RESEARCH ARTICLE

Frontiers of Biogeography
the scientific journal of
the International Biogeography Society

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

Philipp Laeseke[1]*, Brezo Martínez[2], Andrés Mansilla[3] and Kai Bischof[4]

[1] Department of Marine Botany, University of Bremen, Department 2, Leobener Straße NW2, 28359 Bremen, Germany; [2] Universidad Rey Juan Carlos, Área de Biodiversidad y Conservación, c/ Tulipán s/n., E-28933 Móstoles, Madrid, Spain; [3] Laboratory of Antarctic and Sub-Antarctic Marine Ecosystems (LEMAS), University of Magallanes, Institute of Ecology and Biodiversity (IEB), Avenida Bulnes 01855, Punta Arenas, Chile; [4] Department of Marine Botany & MARUM, University of Bremen, Department 2, Leobener Straße NW2, 28359 Bremen, Germany

*Correspondence: Philipp Laeseke, philipp.laeseke@posteo.de

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

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

e-ISSN: 1948-6596 https://escholarship.org/uc/fb doi:10.21425/F5FBG50879

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 (Ruiz et al. 1997, Casas et al. 2004, Raffo et al. 2009, Vilà et al. 2010). 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 (Leung et al. 2002, Chapuis et al. 2004, Wotton et al. 2004, Bergstrom et al. 2009, Convey and Peck 2019). Ecological niche models (ENM) can help predict the invasive potential of alien species and identify the geographic space at risk of invasion (Guisan and Thuiller 2005, Peterson 2005, Jiménez-Valverde et al. 2011). 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, (Hutchinson 1957)] 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 (Atwater et al. 2018, Cárdenas et al. 2020) 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 (Peterson 2005).

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. Peterson et al. 1999, Losos 2008, Warren et al. 2008). Ample examples exist for niche shifts for a variety of organisms, such as terrestrial plants (Broennimann et al. 2007, Atwater et al. 2018), freshwater fish (Lauzeral et al. 2011), insects (Fitzpatrick et al. 2007, Medley 2010, Hill et al. 2017), and a bivalve in Antarctica (Cárdenas et al. 2020). In all these examples, the invaders occupy environmental space which they did not occupy in their native ranges. Contrary to this, Petitpierre et al. (2012) 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 (Guisan et al. 2014). 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 (Clayton et al. 1997, Gallardo et al. 1999, Wiencke and Clayton 2002, Yoneshigue-Valentin et al. 2013, Pellizzari et al. 2017). 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 (Lowe et al. 2000, Williams and Smith 2007). Antarctica, the "final frontier for marine biological invasions" (McCarthy et al. 2019), 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 (Lüning 1990). 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 (Lüning 1990, Clarke et al. 2005, Chown et al. 2015). 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 (Barnes et al. 2010, Lynch et al. 2010, Chown et al. 2012). 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 (Fraser et al. 2018, Avila et al. 2020). 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 (Braun and Gossmann 2002, Zacher et al. 2009, Fraser et al. 2018). 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 (Clayton et al. 1997, Gallardo et al. 1999, Frenot et al. 2005, Chown et al. 2012, Hughes et al. 2015, McGeoch et al. 2015, Fraser et al. 2018). Evidence indicates that Antarctic invaders, like the mussel *Mytilus* cf. *platensis* (Cárdenas et al. 2020) or the terrestrial grass *Poa annua* (Chwedorzewska 2008) 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 (Hughes and Convey

2012). 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.

Materials 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 Papenfuss (1964), Wiencke and Clayton (2002), Wiencke et al. (2014), references therein and references listed on www.algaebase.org (Guiry and Guiry 2020) and under inclusion of former nomenclature to verify true novel records. For all species, distributional data were collected from www.gbif.org (link to dataset: https://www.gbif.org/occurrence/download/0078530-200221144449610, accessed June 4th, 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 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 (Assis et al. 2017)]. 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. Lüning (1990) and Peters and Breeman (1993) 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 (Lüning 1990) 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 (Davison et al. 1989, Lüning 1990, Becker et al. 2009).

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 Nyberg and Wallentinus (2005). Nyberg and Wallentinus (2005) 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. Nyberg and Wallentinus (2005) 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 assessment in a category, we include information from related species occurring in the same biogeographic regions. Note that we do not assign definitive values

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 Nyberg and Wallentinus (2005).

