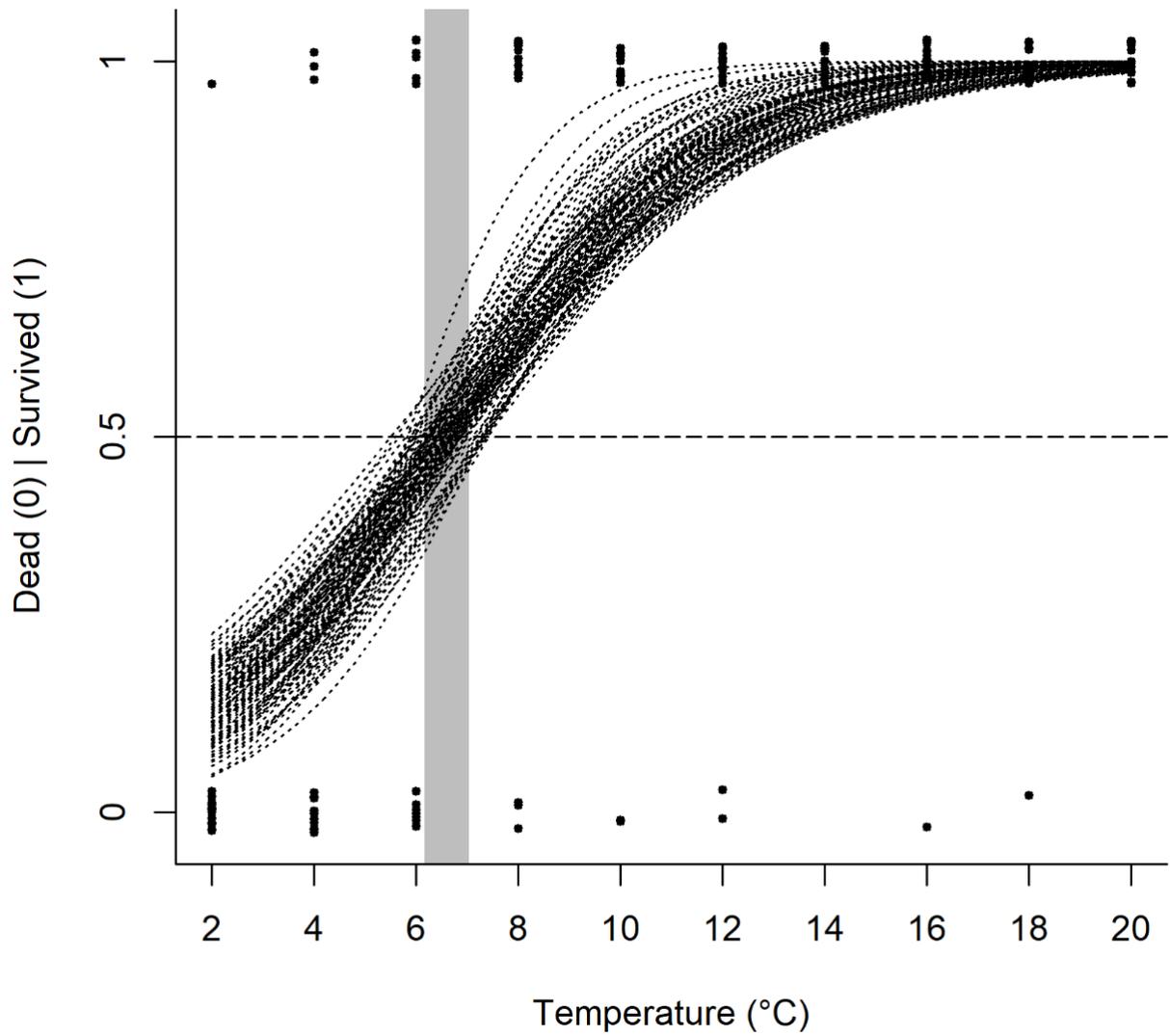


Figure 7. Number of survived (1) versus dead (0) individuals of *C. implexa* over the experimental temperature range after 28 days. Data points are jittered for better visualization but are in fact only 1 or 0. The dotted lines display the binomial generalized linear models fitted on survival rate (100 repetitions).  $Lt_{50}$  lies at  $6.6 \pm 0.44$  °C (grey area); AUC averaged =  $0.9 \pm 0.04$ .

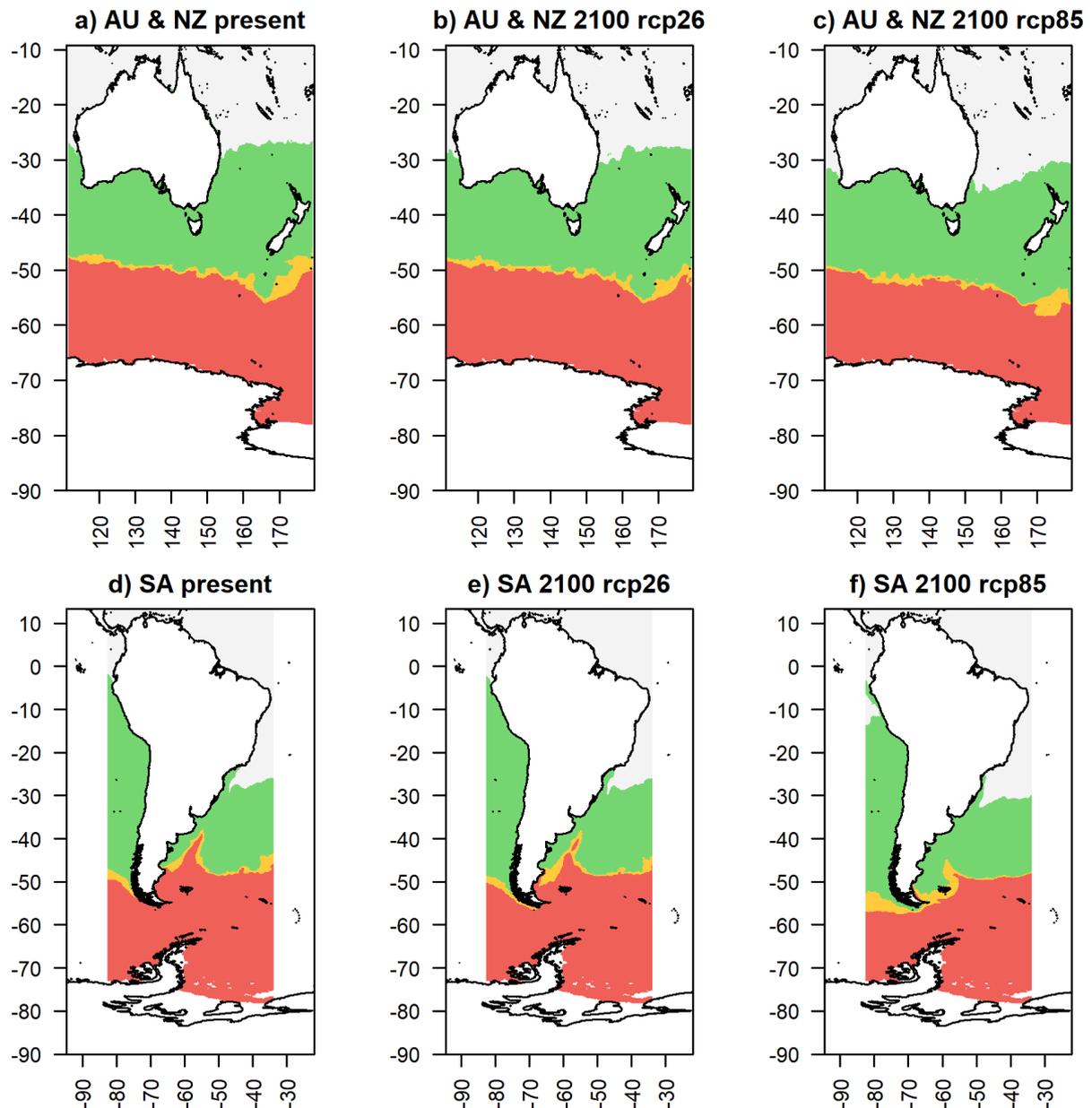


Figure 8. Projection of the southern distributional limit of *C. implexa* in Australia, New Zealand (a–c) and South America (d–f) for present and future climate scenarios by applying the  $lt_{50}$  temperature threshold from physiological experiments. Red >  $lt_{50}$ , green <  $lt_{50}$ , yellow =  $6.6 \pm 0.44$  °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.

#### 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 ( $0.782 \pm 0.082$ ) and higher model gain (0.683) than

models with max SST (AUC:  $0.738 \pm 0.75$ ; gain: 0.579). Hence, final projections were based on min SST as single predictor variable in Maxent and biomod2 (Table 2 and Table 3). The response curve of habitat suitability dependent on min SST from Maxent is shown in Figure 9. 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 (Figure 5b). The occupied maximum SST in the native range lies between 14.2 and 23.9 °C (not shown).

Table 2. Model contributions of predictor variables and model performances of different predictor combinations. 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  $\geq 20\%$ , bold letters). Asterisks mark predictors with significant contribution to the models.

Predictor variable	Model1	Model2	Model3	Model4	Model5
Minimum Sea Surface Temperature (Min SST)	<b>76.6 (0.58)*</b>	-	<b>79 (0.68)*</b>	-	<b>51.8 (0.68)*</b>
Maximum Sea Surface Temperature (Max SST)	-	<b>70.1 (0.57)*</b>	-	<b>72.3 (0.57)*</b>	<b>27.5 (0.57)*</b>
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) <sup>1</sup>	0.3	0.2	0.1	0.2	0.1
Maximum Photosynthetically Active Radiation (Max PAR)	1.1	1.9	1	1.6	0.8
Precipitation of driest month (Min Prec)	10.7	17.1	7.5	14	6.9
Precipitation of wettest month (Max Prec) 6	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

Table 3. Model parameter of the model with Min SST as single predictor variable. AUC = Area Under Curve, Df = degrees of freedom, AIC = Akaike Information Criterion, ROC = Receiver Operating Characteristic.

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

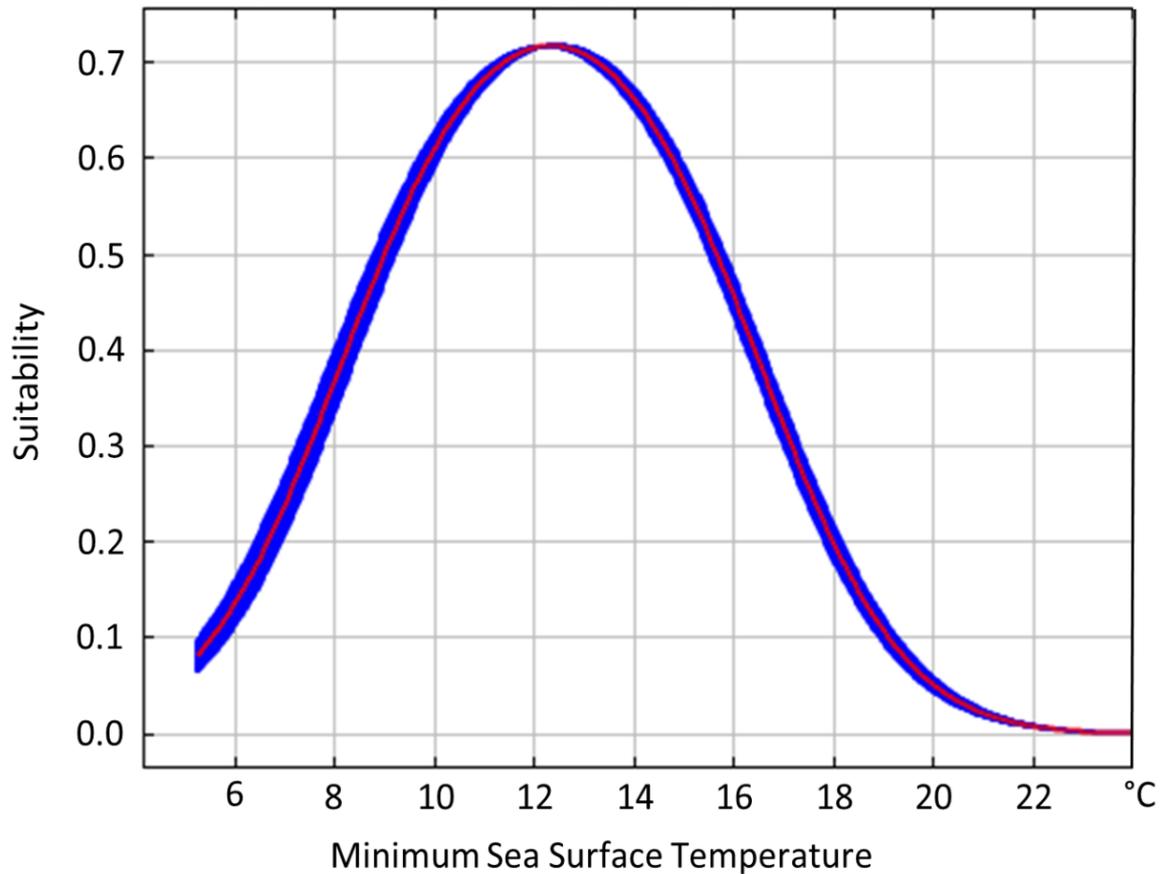


Figure 9. Maxent response curve of *Capreolia implexa*, showing the predicted habitat suitability dependent on min SST. Black line is the average of 10 replicated runs  $\pm$  SD (grey area).

#### 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 (Figure 10a). 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 (Figure 10b 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  $\sim$  528 km of coastline under rcp 2.6 conditions and  $\sim$  4226 km under rcp 8.5 conditions and gain as  $\sim$  163 km. Gain in suitable habitat is, however, predominantly predicted for coasts with soft substrate habitats.

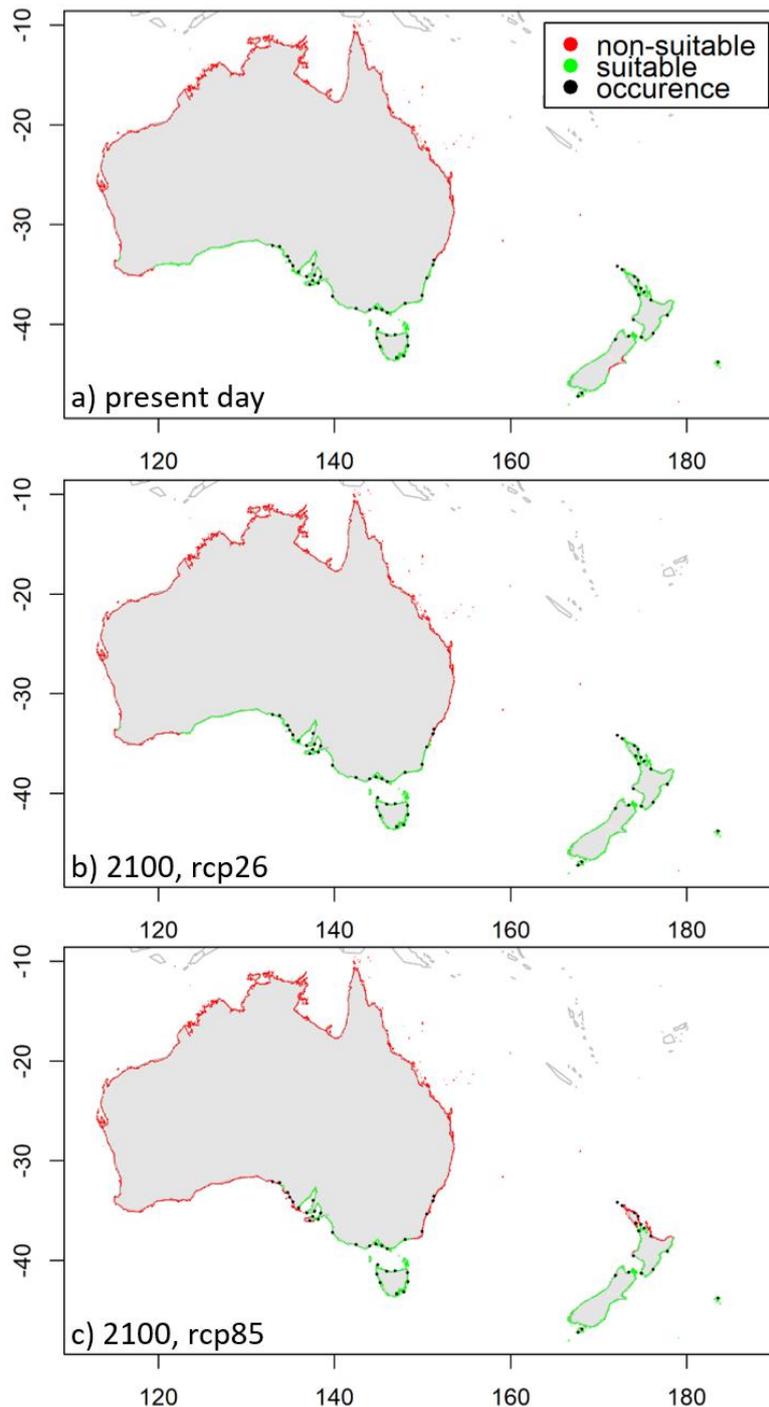


Figure 10. Binary habitat suitability predictions for Australia and New Zealand based on correlative SDMs for a present, b 2100 rcp 2.6 and c 2100 rcp 8.5 climate scenarios.

#### Predicted habitat suitability for South America under present and future conditions

Projections for South America included the reported invaded regions as suitable habitat (Figure 11). Under present day climate conditions (Figure 11a) 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 Chiloe' island), and between 28° 28' S and 42° 58' S along the Atlantic coast (San Matías Gulf and south of the Rio de la Plata in Argentina, most of Uruguay and parts of Brazil). Under future conditions (Figure 11b 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° 58' S on the Pacific coast and 29° 12' on the Atlantic coast. Southern limits are predicted at approximately 51° 48' S in Chile and 47° 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 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.

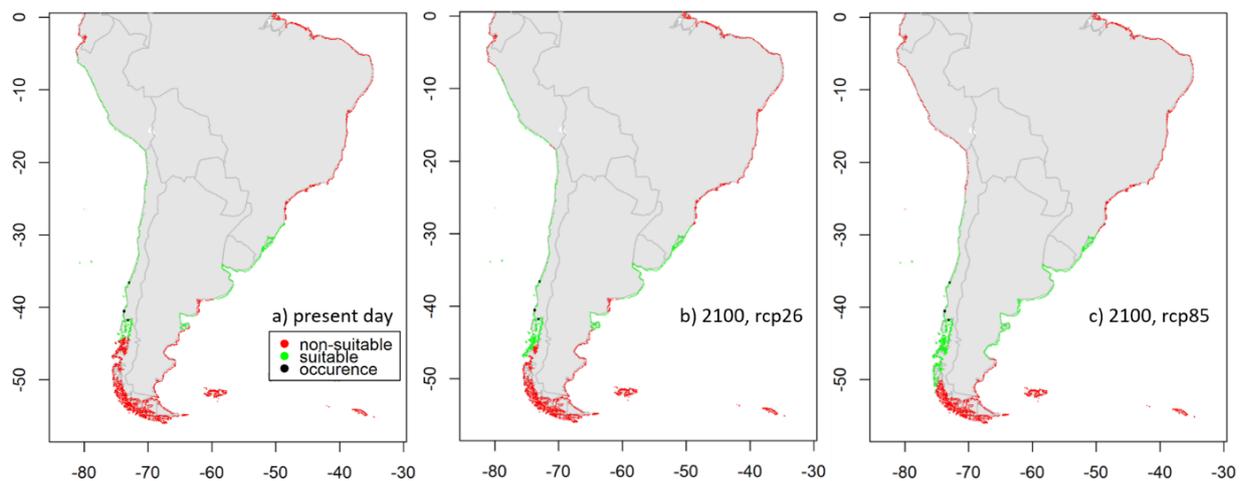


Figure 11. Binary (suitable vs. non-suitable) habitat suitability predictions for South America from Maxent. Model trained on native area (Australia & New Zealand) and projected to the invaded area under a present, b 2100 rcp 2.6 and c 2100 rcp 8.5 climate scenarios.

## 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<sup>[15]</sup>. 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. Our Maxent model correctly identified the currently occupied Chilean coasts as suitable areas and with an AUC of  $0.782 \pm 0.082$  can be evaluated as “good”<sup>[130, 131]</sup>. 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  $6.6 \pm 0.4$  °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 response curves <sup>[95]</sup>. 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 <sup>[93]</sup>. <sup>[15]</sup> 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 Valparaiso 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  $6.6 \pm 0.4$  °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 <sup>[132]</sup>. Hence, the distributional range might be limited by much lower than the highest occupied SST in the native range. <sup>[132]</sup> found that most of their investigated species exhibited a "safety margin" of at least 2 - 3 °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.<sup>[64, 133-135]</sup>). It is hitherto unknown what factors define this biogeographic break, but<sup>[134]</sup> identified low dispersal capacity as a main predictor for phylogeographic structure across this break.<sup>[113]</sup> 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<sup>[15]</sup> 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<sup>[106]</sup>. 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<sup>[114]</sup> and has also been found on wooden structures and even fallen tree trunks<sup>[15]</sup>, 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<sup>[109]</sup>. Moreover, *C. implexa* has a biphasic life cycle and different life-history stages might have different temperature tolerances (e.g.,<sup>[136]</sup>) and reproduction may depend on certain temperature and/or light-regimes<sup>[26]</sup>. 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*<sup>[137, 138]</sup>. 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<sup>[6]</sup> and<sup>[39]</sup>, 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<sup>[6]</sup>.

<sup>39, 139]</sup>. Effects can be dramatic as these shifts affect ecosystem engineers such as large kelps, which can provide habitat for large numbers of associated organisms <sup>[140]</sup>. *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 matforming 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 <sup>[65]</sup>. 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 <sup>[141]</sup>. 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

Conflict of interest

The authors are not subject to any conflicts of interest regarding this report.