Niche metric analysis

To calculate climatic niche sizes, we used the "dynRB-Vpa()"-function of the "dynRB"-package (Junker et al. 2016) in R (R Core Team 2020). 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 Qiao et al. (2016). 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 (Junker et al. 2016) was used to allow comparisons. For a detailed method description for size and overlap calculation in the dynRB-package consult the original publication by Junker et al. (2016).

Geospatial data for this study was processed with the "raster" (Hijmans 2020) and "rgdal" (Bivand et al. 2020) packages in R (R Core Team 2020). Graphs and maps were made with the "ggplot2" (Wickham 2016) and "tmap" packages (Tennekes 2018), also in R (R Core Team 2020).

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 1, Fig. 1). The species occur in varying amounts, ranging from small, localized populations (e.g. *Dictyota decumbens*, Pellizzari et al. 2017) to wide-spread populations across several islands and coastlines along the South Shetland Islands [e.g. *Ulva intestinalis*, Clayton et al. (1997); Pellizzari et al. (2017)]. Four of the species (*Blidingia minima, Ulva intestinalis, Ulva compressa, Petalonia fascia*) are treated in the literature as introduced species (Wiencke and Clayton 2002). For one species, introduction via anthropogenic vectors is discussed as a possibility (*Monostroma grevillei,* Pellizzari et al. 2020).

Except for one species (*D. decumbens*), all species have well-documented distributions throughout other climatic zones in the Northern and/or Southern Hemisphere(s) (Fig. 2) 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 limits in this category are between 47 and 55.5°S. *M. grevillei* has one record at 40.6°S from Chile (Navarro et al. 2019) 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 (Bolton et al. 2007) and *D. decumbens*, which is exclusively known from Macquarie Island (Ricker 1987).

Introduction potential

We evaluated the potential for successful introduction in accordance with the publication by Nyberg and Wallentinus (2005) and assigned the following potentials to the species based on species

Table 1. Pre-Antarctic distributions of the newly recorded Antarctic seaweeds with northern & southern latitudinal limits and number of global records from 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
Blidingia minima (Chlorophyta – Ulvales – Blidingia)	I	Cosmopolitan or amphiequatorial	76.96	-54.04	752	Gallardo et al. (1999), Wiencke and Clayton (2002)
Monostroma grevillei (Chlorophyta – Ulotrichales – Monostroma)	I	Cosmopolitan or amphiequatorial	70.38	- 40.58	502	Pellizzari et al. (2017)
Petalonia fascia (Phaeophyta – Ectocarpales – Petalonia)	I	Cosmopolitan or amphiequatorial	74.71	-54.54	1074	Clayton et al. (1997), Pellizzari et al. (2017)
Ulva compressa (Chlorophyta – Ulvales – Ulva)	I	Cosmopolitan or amphiequatorial	70.37	-51.54	1004	Clayton et al. (1997), Pellizzari et al. (2017)
Ulva intestinalis (Chlorophyta – Ulvales – Ulva)	I	Cosmopolitan or amphiequatorial	71.29	-55.21	2383	Clayton et al. (1997), Pellizzari et al. (2017)
Callophyllis pinnata (Rhodophyta – Gigartinales – Callophyllis)	II	Pacific coast of North America	60	30.43	81	Yoneshigue-Valentin et al. (2013)
Asteronema ferrugínea (Phaeophyta – Scytothamnales – Asteronema)	III	Southern Australia, Tasmania, Argentina, Macquarie Island	-37.17	-54.61	16	Pellizzari et al. (2017)
Cladodonta lyallii (Rhodophyta – Ceramiales – Cladodonta)	III	South America, Subantarctic Islands	-42.36	-55.53	25	Pellizzari et al. (2017)
Dictyota decumbens (Phaeophyta – Dictyotales – Dictyota)	III	Macquarie Island	-54.62	-54.62	(*)	Pellizzari et al. (2017)
Microzonia velutina (Phaeophyta – Syringodermatales – Microzonia)	III	New Zealand, Subantarctic Islands, Argentina	-34.13	-54.79	45	Pellizzari et al. (2017)
Rhizoclonium ambiguum (Chlorophyta – Cladophorales – Rhizoclonium)	III	South America, Subantarctic Islands	-3.6	-54.77	26	Pellizzari et al. (2017)
Rhodophyllis centrocarpa (Rhodophyta – Gigartinales – Rhodophyllis)	III	New Zealand, South America	-35.25	-54.76	38	Pellizzari et al. (2017)