### References

*Moved to the comprehensive reference list at the end of this thesis.*

Supplementary material

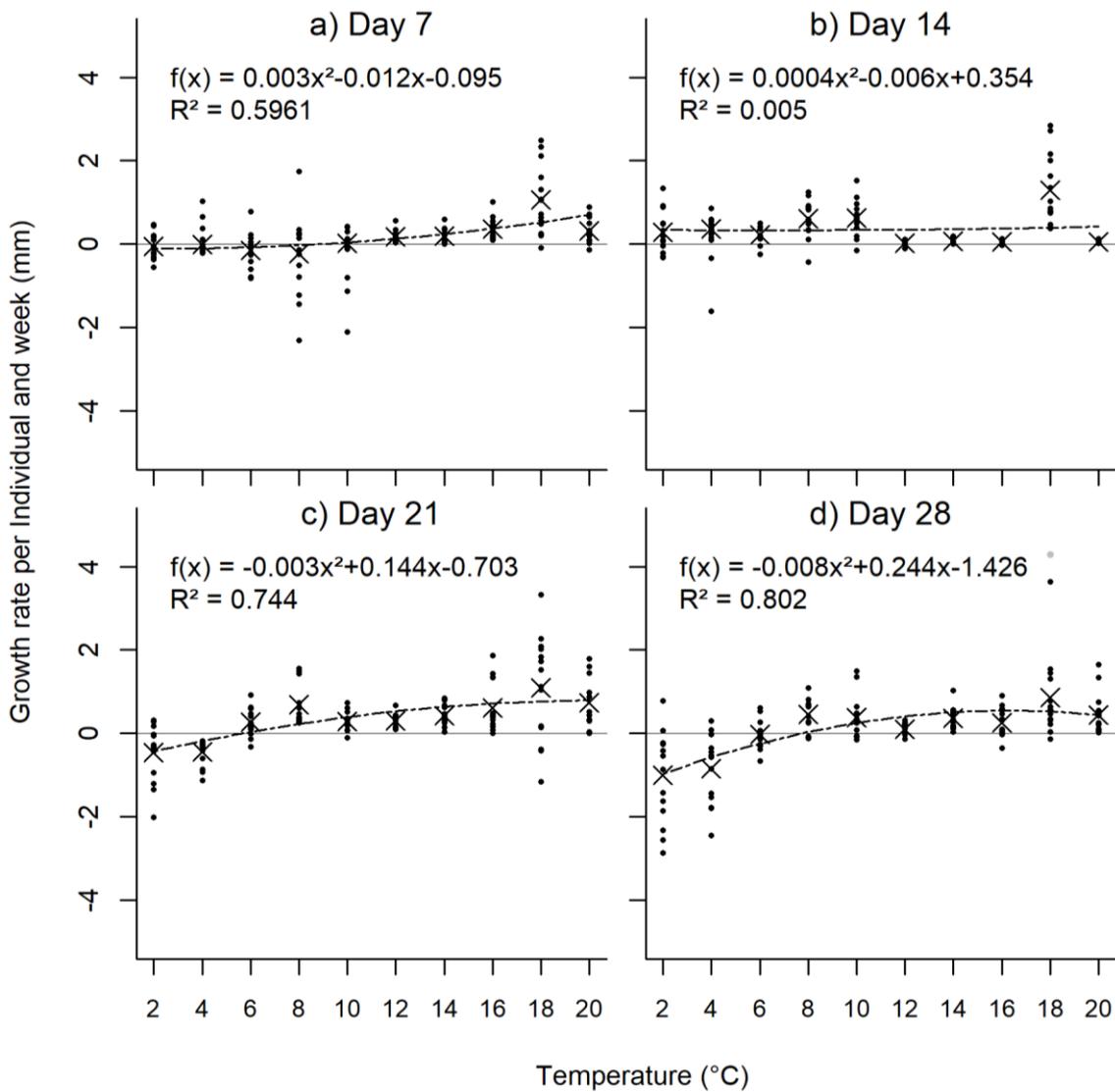


Figure S1-1. Growth rates per individual and week over four weeks. Black dots represent individual replicates, crosses the average per temperature without outliers and the dashed-dotted line the 2<sup>nd</sup> order polynomial trend line. For the trend line the equation and  $R^2$  are given.



## Research chapter 2 – publication 2

Title: **Invaders in waiting? – Non-equilibrium in Southern Hemisphere seaweed distributions may lead to underestimation of Antarctic invasion potential**

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### Abstract

Bioinvasions pose a major threat to global biodiversity. Correlative Ecological Niche Models (ENMs) can be a valuable tool to identify invaders and invasion sites. However, in cases when species are in non-equilibrium with their native environment (i.e. do not fill their niche), correlative approaches have limited power and invasions lead to shifts of the realized niche. In recent years, several new seaweed species have been reported in Antarctica. It is impossible to unequivocally identify which of these species are truly non-natives, however, here, we provide literature-based evidence that seaweed species have been introduced to Antarctica. Under this assumption, we reconstruct pre- and post-introduction niches of these species, calculate relative niche sizes and overlap between pre-Antarctic and Antarctic sites, and evaluate increase in niche size due to inclusion of Antarctic habitats. In seven species, the absolute occupied temperature range is dramatically enlarged, with minimum sea surface temperature (SST) being 2-5°C lower than in the pre-Antarctic ranges. In all species except one, summer SST is 5-20°C lower than in the pre-Antarctic ranges. As a result, several species' niches increase dramatically. We hypothesize that species from the Southern Hemisphere do not cover their whole abiotically suitable range due to lack of settling substrate in cold-water regions while species from the Northern Hemisphere tend to fill their niches to a greater degree due to higher connectivity between tropic and polar regions along coastlines. Thus, while correlative ENMs for Northern Hemisphere species will probably be successful in predicting Antarctica as a suitable habitat, such models will likely be insufficient to do so for Southern Hemisphere species. From a precautionary standpoint, we argue that not only species from climatically matching regions pose an invasion threat for Antarctica, but that also species from other, climatically non-matching regions, might be potential invaders. In light of higher connectivity of the Antarctic continent with other continents this finding significantly increases invasion risk for Antarctica.

## Highlights:

- Non-native Antarctic species likely originate from climatically non-matching and distant habitats
- Shifts in realized niches might be common during introductions to Antarctica
- Southern Hemisphere seaweeds in particular, and perhaps other intertidal organisms, in the Southern Hemisphere exhibit non-equilibrium distributions and might be “invaders in waiting”
- Purely correlative approaches to identify potential Antarctic invaders are insufficient

**Key words:** barrier, bioinvasions, ecological niche modelling, intertidal, marine, niche shifts, polar, South Shetland Islands, species distribution modelling

## Introduction

Bioinvasions can have disastrous impacts on affected ecosystems and are recognized as a major threat to global biodiversity, ecosystem health, economy, and human health <sup>[11-13, 142]</sup>. Anticipation of invasions and early prevention are preferable over eradication measures, since the latter are extremely labor-intensive, costly, and have uncertain chances for success <sup>[34, 49, 143-145]</sup>. Ecological niche models (ENM) can help predict the invasive potential of alien species and identify the geographic space at risk of invasion <sup>[93, 108, 146]</sup>. Such models make estimations of a species' realized niche [the occupied multidimensional space, which, in contrast to the fundamental niche, can be limited by other factors, <sup>[84]</sup>] based on correlations between distributional and environmental data. This information can then be used to identify suitable but unoccupied geographic space. Hence, identification of suitable habitat in unoccupied geographic space follows the premise of climate matching, i.e. that species will likely occupy environmental conditions similar to those in their native habitat. However, realized niches can be extended during invasions <sup>[82, 147]</sup> when species are in non-equilibrium with their native environment and originally unavailable niche space becomes accessible. As a consequence, correlative ENMs, trained on non-equilibrium data, will likely underestimate the potential suitable range of a species <sup>[93]</sup>. Given the power of ENMs for forecasting invasions and the significance of bioinvasions as a global problem, the frequency and mechanisms of niche shifts and their implications for reliable ecological niche models are debated (e.g. <sup>[148-150]</sup>). Ample examples exist for niche shifts for a variety of organisms, such as terrestrial plants <sup>[147, 151]</sup>, freshwater fish <sup>[152]</sup>, insects <sup>[153-155]</sup>, and a bivalve in Antarctica <sup>[82]</sup>. In all these examples, the invaders occupy environmental space which they did not occupy in their native ranges. Contrary to this, <sup>[156]</sup> examined niche shifts in 50 holarctic invasive terrestrial plant species and found that substantial niche shifts occurred in only 14% of the investigated species. However, the authors stressed that the respective native and recipient ecosystems were similar. Hence, ENMs are valuable tools provided that recipient habitats are comparable to native ones, although outside this

range, predictions may be inaccurate <sup>[157]</sup>. In cases where donor and recipient ecosystems do not match environmentally, correlative ENMs for assessments of invasion risk may underestimate invasive potential.

In recent years and decades, novel and non-native seaweed species have been reported from Antarctic sites <sup>[75, 81, 83, 158, 159]</sup>. Seaweeds are highly important ecosystem engineers and provide invaluable ecosystem services to coastal marine habitats throughout all ecoregions. Some seaweed species (e.g. *Undaria pinnatifida*, *Caulerpa taxifolia*) are ranked among the 100 worst invasive species worldwide and have disastrous impacts on recipient ecosystems, making seaweeds a highly relevant target group and model organism for our study <sup>[53, 59]</sup>. Antarctica, the “final frontier for marine biological invasions” <sup>[71]</sup>, is highly isolated latitudinally from other continental masses by natural physical barriers, such as the Antarctic Polar Front (APF) and the Antarctic Circumpolar Current (ACC), and has the harshest climatic conditions on Earth <sup>[26]</sup>. Therefore, non-native species have to cross a major biogeographic barrier across a large latitudinal range and face highly contrasting environmental conditions on either side of this barrier. These factors have led to a high level of endemism in Antarctica, and the APF has been perceived as an almost impenetrable protective barrier against invasions into Antarctic ecosystems <sup>[26, 73, 74]</sup>. However, in recent decades, the continent’s isolation has decreased as shipborne activities, scientific research, and the amount of long-lasting floating litter reaching Antarctica have increased <sup>[70, 77, 160]</sup>. In addition, natural rafts like the kelps *Durvillaea antarctica* and *Macrocystis pyrifera* frequently reach Antarctica and offer the possibility for attached species to hitchhike to Antarctica <sup>[16, 78]</sup>. Simultaneously, global warming is leading to higher suitability of Antarctic habitats for non-native species, and the reduction of the impact of ice and ice-scouring along the coasts will increase substrate availability to intertidal species such as seaweeds <sup>[16, 41, 161]</sup>. Today, several non-native species are reported from the terrestrial and marine realms of Antarctica, showing that natural barriers like the ACC can be crossed and that non-native species successfully reach and establish in Antarctica <sup>[16, 70, 83, 158, 162-164]</sup>. Evidence indicates that Antarctic invaders, like the mussel *Mytilus* cf. *platensis* <sup>[82]</sup> or the terrestrial grass *Poa annua* <sup>[165]</sup> do not necessarily originate from polar habitats but also from climatically non-matching regions.

Here, we critically review the literature on new records of seaweed species in Antarctica and discuss the possibility that the reported species are non-natives. Three scenarios are possible: (a) they are native species, which have not previously been found in Antarctica, (b) they are colonists, which were introduced naturally (e.g. floating on rafting species), or (c) they are new colonists which were introduced via human-mediated activities <sup>[166]</sup>. In the light of decreasing isolation of Antarctica, scenarios (a) and (b) in particular have to be evaluated from a precautionary perspective. The authors of the original reports state that the novel species might have been overlooked in previous campaigns and that it is unclear which species are true non-natives. However, we examine the species’ potentials

of being successfully introduced, and provide evidence that there are truly non-native species among them. We explore the respective scenarios, and postulate that seaweed introductions to Antarctica will coincide with shifts of the realized niches of non-native species. Here, we analyze pre- and post-introduction niches to quantify the magnitude of niche shifts and hypothesize that Antarctic non-native seaweeds can originate not only from climatically matching regions, but that niche shifts can occur as a consequence of introduction to Antarctica and prior niche unfilling, and that the respective species simply need transportation vectors to reach Antarctica to fill their niches. The risk of invasion for Antarctica might therefore be higher than assumed, and correlative approaches alone might not be sufficient to determine Antarctica's invasion risk.

## Material and methods

### Literature search for new reports of species and gathering of distributional information

We conducted an extensive literature search for new additions to the Antarctic seaweed flora. Every report was cross-validated with comprehensive literature such as [75, 167, 168], references therein and references listed on [www.algaebase.org](http://www.algaebase.org) [169] and under inclusion of former nomenclature to verify true novel records. For all species, distributional data were collected from [www.gbif.org](http://www.gbif.org) (link to dataset: <https://www.gbif.org/occurrence/download/0078530-200221144449610>, accessed June 4<sup>th</sup>, 2020), and from the published literature. We included the key references for species' distributions as accessible in each single species' entry on [www.algaebase.org](http://www.algaebase.org) and conducted literature searches for each species with Google.Scholar for further references. Gbif information was cross-checked for reliability and validity with literature references and the meta-data of the datasets. From the literature, information with coordinate reference or location description was included. Imprecise information, e.g. simple mentioning of a certain country, sea region or county coast, was not included. We removed duplicates in the sense of multiple mentions per raster grid cell (5 arcmin resolution). In total, 5946 records from the database and literature were used for niche analyses.

Distributional data were used to sample minimum and maximum sea surface temperature (SST) over the entire pre-Antarctic distributional ranges from bio- Oracle v2.0 Long-Term Minimum and Maximum SST layers [average temperatures of coldest and warmest month, respectively, over the years 2000-2014, 5 arcmin resolution [125]]. For comparison, SST data from occurrence sites at the South Shetland Islands (SSI) were sampled from the same SST data layers. These two data sets were then used to i) compare absolute SST ranges prior to and after Antarctic occurrence and ii) to build respective climatic envelopes for consecutive analyses of niche metrics (see below). We restricted our niche approach to SST, following traditional works on seaweed biogeography by e.g. [26] and [132] who built their biogeographic predictions mainly on experimentally tested thresholds for survival, reproduction and growth, as well as correlations of distributional data and SST isotherms. SST, next to availability of hard substrate, is the most important factor for macroalgal distributions [26] and its

importance is underlined by its prevalence as determining factor in modern seaweed ENMs available in the literature. Intertidal seaweeds are also exposed to air temperature during low tide but freezing during emergence does not necessarily damage intertidal seaweeds because they can tolerate more extreme conditions in a dry state, making this factor less relevant for biogeographic predictions <sup>[26, 170, 171]</sup>.

#### Assessment of introduction potential

In addition to the compilation of distributional data, we assessed each species' potential for successful introduction in accordance with the publication by <sup>[172]</sup>. <sup>[172]</sup> analyzed features of 113 known introduced seaweeds in Europe to identify key traits for prediction of successful introduction, the most relevant being "Distribution," "Probability of being transported," "Temperature and Salinity Ranges," "Reproductive Mode," and "Growth Strategies & Surface: Volume Ratio." In contrast to their approach, we assume that a wider geographic distribution leads to a higher ranking, since more potential source locations are available for transport to Antarctica. In the other categories we follow their ranking: In the category "Probability of being transported," the highest ranks are assigned in ascending order to species which grow on artificial substrates, oysters and mussels, or ship and platform hulls. For salinity and temperature ranges, wider ranges indicate a higher potential for successive introduction. In the category "Reproductive Mode," the highest ranks are assigned in ascending order to species which reproduce via asexual spores, vegetative propagules, or via fragmentation. In "Growth Strategies & Surface:Volume Ratio" highest ranks are assigned to *r*-strategists. Reliable and comparable information for "Surface:Volume Ratio" was impossible to find, thus, this category is limited to growth strategy in this study. <sup>[172]</sup> also tested other categories for their predictive power for introduction potential, however, these were rated less informative and are therefore not included in this study. In cases where sufficient information is not available for to each species in the categories but rather follow a qualitative weight-of-evidence approach. This was done because the species are unequally well documented and investigated and comparison based on exact numbers would possibly introduce a higher resolution than the information allows. For details on the methodology, other categories and the ranking system please consult the original publication by <sup>[172]</sup>.

#### Niche metric analysis

To calculate climatic niche sizes, we used the "dynRB-Vpa()" -function of the "dynRB" -package <sup>[98]</sup> in R <sup>[123]</sup>. Distributional data suffered from geographical biases, in the sense that some regions were heavily oversampled, while others were undersampled, leading to strong biases in geographic distribution of occurrence data. Although the "dynRB-Vpa()" method is robust towards sampling bias, we added an additional step to overcome sampling bias and used virtual species based on the original distributional data.

To construct virtual species, we followed the procedure described by <sup>[173]</sup>. First, we identified the climatic envelopes with combined minimum and maximum SST in the pre-Antarctic distributional

range. We then used these envelopes as masks to limit the environmental data raster files to geographic regions enclosed by this volume. This subset was further reduced with the GEBCO-bathymetry raster layer to coastal areas between -50 and +10m around sea-level and to regions within or adjacent to the occupied pre-Antarctic range. From this final subset, we randomly sampled a maximum of 500 occurrence records per species. For *Dictyota decumbens*, this approach was not feasible due to its extremely limited distributional range and environmental data were sampled from the entire Macquarie Island instead. The final datasets were further reduced by fitting a minimum volume ellipse around the original data and reducing the virtual niche to the space within this ellipse. In this way, we constructed virtual climatic niches comparable to the original real-world niches, but without sampling bias. For a second, Antarctica-inclusive dataset, we added data from the Antarctic sites at the SSI to the pre-Antarctic data sets.

These datasets were then used to calculate respective niche sizes and overlaps between pre-Antarctic and Antarctica-inclusive distributions. Since niche sizes were unequally large, the “mean”-aggregation method <sup>[98]</sup> was used to allow comparisons. For a detailed method description for size and overlap calculation in the dynRB-package consult the original publication by <sup>[98]</sup>. Geospatial data for this study was processed with the “raster” <sup>[128]</sup> and “rgdal” <sup>[174]</sup> packages in R <sup>[123]</sup>. Graphs and maps were made with the “ggplot2” <sup>[175]</sup> and “tmap” packages <sup>[176]</sup>, also in R <sup>[123]</sup>.

## Results

### Distributions of newly reported Antarctic seaweeds

In total, 12 seaweed species of 11 genera (10 orders) and of different organizational complexity (filamentous green algae to *Rhodophyta*) are reported in the literature as new additions to Antarctic flora (Table 4, Figure 12). The species occur in varying amounts, ranging from small, localized populations (e.g. *Dictyota decumbens*, <sup>[81]</sup>) to wide-spread populations across several islands and coastlines along the South Shetland Islands [e.g. *Ulva intestinalis*, <sup>[81, 83]</sup>]. Four of the species (*Blidingia minima*, *Ulva intestinalis*, *Ulva compressa*, *Petalonia fascia*) are treated in the literature as introduced species <sup>[75]</sup>. For one species, introduction via anthropogenic vectors is discussed as a possibility (*Monostroma grevillei*, <sup>[81]</sup>).

Table 4. Pre-Antarctic distributions of the newly recorded Antarctic seaweeds with northern & southern latitudinal limits and number of global records from [www.gbif.org](http://www.gbif.org) and literature used for analyses. Categories based on distribution (Category I = cosmopolitan or amphiequatorial, category II = Pacific coast of North America, category III = Southern Hemisphere).

Species (Phylum – Order – Genus)	Category	Pre-Antarctic distribution	Pre-Antarctic northern limit [°]	Pre-Antarctic southern limit [°]	Number of global records	Reference
<i>Blidingia minima</i> (Chlorophyta – Ulvales – Blidingia)	I	Cosmopolitan or amphiequatorial	76.96	-54.04	793	[75, 158]
<i>Monostroma grevillei</i> (Chlorophyta – Ulotrionales – Monostroma)	I	Cosmopolitan or amphiequatorial	70.38	-40.58	505	[81]
<i>Petalonia fascia</i> (Phaeophyta – Ectocarpales – Petalonia)	I	Cosmopolitan or amphiequatorial	74.71	-54.54	1119	[81, 83]
<i>Ulva compressa</i> (Chlorophyta – Ulvales – Ulva)	I	Cosmopolitan or amphiequatorial	70.37	-51.54	1019	[81, 83]
<i>Ulva intestinalis</i> (Chlorophyta – Ulvales – Ulva)	I	Cosmopolitan or amphiequatorial	71.29	-55.21	2642	[81, 83]
<i>Callophyllis pinnata</i> (Rhodophyta – Gigartinales – Callophyllis)	II	Pacific coast of North America	60	30.43	85	[81, 177]
<i>Asteronema 62erruginea</i> (Phaeophyta – Scytothamiales – Asteronema)	III	Southern Australia, Tasmania, Argentina, Macquarie Island	-37.17	-54.61	16	[81]
<i>Cladodonta lyallii</i> (Rhodophyta – Ceramiales – Cladodonta)	III	South America, Subantarctic Islands	-42.36	-55.53	24	[81]
<i>Dictyota decumbens</i> (Phaeophyta – Dictyotales – Dictyota)	III	Macquarie Island	-54.62	-54.62	(*)	[81]
<i>Microzonia velutina</i> (Phaeophyta – Syringodermatales – Microzonia)	III	New Zealand, Subantarctic Islands, Argentina	-34.13	-54.79	47	[81]
<i>Rhizoclonium ambiguum</i> (Chlorophyta – Cladophorales – Rhizoclonium)	III	South America, Subantarctic Islands	-3.6	-54.77	22	[81]
<i>Rhodophyllis centrocarpa</i> (Rhodophyta – Gigartinales – Rhodophyllis)	III	New Zealand, South America	-35.25	-54.76	30	[81]

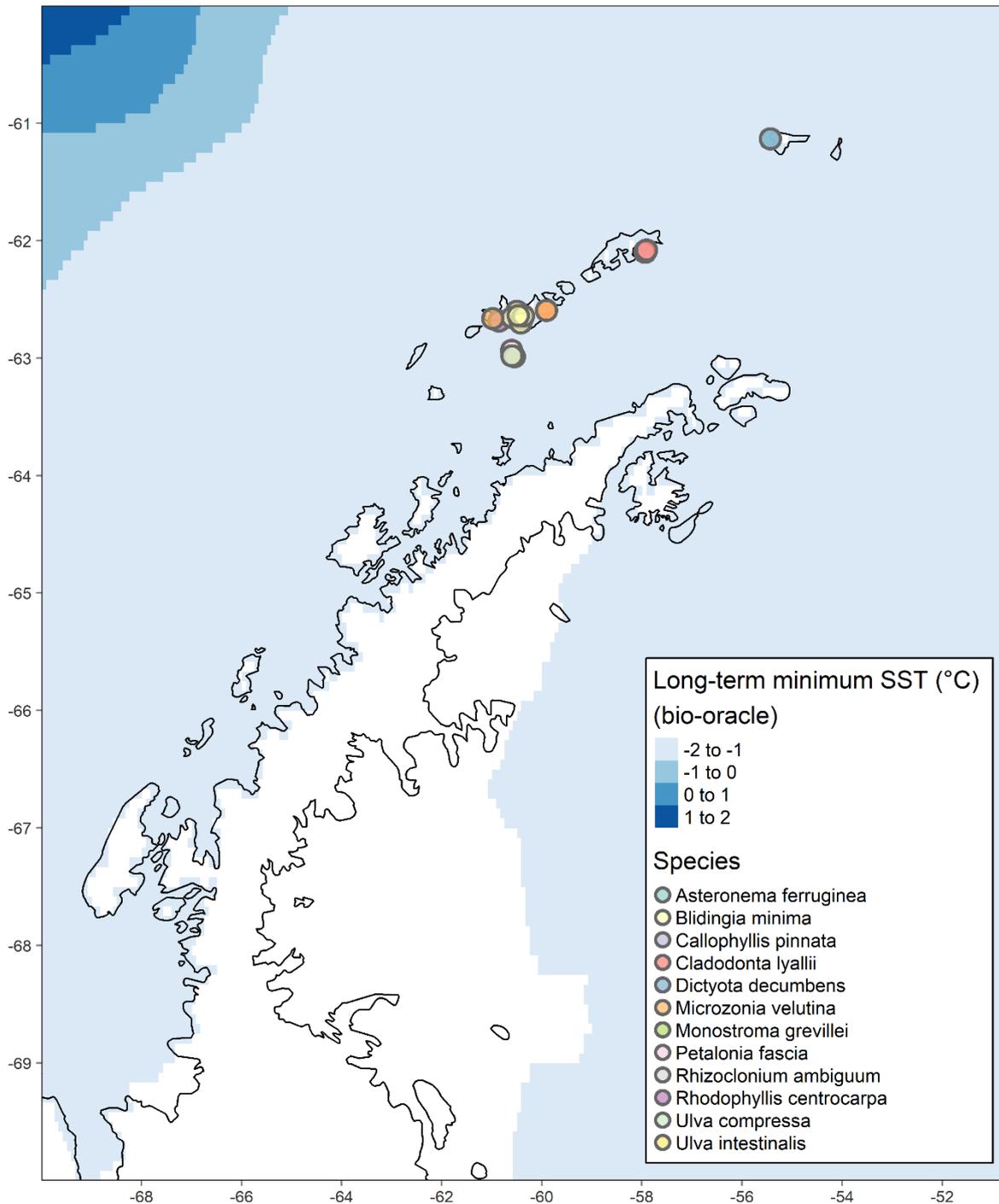


Figure 12 Locations where the novel species were reported at the South Shetland Islands (references in Table 4) and long-term minimum sea surface temperature from bio-oracle v2.0 [125].