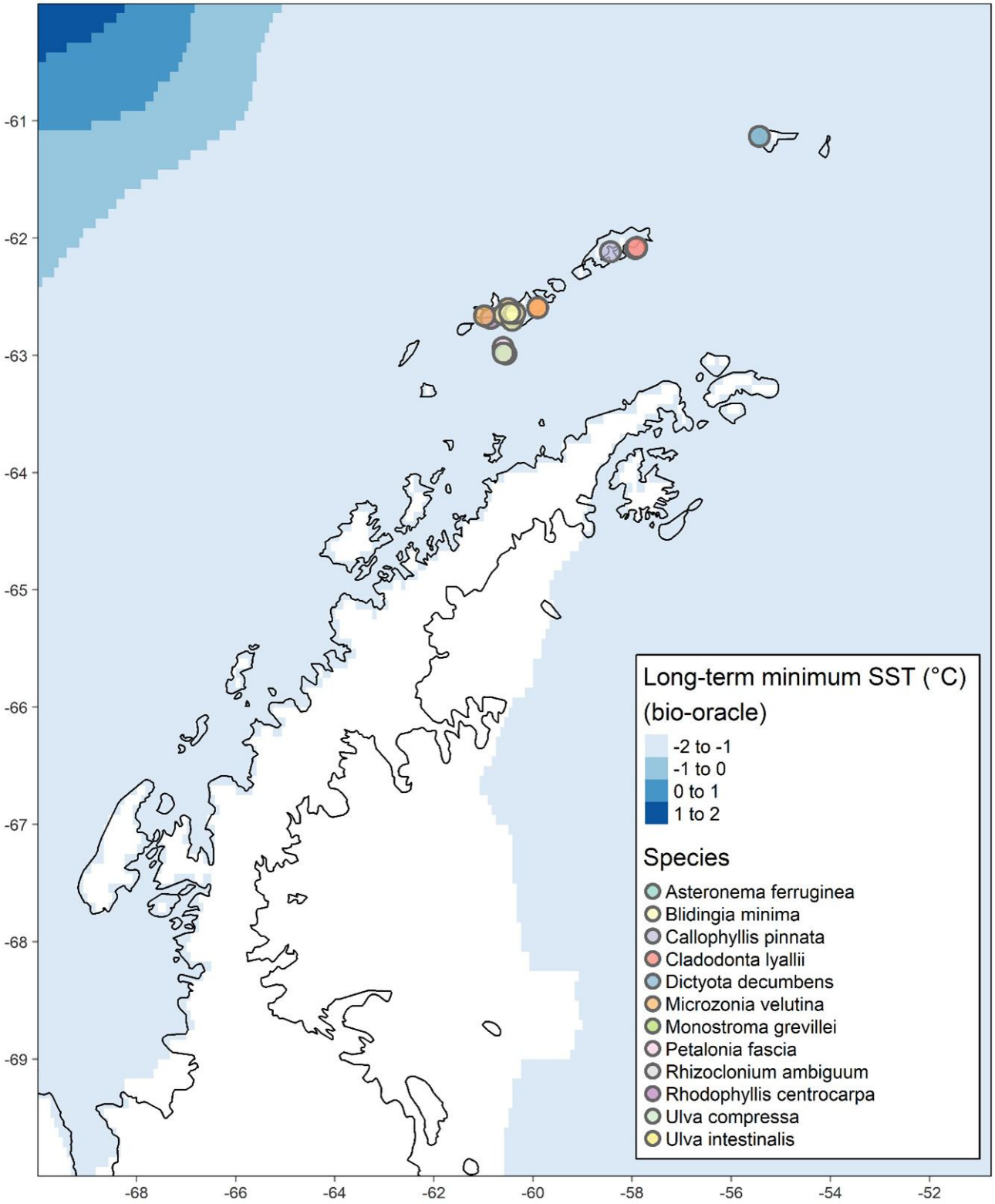

Figure 1. Locations where the novel species were reported at the South Shetland Islands (references in Table 1) and long-term minimum sea surface temperature from bio-oracle v2.0 (Assis et al. 2020).

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,

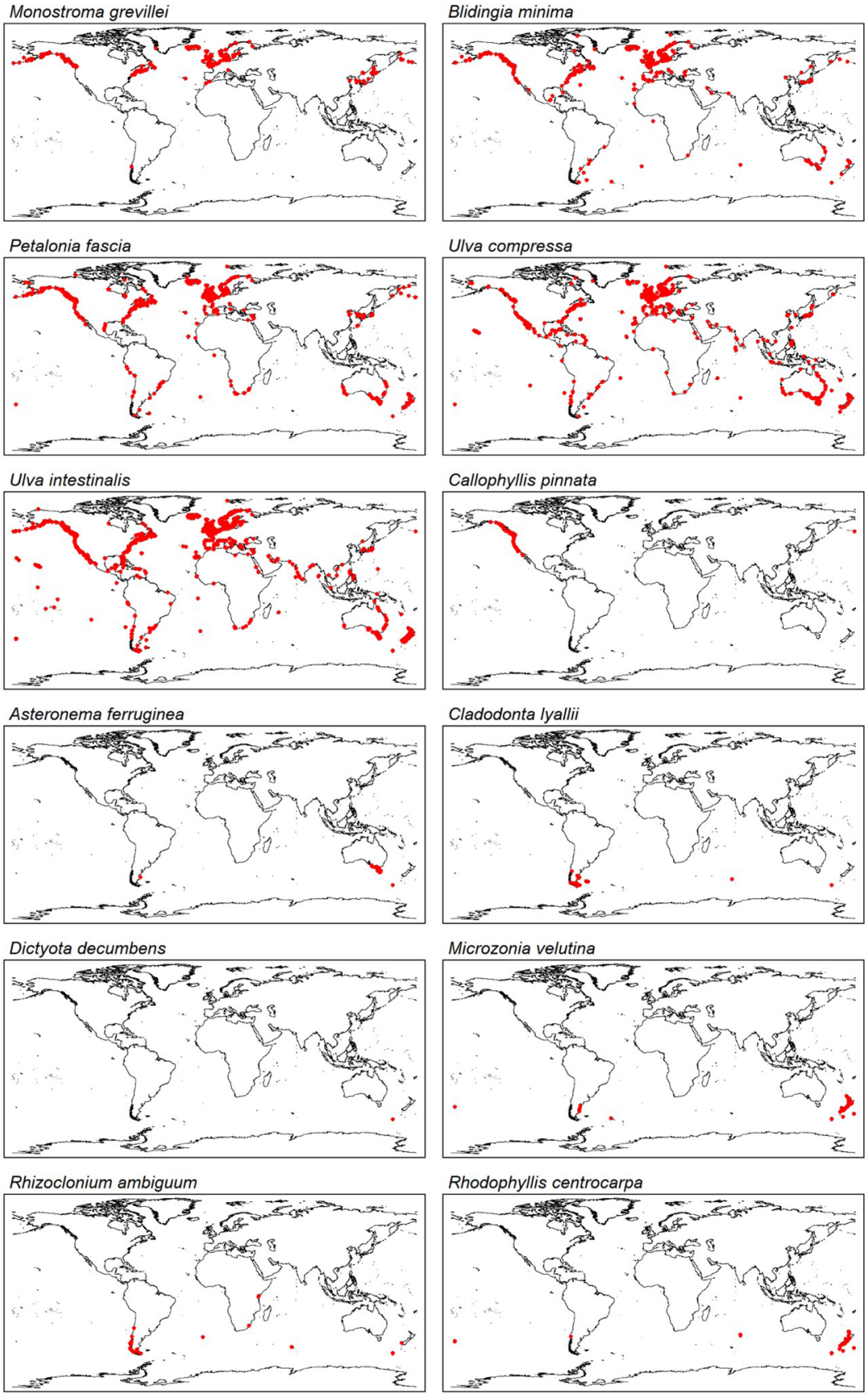

Figure 2. Pre-Antarctic distributions of all species. Records from www.gbif.org and www.algaebase.org (Guiry and Guiry 2020). Pre-Antarctic data were thinned to one record per grid-cell to remove duplicates.