Except for one species (*D. decumbens*), all species have well-documented distributions throughout other climatic zones in the Northern and/or Southern Hemisphere(s) (Figure 14) and we categorized them based on their pre-Antarctic distributions: Category I (cosmopolitan and amphiequatorial species) contains five species distributed throughout polar to warm-temperate or polar to tropical regions, respectively: *B. minima*, *M. grevillei*, *P. fascia*, *U. compressa* and *U. intestinalis*. Pre-Antarctic northern distributional limits in category I were between 66 and 77°N. Pre-Antarctic southern range

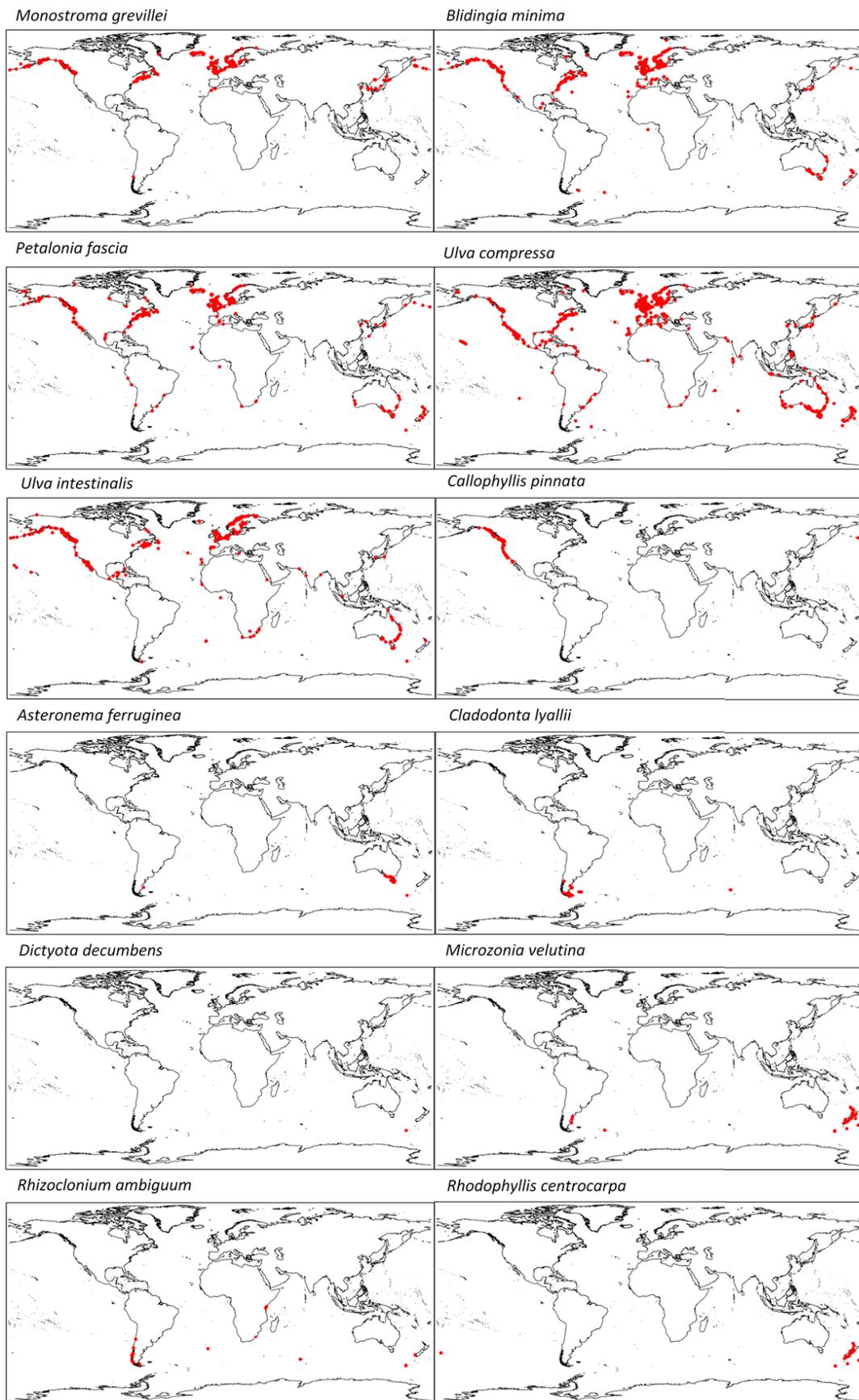


Figure 13. Pre-Antarctic distributions of all species. Records from [www.gbif.org](http://www.gbif.org) and [www.algaebase.org](http://www.algaebase.org) <sup>[169]</sup>. Pre-Antarctic data were thinned to one record per grid-cell to remove duplicates.

limits in this category are between 47 and 55.5°S. *M. grevillei* has one record at 40.6°S from Chile <sup>[178]</sup> but is otherwise only reported in the Northern Hemisphere. *B. Minima*, *P. fascia*, *U. compressa* and *U. intestinalis* are also distributed throughout the tropics, while *M. grevillei* is not known to occur in tropical regions. Category II (Pacific coast of North America) contains only one species (*Callophyllis pinnata*), which is only found along the North American Pacific Coast between 60°N and 30.4°N. The remaining species are assigned to Category III (i.e. *Asteronema ferruginea*, *Cladodonta lyallii*, *D. decumbens*, *Microzonia velutina*, *Rhizoclonium ambiguum* and *Rhodophyllis centrocarpa*). These species are distributed along temperate coasts in the Southern Hemisphere with most records along cold-temperate coasts of New Zealand, Australia, the Subantarctic Islands and South America and only a few along warm-temperate coasts, and have their pre-Antarctic southern distributional limit between 54.6 and 55.5°S (corresponding to the southern tip of South America and Subantarctic Islands). In this category, northern distributional limits are between 34.1 and 42.4°S with two exceptions: *R. ambiguum*, which is also found at 3.6°S in Kenya <sup>[179]</sup> and *D. decumbens*, which is exclusively known from Macquarie Island <sup>[180]</sup>.

#### Introduction potential

We evaluated the potential for successful introduction in accordance with the publication by <sup>[172]</sup> and assigned the following potentials to the species based on species descriptions in the literature: Category I species (cosmopolitan and amphiequatorial) are assigned a high potential for introduction due to their wide geographic distribution. Species from Categories II (Pacific coast of North America) and III (Southern Hemisphere) are assigned a very low (*C. pinnata*, *D. decumbens*) to intermediate potential based on more limited geographic distribution. However, Category III species grow in regions where, in addition to anthropogenic vectors, natural rafting (e.g. via kelps), is a possible vector for transportation to Antarctica. Thus, such regions show a higher connectivity to Antarctica and lead to a higher rating. Most species grow on artificial substrates such as ships hulls (*B. minima*, *Ulva* spp., *Dictyota* spp., *Rhizoclonium* spp.) and/or holdfasts of *Durvillaea antarctica* (*A. ferruginea*, *Petalonia* spp.) and/or *Macrocystis pyrifera* (*Ulva* spp., *Dictyota* spp., *Callophyllis* spp., *C. lyallii*). We did not find similar reports for species of the genera *Monostroma*, *Microzonia*, or *Rhodophyllis*. *D. antarctica* and *M. pyrifera* are both rafting species which are washed ashore at the South Shetland Islands and WAP, carrying attached epibionts <sup>[16, 78, 158]</sup>. Therefore, information from the literature suggests that all species except for *M. grevillei*, *M. velutina*, and *R. centrocarpa* have a high “Probability of being transported.” The categories of temperature and salinity ranges are less relevant for this study, since the species have been reported from the Antarctic region, indicating that their tolerable ranges include Antarctic conditions. Nevertheless, Category I species, in particular, are assigned high introduction potential, since they grow in habitats from the tropics to the Arctic and are, therefore, adapted to a wide range of SSTs and salinity conditions. Species in Categories II and III have more limited

distributional ranges and cover a smaller range of environmental conditions (Figure 14). In the category “Reproductive Mode,” only *A. ferruginea*, *C. pinnata* and *C. lyallii* are not evaluated due to a lack of sufficient literature on this aspect. All other species are assigned a high score, since they have the potential for asexual reproduction or reproduction via fragmentation (*Rhizoclonium* spp., *Ulva* sp.). Information on growth strategy is also sparse and mostly insufficient to reliably evaluate the species in accordance with the publication of [172]. In addition, species of the genera *Dictyota*, *Rhizoclonium*, *Ulva*, *Blidingia*, and *Monostroma* are known to be fast-growing and dominant species in other habitats. In conclusion, the species investigated in this study show an intermediate to high potential for successful introduction into new geographic areas via natural or anthropogenic vectors.

#### Niche metrics

Absolute temperature ranges and sizes of pre-Antarctic climatic niches increase with latitudinal range. Species from Category I (five species, cosmopolitan or amphiequatorial) exhibit the largest distributional and temperature ranges and have the largest niches (Figure 14, Table 5). All of them occupy sites with SSTs from -1.9°C to >30°C. Category II (*C. pinnata*, Pacific Coast of North America) and III species (six species, Southern Hemisphere) are separated geographically, but their climatic niches overlap (Figure 15). These species are not as widely distributed as species from Category I and their temperature ranges and niches are smaller, and do not extend below 0°C. Within Categories II and III, *M. velutina* has the overall lowest minimum SST of 0.3°C while the other species have pre-Antarctic lower limits ranging from 3-3.7°C. Maximum SSTs in Categories II and III range from 4°C (*D. decumbens*) to 29°C (*R. ambiguum*). Therefore, the temperature niches of all seven species from Categories II and III are extended at the lower end by 2.1 to 5.5°C when Antarctic conditions are added. In contrast, we observe no extension of absolute temperature ranges in the five cosmopolitan and amphiequatorial species of Category I.

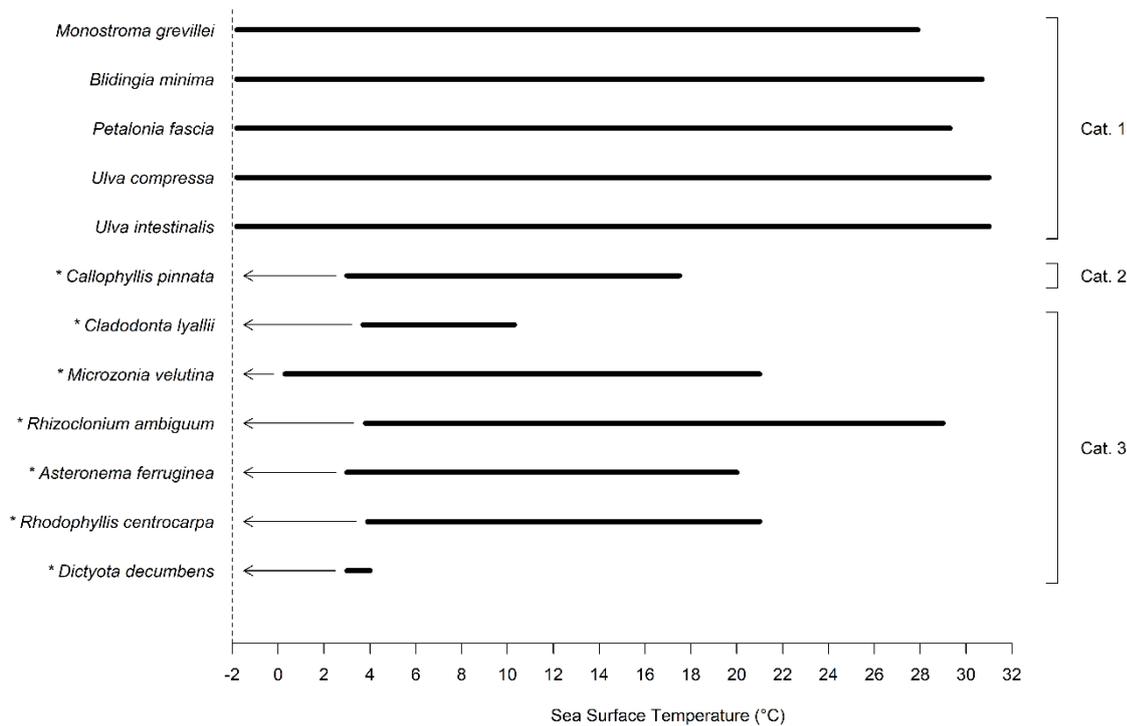


Figure 14. Absolute pre-Antarctic SST ranges (black lines) as sampled from bio-Oracle v2.0 layers with all available distributional data from www.gbif.org and the literature. Minimum sea surface temperature at the Antarctic sites is approximately -1.9°C (y-axis, dashed). Species with range extensions are marked with an asterisk and arrows indicate shift of the minimum SST. Categories based on native latitudinal distribution as in Figure 13 (Category I = cosmopolitan or amphiequatorial; Category II = endemic to Pacific coast of North America; Category III = distributed only in the Southern Hemisphere).

Table 5. Relative pre-Antarctic niche sizes per species and respective size increases. Niches here are volumes of minimum and maximum sea surface temperature data from the virtual niches. Virtual niches were built to match with the respective pre-Antarctic niches, but without sampling bias (see Methods section for details). Calculations were conducted using the “dynRB\_Vpa()” function of the “dynRB” package for R and represent “mean”-aggregation results [98].

	Species	Relative niche size without Antarctic sites	Relative niche size including Antarctic sites	Difference in relative niche size	Percentage increase in relative niche size
Cat. I	<i>Monostroma grevillei</i>	0.608862569	0.687181726	0.078	12.9
	<i>Blidingia minima</i>	0.960385456	0.986921535	0.027	2.8
	<i>Petalonia fascia</i>	0.608360130	0.714795528	0.106	17.5
	<i>Ulva compressa</i>	0.972191388	0.994561049	0.022	2.3
	<i>Ulva intestinalis</i>	0.977391961	0.994356300	0.017	1.7
Cat. II	<i>Callophyllis pinnata</i>	0.282159610	0.727445728	0.445	157.8
Cat. III	<i>Cladodonta lyallii</i>	0.159983510	0.563450574	0.403	252.2
	<i>Microzonia velutina</i>	0.633667207	0.885464204	0.252	39.7
	<i>Rhizoclonium ambiguum</i>	0.910290667	0.986724482	0.076	8.4

<i>Asteronema ferruginea</i>	0.323343954	0.866235802	0.543	167.9
<i>Rhodophyllis centrocarpa</i>	0.521627662	0.883306074	0.362	69.3
<i>Dictyota decumbens</i>	0.009891661	0.511214360	0.501	5068.1

The cosmopolitan and amphiequatorial species do not extend their absolute temperature range when Antarctica is included, but summer temperatures at the Antarctic sites are much lower than in their pre- Antarctic ranges. Given the combination of winter and summer SSTs, the Antarctic sites are climatically not contained within any of the species' pre-Antarctic niches and overlap values are close to zero. Only the pre-Antarctic range of *P. fascia* slightly overlaps with the Antarctic site as it thrives at high Arctic locations with winter SSTs of -1.9°C and summer SSTs of around 2°C. In all other species, at pre-Antarctic sites with winter temperatures <0°C, summer SSTs are 4.3 to >20°C higher than at the Antarctic sites. Thus, Antarctic and pre-Antarctic habitats are separated climatically despite comparable low temperature extremes (Figure 16). Although the absolute temperature ranges are not extended by inclusion of Antarctic records, niches are still extended by lower summer SSTs.

Percentage increases in niche size are highly heterogenous among species. Increases are on average smaller for cosmopolitan and amphiequatorial species (+1.7% to +17.5%) than in Categories II (+157.8%) and III (+8.4 to + 252.2%, with one extreme case, +5,068.1% in *D. decumbens*, for which the pre-Antarctic niche makes almost no contribution to the Antarctic-inclusive niche size). Pre-Antarctic niche sizes in Category I are much larger than in the other categories due to the very wide occupied distributional and environmental pre-Antarctic ranges. Here, absolute temperature ranges already include Antarctic winter temperatures in the pre-Antarctic geographic ranges. Therefore, the addition of Antarctic environmental conditions does not contribute substantially to the absolute niche size and causes only minor relative increases. In Categories II and III, with more limited distributions, pre-Antarctic niches are smaller and Antarctic conditions are out of the environmental space. Therefore, additions lead to a higher percentage increase. Still, for all species, irrespective of the magnitude of the increase, addition of Antarctic environmental conditions to the environmental niche space opens a new climatic ecoregion with previously unoccupied climatic conditions as potential suitable range.

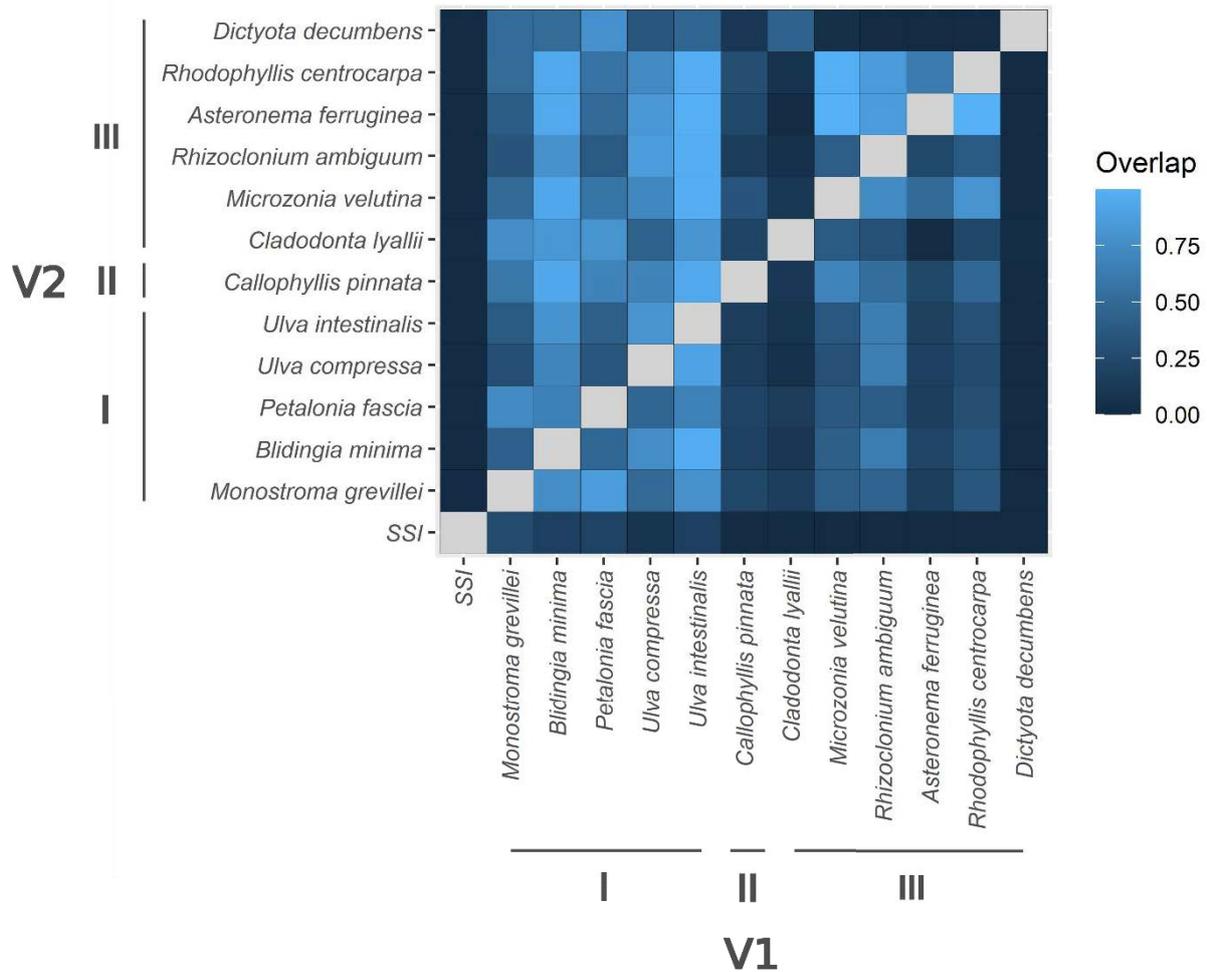


Figure 15. Niche overlaps between pre-Antarctic niches and Antarctic sites (SSI = South Shetland Islands). V1 = Volume 1, V2 = Volume 2. Read like this: *D. decumbens*' niche (as V1) does not contain any other species' niche (V2) and has therefore overlap values around 0 along the y-axis but is contained within the niches of most other species and has therefore higher overlap values along the x-axis<sup>[98]</sup>. Data included: Minimum and maximum sea surface temperature data from the pre-Antarctic virtual species' niches. Aggregation method = "mean".

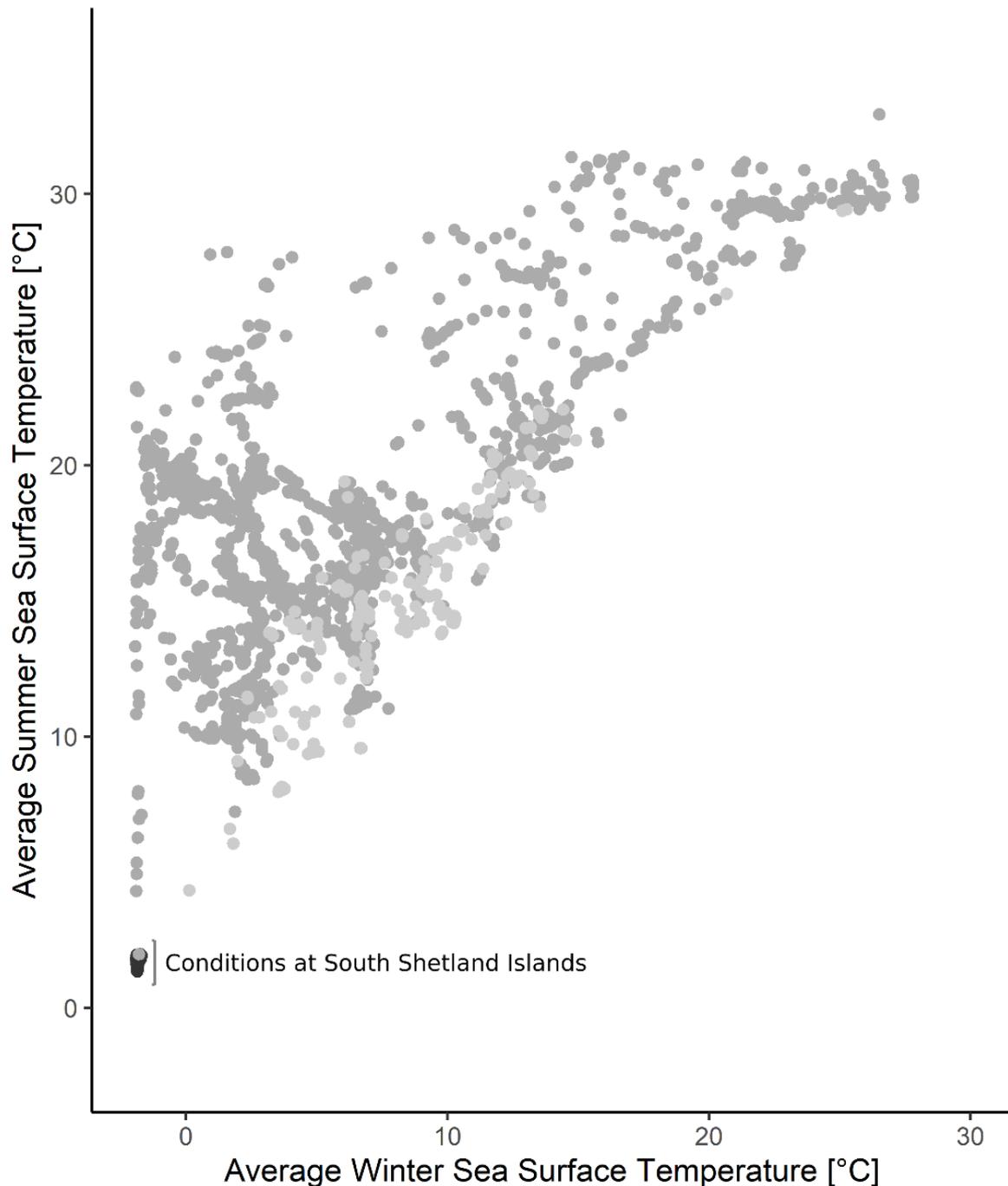


Figure 16. Winter and summer sea surface temperatures at pre-Antarctic and Antarctic occurrence sites of all species. Dark grey = species of category I (cosmopolitan & amphiequatorial), light grey = species of categories II (Pacific coast of North America) and III (Southern Hemisphere), black = conditions at Antarctic sites (South Shetland Islands). The dark grey dot within the range of the Antarctic sites belongs to *Petalonia fascia*.

### Discussion

Twelve seaweed species have been reported in the literature as new additions to the Antarctic flora [75, 81, 83, 158, 159]. Our study indicates that some of these species are, in fact, non-native (see below). Under this assumption, species from the Southern Hemisphere in particular extend their realized niches during introductions to Antarctica. Our results have implications for invasion forecasting and conservation biology. Due to the climatic mismatch of pre-Antarctic and Antarctic sites, correlative ENMs are not appropriate to fully describe the invasive potential of potential Antarctic invaders (see

<sup>[157]</sup>). In our case study, we explicitly used a model system with unconnected donor (pre-Antarctic) and recipient (Antarctic) sites, characterized by a strong latitudinal gradient in environmental conditions and a high degree of isolation via a geographic barrier (the Antarctic Polar Front). The non-native species crossed the Antarctic Polar Front, thereby dramatically extended their latitudinal range southward, and settled in a region with extremely harsh environmental conditions previously not occupied in their distributional ranges.

In all species, except for *P. fasciata*, the realized niches are extended when Antarctica is added to the distributional range. In most species, the absolute temperature ranges are extended, but also in species which already thrived under extreme low conditions in their pre-Antarctic ranges, the summer SSTs are considerably higher in the pre-Antarctic ranges than at Antarctic sites. Only *P. fasciata* is reported from high Arctic sites where both extreme low winter as well as low summer temperatures prevail and match conditions at the Antarctic sites. Classic works on seaweed biogeography point out that not only lethal low winter and high summer temperatures define distributional limits, but also that summer temperatures have to be adequate for growth and reproduction <sup>[26, 132, 181]</sup>. Hence, taking into account the combination of extreme low winter and low summer temperatures, we observe extensions of realized niches in all species except *P. fasciata*. Regions with SST conditions comparable to the Antarctic are only found in the high Arctic. We compared data on Arctic and Antarctic sea-ice concentrations from the years 2003 – 2014 (corresponding to the data time frame of the SST raster layers; <sup>[182]</sup>) to evaluate the availability of settling substrate and found that in large parts of the Arctic, sea ice is much more prevalent along the coasts than at the sites at the South Shetland Islands. As an exemplar we compare the North American Arctic and the Antarctic sites in Box 1. At the South Shetland Islands, many more days are ice free per year than in the North American Arctic and relatively ice-free sites in the Arctic are characterized by SST conditions not comparable to Antarctic sites. Hence, it is possible that the higher accessibility of the SSI allows species to colonize niche space beyond the North American Arctic conditions.

Some of the niche extensions are very small, especially for already widespread species. In the methodology used here, the maximum niche space is defined by all the included data <sup>[98]</sup> and widespread species naturally experience small relative niche extensions by lowering the occupied minimum summer SST by a few degrees Celsius. Still, these minor increases in relative niche size have large ecological implications, since a new ecoregion will become classified as suitable for the respective species. Thus, our results have implications for invasion forecasting and conservation biology. Due to the climatic mismatch of pre-Antarctic and Antarctic sites, correlative ENMs are not appropriate to fully describe invasive potential of these species <sup>[157]</sup>. The observed niche extensions are probably a result of non-equilibrium distribution in the pre-Antarctic ranges, especially in species which occur as natives in temperate zones of the Southern Hemisphere. Here, the southernmost pre-Antarctic

distributional limit was around 55°S. This latitude matches the southern tip of South America and the Subantarctic Islands. Unlike in the Northern Hemisphere, there is no continuous coastline between temperate and polar regions in the Southern Hemisphere, while tropical and Arctic regions in the Northern Hemisphere are connected via continuous coastlines and stepping stones (Iceland, Labrador, Greenland). These connections allow migrations either via passive dispersal or via other organisms, even against currents and, in theory, over the whole tolerable environmental range of species [26]. In contrast, in the Southern Hemisphere, the APF and large gaps between temperate and polar continental masses act as a dispersal barrier between temperate zones and Antarctica [16]. Hence, in the Southern Hemisphere, species are not necessarily restricted by adverse environmental conditions but perhaps simply by the lack of settling substrate, leading to failure to fill the fundamental niche at the lower end of the suitable temperature range [183]. Under this assumption, correlative ENMs are predestined to be incomplete and to underestimate suitable ranges of southern species in the climatically non-matching habitats of Antarctica [93, 157, 184].

The results from our scenario analysis indicate that potential cold-tolerant invaders may not only originate from climatically matching polar regions, but may also originate from temperate regions of the Southern Hemisphere. [82] reported this for the mussel *Mytilus cf. platensis*. Like some species in our study, *M. cf. platensis* is native to South American coasts in Southern Patagonia and migrated to the SSI. These regions do not match climatically, but the species successfully recruits in the Antarctic environment, regardless of considerably lower winter and summer temperatures than in their native range in Southern Patagonia. In addition, [78] reported that a non-Antarctic bryozoan, *Membranipora membranacea*, has established a population under relatively mild water conditions in a caldera at Deception Island, but the authors suspect that it may already be adapted to Antarctic cold-water conditions and will spread beyond Deception Island in the future. *M. membranacea* has a global invasion history and the authors reported it as hitchhiking on kelp rafts of *M. pyrifera* and *D. antarctica* to Antarctica.

It is difficult to clearly identify non-native species among the Antarctic seaweed flora without further investigations (e.g. molecular analyses). Due to the remoteness of Antarctica and harsh climatic conditions which make expeditions a demanding endeavor, there is only incomplete information available on Antarctic biodiversity. The authors of the cited studies emphasize that the reported species might well have been overlooked in previous sampling campaigns. However, studies on Antarctic seaweed biodiversity date back to 1817 [75] and [168] reported 124 known seaweed species for Antarctica with reference to numerous macroalgal community analyses. The focus of Antarctic seaweed biodiversity studies has been on the SSI, South Orkneys and the Western Antarctic Peninsula [168, 185], making these areas of Antarctica the most studied ones in this respect. Hence, although most of the Antarctic continent is clearly understudied, the new species have been reported from sites with

a long history of seaweed biodiversity research. At the same time, these sites are known to be target sites of natural and anthropogenic transportation vectors from other regions to Antarctica <sup>[16, 71, 78]</sup> and we have shown that the species have traits which indicate an intermediate to high potential for successful introductions. In addition, the species are conspicuous and well-known and have well-documented distributions in other regions (especially *U. intestinalis*, *U. compressa*, *M. grevillei*, *B. minima*, *R. ambiguum*, *D. decumbens* and *P. fascia*). Therefore, given the long history of seaweed research at the South Shetland Islands and Western Antarctic Peninsula by pioneering seaweed experts such as Skottsberg, Kylin, Harriot and Gain at the turn of the last century and in the second investigation period of Antarctic seaweeds 55 to 80 years ago by Levring, Neushul, Zaneveld, Moe, Delépine, Lamb and Zimmermann, we have to assume that (among) these species are truly neophytes (C. Wiencke, personal communication), which have been either naturally or anthropogenically introduced. Examples exist where species have successfully been introduced to Antarctica from regions where the climate does not match Antarctic conditions. From this perspective it is imperative to take a precautionary point of view and consider that seaweeds might have been successfully introduced to Antarctica as well.

In future studies, other methods next to correlative ENMs should be considered to assess species' invasion potential for Antarctic habitats. Fundamental niches of species, and hence adaptations to certain environmental conditions, can be conserved over evolutionary timescales <sup>[26, 148-150]</sup>. It may, therefore, be useful to include distributional data from higher taxonomic levels in ENMs for distribution modelling to fill gaps in non-equilibrium data <sup>[186]</sup>. In our study, the genera *Monostroma* and *Ulva* were already distributed in Antarctica and species of the genera *Callophyllis* and *Rhizoclonium* settle at sites with minimum SSTs of -1.9°C, hinting at the cold tolerance of the species included here. Inclusion of this kind of information might prove to be useful to fill knowledge gaps on fundamental but not realized niches and suitability of habitats for potential invaders <sup>[148]</sup>. Further, experimentally tested temperature tolerances could inform about fundamental niches in a mechanistic approach <sup>[14]</sup>. Experimentally-tested temperature tolerances are available for many species in the literature (e.g. <sup>[187]</sup>). However, it is important to note that temperature tolerances of seaweeds can vary between populations and species are not a homogenous entity in this respect <sup>[188]</sup>. Still, such data could be useful to estimate how many Southern Hemisphere species are adapted to extreme cold conditions and could pose an invasion threat for Antarctica under present-day or future conditions. Next to temperature tolerance, adaptation to extremely variable light conditions will have to be addressed. Light availability will be a crucial factor in forecasting suitability of habitats at higher latitudes for photoautotrophic organisms such as seaweeds, where photoperiod and temperature conditions play an important role for growth and reproduction <sup>[26]</sup>. The SSI are situated north of the polar circle and, therefore, do not have phases of polar night in winter. Still, light follows strong seasonal variations with around 5 hours

to 20 hours of sunlight, depending on season. In polar areas, incoming light is further reduced by occurrence of ice, posing a challenge to seaweeds, and polar night and harsher environmental conditions might prevent further spread of non-native species beyond the SSI. Nonetheless, the SSI might serve as an entry point for additional non-native species<sup>[70]</sup>. Future introductions of land-bound (e.g. intertidal seaweeds) and terrestrial species across the APF to Antarctica might coincide with sudden large latitudinal range extensions and hence extensions of realized niches. It appears likely that non-native species only need vectors to cross the APF and fill their fundamental niches in Antarctic geographic and environmental space. Ongoing climate change will further increase the suitability of Antarctic habitats for non-Antarctic species via increased temperatures. In addition, reduction of ice-cover and -scouring in the intertidal will make more habitat available to native and non-native species<sup>[16, 41, 161]</sup>. Therefore, the invasion risk of Antarctica should not be underestimated<sup>[189]</sup> and invaders should not only be expected from climatically matching regions. Climate change is often seen as increasing the likelihood of successful invasions, and it is generally assumed that species from climatically similar regions are more likely to become successful invaders (e.g.<sup>[71]</sup>). However, already under present day conditions, temperate species might pose a threat to the Antarctic marine environment.

### Acknowledgements

We wholeheartedly thank Christian Wiencke, Gunnar Spreen and Christian Melsheimer for their advice and support on Antarctic seaweed biodiversity and polar ice remote sensing. This study was funded by the Priority Program on Antarctic Research of the Deutsche Forschungsgemeinschaft (Schwerpunktprogramm 1158 Antarktisforschung), Project Number DFG Bi772/17-1.

### Data accessibility

The original gbif dataset used for this study can be found at: <https://doi.org/10.15468/dl.hbaaag> (www.gbif.org, 04 June 2020). The modified and completed distributional dataset can be requested from the corresponding author.

### References

*Moved to the comprehensive reference list at the end of this thesis.*

## S1 - Development of ice-maps

### Box 1. Sea-ice prevalence

We here provide exemplar maps for sea-ice prevalence in the North American Arctic and at the South Shetland Islands and Western Antarctic Peninsula. For these maps, we summarized daily sea ice concentration data for the years 2003 – 2014, except 2011 due to incompleteness of data for this year. This period overlaps with the bio-oracle sea surface temperature layers which cover the years 2000 – 2014. Daily maps for sea ice concentration in the Arctic and Antarctic regions were downloaded from <https://seoice.uni-bremen.de/start/> (Spreen et al. 2008). For each day, a pixel with concentration  $\geq 50\%$  was assigned as ice-covered,  $< 50\%$  as ice-free. For each year, the total number of ice-free days per year was counted and averaged over the included years. Coastal pixels rather show overestimations of ice cover due to technical reasons, hence, actual ice concentrations might be lower than shown in the maps (G. Spreen, personal communication).

Other Arctic records of the investigated species were from sites where ice concentrations are less or similar to the conditions in the North American Arctic (e.g. Iceland, Norway, western Svalbard). Hence, only the North American Arctic is shown here exemplarily.

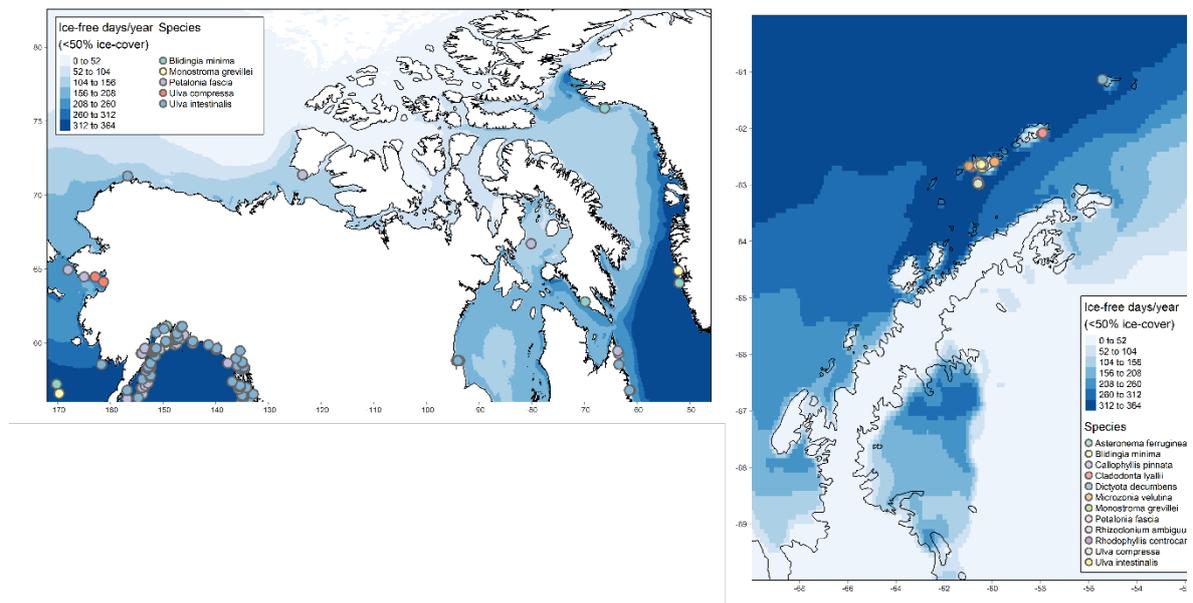


Figure 6. Comparison of ice-prevalence in the North American Arctic and at the South Shetland Islands. Data is averaged over the years 2003 – 2014, except for the year 2011. Data source: <https://seoice.uni-bremen.de/start/> (Spreen et al. 2008).

## Research chapter 3 – publication 3

Title: **Patterns in thermal niche equilibria in global seaweed distributions** (*in preparation for submission*)

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### Abstract

Thermal niches are central in biogeography, and in seaweeds distribution patterns are largely explained by temperature preferences. Seaweeds are important intertidal species which shape intertidal communities throughout all marine realms but are under threat via global warming, and knowledge of tolerance thresholds is therefore important to assess impacts of global warming on seaweed distributions. Here, we compared the realized and fundamental niches of 126 seaweed species to elucidate how well fundamental thermal tolerance limits explain the limits of distribution. Further, we describe patterns of non-equilibrium as a function of latitudinal range. In 40% of the species, there was an underfilling of the thermal niche at the lower survival threshold (LST) and in 43% of the species, there was an underfilling of the upper survival threshold (UST) (i.e. the thermal niches were narrower than the fundamental niches). In addition, 3 of the 126 species had distributions in areas with colder average minimum sea surface temperatures than their reported cold-tolerances, while 23 species had distributions in areas with average maximum sea surface temperatures higher than their reported upper survival temperature (i.e. they showed an overfilling of their fundamental niches). Further, the state of non-equilibrium at the LST was dependent on maximum distributional latitude (i.e. poleward distributional limit), while there was no such relationship between the UST and the equatorward distributional limit. Our analyses yield two main findings: First, that the match between fundamental thermal limits and realized distributional limits may be lower than in other marine organisms and that deviations may be large. This indicates that responses towards climate change might be highly variable in seaweed species. Second, distributional patterns & realized conditions and lower survival temperatures are rather independent. These findings are important for the assessment of climate change effects on seaweed distributions, and for the identification of suitable distributional ranges, especially in the light of climate change-induced higher suitability of polar environments for non-polar seaweed species, and thus invasion biology. Finally, nearly 60% of the species had populations which are close to or beyond their reported upper survival limits, and are thus probably under threat of eradication by elevations of sea surface temperatures.

Main conclusions:

- Distributional ranges show deviations from fundamental thermal tolerances
- Underfilling and overfilling of thermal niches are common in seaweeds
- Non-equilibrium at cold-tolerance increases with reduction in latitudinal distributional limit, while equilibrium at heat tolerance does not follow a distributional pattern, indicating independence of lower survival temperatures and biogeographic patterns
- Nearly 60% of the species have distributional limits at or beyond their upper thermal tolerance limits and are thus probably threatened by global warming

Keywords: climate change, ecology, evolution, heat waves, invasion, macroalgae, niche conservation, physiology, range shift, thermal tolerance limits

## Introduction

Temperature is a main predictor of species distributions, and global warming is a threat to global and diverse populations, causing range shifts and having profound effects on community structures and biodiversity in both terrestrial and marine environments [5, 99, 190-192]. Thus, temperature tolerances play an important role in explaining and forecasting effects of a changing climate on the distribution of species (e.g. [192]). Thermal niches can be reconstructed either from correlation analyses of known distributions and environmental data via ecological niche models (ENMs) [1], or via experimental testing [14]. However, non-equilibrium distributions (i.e. distributions where the geographic extent of a species' distribution does not match the potential suitable range as predicted by the estimated niche extents [1, 193]) are widespread in species [96]. Thus, forecasting of suitable habitats and effects of temperature change are subject to uncertainty [1]. In addition, both approaches have methodological limitations in applicability and transferability, the former tend to underestimate niches, while the latter tend to overestimate realized niches [95]. Attempts have been made to describe and explain the state of equilibrium in species distributions ([96] and references therein). E.g., [96] did an analysis of how well thermal tolerances and geographic range extent match in marine and terrestrial ectotherm species and concluded that in marine species thermal tolerances and geographic range extents match well, and that therefore species distribution models (SDMs) will yield rather accurate predictions of range shifts under changing climate. Further, in [97], they showed that especially mobility explains how fast species track climate change, with highly mobile species being faster in changing their ranges. However, (marine) primary producers did not play a major role in these studies.

Therefore, in this study, we will focus on marine seaweeds. Seaweeds are highly important ecosystem engineers and provide invaluable ecosystem services to coastal marine habitats [6]. At the same time, seaweed populations are facing major threats by changing climate, leading to loss of habitat and local

extinctions <sup>[6, 7, 42]</sup>. Further, seaweed species (*Undaria pinnatifida*, *Caulerpa taxifolia*) are ranked among the 100 worst invasive species worldwide and can have disastrous impacts on recipient ecosystems, making seaweeds a highly relevant group of study organisms <sup>[53, 59]</sup>. Unlike animals, seaweeds are not able to actively migrate, but are restricted to short-range dispersal via spores (usually in the range of meters, <sup>[38]</sup> and references therein), transport via independent vectors or occasional long-range rafting <sup>[194]</sup>. Thus, the proposed match of distributions and underlying thermal adaptation, have to be tested for seaweeds, since here, the generalized set of the possibilities “adaptation / migration / extinction” in response to climate change <sup>[195]</sup> is lacking the possibility of active migration as opposed to animals with mobile life-history stages. Since sea surface temperature and thermal niches are of major importance to describe global seaweed distributions <sup>[26]</sup>, information on temperature requirements and habitat suitability is central in the assessment of effects of climate change on distribution patterns <sup>[39, 95]</sup>, or in the context of invasion-biology to forecast invasive potential of non-native species <sup>[105]</sup>. It is important to understand to what degree seaweed distributions match their fundamental niches because only before this background, expectations can be formulated how changing temperatures will affect distribution patterns. This assessment is also relevant for the forecasting of seaweed invasions, as it describes patterns in niche-equilibrium which might help to better predict suitability of recipient habitats <sup>[105]</sup>.

Here, we compare experimentally tested lower and upper survival temperatures (LST and UST, respectively) of 126 species of marine macroalgae with distributional data. The comparison of experimental survival limits and distributional data will allow us to test how well fundamental temperature tolerances predict distributions, and how wide-spread non-equilibrium distributions are. This will help to understand patterns in state of equilibrium and will be important for future studies to predict effects of climate change on seaweed distributions, and to estimate uncertainty in habitat suitability predictions. Further, we will test, how non-equilibrium states are distributed across latitudes and how variable survival temperatures and realized thermal niches are across species. In addition, our analyses provide information on how many of the investigated species are thriving at the edge of their tolerable ranges and might therefore be threatened by global warming and extreme climate events such as marine heatwaves <sup>[42, 43]</sup>.

## Materials and methods

### Collection of experimental data for fundamental niche identification

We did a literature search with google scholar and followed reference lists of included studies to collect experimentally determined upper and lower survival temperatures from the respective literature on seaweed biogeography. Survival temperatures were the temperatures beyond which death or extensive necrosis to tissues appeared and no recovery was possible under optimal conditions. We included only data from tests with exposure times of at least 1 week and only when the test material

was tested submerged in medium (i.e. not under air-exposure as occasionally reported for freezing-tolerance experiments). Light intensity in the reported experiments was low (in the majority  $\leq 40 \mu\text{mol m}^{-2} \text{ s}^{-1}$ ). In cases where the taxonomic status changed and the current identity of the species was not clear, data were not further included. Data from studies where a limit was reported but the tested intervals or a graphical presentation of the experimental results was missing was also not included because in such cases it was not possible to comprehend the derivation of the threshold temperature. If an interval for the survival limit was reported (e.g. the species died at  $0^\circ\text{C}$  but survived at  $3^\circ\text{C}$  with no tested temperatures in between), the mean was selected as lower survival temperature ( $1.5^\circ\text{C}$  in this example). In some publications, the authors did not test below  $0^\circ\text{C}$  but reported that the tested material still showed photosynthetic activity at  $0^\circ\text{C}$  (e.g. <sup>[196-199]</sup>). In such cases, we arbitrarily chose  $-1^\circ\text{C}$  as lower survival temperature to account for the limitation in experimental information.

If there were different values for LST and/or UST available, e.g. for specimens from different sampling locations or life-history stages, we used the overall lowest LST and overall highest UST to define the maximum suitable range of a species (even if then the UST and LST were then from different populations).

#### Collection of distributional data for realized niche identification

To identify the current realized niches, we used distributional data to extract the minimum and maximum sea surface temperatures for each species from bio-oracles SST layers (see below). Distributional data were downloaded from [www.gbif.org](http://www.gbif.org) (GBIF.org (14 June 2021) GBIF Occurrence Download <https://doi.org/10.15468/dl.d287a7>; GBIF.org (30 March 2021) GBIF Occurrence Download <https://doi.org/10.15468/dl.t94mm6>). For every species, we used the current (September 2020 to June 2021) taxonomy as on [www.algaebase.org](http://www.algaebase.org) <sup>[169]</sup>. Therefore, some species appear here with different names than in the original publications and might have been moved to another genus. For each species, we used the “Detailed distribution with sources” section on [algaebase.org](http://algaebase.org) as a reference for additional distributional data, to check for completeness of gbif data and to verify edge populations (i.e. distributional records which represented occurrences with the minimum or maximum observed SST). If [algaebase](http://algaebase.org) or [gbif](http://gbif.org) data did not agree with the respective other, we searched with google scholar for additional reports and complemented the dataset with missing data or references. Dubious records were excluded from the [gbif](http://gbif.org) dataset, such as wrong coordinates (e.g. latitude 0, longitude 0), single data points far outside the rest of the distributional range and not being covered with reliable evidence or support from other resources, or locations of museums rather than actual occurrences. In addition to the distributional minimum and maximum SST values, we extracted the minimum and maximum SSTs for the reported sample locations to check for correlations between the STs and the conditions at the sample locations.

### Sea surface temperature data

We sampled sea surface temperatures (SST) data from the long-term minimum and maximum SST raster layers from bio-oracle v2 <sup>[125]</sup>. These layers provide the minimum and maximum of the coldest and warmest months, respectively, averaged over the years 2000-2014 in resolution of 5 arc minutes. SST layers are derived from satellite and *in situ* data and have an average error of 0.39°C <sup>[125]</sup>.

### Precision of experimental data and definition of non-equilibrium distributions

References for the classification of distributions as representative of under- or overfilling are scarce (but see <sup>[96]</sup>), and to our knowledge there is no definition of a certain threshold in deviation from the fundamental temperature limits as being representative of a non-equilibrium distribution in seaweeds (niche underfilling refers to a state where the realized thermal niche is narrower than the fundamental niche, niche overfilling refers to the opposite (e.g. <sup>[96]</sup>). Thus, we defined a threshold based on the precision of experimental and environmental data. To do so, we first identified the precision of the experimental data from each included reference: Usually, survival limits were tested in experiments with temperature steps of between 1 and 5°C (see literature references in Table S1). Here, as precision, we used the tested temperature interval closest to the reported survival limit. For example, if a LST of 1°C was reported and the next lower tested temperature step was 0°C, then the precision is set as 1°C. However, for minimum SST there are physical limits as the seawater temperature cannot drop below -1.9°C. Thus, if a LST of -1.5°C was reported, and no lower temperature was tested, we assigned a precision of 0.4°C. We did such a precision estimation for every included LST and UST and the average precision of the LST was 0.96°C (SD = 1.14) and for the UST 1.98°C (SD = 1.03), both being larger than the standard error of the SST layers (see below). Corresponding to the larger of the values, we used a threshold of ±2°C around the survival temperatures for the classification as non-equilibrium distributions. We compared the survival temperature limits with the realized temperature limits as sampled from the bio-oracle SST layers, and deviations of more than 2°C from the survival thresholds were counted as under- or overfilling of the fundamental thermal niche. In general, we set LSTs lower than -1.9°C to this value to restrict the fundamental survival temperatures to an ecologically meaningful range.

### Statistical analyses

We fitted linear(mixed effects) models with and without reference as a random effect, respectively, with functions from the R package “lme4” <sup>[200]</sup>. Reference was included as a random effect to account for methodological differences <sup>[96]</sup>. We tested the significance of random effects by fitting one model with and one without the random term and compared the models in a likelihood ratio test via `anova()` from R “stats” <sup>[123]</sup>. We tested for relationships of *LST ~ SST at sampling location*, *UST ~ SST at sampling location*, *realized minimum SST ~ LST*, *realized maximum SST ~ UST*, and *state of equilibrium ~ latitude*. Prior to analyses, outliers

were removed (threshold for exclusion: 25<sup>th</sup> percentile – 1.5\*interquartile range and 75<sup>th</sup> percentile + 1.5\*interquartile range, respectively). Residuals were inspected visually for patterns, and for model selection we used the AIC. For the relationship *realized minimum SST* ~ *LST* we tested for breakpoints in the data with the segmented()-function from the “segmented” package for R [123, 201] and fitted models to the resulting data sections. All analyses were done with the software R (version 4.1.2) [123]. Additional R-packages used for the data analyses and visualizations in this work included “raster” [128], “tidyverse” [175], “car” [202], and “ggplot2” [175] for R [123].

## Results

Our final dataset included survival temperatures for 126 species from 94 genera from 22 studies [132, 187, 196-198, 203-219] (Table S1). In all cited studies, experimental exposure periods varied from one week [210] to three months [211]. Test material included “algal material”, which refers to spores, fragments of sporophytes, entire sporophytes, gametophytes or a combination. Most reported experiments were conducted with cultured material ( $n_{\text{species}} = 97$ ), but some authors directly applied field material to the experimental conditions ( $n_{\text{species}} = 29$ ). Test material was mostly collected from cold- to warm-temperate sites ( $n = 119$ ) with fewer samples from tropical ( $n = 4$ ) or polar regions ( $n = 4$ ), but the species had distributions throughout all marine biogeographic realms (*sensu* [220]). For more details on test material, sampling site, precise distributional and experimentally determined temperature limits and literature references, see Table S1 in the Appendix.

After we limited LST to the ecologically meaningful value of  $-1.9^{\circ}\text{C}$ , 88 red green and brown species from 65 genera had an LST  $<0^{\circ}\text{C}$  (see appendix for details in which species this was done). 38 species from 32 genera had an LST of  $\geq 0^{\circ}\text{C}$  (maximum =  $15^{\circ}\text{C}$ ). The genera *Alaria* Greville (2), *Ceramium* (3), *Cladophora* (10), *Desmarestia* J.V. Lamouroux (4), *Dictyopteris* (2), *Fucus* L. (3), *Laminaria* J.V. Lamouroux (7), *Lessonia* Bory de Saint-Vincent (3), *Phycodrys* Kützing (2), *Polyneura* (2), *Saccharina* (2), *Saccorhiza* Bachelot de la Pylaie (2), and *Ulva* L. (3) were represented by more than one species (number of species per genus in brackets). Upper survival temperature limits were overall more variable than LSTs and ranged from  $14^{\circ}\text{C}$  (*Ballia callitricha*, *Phycodrys austrogeorgica*) to  $35^{\circ}\text{C}$  (*Cladophora* spp., *Grinnellia americana*). The overall variance among LSTs was 14.06, which was significantly different from the variance among USTs 23.76 (levene test:  $F = 23.845$ ,  $p < 0.001$ ; see also Figure 17). The variance in distributional minimum SSTs in species was 28.47 and in maximum SSTs 25.8, with both being statistically equal. Variances among LSTs and among realized minimum SSTs were significantly different from each other (levene test:  $F = 11.868$ ,  $p < 0.001$ ), while variances among USTs and realized maximum SSTs were equal (levene test:  $F = 0.3533$ ,  $p = 0.5528$ ).

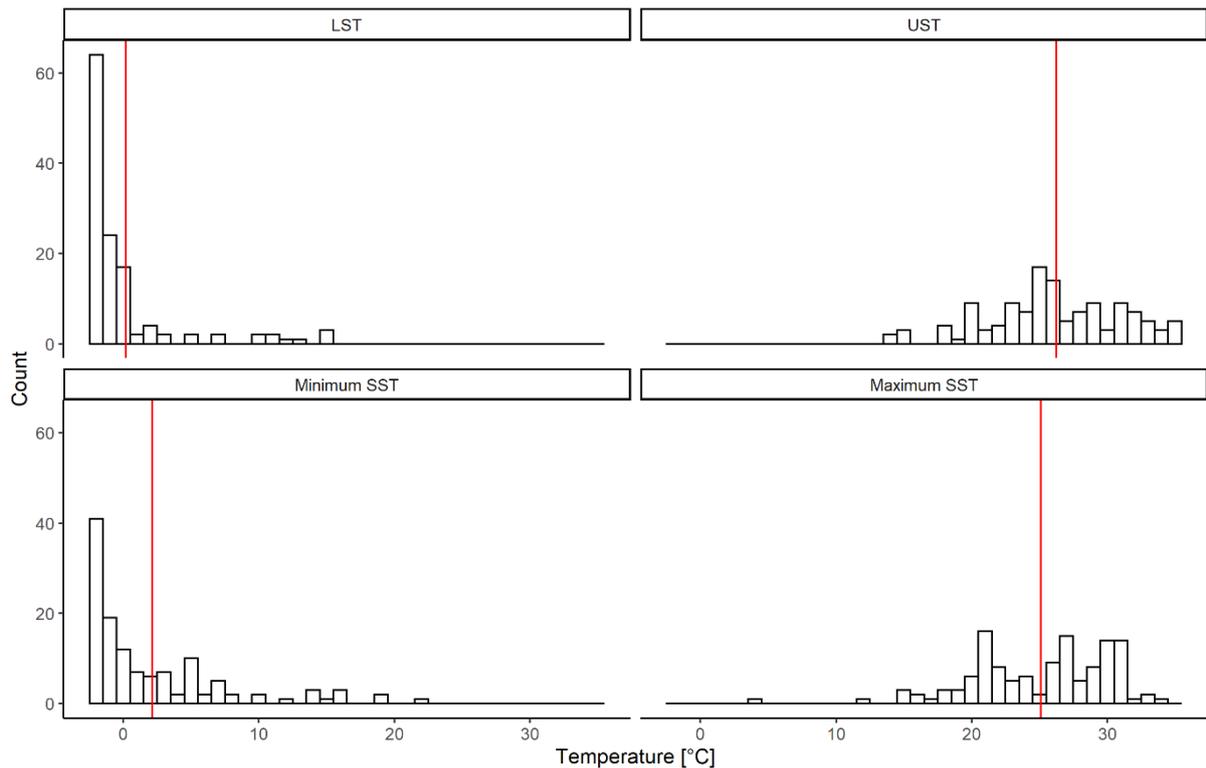


Figure 17. Histograms of LST, UST, minimum and maximum realized SST in °C. Variances of LST and Minimum SST were significantly different, while UST and Maximum SST had equal variances (see text). Red lines represent means per panel.

Absolute distributional temperature ranges were highly variable in size, ranging from 5.9°C in *Phycodrys austrogeorgica* (distributed in subantarctic Islands to Antarctica) to over 30°C in cosmopolitan species which were distributed throughout cold-temperate and polar environments and the tropics. The physiological survival ranges were 15°C (*Dictyopteris justii*) to 37°C large (*Cladophora* spp.). At the LST, 3 species showed an overfilling, 51 species equilibrium and 72 species a state of underfilling (Figure 18). At the UST, 77 species showed an under- (n = 54) or overfilling (n = 23) of their fundamental niche and 49 species were in equilibrium.

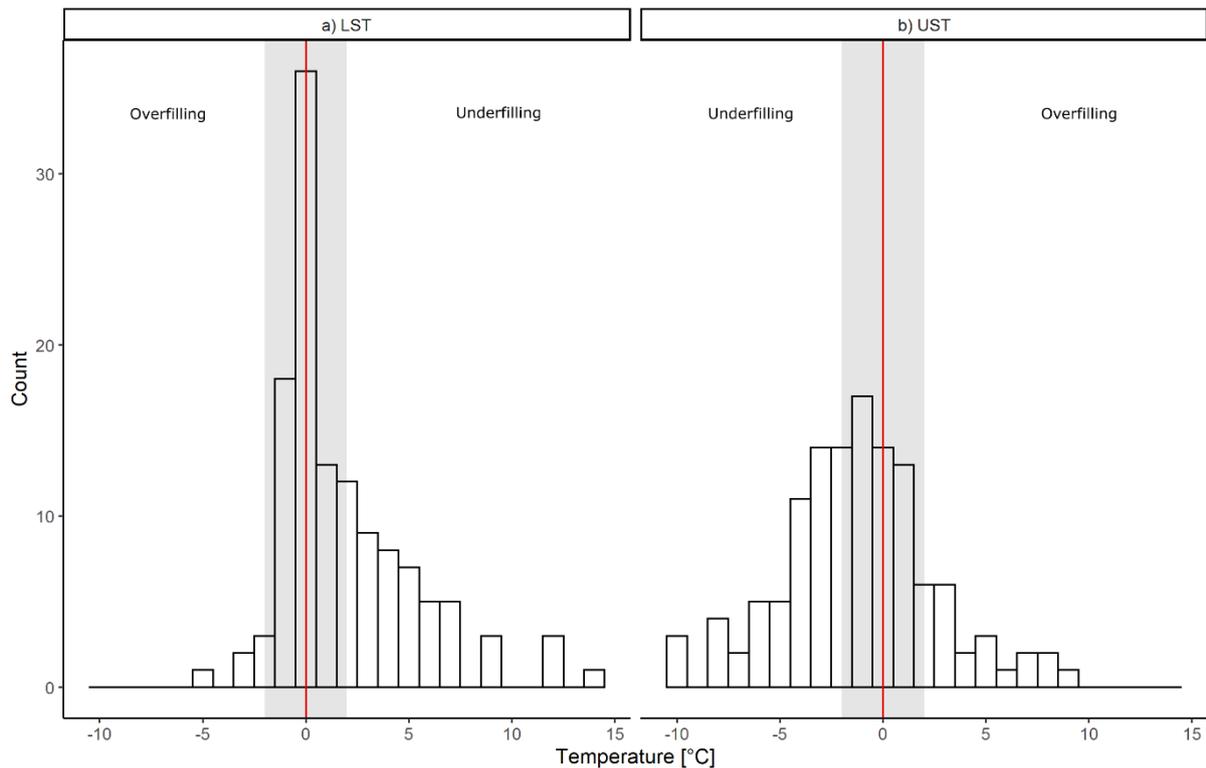


Figure 18. Deviations from normalized lower survival temperatures (LST, a) and normalized upper survival temperatures (UST, b) in species distributions. a) Negative numbers = distributional limit colder than the LST (i.e. overfilling), positive number = distributional limit warmer than the LST (underfilling). Three species had a realized thermal niche beyond the LST (overfilling), 51 species showed an underfilling, and 72 species were in equilibrium with the LST. b) Deviations from upper survival temperatures (UST) in species distributions. Negative numbers = distributional limit colder than the UST (underfilling), positive number = distributional limit warmer than the UST (overfilling). 23 species had a realized thermal niche beyond the LST (overfilling), 54 species showed an underfilling, and 49 species were in equilibrium with the LST. Grey areas mark the  $\pm 2^\circ\text{C}$  range around the normalized LST or UST, respectively, beyond which a distribution was classified as being not in equilibrium with the fundamental niche.

### Results from the linear models

#### *LST and UST as functions of temperature at sampling locations*

LST and UST were significantly correlated with minimum and maximum SST at the locations where the sampling materials were collected, respectively, and in both cases, there was a significant reference effect. Both parameter estimates of the location SST were low with 0.17 for minimum SST (Table 6) and 0.25 for maximum SST (Table 7).

Table 6. Parameter estimates for the linear model with  $LST \sim \text{minimum SST at sampling location} + (1|ref)$ . Residual standard deviation = 1.252.

Variable	$\beta$ -Estimate (95% confidence interval)	p-value
Intercept	0.39 (-1.37 – 2.2)	0.7
Min. SST	0.17 (0.11 – 0.24)	<0.001

Table 7. Parameter estimates for the linear model with  $UST \sim \text{maximum SST at sampling location} + (1|ref)$ . Residual standard deviation = 3.06.

Variable	$\beta$ -Estimate (95% confidence interval)	p-value
Intercept	23.3 (19.27 – 27.25)	<0.001
Max. SST	0.25 (0.08 – 0.41)	<0.001

#### *Realized temperature limits as a function of survival temperatures*

For *realized minimum SST*  $\sim$  *LST*, a linear model was not suited for the analysis, as residuals from a linear model indicated a non-linear relationship. Based on visual inspection and confirmed by breakpoint analysis, data were split into two cohorts, the first with  $LST \leq 9^\circ\text{C}$  and the second with  $LST \geq 9^\circ\text{C}$  (Figure 19). For each cohort a model was fitted. For cohort 1, there was a significant effect of *LST* on minimum *SST* and a significant reference effect (Table 8). However, note that variability in minimum *SST* is large, especially for species with an  $LST \leq 0^\circ\text{C}$ . For these species with a  $LST \leq 0^\circ\text{C}$ , minimum *SST* values range from  $-1.9$  to  $12.2^\circ\text{C}$  (mean = 0.5, median =  $-1^\circ\text{C}$ , variance =  $9.9^\circ\text{C}$ ) and there was no correlation or significant effect found when examining this further restricted sub-dataset only. Further note that cohort 1 includes 117 species, of which 109 have  $LST \leq 0^\circ\text{C}$ , which makes the described relationship doubtful for low *LST*s. For cohort 2 ( $n = 9$ ), no significant effect was found.

For the relationship *realized maximum SST*  $\sim$  *UST*, a linear model was fitted (Table 9, Figure 20). Here, realized maximum *SST* significantly increased by  $0.78^\circ\text{C}$  with increasing *UST*. There was no significant effect of the reference as random term. Residual standard deviation here was 2.766 and adjusted  $R^2 = 0.64$ . Thus, a correlation as well as some deviation from the prediction are evident.

Table 8. Parameter estimates for the linear model with *realized minimum SST*  $\sim$  *LST* + (1|ref) for cohort 1. Residual standard deviation = 2.765.

Variable	$\beta$ -Estimate (95% confidence interval)	p-value
Intercept	1.89 (0.35 – 3.41)	0.01
<i>LST</i>	0.79 (0.37 – 1.2)	<0.001

Table 9. Parameter estimate from the linear model with *realized maximum SST*  $\sim$  *UST*. Residual standard deviation = 2.766 on 115 degrees of freedom, adjusted  $R^2 = 0.638$ .

Variable	$\beta$ -Estimate (95% confidence interval)	p-value
Intercept	4.72 (1.82 – 7.63)	<0.001
<i>UST</i>	0.78 (0.67 – 0.88)	<0.001

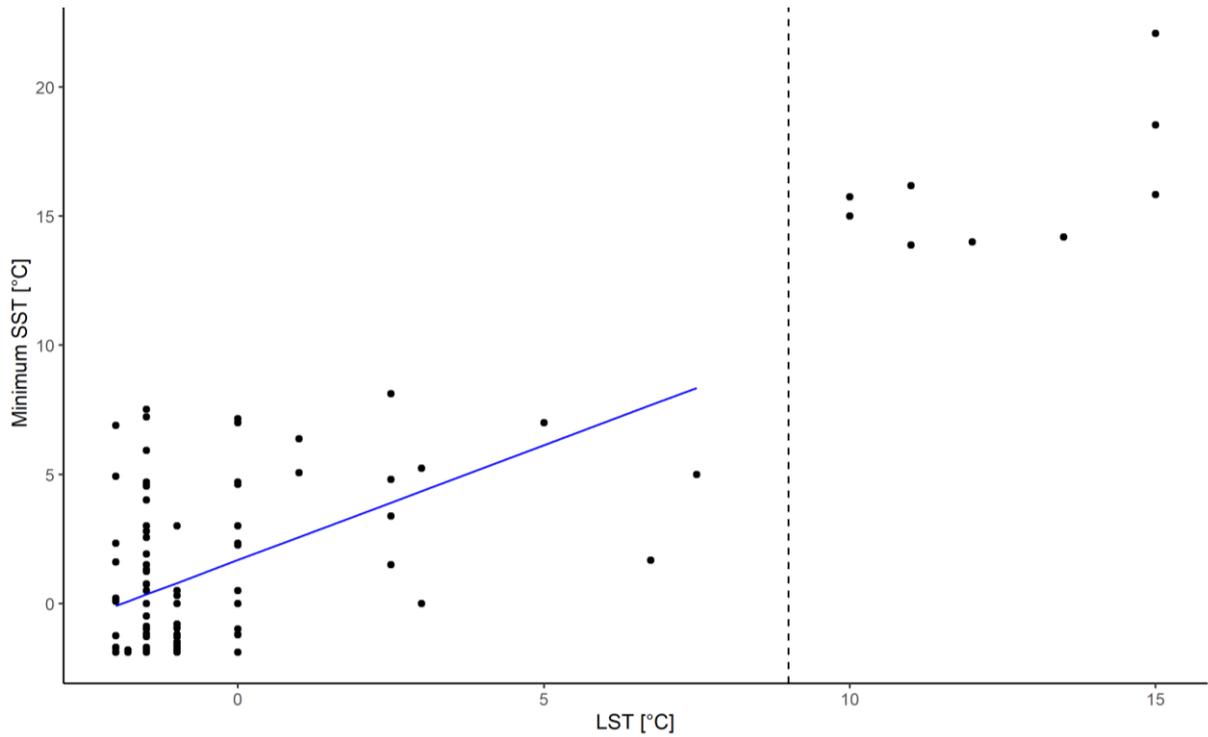


Figure 19. Realized minimum SST as a function of LST (blue line) for cohort 1 (to the left of the dashed line). For the cohort to the right of the line, no significant effect of LST on minimum SST was found.

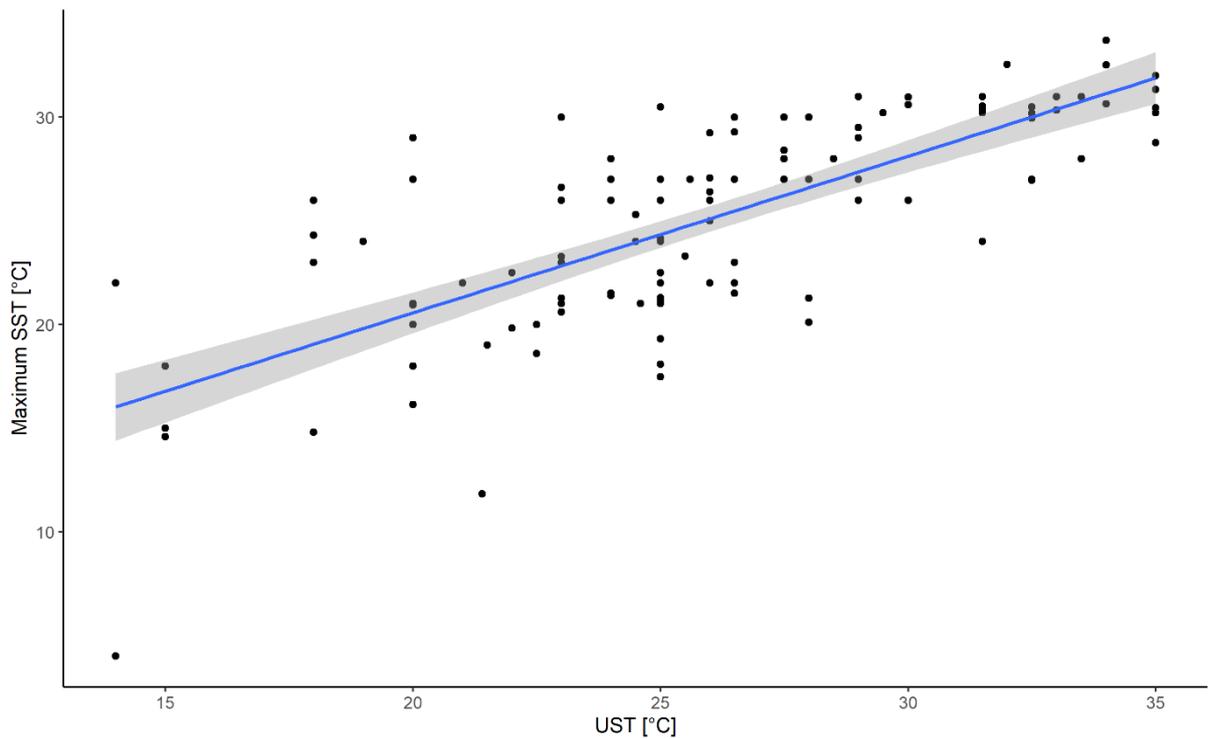


Figure 20. Linear regression line (blue) with 95% confidence interval (grey) for *realized maximum SST ~ UST*.

*State of equilibrium as a function of latitudinal distribution*

For state of equilibrium as a function of latitudinal distributions, we used linear models. The state of equilibrium at the LST followed a significant decreasing trend of  $-0.14^{\circ}\text{C}$  with increasing maximum latitude (Table 10, Figure 21). Here, the smaller the latitudinal range toward the pole is, the larger is

the niche underfilling. Hence, with equatorward range limitation, survival temperatures remain unaffected, leading to a higher degree of niche underfilling. There was no significant effect of reference. Residual standard error was 2.177 and adjusted  $R^2 = 0.289$ . This indicates large variation around the fitted linear regression line.

There was no significant effect for *state of UST equilibrium ~ minimum latitude* and no significant effect of reference as a random effect (Table 11, Figure 22).

Table 10. Parameter estimate from the linear models with *state of LST equilibrium ~ maximum latitude*. Residual standard error = 2.177 on 111 degrees of freedom, adjusted  $R^2 = 0.289$ .

Variable	$\beta$ -Estimate (95% confidence interval)	p-value
Intercept	9.07 (6.8 – 11.33)	<0.001
Max. lat.	-0.14 (-0.16 - -0.09)	<0.001

Table 11. Parameter estimate from the linear models with *state of UST equilibrium ~ minimum latitude*. Residual standard error = 2.913 on 107 degrees of freedom, adjusted  $R^2 = 0.013$ .

Variable	$\beta$ -Estimate (95% confidence interval)	p-value
Intercept	-0.51 (-1.52 – 0.49)	0.314
Min. lat.	-0.03 (-0.07 – 0.008)	0.12

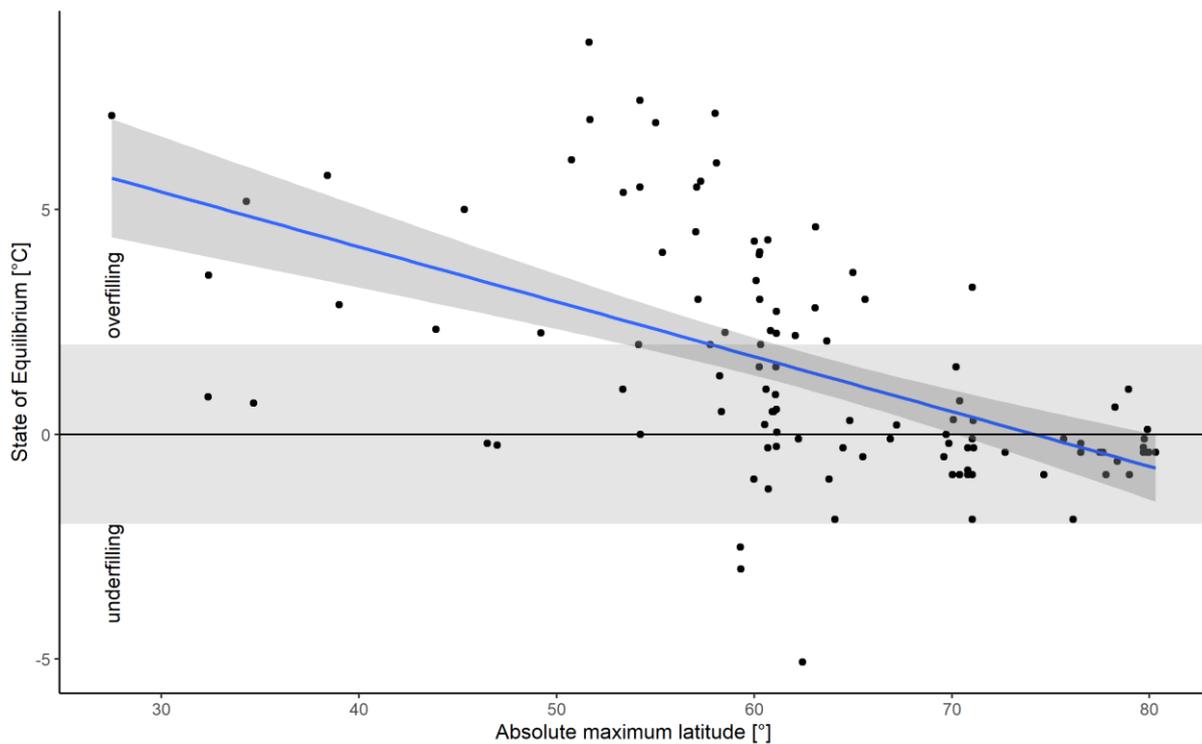


Figure 21. State of LST-Equilibrium versus absolute latitudinal maximum (i.e. poleward distributional limit) with regression line (blue) with 95% confidence interval (grey area around the line), adjusted  $R^2 = 0.289$ , for regression

parameters see Table 10. State of equilibrium is highlighted by the grey-shaded region around  $0\pm 2^\circ\text{C}$ , regions of under- and overfilling are annotated. LST is normalized to  $0^\circ\text{C}$  (black line).

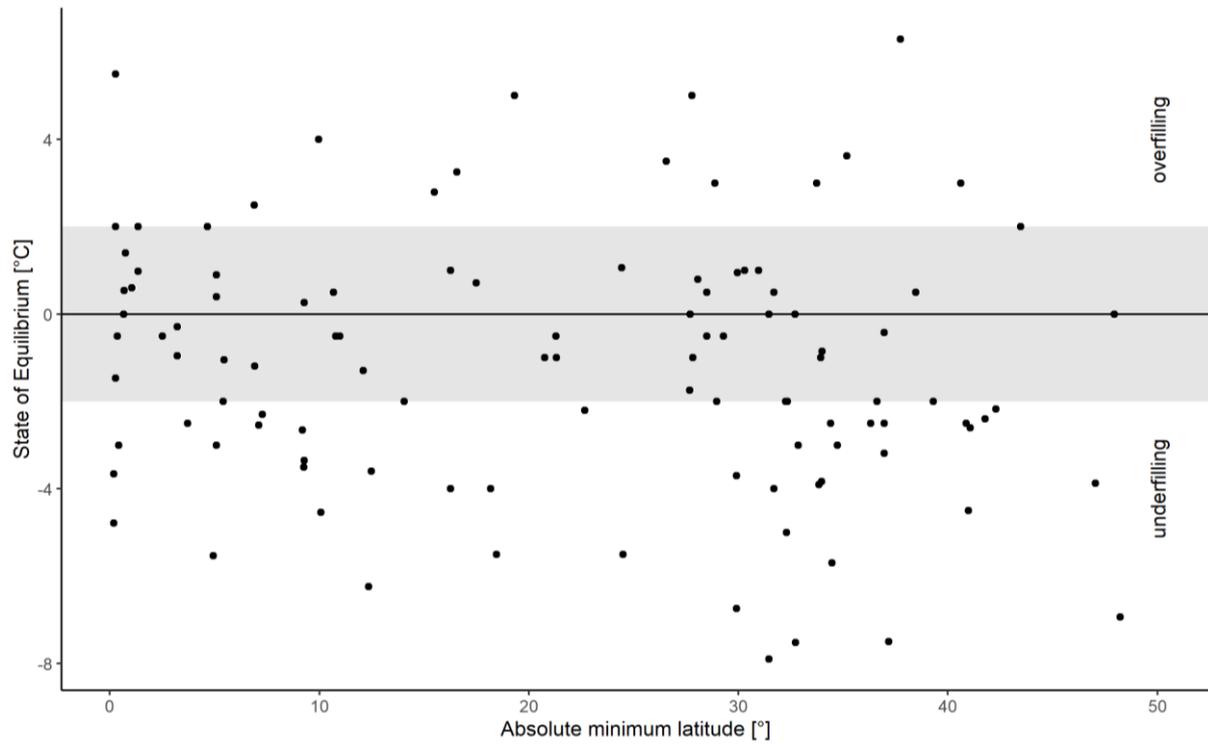


Figure 22. State of UST-Equilibrium versus absolute latitudinal minimum (i.e. equatorward distributional limit), no significant relationship was found. State of equilibrium is highlighted by the grey-shaded region  $0\pm 2^\circ\text{C}$ , regions of under- and overfilling are annotated. UST is normalized to  $0^\circ\text{C}$  (black line).

## Discussion

In this study, we compared upper and lower survival temperature limits of 126 seaweed species from 94 genera with the thermal limits of their distributions. The here included species were distributed throughout all marine realms (*sensu* <sup>[220]</sup>) from the poles to the tropics. Thus, the dataset can be treated as representative for global seaweed populations. The results of our analyses show that the experimental upper and lower survival temperatures are not necessarily the limits of distribution, but rather that niche underfill and -overfill, are common in a large number of seaweed species. We observed considerable deviations in the form of under- and overfilling of more than  $2^\circ\text{C}$ . At the LST, approximately 58% of the species and at the UST approximately 39% of the species were in equilibrium with the temperature survival limit, while the remaining species were in non-equilibrium and showed under- or overfilling of their thermal niches. This indicates that responses towards climate change might be highly variable between species. Further, this has implications for biogeographic studies which aim at identifying suitable habitat ranges of species. Temperature gradients along coasts over latitudes can be steep. Compare e.g. the SST isotherms between the Eastern and Western Atlantic in <sup>[26]</sup>: Here, the latitudinal distance between isotherms is much larger on the Eastern shores than on the Western shores. Thus, a deviation in  $2^\circ\text{C}$  from the expected tolerable limits can have large implications for the projection of suitable ranges, and geographic extent of projected ranges might differ

substantially. Overall, the state of underfilling significantly decreased with increasing overall distributional range, and such species with a large distributional range rather had overfilling at the UST (not shown), which is in line with <sup>[97]</sup>, who reported that species with smaller distributional ranges showed a higher degree of niche underfilling.

A large share of the here included species thrives at or beyond their experimental upper survival temperature limits. In these species, upper survival limits might regularly be exceeded during marine heatwave events which lead to temporary increases of the SST. Frequency and durations of these events are increasing globally as a consequence of global warming <sup>[43]</sup>. <sup>[42]</sup> reported that a temperature of 0.5°C above the mortality threshold led to mortality rates of ≥58%, and excess by 2°C led to 100% mortality in the sugar kelp *Saccharina latissima*. Thus, species which thrive at or beyond the temperature limits are potentially facing high risk of local extinction.

#### Reference effects and effects of sampling location

Reference and SST at sampling location both had significant effects in our models, although effects were rather small. Still, this underlines that experimental set-ups and origin of the sample material play a role in identification of temperature tolerances, especially given that we already constrained our dataset on survival temperatures by applying selection criteria for inclusion of data. The original data sources do not allow to unequivocally identify factors which led to the reference and sampling location effects. Temperature tolerances can vary between life-cycle stages and seasons <sup>[68, 187, 188, 221]</sup>, and survival temperatures which are derived from the “non-hardest” life-cycle stage are probably not adequate to describe tolerance limits <sup>[187]</sup>. The experimental set-up (e.g. duration, pre-acclimation) or other conditions (e.g. photon fluence rate) can also have an effect on the LST and UST (and comparability of data from different studies), making experimental design for determination of temperature limits highly complex (<sup>[222]</sup> and references therein). <sup>[186]</sup> showed how populations of a single species cover different areas of a species’ fundamental niche. Within a species’ niche, several sub-populations might inhabit different sub-volumes of the niche, and populations might be adapted to local conditions. Indeed, seaweed species must not be treated as homologous entities when it comes to temperature tolerances and local adaptations can lead to niche differentiation <sup>[42, 188, 204, 221]</sup>. Thus, data from single populations, seasons or experiments might not be valid on a species level and could lead to over- or underestimation of a species’ suitable range. Most of the here cited authors used material from Northern Atlantic or Northern Pacific sites and tested tolerances only in one life-history stage (seaweeds have two to three life-history stages, which might differ with respect to temperature tolerance, <sup>[187]</sup>). This might explain both reference and location effects, as well as non-equilibrium distributions (see below). Both factors, reference as proxy for experimental set-up, and sample origin, will need to be addressed in future studies when data from different studies are compared. Otherwise, effects might be masked by differences in study execution.

### Independence of survival temperatures and environmental conditions

Lower survival temperatures were not a suitable indicator of distributional temperature limits. Upper survival temperatures on the contrary were a valid predictor. Variances between temperature tolerance limits and realized SST limits suggest that distributions rather follow UST, but to a lesser extent LST: While the variance in realized temperature limits was equal between the lower and upper distributional limits, the variance in LSTs was significantly smaller than in USTs. This was further illustrated by the linear model for *realized minimum SST*  $\sim$  *LST* + (1|ref), where the data had to be split into cohorts and variations in realized minimum SST were still extremely large in the cohort with LST restricted to  $< 9$  and  $\leq 0^\circ\text{C}$ , respectively. This indicates an independence of distributional limits from the LST. Further, it might indicate that LSTs are retained irrespective of the realized, distributional minimum SST, which can be much higher than the LST. This is further supported by (1.) the low beta estimate of 0.17 for minimum SST at sampling location as a predictor of LST, and (2.) the finding that state of equilibrium at the LST was a function of latitudinal distribution. Here, for the LST, the state of underfilling increased with decreasing maximum absolute latitude, meaning that with a more equatorward distributional limit the discrepancy between the lowest experienced and the lowest tolerated temperature increased. This clearly indicates that even with relatively high winter SSTs, cold-tolerances are present in seaweeds. The relationship of LST underfilling and latitudinal range is surprising because without a selection pressure, thermal tolerances can be lost <sup>[223]</sup>, which would explain the close match of distributional limits and thermal tolerances in other organisms, as reported by <sup>[96]</sup>.

The independence of LST and realized temperature patterns in our study is surprising as temperature is the most important variable to explain seaweed distributions on a global scale (see e.g. the standard work by Lüning on seaweeds and their biogeography <sup>[26]</sup>). Our observations might be explained phylogenetically: SST data in this study represent present-day climatic conditions while survival temperatures might represent ancestral adaptations to climatic conditions. The literature on the legacy of ancestral niches in seaweed survival temperatures, the radiation of seaweed genera from prehistoric times until today, and the corresponding temperature regimes is extensive <sup>[26, 132, 187, 224-229]</sup>. Authors conclude that depending on the ancestral place of origin, survival temperatures reflect either heat tolerance (corresponding to a tropical origin) or cold-tolerance (corresponding to a polar origin). We want to point out that, although we included species with distributions throughout all realms, the species selection and the sampling sites in the quoted references have a bias towards rather (cold-)temperate species and sites, and that tropical species are rather underrepresented. Thus, the here observed independence between realized minimum SST and LSTs might be explained by inherited cold-tolerances. It will therefore be interesting to map climatic niches along phylogenetic trees to comprehend the evolution of thermal niches in seaweeds (e.g. <sup>[230]</sup>), especially given the here described

continuity of LSTs irrespective of environmental conditions. In future studies this might be important to refine predictions of climatic adaptations and predictions of responses to climate change.

#### Equilibrium distributions

At the UST, 51 and at the UST 49 species showed equilibrium distributions. <sup>[193]</sup> wrote that extreme climate events determine distributions. On the one hand, this indicates a good predictability of geographic distribution based on physiological knowledge. On the other hand, <sup>[95]</sup> underlined that mechanistic models rather tend to overestimate distributional ranges since limiting factors such as biotic interactions, which might restrict a distribution, are not included. In addition, these species would not be subjected to a “safety margin” between survival temperature limit and actual SST, as reported by <sup>[132]</sup> for seaweed distributions. Therefore, equilibrium distributions which match survival temperature limits contradict previous assumptions about seaweed distributional patterns. Further, for these species future global warming might pose a threat and cause range shifts in response to increasing SST since they already thrive in regions which are characterized by average summer temperatures which are close to their tolerance limits.

#### Non-equilibrium distributions - underfilling

Underfilling of the fundamental niche can be explained by e.g. dispersal barriers or biotic interactions (see <sup>[181]</sup> and <sup>[1]</sup>). For example, in a previous study we showed that southern hemisphere species are limited in their geographic distribution by lack of substrate to the south of the landmasses of New Zealand, Australia, South Africa and South America <sup>[183]</sup>. Still, <sup>[96]</sup> reported that especially marine ectotherms show close match of distributional and thermal tolerance limits and concluded that climate related range shifts will be more predictable than in terrestrial species. <sup>[97]</sup> reported that especially at the equatorward range edge underfilling was more pronounced. Although they did not include primary producers in their study, this is in line with our findings. An explanation is that at equatorward range edges factors such as competition limit the potential distributional range <sup>[96]</sup>. Further, <sup>[132]</sup> reported that seaweeds rather tend to keep a “safety margin” of 2-3°C between their USTs and maximum temperatures at the distributional limits to avoid adverse temperature conditions.

#### Non-equilibrium distributions - overfilling

Occurrences beyond the survival temperature limits (i.e. state of niche overfilling) need further discussion of the underlying mechanisms. Ecological as well as methodological explanations can be used to explain the finding of non-equilibrium states. Methodological aspects have been discussed above already, and effects of experiment conduction and/or selection of sample material might well lead to underestimations of the fundamental niches, leading to a perceived non-equilibrium distribution. Ecologically, overfilling might be explained by overwintering strategies. Seaweeds possess complex life-cycles with two to three alternating multicellular life-history stages with unicellular stages in between (e.g. <sup>[231]</sup>). Life-history stages with wide tolerances could allow to maintain populations

during seasons of unfavorable conditions <sup>[187]</sup>. <sup>[232]</sup> wrote that heteromorphic life-history stages in seaweeds might allow species to “exploit seasonally or spatially dissimilar niches”. I.e. that different life-history stages might express different tolerance levels to environmental conditions (e.g. <sup>[136, 233]</sup>) and their alternation might allow populations to survive unfavorable condition in the state of a more tolerant life-history stage <sup>[232]</sup>. In addition, “seed banks” can be important to maintain populations with seasonally occurring unfavorable conditions (see chapter 3.5 in <sup>[38]</sup>, and references therein). These “seed banks” might be constituted of tolerant propagules which then develop into populations when conditions become favorable again for consecutive life-history stages <sup>[234]</sup>. <sup>[235]</sup> described how Chilean *Macrocystis* populations produce an enormous number of gametophytes before the annual population collapse, and how these gametophytes reconstitute the population under favorable seasonal conditions, ensuring its persistence. Thus, seaweed populations beyond the thermal survival limits might be maintained by alternating and adapted life-history stages, or “seed banks”. In other ecological contexts, the concept of source and sink populations is often used to explain how populations are maintained outside their suitable range <sup>[87]</sup>. According to this concept, populations can be maintained even under unfavorable conditions via constant migration of individuals or reproductive material from sites where conditions are more favorable. Like this, populations could be maintained in spaces where conditions are outside the fundamental niche and prevent establishment of independent populations. Such populations then clearly display a state of niche overfilling <sup>[1]</sup>. However, in seaweeds, dispersal of reproductive material is very limited, to few meters to kilometers (<sup>[236]</sup>, <sup>[38]</sup>, chapter 3.5 and references therein). Thus, the concept of source- and sink-populations is probably not adequate to explain how seaweed populations are maintained in regions with several degree deviation from the respective lower and upper survival temperatures, as observed here. Such variations in SST are usually found across larger latitudinal distances than the dispersal distance.

Irrespective of the tolerance strategies or methodological constraints, species with overfilling distributions have distributional limits which are beyond their experimentally tested thermal tolerance limits. Although they might have strategies to evade temperature stress, large scale range shifts in seaweeds have been reported as a response to global warming <sup>[6]</sup> and heat stress is expected to increase in the future <sup>[42]</sup>. Thus, these species will probably face temperature pressure which exceed their potential for adjustment and we have to expect further range shifts for these species in the future. Given the significance of macroalgal ecosystems as coastal foundation species, this is alarming and underlines the urgency to install protection measures <sup>[7]</sup>.

#### Implications for forecasting of habitat suitability

Our findings have implications for forecasting of distributional changes under global warming. Range shifts of species, including seaweeds, in response to climate change have extensively been documented <sup>[5, 6, 39, 96, 97, 99, 190-192]</sup>. Thus, seaweeds are evidently responding to changing temperature

conditions with range shifts. However, as our results indicate, responses might differ between species, since species show different states of niche-equilibrium, and predictions thus have to be treated with caution to account for uncertainties. <sup>[95]</sup> have shown the importance of including physiological data into forecasting of seaweed distributions, and explained mechanisms of uncertainty. Our study underlines that fundamental and realized niches of seaweeds can show large deviations. Thus, while seaweeds are shifting their distributions away from the equator and toward colder environments <sup>[5, 6, 39]</sup>, responses may be very heterogenous among species and some species might be more adaptive than others. Such species might e.g. maintain populations under warming conditions and perhaps even profit from the disappearance of less heat-tolerant competitors <sup>[6, 237]</sup>. In general, fundamental niches seem to have a more limited predictive power than for other marine ectotherms <sup>[97]</sup>, which might in parts be explained by the lack of active dispersal mechanisms, which would perhaps allow for more direct response towards changing environmental conditions.

We further illustrate consequences of our findings for biogeographic research objectives with respect to polar environments. With increasing temperatures, habitat at the poles becomes more available and easier accessible, due to retreat of sea-ice and increasing connectivity <sup>[16, 41, 70, 71, 78, 189, 238-241]</sup>. Thus, with increasing connectivity, non-native species will probably pose competitive pressure on polar native species. Here, the finding that LST might be preserved irrespective of environmental conditions is highly relevant, as it indicates that non-polar species might have cold-tolerances which might enable them to successfully establish in, and invade, regions with cold conditions, although they do not encounter such conditions in their native ranges. <sup>[242]</sup> and <sup>[82]</sup> have provided evidence that in Antarctica this might already be happening. In such cases, distributional data are not sufficient to identify the temperature tolerances of these species and purely correlative approaches will fail to identify these species as potential invaders. Further, this opposes the assumption of a climate matching hypothesis, under which predominantly species from climatically comparable habitats pose an invasion risk to polar environments (e.g. <sup>[70, 71, 79]</sup>). Thus, it is important to identify invasion potential of potential invaders beyond their native realized niches. Here, our findings are important as they underline that species might have hidden, perhaps inherited, cold-tolerances.

## Conclusion

With a dataset which represents global seaweed species we showed that many macroalgal species have distributions which deviate from their fundamental thermal niches in both states of over- as well as underfilling, i.e. non-equilibrium distributions are widespread in this species group. We discussed possible phylogenetic, ecological, as well as, methodological underlying explanations for this finding. Irrespective of the underlying mechanisms, the extent of the deviations is surprising when compared to literature references which indicated good fit of temperature tolerances and realized niches for marine ectotherms. Our findings highlight that the accuracy of predictions of the effects of climate

change is probably highly heterogenous among seaweed species and that responses will be so as well. Further, our findings are important for identification of invasive species, since temperature tolerances, especially towards cold-temperatures, are to some degree independent of environmental conditions and not suitable to forecast habitat suitability. As additional finding, we report that many species' distributions have limits at or beyond their upper survival temperature limits and are thus probably threatened by global warming and marine heatwave events. Thus, large scale redistributions are to be expected under global warming.

## References

*Moved to the comprehensive reference list at the end of this thesis.*

## Appendix

Table S1. Collected lower and upper survival temperatures for this study with references. LST = lower survival temperature limit as reported in the reference with the ecologically meaningful value if indicated, UST = upper survival temperature limit. Dist. Min. and Max. SST = the overall minimum and maximum sea surface temperature of the species distributional range, based on distributional data and extracted from bio-Oracle layers<sup>[125]</sup>. Experimental material as reported in the original publications. Location of the sample collections as reported in the respective reference. Climatic regions follow<sup>[220]</sup> and are based on the sampling location as reported in the literature. Here, cosmopolitan refers to studies with material from different and far apart sites. In such cases, the overall reported minimum and maximum values of all tested specimens were used as LST and UST in this study. Min. and Max. SST at coll. site are the minimum and maximum SST at the reported collection sites of the tested material, based on the reported information on collection site and extracted from bio-Oracle layers. CAN = Canada, FR = France, GER = Germany.

Genus	Species (as in publication if different)	LST (adjusted, see text for explanation) (°C)	UST (°C)	Dist. Min. SST (°C)	Dist. Max. SST (°C)	Experimental Material	Location of original collection as reported in the reference	Climatic region	Min. SST at coll. site (°C)	Max. SST at coll. site (°C)	Reference
<i>Acrosiphonia</i>	<i>Acrosiphonia arcta</i>	-1.8	25.5	-1.9	23.3	cultured field-collected specimens (sporophytes and gametophytes)	Puerto Williams, Chile	temperate	4.8	9.1	[203]
<i>Agardhiella</i>	<i>Agardhiella subulata</i>	0	32.5	2.3	30.5	cultured gametophytes and tetrasporophytes	Waterford, CT, USA	temperate	2.2	25.9	[216]
<i>Ahnfeltia</i> (Hudson) E.M.Fries	<i>Ahnfeltia plicata</i>	-1.5	28	-1.9	30.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Alaria</i> Greville	<i>Alaria esculenta</i>	-1.5	21	-1.9	22.0	gametophytes	Iceland	temperate	0.63	12.70	[187]
<i>Alaria</i> Greville	<i>Alaria marginata</i>	-1.5	22.5	-1.0	20.0	gametophytes	Friday Harbor, San Juan Island, Washington, USA and Pilar Point, California, USA	temperate	6.20	18.40	[187]
<i>Analipus</i>	<i>Analipus japonicus</i>	-1.5	25	0.0	24.2	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]

<i>Ascophyllum</i>	<i>Ascophyllum nodosum</i>	0 (-1)	29	-1.9	27.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Asparagopsis</i>	<i>Asparagopsis armata</i>	1.0	26	5.1	29.3	sporophytes from cultures	Ville-france sur Mer, FR	temperate	13.3	24.7	[213]
<i>Ballia</i>	<i>Ballia callitricha</i>	-1.8	14	-1.9	22.0	cultured field-collected specimens (sporophytes and gametophytes)	King George Island	Antarctic	3.7	10.9	[203]
<i>Blidingia</i>	<i>Blidingia minima</i>	0 (-1)	26.5	-1.9	29.3	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Bonnemaisonia</i>	<i>Bonnemaisonia asparagoides</i>	6.8	23	1.7	26.6	sporophytes from cultures	Herdla, Norway	temperate	4.5	15.4	[214]
<i>Bryopsis</i>	<i>Bryopsis hypnoides</i>	0 (-1)	31.5	-1.0	31.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Calliblepharis</i>	<i>Calliblepharis ciliata</i>	2.5	27.5	4.8	28.0	Tetrasporophytes	Roscof, FR	temperate	8.1	19.9	[215]
<i>Callophyllis</i>	<i>Callophyllis flabellulata</i>	0	20	-1.9	21.0	Field collected algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.2	18.4	[210]
<i>Ceramium</i>	<i>Ceramium deslongchampsii</i>	0 (-1)	26.5	0.5	23.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Ceramium</i>	<i>Ceramium nitens</i>	15.0	33	15.8	30.3	large fully grown plants from cultures	Virgin Islands, USA	temperate	26	29.2	[218]
<i>Ceramium</i>	<i>Ceramium virgatum</i> Roth	0 (-1)	26.5	-1.7	29.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Champia</i>	<i>Champia parvula</i>	3.0	32	0.0	32.5	sporophytes from cultures	Rhode Island, USA	temperate	3.9	21.3	[219]
<i>Gigartina</i> Stackhouse	<i>Chondracanthus exasperatus</i> ( <i>Gigartina exasperata</i> )	-1.5	25	3.0	21.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Chorda</i> Stackhouse	<i>Chorda filum</i>	-1.5	28	-1.7	27.0	gametophytes	Ireland	temperate	4.75	18.90	[187]
<i>Cladophora</i>	<i>Cladophora albida</i>	-2	35	-1.3	32.0	cultured field-collected specimens	Corsica	temperate	12.8	26.4	[196]
<i>Cladophora</i>	<i>Cladophora coelothrix</i>	2.5	35	8.1	30.2	cultured field-collected specimens	Florida, USA, Brittany, FR	tropical and temperate	15.2	30.6	[205]

<i>Cladophora</i>	<i>Cladophora dalmatica</i>	-2	32.5	1.6	30.0	Sporophytes Cultured from Field Selction	Roscoff, FR	temperate	8.1	19.9	[206]
<i>Cladophora</i>	<i>Cladophora hutchinsiae</i>	2.5	32.5	3.4	27.0	Sporophytes Cultured from Field Selction	Roscoff, FR	temperate	8.1	19.9	[206]
<i>Cladophora</i>	<i>Cladophora laetevirens</i>	0	32.5	-1.0	30.2	cultured field-collected specimens	Roscoff, FR	temperate	8.1	19.9	[205]
<i>Cladophora</i>	<i>Cladophora prolifera</i>	0.0	30	7.1	31.0	cultured field-collected specimens	Calvi, Corsica	temperate	13.20	25.70	[205]
<i>Cladophora</i>	<i>Cladophora ruchingeri</i>	0 (-1)	32.5	-1.2	27.0	cultured field-collected specimens	Iceland	temperate	0.63	12.7	[196]
<i>Cladophora</i>	<i>Cladophora rupestris</i>	-5	27.5	-1.7	30.0	field-collected specimens	Roscoff, FR	temperate	8.1	19.9	[196]
<i>Cladophora</i>	<i>Cladophora submarina</i>	5.0	35	19.5	30.5	cultured field-collected specimens	Curacao, BR	tropical	25.9	29.2	[205]
<i>Cladophora</i>	<i>Cladophora vagabunda</i>	-2	35	2.3	31.3	field-collected specimens	Roscoff, FR	temperate	8.1	19.9	[196]
<i>Cladostephus</i>	<i>Cladostephus spongiosus</i>	0 (-1)	29	-0.8	27.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Codium</i>	<i>Codium fragile</i>	0 (-1)	31.5	-1.5	31.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Corallina</i>	<i>Corallina officinalis</i>	0 (-1)	29	-1.3	26.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Costaria</i> Greville	<i>Costaria costata</i>	-1.5	26	-1.8	25.0	gametophytes	Japan	temperate	-1.35	21.60	[187]
<i>Cryptopleura</i>	<i>Cryptopleura ramosa</i>	2.5	27.5	1.5	28.4	Tetrasporophytes	Roscoff, FR	temperate	8.1	19.9	[215]
<i>Cymathere</i>	<i>Cymathere triplicata</i>	-1.5	15	-0.5	15.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Cystoclonium</i>	<i>Cystoclonium purpureum</i>	0 (-1)	24	-1.9	27.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Dasya</i>	<i>Dasya baillouviana</i>	0.0	34	-1.2	32.5	Tetrasporophytes from cultures	Southern Gulf of St Lawrence Gulf (Nova Scotia), CAN	temperate	-1.2	19.7	[198]
<i>Delesseria</i>	<i>Delesseria sanguinea</i>	0 (-1)	24	-1.9	26.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Desmarestia</i> J.V.Lamouroux	<i>Desmarestia aculeata</i>	-1.5	23	-1.9	21.0	cultured field-collected specimens	Friday Harbor, San Juan	temperate	6.20	18.40	[203]

<i>Desmarestia</i> J.V.Lamouroux	<i>Desmarestia firma</i>	-2	28.5	10.5	21.0	(sporophytes and gametophytes) gametophytes (f&m)	Island, Washington, USA Herradura, Coquimbo & Bahia Mendieta, Peru	temperate	11.90	25.20	[132]
<i>Desmarestia</i> J.V.Lamouroux	<i>Desmarestia ligulata</i>	-2	25.6	-1.7	27.0	gametophytes	Chiloe bis Navidad, Chile	temperate	9.00	19.60	[132]
<i>Desmarestia</i> J.V.Lamouroux	<i>Desmarestia viridis</i>	-1.5	23	-1.9	26.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Devaleraea</i> Guiry	<i>Devaleraea ramentacea</i>	-2	22	-1.9	19.8	sporophytes	Nova Scotia, CAN	temperate	-1.30	24.90	[211]
<i>Dictyopteris</i>	<i>Dictyopteris delicatula</i>	12.0	31.5	14.0	30.6	full grown plants from culture	Cap Verde and Bonaire, Antilles	tropical	21.7	28.10	[209]
<i>Dictyopteris</i>	<i>Dictyopteris justii</i>	15.0	30	18.5	30.6	large fully grown plants from cultures	Virgin Islands, USA	temperate	26	29.2	[218]
<i>Dictyurus</i>	<i>Dictyurus occidentalis</i>	15.0	31.5	22.1	30.3	large fully grown plants from cultures	Virgin Islands, USA	temperate	26	29.2	[218]
<i>Digenea</i>	<i>Digenea simplex</i>	10.0	34	15.0	33.7	Sporophytes from cultures	Lemnos Island, Greece	temperate	13.6	25.1	[219]
<i>Dumontia</i>	<i>Dumontia contorta</i>	0 (-1)	26.5	-1.9	21.5	Field-collected Sporophytes	Iceland to Brittany, FR	temperate	0.62	12.7	[197]
<i>Ectocarpus</i>	<i>Ectocarpus siliculosus</i>	-1.8	33	-1.9	31.0	Sporophytes	cosmopolitan	several	-1.784723	30.500301	[204]
<i>Egregia</i> Areschoug	<i>Egregia menziesii</i>	-1.5	18	4.0	23.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Eisenia</i>	<i>Eisenia arborea</i>	1.0	26	6.4	27.1	gametophytes	Bamfield, CAN	temperate	22.5	30.5	[187]
<i>Endocladia</i> J.Agardh	<i>Endocladia muricata</i>	-1.5	28	1.5	20.1	Algal material	Friday Harbor, San Juan Island,	temperate	6.20	18.40	[210]

<i>Eudesme</i>	<i>Eudesme virescens</i>	-1.8	30	-1.8	26.0	cultured field-collected specimens (sporophytes and gametophytes)	Washington, USA					
<i>Fucus</i> L.	<i>Fucus serratus</i>	0 (-1)	26.5	-1.3	22.0	Field-collected Sporophytes	Disko Island Greenland	Arctic	-1.8	7.1		[203]
<i>Fucus</i> L.	<i>Fucus spiralis</i>	-1.5	25	-1.2	24.0	Algal material	Helgoland, GER	temperate	1.44	19.7		[197]
<i>Fucus</i> L.	<i>Fucus vesiculosus</i>	0 (-1)	29	-1.6	27.0	Field-collected Sporophytes	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40		[210]
<i>Gongolaria</i>	<i>Gongolaria barbata</i> ( <i>Cystoseira barbata</i> )	3.0	33	5.2	29.0	Sporophytes from cultures	NW England Helgoland, GER	temperate	4.75	18.9		[197]
<i>Gongolaria</i>	<i>Gongolaria barbata</i> ( <i>Cystoseira barbata</i> )	3.0	33	5.2	29.0	Sporophytes from cultures	Thessaloniki, Greece	temperate	12.4	26.8		[213]
<i>Grateolupia</i>	<i>Grateloupia lanceolata</i> ( <i>Prionitis lanceolata</i> )	-1.5	25	4.6	26.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40		[210]
<i>Griffithsia</i>	<i>Griffithsia globulifera</i>	0 (-1)	29.5	-1.2	30.2	Tetrasporophytes	Nova Scotia, CAN	temperate	-1.3	24.9		[198]
<i>Grinnellia</i>	<i>Grinnellia americana</i>	0	35	2.3	28.8	cultured gametophytes and tetrasporophytes	Waterford, CT, USA	temperate	2.2	25.9		[216]
<i>Gymnogongrus</i> Martius	<i>Gymnogongrus linearis</i>	-1.5	25	4.0	17.5	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40		[210]
<i>Haloplegma</i>	<i>Haloplegma duperreyi</i>	13.5	31.5	14.2	30.5	large fully grown plants from cultures	Virgin Islands, USA	temperate	26	29.2		[218]
<i>Halosaccion</i> Kützing	<i>Halosaccion americanum</i>	-1.5	18	0.5	14.8	Algal material	Friday Harbor, San Juan Island,	temperate	6.20	18.40		[210]

<i>Halosiphon</i>	<i>Halosiphon tomentosus</i> ( <i>Chorda tomentosa</i> )	-1.5	25	-1.7	22.5	gametophytes	Washington, USA Brittany, FR	temperate	8.10	19.90	[187]
<i>Halurus</i>	<i>Halurus equisetifolius</i>	7.5	27.5	5.0	27.0	Tetrasporophytes	Roscoff, FR	temperate	8.1	19.9	[216]
<i>Haplogloia</i>	<i>Haplogloia andersonii</i>	-1.5	26.5	2.8	30.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Hedophyllum</i> Setchell	<i>Hedophyllum sessile</i>	-1.5	15	2.6	14.6	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Heterosiphonia</i>	<i>Heterosiphonia gibbesii</i>	11.0	34	16.2	30.7	large fully grown plants from cultures	Virgin Islands, USA	temperate	26	29.2	[218]
<i>Hooperia</i>	<i>Hooperia divaricata</i>	0	32.5	-1.2	31.0	cultured gametophytes and tetrasporophytes	Waterford, CT, USA	temperate	2.2	25.9	[216]
<i>Kuckuckia</i> G.Hamel	<i>Kuckuckia spinosa</i>	-1	29	0.3	29.0	unclear cultured	Naples, Italy	temperate	12.30	27.00	[212]
<i>Laminaria</i> J.V.Lamouroux	<i>Laminaria digitata</i>	-1.5	23	-1.8	23.3	gametophytes	Helgoland, GER	temperate	1.44	19.70	[187]
<i>Laminaria</i> J.V.Lamouroux	<i>Laminaria hyperborea</i>	-1.5	22	-0.9	22.5	gametophytes	Helgoland, GER	temperate	1.44	19.70	[187]
<i>Laminaria</i> J.V.Lamouroux	<i>Laminaria longicuris</i>	-1.5	24	-1.9	21.4	gametophytes	Faroe Islands	temperate	6.60	11.20	[187]
<i>Laminaria</i> J.V.Lamouroux	<i>Laminaria ochroleuca</i>	-1.5	24.5	7.2	25.3	gametophytes	Roscoff, FR	temperate	8.10	19.90	[187]
<i>Laminaria</i> J.V.Lamouroux	<i>Laminaria setchellii</i>	-1.5	23	1.9	23.0	gametophytes	Bamfield, CAN	temperate	6.20	18.40	[187]
<i>Laminaria</i> J.V.Lamouroux	<i>Laminaria sinclairii</i>	-1.5	22.5	7.5	18.6	gametophytes	Pilar Point California, USA	temperate	9.60	17.40	[187]
<i>Laminaria</i> J.V.Lamouroux	<i>Laminaria solidungula</i>	-1.5	20	-1.9	16.1	gametophytes	Igloolik, CAN	Arctic	-1.80	3.60	[187]

<i>Leathesia</i> S.F.Gray	<i>Leathesia marina</i> ( <i>Leathesia difformis</i> )	-1.5	18	-1.2	26.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Lessonia</i> Bory de Saint-Vincent	<i>Lessonia nigrescens</i>	-2	24.6	6.9	21.0	gametophytes (f&m)	Valdivia, Chile	temperate	10.20	17.20	[132]
<i>Lessonia</i> Bory de Saint-Vincent	<i>Lessonia trabeculata</i>	-2	26.7	10.1	16.3	gametophytes (f&m)	San Juan, Peru	temperate	15.10	25.20	[132]
<i>Lessonia</i> Bory de Saint-Vincent	<i>Lessonia vadosa</i>	-2	21.4	4.9	11.8	gametophytes (f&m)	Beagle Channel, Chile	temperate	4.80	9.10	[132]
<i>Lomentaria</i>	<i>Lomentaria articulata</i>	0	28.5	4.6	28.0	cultured gametophytes and tetrasporophytes	Waterford, CT, USA	temperate	2.2	25.9	[215]
<i>Lophocladia</i>	<i>Lophocladia trichoclados</i>	11.0	31.5	13.9	31.0	full grown plants from culture	Tenerife (Canary Islands)	temperate	19	24.1	[209]
<i>Macrocystis</i> C.Agardh	<i>Macrocystis pyrifera</i>	-2	26	0.2	26.4	gametophytes	California, USA	temperate	9.60	17.40	[187]
<i>Mastocarpus</i> Kützinger	<i>Mastocarpus papillatus</i>	-1.5	28	1.2	21.3	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Mazzaella</i> G. de Toni f.	<i>Mazzaella splendens</i> ( <i>Iridaea cordata</i> var. <i>splendens</i> )	-1.5	20	1.3	20.4	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Membranoptera</i>	<i>Membranoptera alata</i>	0 (-1)	21.5	-1.8	19.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Microdictyon</i>	<i>Microdictyon boergesenii</i>	10.0	31.5	15.8	30.2	sporophytes from cultures	Bahamas Islands	tropical	22.5	30.5	[207]
<i>Neoagarum</i> H. Kawai & T. Hanyuda 2017	<i>Neoagarum fimbriatum</i> ( <i>Agarum fimbriatum</i> )	-1.5	20	4.7	20.6	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Neodilsea</i> Tokida	<i>Neodilsea borealis</i>	-1.5	25	0.7	18.1	Algal material	Friday Harbor, San Juan Island,	temperate	6.20	18.40	[210]

<i>Neorhodomela Masuda</i>	<i>Neorhodomela larix</i>	-1.5	25	-1.0	19.3	Algal material	Washington, USA Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Odonthalia Lyngbye</i>	<i>Odonthalia floccosa</i>	-1.5	25	-1.0	21.2	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Opuntiella Kylin</i>	<i>Opuntiella californica</i>	-1.5	20	-1.3	20.9	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Osmundea</i>	<i>Osmundea spectabilis</i>	0	23	4.7	21.3	Field collected algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.2	18.4	[210]
<i>Petalonia</i>	<i>Petalonia fascia</i>	0 (-1)	24	-1.9	28.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Phycodrys Kützing</i>	<i>Phycodrys austrogeorgica</i>	-1.8	14	-1.9	4.0	cultured field-collected specimens (sporophytes and gametophytes)	King George Island	Antarctic	3.7	10.9	[203]
<i>Phycodrys Kützing</i>	<i>Phycodrys rubens</i>	-2	19	-1.9	24.0	sporophytes	Brittany, FR	temperate	8.10	19.90	[211]
<i>Phyllophora</i>	<i>Phyllophora pseudoceranooides</i>	0 (-1)	31.5	-1.5	24.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Pleurophycus Setchell &amp; Saunders ex J.Tilden</i>	<i>Pleurophycus gardneri</i>	-1.5	20	0.0	18.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Plocamium</i>	<i>Plocamium cartilagineum</i>	0	23	-1.9	30.0	Field collected algal material	Helgoland, GER, Friday Harbor, San Juan	temperate	1.44	19.7	[210]

							Island, Washington, USA					
<i>Plumaria</i>	<i>Plumaria plumosa</i>	0	25	-1.9	22.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]	
<i>Polyneura</i>	<i>Polyneura bonnemaisonii</i> ( <i>Polyneura hilliae</i> )	5.0	25	7.0	20.0	Tetrasporophytes	Roscoff, FR	temperate	8.1	19.9	[215]	
<i>Polyneura</i>	<i>Polyneura latissima</i>	0	23	0.5	21.3	Field collected algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.2	18.4	[210]	
<i>Porphyra</i>	<i>Porphyra umbilicalis</i>	0 (-1)	26.5	-1.9	27.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]	
<i>Postelsia</i> Ruprecht	<i>Postelsia palmaeformis</i>	-1.5	15	5.9	18.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]	
<i>Pterygophora</i> Ruprecht	<i>Pterygophora californica</i>	-1.5	25	4.5	21.3	gametophytes	Bamfield, CAN	temperate	6.20	18.40	[187]	
<i>Rhodochorton</i>	<i>Rhodochorton purpureum</i>	-1.8	25	-1.9	22.0	cultured field-collected specimens (sporophytes and gametophytes)	Ems-Dollard Estuary, Netherlands	temperate	2.45	19.7	[203]	
<i>Rhodomela</i>	<i>Rhodomela confervoides</i>	0 (-1)	24	-1.9	21.5	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]	
<i>Saccharina</i>	<i>Saccharina japonica</i> ( <i>Laminaria japonica</i> )	-1.5	26	-0.5	26.0	gametophytes	Hokkaido, Japan	temperate	-1.35	23.20	[187]	
<i>Saccharina</i>	<i>Saccharina latissima</i>	-1.5	26	-1.9	22.0	gametophytes	Helgoland, GER	temperate	1.44	19.70	[187]	
<i>Saccorhiza</i> Bachelot de la Pylaie	<i>Saccorhiza dermatodea</i>	-1.5	23	-1.9	20.6	gametophytes	Newfoundland	temperate to Arctic	-1.40	17.20	[187]	
<i>Saccorhiza</i> Bachelot de la Pylaie	<i>Saccorhiza polyschides</i>	0	24.5	3.0	24.0	gametophytes	Port Erin breakwater, Isle of Man, UK	temperate	4.75	18.9	[187]	

<i>Sarcodiotheca</i>	<i>Sarcodiotheca gaudichaudii</i>	0	25	3.0	27.0	Field collected algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.2	18.4	[210]
<i>Sargassum C.Agardh</i>	<i>Sargassum muticum</i>	-1.5	28	1.3	27.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Schizymenia</i>	<i>Schizymenia pacifica</i>	0	20	0.0	27.0	Field collected algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.2	18.4	[210]
<i>Smithora Hollenberg</i>	<i>Smithora naiadum</i>	-1.5	20	0.8	29.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Solieria</i>	<i>Solieria filiformis</i>	0	33.5	7.0	31.0	cultured gametophytes and tetrasporophytes	Port Isabel, Brownsville, TX, USA	temperate	16.9	30.1	[216]
<i>Soranothera</i>	<i>Soranothera ulvoidea</i>	-1.5	20	0.5	20.0	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Sparlingia G.W.Saunders I.W.Strachan &amp; Kraft</i>	<i>Sparlingia pertusa (Rhodymenia pertusa)</i>	-1.5	18	-1.8	24.3	Algal material	Friday Harbor, San Juan Island, Washington, USA	temperate	6.20	18.40	[210]
<i>Striaria Greville</i>	<i>Striaria attenuata</i>	-2	33.5	0.1	28.0	gametophytes (f&m)	Chiloé, Chile	temperate	8.50	16.60	[132]
<i>Ulva L.</i>	<i>Ulva curvata</i>	0 (-1)	29	3.0	26.0	Field-collected Sporophytes	Helgoland, GER	temperate	1.44	19.7	[197]
<i>Ulva L.</i>	<i>Ulva fenestrata</i>	-1.5	25	-1.8	30.5	Algal material	Friday Harbor, San Juan Island,	temperate	6.20	18.40	[210]

<i>Ulva</i> L.	<i>Ulva lactuca</i>	0 (-1)	29	-1.9	31.0	Field-collected Sporophytes	Washington, USA	cosmopolitan	several	-1.789672	31.079992	[197]
<i>Undaria</i>	<i>Undaria pinnatifida</i>	-1	29	0.0	29.5	gametophytes	Japan	temperate	-1.35	21.6		[187]
<i>Valonia</i>	<i>Valonia utricularis</i>	0	31.5	12.2	31.0	sporophytes from cultures	Mediterranean	temperate	8.5	30		[207]



## Synoptic discussion

In this section, the results from the individual research chapters are put into context. A detailed repetition of the results and discussions from the individual research chapters is omitted here.

Key finding 1 – Continental margins in the southern hemisphere prevent equilibrium distributions with consequences for biogeography of seaweeds and invasion biology

The first key finding of this thesis was found in research chapter 1, and further consolidated in research chapter 2. In research chapter 1, I concluded that the fundamental niche of *C. implexa* is restricted to its realized niche by the lack of rocky coasts as settling substrate south of the continental margins of Australia, New Zealand and South America. Thus, while this alga could grow at colder temperatures than found in its native range, the abiotically suitable sites are sparsely distributed over vast distances, in the form of small islands across the Southern Ocean. As such, it has little to no opportunity to unaidedly migrate further south due to the large distances between sparse suitable sites. This leads to a state of niche underfilling in this alga. This finding was the basis of the research objective in research chapter 2: To what extent do other temperate species have cold-tolerances towards conditions beyond those found in their native ranges? In order to address this question, I used recently discovered, presumably non-native Antarctic seaweed species for the assessment. The results indicate that the finding from research chapter 1 can be extended to other species, and that indeed many temperate species could have cryptic extreme cold-temperature adaptations which allow them to settle in polar habitats (see also key finding 2). Hence, I conclude that especially southern hemisphere seaweed species can have hidden cold-tolerances, but are restricted to their realized niches by the absence of further settling substrate and large distances between habitats. In the framework of the BAM diagram by <sup>[1]</sup>, this can be regarded as a restriction in the M (“movement”) dimension. Although the Polar Front is not as strict barrier as historically assumed and permeable via eddies and drifting material <sup>[16, 74]</sup>, it is still a major barrier for most organisms because of the lack of settling substrate at the sea surface and extreme depth of the seafloor <sup>[243]</sup>, which can restrict geographical distributions. With respect to southern hemisphere distributions and especially the Antarctic ecosystem, this is a highly relevant finding, since previous studies on the invasiveness of Antarctica have adopted the climate-matching hypothesis for the assessment of Antarctic invasion risk <sup>[70, 162]</sup>. Under the assumption that not only species which already thrive under polar conditions pose an invasion risk, but also temperate species do so, the pool of potential invaders is dramatically enlarged and the invasion pressure might be much higher than previously assumed. The implications for Antarctic biodiversity will be discussed below.

## Key finding 2 – Patterns in non-equilibrium distributions in global seaweeds with implications for forecasting of climate change effects and invasion biology

In research chapter 3, I further elaborated on the aspect of non-equilibrium distributions and investigated how well thermal tolerances predict seaweed distributions on a global scale. The analyses showed that non-equilibrium distributions are common in seaweeds and that seaweed distributions regularly show deviations from the predicted range limits. Here, two major results were found: First, that there is an independence of cold-tolerance and distribution limit, as the state of niche underfilling increased with the decrease of the latitudinal poleward distribution limit. This confirms the findings from research chapters 1 and 2, in which I already showed that temperate species can have cold-tolerances although they are not reflected in their actual distributions. Upper survival temperatures seemed to better predict distributional patterns, although also here, under- and overfilling were present in many species. This is important in context of the second major finding from this chapter. Namely, that a large share (56%) of the investigated 126 species had distributional limits at or beyond their survival limits. This indicates that the upper survival temperature limits might be rather adaptive (i.e. match realized temperature conditions), and strengthens that subpopulations might have different tolerances <sup>[188]</sup>, but also that a large share of species is thriving at their upper temperature limits and thus under threat of global warming. This is in line with the finding from research chapter 1, where I predicted a range contraction for *C. implexa* under global warming. The effects of global warming on seaweed distributions are discussed below.

## Outlook on Antarctic biodiversity

The results from research chapters 1 and 2 indicated that the pool of potential invaders for Antarctica is considerably larger than previously assumed. The results from research chapter 3 strengthen the assumption that cold-tolerances can be independent of geographic distributions and thus confirm this estimation.

On a global scale, climate change and bioinvasions are the main drivers of biodiversity loss <sup>[44, 244]</sup>. Climate change leads to redistribution of communities via changes in abiotic conditions and, in polar systems, via retreat of sea-ice. The majority of endemic Antarctic species, which thrive south of the polar front, will experience a significant reduction in the amount of suitable habitat due to global warming, leading to localized extinctions <sup>[245]</sup>. For these species, the potential to migrate to colder waters is extremely limited if not entirely impossible. Further, <sup>[246]</sup> wrote that the increasing extent of ice-free areas in Antarctica might lead to biotic homogenization and loss of less competitive species. They forecast that the number of ice-free patches will decrease while area per patch increases, due to coalescence of today's individual ice-free patches. Thus, species which thrive in largely isolated patches will come in contact with other species and might lose habitat to competitively superior species, potentially including non-natives, since emergence of larger ice-free areas will give opportunity for

restructuring of Antarctica's species distributions both for Antarctic as well as non-Antarctic species. Antarctic species are especially vulnerable to invasions, since they show a high level of endemism, and low interspecies competition in their native habitats and communities [163, 247, 248]. It is not clear, whether the immigration of other Antarctic or non-Antarctic species could outweigh the loss of species. Still, [243] project a "substantial redistribution rather than wholesale extinction or invasion" for Antarctic benthic species. In this scenario, immigration of species to abandoned niche space might even increase absolute biodiversity locally. Thus, effects on Antarctic biodiversity will be spatially heterogeneous with some regions experiencing increases and others experiencing decreases in diversity [245]. Nevertheless, climate change leads to a disturbance of the Antarctic ecosystems and therefore increases its vulnerability towards invasions [53].

Alien or invasive species are rare in continental Antarctica, but more common on sub-Antarctic islands and include plants, invertebrates, vertebrates, microorganisms, and marine macroalgae [162]. The effects of non-native species on Antarctic ecosystems are mostly not yet understood but some have documented significant negative effects on native Antarctic biodiversity [162]. Many of these reported non-native species are globally widespread, and have invasion histories in other regions of the world. Of the (sub-)Antarctic alien species, most are of European origin, i.e. of temperate origin [162]. Given that the majority of alien species is found in sub-Antarctic habitats, [162] concluded that the climate matching hypothesis (i.e. that species will be more successful at establishing in habitats matching their native conditions) mostly applies to (sub-)Antarctic non-native species. However, next to my findings, [82] provided an example (the mussel *Mytilus cf. platensis*) where this hypothesis might not apply. In addition, the non-native grass *Poa annua* in Antarctica is of Polish origin and thus from a non-polar source population [165]. These species are therefore apparently not excluded from Antarctica by extreme environmental conditions, but by geographic barriers. Thus, the global pool of potential invaders might be much larger than under the assumption that only (sub-)polar species could establish in Antarctica. For these species, warming of Antarctica is not a prerequisite for successful settlement and there is an urgent need to assess on a larger scale to what extent the climate-matching hypothesis is valid for Antarctica's non-natives. It is important to point out that among the species which I included in research chapter 2 are species which have introduction histories in other parts of the world or are successful and defining elements of the native flora in their native habitats. Thus, their establishment in Antarctica might strongly change the local community structure.

A prerequisite for introduction is arrival. [162] named human activities a main driver of introductions (and degree of climate matching between source and target habitat as a major predictor for a successful outcome). Human activities in Antarctica are increasing and the climate is changing, making introductions more likely and potentially more successful. There are natural long-distance vectors [16, 162], and an increase in floating non-natural objects [77] in concert with a weakening of Antarctica's

isolative forces <sup>[16]</sup>, thus, propagule pressure and introductions might considerably increase. Based on my findings, it is not sufficient to focus on transportation vectors between polar regions, but also vectors between temperate and Antarctic regions might be potential introduction vectors for cold-tolerant species and have to be considered in invasion risk assessments.

To broaden the view on expected effects of global warming and sea-ice retreat on polar ecosystems, the Arctic environment will shortly be discussed here. Both Antarctica and the Arctic are facing major changes with respect to both climate change and connectivity <sup>[3, 16, 240]</sup>. Both regions are remote and climatically extreme, making field research difficult (for impressive historic reference see <sup>[249]</sup> and references therein) and making them relatively understudied when compared to e.g. European or North American temperate coasts (compare e.g. availability of species occurrence data, and data on species inventories <sup>[81]</sup>). Thus, it is beneficial to add insights from the Arctic to complement assumptions on the expected changes in Antarctica. <sup>[238]</sup> predicted a sea-ice free summer in the Arctic for as early as 2037, and effects of climate change include a variety of organism-specific responses <sup>[250]</sup>. <sup>[251]</sup> investigated Western Greenland's intertidal ecosystems and predict a high resilience towards climate change with probably increased productivity under warmer temperatures and prolonged ice-free seasons <sup>[40, 252]</sup>. They also rate the introduction of non-native species as more threatening than global warming for Arctic biodiversity and communities <sup>[239]</sup>. The risk of invasion will increase under future climatic conditions, since sea-ice retreat opens new habitats and new navigable shipping routes through Arctic waters, with shipping being a major vector for non-native species <sup>[8, 240, 241]</sup>. Thus, both polar regions will face dramatic changes in the future via climate change and increased number of transportation vectors for non-native species. While it is naturally difficult to accurately predict effects on the recipient ecosystems, researchers working in polar regions have come to comparable conclusions: Global warming will have dramatic effects on species, community-structures and productivity in both polar systems, and species will experience range shifts towards colder habitats where possible. For both poles, the introduction of non-native species is seen as a major, perhaps more serious, threat for biodiversity and there is a recognized increase in transportation vectors due to human activities. Identification of potential invaders and invasions sites is therefore crucial <sup>[70, 239]</sup>. Based on my results, these potential invaders might stem also from non-polar environments and might have cold-tolerances which are not visible from their current distributions, leading to an increase in numbers of potential invaders.

#### Effects of global warming on seaweed distributions

From both publications 1 and 3, conclusions can be drawn on how climate change will affect species distributions in the future. In these chapters, I used present-day distributional data to identify the species realized niches (research chapter 1) and climatic envelopes (research chapter 3), respectively. These were then used to discuss effects of changing climate on species distributions. For *Caprella*

*implexa* (research chapter 1), I explicitly used projections for future SSTs to make predictions of habitat suitability under future climate scenarios. In research chapter 3, I used information from the literature to discuss effects of rising SSTs on seaweed distributions. Research chapter 1, provides a vivid example of how the conclusions translate to individual consequences for future range projections on a species-level scale, while the results from research chapter 3 are of a more general nature and effects are discussed in a global context. In both cases, global warming will decrease the habitat suitability at the equatorward distributional edge and therefore probably cause poleward range-shifts of the distributions, potentially leading to overall loss of total amount of available habitat. For *C. implexa*, this conclusion is based on the projection of its suitable range under assumption of climate projections for the year 2100 with rcp 2.6 and rcp 8.5, respectively. In research chapter 3, I found that 56% of the investigated species thrive at or even beyond their upper survival temperature limit. Here, warming might lead to shifts in distributions as well, as populations might face local extinctions [6, 39, 99]. [6, 39] reported that seaweed populations are in retreat of global warming, and thus, losing substantial amounts of settling habitat in temperate environments along the shores of southern continents. Here, between the continental masses of South America, South Africa, New Zealand & Australia and Antarctica, rocky shores are limited mostly to small islands in the Southern Ocean. Thus, loss of suitable habitat in these temperate zones leads to absolute loss of suitable habitat, since range shifts are only possible to a very limited extent. The example of *C. implexa* illustrates how a poleward range-shift leads to overall reduction of suitable habitat. In both its native (Australia & New Zealand) as well as novel range (Chile), the Southern Ocean represents a strict distributional barrier at the southern distributional limit, since settling habitat is scarce and distances between potentially suitable sites are vast. *C. implexa*'s suitable range will not entirely be shifted beyond the continental margins, but for other species this is true and extinctions have to be expected [6, 39]. The projected southward range shift of *C. implexa* illustrates how seaweeds are retreating from rising temperatures on a global scale and losing overall suitable habitat [5, 6, 39, 139]. Losses of species from local habitats can have cascading effects on associated organisms and overall biodiversity, as has been shown for Tasmanian kelp habitats [253]. *C. implexa* is not known as a foundation species, but being a mat-forming species, it likely provides shelter from desiccation to associated flora and fauna [65], and its loss might thus have effects on abandoned sites and its species composition. It might be replaced by other southward shifting species, which provide comparable shelter functions. However, species associations can be highly specialized and not be transferable to another combination of species (e.g. [254] [255]). Thus, replacement of *C. implexa* by other, functionally similar (i.e mat-forming) species, might not lead to a functional substitution for associated taxa. The species-pool in research chapter 3 includes more prominent foundation species, such as the Laminariales *Saccharina japonica* and *Macrocystis pyrifera* among others, which provide highly important functions to their communities. Changes in their abundance

will cause profound changes in habitat configuration, by altering its three-dimensional structure, currents, radiation and overall biomass, and have huge impacts on community composition and biodiversity of associated taxa <sup>[256]</sup>.

Heat stress at the warm edge of species distributions is not a stable phenomenon but subject to fluctuations, known as heat-waves <sup>[43]</sup>. Heat-waves increase in the course of global warming, can periodically increase heat stress on populations, and cause high rates of mortality <sup>[42]</sup>. This variability was not included in the projection of *C. implexa*'s suitable future range, and thus, the overall loss of habitat might be underestimated. <sup>[132]</sup> reported how seaweed species keep a safety-margin between its fundamentally suitable limit and the realized suitable limit, corresponding to a temperature range of 2 - 3°C. With an increase in extreme temperature events, the geographic extent of such a safety margin might increase to not only account for a higher mean SST, but also higher occurrence of unsuitable extreme temperature events. Without the inclusion of heat-waves, the SDM in research chapter 1 predicted a loss of approximately 50% of suitable habitat for the year 2100 under the rcp 8.5 scenario and in research chapter 3, already 56% of the species were close to or beyond their tolerance limits. Extreme temperature events will largely increase the temperature pressure on these species and probably lead to larger range-shifts than mean SST alone <sup>[42]</sup>.

### Conclusions on the research objectives

Research objective 1: Identification of the potential distributional range of the non-native red alga *Capreolia implexa*'s via correlative SDM and physiological data – identification of the Southern Ocean as dispersal barrier

In research chapter 1, I identified the realized thermal niche and the lower temperature tolerance limit of *C. implexa*. The results showed that the fundamental niche is not filled, and that the geographic limit corresponding to the temperature tolerance limit is projected to lie south of the southern hemisphere landmasses. Thus, lack of settling substrate probably leads to a niche underfilling situation in *C. implexa*. Further, under global warming, *C. implexa*'s suitable habitat will shrink between the northern boundary and continental margins to the south. At the same time, the suitable habitat range in South America is larger than previously assumed.

Research objective 2: Assessment of invasion potential of non-polar seaweeds for Antarctica

In the second research chapter, the findings of research chapter 1 were applied to Antarctic seaweeds and how it may have implications for bioinvasions into Antarctica. I hypothesized that especially species in the southern hemisphere might have truncated realized niches by the lack of settling substrate between Antarctica and other landmasses in the southern hemisphere. I argued further that species in South America, Australia, New Zealand, Southern Africa and other isolated temperate regions might have cold-tolerances which they cannot occupy due to lack of substrate. However, these tolerances would perhaps allow them to successfully establish in Antarctica, while it is not possible to

derive such tolerances from their original distributions. I used data on the distributions of newly discovered Antarctic seaweeds, and compared pre-Antarctic and Antarctic-inclusive realized thermal niches. To do so, I used data on their distributions from databases and the literature and applied the methods described by <sup>[98]</sup> to assess niche overlaps. The results indicated that temperate seaweed species might indeed be able to successfully establish populations in Antarctica and that the climate-matching hypothesis is not sufficient to describe invasive potential. This is especially relevant in the light of declining isolation of Antarctica <sup>[16]</sup>, as it extends the pool of potential invaders by adding temperate species without a polar distribution.

Research objective 3: Comparison of realized and fundamental thermal niches of seaweeds, with implications for real-world niche identification, responses to climate change and threats via global warming

In research chapter 3, I aimed at investigating how well thermal tolerances predict realized distributions of seaweed species. It was surprising that non-equilibrium distributions in seaweeds were widespread to such a large extent. This indicates that responses towards climate change might be highly variable between species. In addition, many species were distributed beyond their upper thermal tolerance limits. These findings are relevant in the context of research chapter two, as it underlines that cold-tolerances are widespread and perhaps not discernable from the distributional ranges. Further, it highlights how many seaweed species thrive already under present-day SST conditions on the edge or even beyond their temperature tolerance limits. These populations are probably under threat of local collapse due to increasing SSTs and increase in intensity and frequency of marine heatwaves.

### Future perspectives

From the here presented results, future research objectives can be derived:

- (1) How widespread are “cryptic” cold-tolerances in seaweeds from the southern hemisphere?

In all three research chapters I investigated how well LST predicts the realized thermal distributional limits, and found that underfilling is common and, in southern species, probably caused by range limitation via continental margins. Especially large-scale habitat forming species such as the wide-spread, southern bull kelp *Durvillaea antarctica* and the kelp *Macrocystis pyrifera* need to be investigated for their cold-temperature tolerances and thus capabilities to tolerate and invade Antarctic conditions and sites, respectively. Both species are frequently observed rafting in the Southern Ocean and even at the WAP <sup>[16, 78]</sup>. Thus, they serve not only as transport vectors for other species to Antarctica, but have themselves a constant supply of individuals which could perhaps found new populations. In the future, sea-ice will further retreat at the WAP and SST rise, thus, conditions might become more hospitable for these kelp species, and allow its establishment. This might cause a profound

regime shift since so far kelps are absent from Antarctica <sup>[257]</sup>. Therefore, knowledge of their potential to establish populations under present and future SST conditions is important.

(2) To what extent are temperature tolerances conserved in seaweeds?

It will be interesting to map fundamental thermal niches along phylogenetic trees of seaweeds with different geographic origins (see e.g. <sup>[230]</sup>). Like this, evolution of tolerances and adaptation potentials and their loss can be followed over evolutionary time and along migration pathways. This will allow to better understand the adaptive potential of seaweeds to react to global warming, but also help to identify and understand tolerances for temperatures outside their distributional range. The latter will be important to assess invasive potential of seaweed species and their vulnerability to global warming.

(3) How do light availability and temperature regime prevent invasions of seaweeds into polar regions?

Light will be an important, and perhaps limiting, factor for the successful establishment of each newcomer to Antarctica. Figure 23 shows the yearly seasonality of daylength as a function of latitude and illustrates the strong difference in light seasonality between polar and non-polar areas (figure made with the `daylength()`-function from the `geosphere` R-package <sup>[258]</sup>, following <sup>[259]</sup>). The northernmost tip of the WAP, from where the species in research chapter 2 were reported, lies north of the southern polar circle and thus does not have polar night, while the vast majority of the WAP and Antarctica as a whole do so. To what extent these species could migrate further poleward, i.e. into latitudes where polar winter and polar summer occur, is unclear. <sup>[260]</sup> summarized that “favorable light conditions for algal growth are present for only 2-3 months per year” in Antarctic habitats. Here, they describe how algae have to face a high seasonality in light conditions throughout the year and have to be able to withstand long periods of darkness, but at the same time be able to make the maximum use out of the short period when light is available <sup>[260]</sup>. <sup>[260]</sup> conclude that the high degree of adaptation to polar light conditions makes polar seaweeds successful in their extreme environments. Thus, newcomers will be exposed to a light environment which is characterized by extreme seasonality and inhabited by highly specialized native species as competitors for space.

Experiments in which both temperature and light effects according to polar conditions are rare (but see <sup>[261]</sup>). For an assessment of invasion potential for Antarctica, both aspects will have to be experimentally tested in future studies.

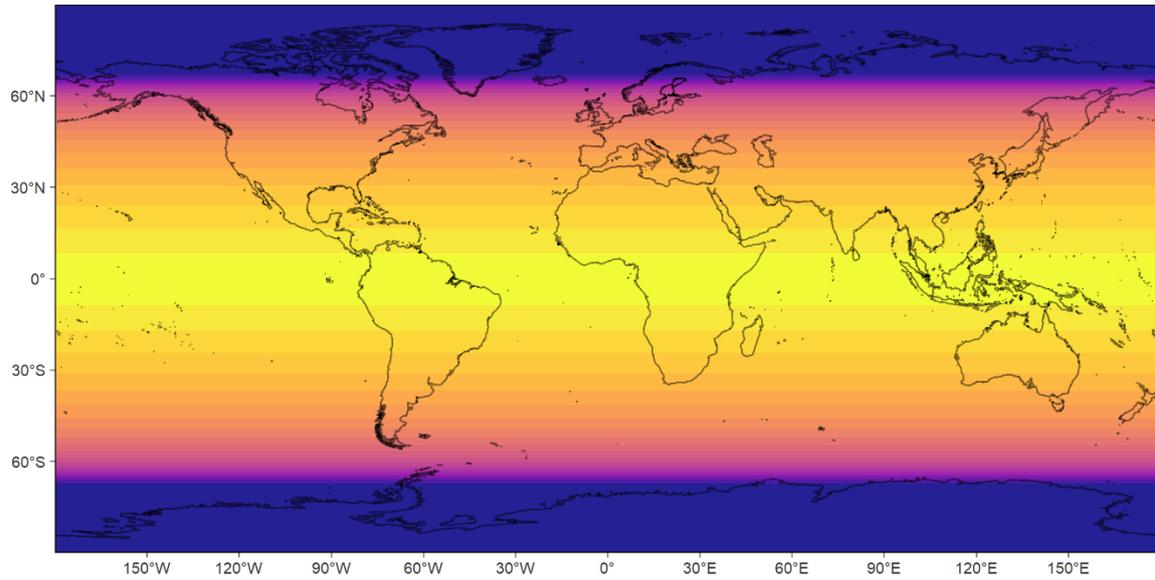


Figure 23. Seasonality of daylength as a function of latitude. The graph shows the absolute difference in hours of daylight between winter and summer solstice. Brightest colors around the equator show low seasonality (difference = 0 hours) which increases to a maximum of 24 hours poleward.



## Versicherung an Eides Statt

Ich,

Philipp Laeseke,

versichere an Eides Statt durch meine Unterschrift, dass ich die vorstehende Arbeit selbstständig und ohne fremde Hilfe angefertigt und alle Stellen, die ich wörtlich oder dem Sinne nach aus Veröffentlichungen entnommen habe, als solche kenntlich gemacht habe, mich auch keiner anderen als der angegebenen Literatur oder sonstiger Hilfsmittel bedient habe. Ich versichere an Eides Statt, dass ich die vorgenannten Angaben nach bestem Wissen und Gewissen gemacht habe und dass die Angaben der Wahrheit entsprechen und ich nichts verschwiegen habe.

Die Strafbarkeit einer falschen eidesstattlichen Versicherung ist mir bekannt, namentlich die Strafandrohung gemäß § 156 StGB bis zu drei Jahren Freiheitsstrafe oder Geldstrafe bei vorsätzlicher Begehung der Tat bzw. gemäß § 161 Abs. 1 StGB bis zu einem Jahr Freiheitsstrafe oder Geldstrafe bei fahrlässiger Begehung.

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*Ort, Datum, Unterschrift*



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