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 (Gallardo et al. 1999, Fraser et al. 2018, Avila et al. 2020). 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 (Fig. 3). 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 Nyberg and Wallentinus (2005). 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 (Fig. 3, Table 2). 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 (Fig. 4). 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

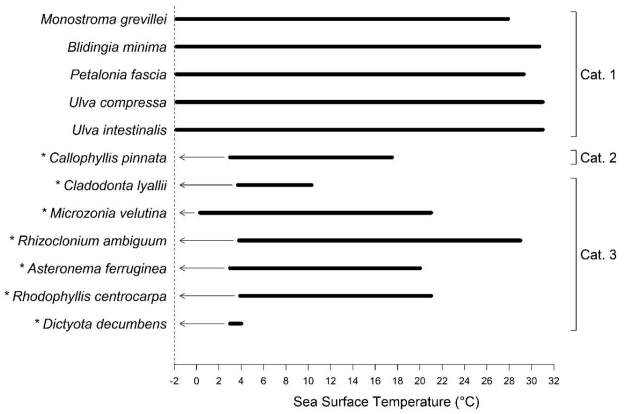

Figure 3. Absolute pre-Antarctic SST ranges (black lines) as sampled from bio-Oracle v2.0 layers with all available distributional data from www.gbif.org and the literature. Minimum sea surface temperature at the Antarctic sites is approximately -1.9°C (y-axis, dashed). Species with range extensions are marked with an asterisk and arrows indicate shift of the minimum SST. Categories based on native latitudinal distribution as in Fig. 2 (Category I = cosmopolitan or amphiequatorial; Category II = endemic to Pacific coast of North America; Category III = distributed only in the Southern Hemisphere).

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.

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 (Fig. 5). 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

Table 2. 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 (Junker et al. 2016).

	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	*Monostroma grevillei*	0.608862569	0.687181726	0.078	12.9
	Blidingia minima	0.960385456	0.986921535	0.027	2.8
	Petalonia fascia	0.608360130	0.714795528	0.106	17.5
	Ulva compressa	0.972191388	0.994561049	0.022	2.3
	Ulva intestinalis	0.977391961	0.994356300	0.017	1.7
Cat. II	*Callophyllis pinnata*	0.282159610	0.727445728	0.445	157.8
Cat. III	*Cladodonta lyallii*	0.159983510	0.563450574	0.403	252.2
	Microzonia velutina	0.633667207	0.885464204	0.252	39.7
	Rhizoclonium ambiguum	0.910290667	0.986724482	0.076	8.4
	Asteronema ferruginea	0.323343954	0.866235802	0.543	167.9
	Rhodophyllis centrocarpa	0.521627662	0.883306074	0.362	69.3
	Dictyota decumbens	0.009891661	0.511214360	0.501	5068.1

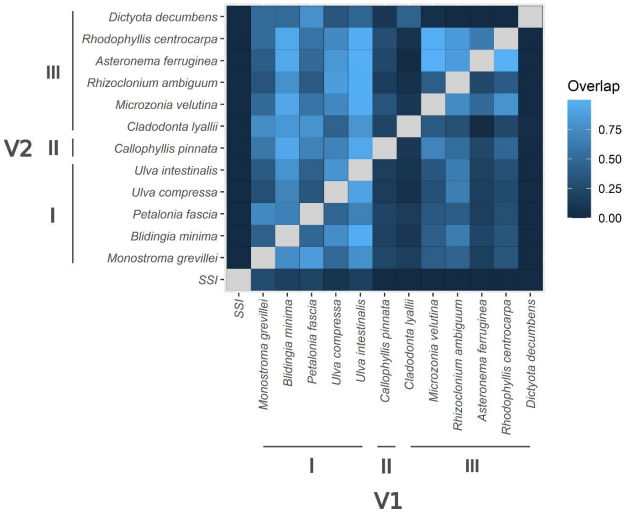

Figure 4. Niche overlaps between pre-Antarctic niches and Antarctic sites (SSI = South Shetland Islands). V1 = Volume 1, V2 = Volume 2. Read like this: *D. decumbens'* niche (as V1) does not contain any other species' niche (V2) and has therefore overlap values around 0 along the y-axis but is contained within the niches of most other species and has therefore higher overlap values along the x-axis (Junker et al. 2016). Data included: Minimum and maximum sea surface temperature data from the pre-Antarctic virtual species' niches. Aggregation method = "mean".

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.

Discussion

Twelve seaweed species have been reported in the literature as new additions to the Antarctic flora (Clayton et al. 1997, Gallardo et al. 1999, Wiencke and Clayton 2002, Yoneshigue-Valentin et al. 2013, Pellizzari et al. 2017). 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 Guisan et al. 2014). In our case study, we explicitly used a model system with unconnected donor (pre-Antarctic) and recipient (Antarctic) sites, characterized by a strong latitudinal

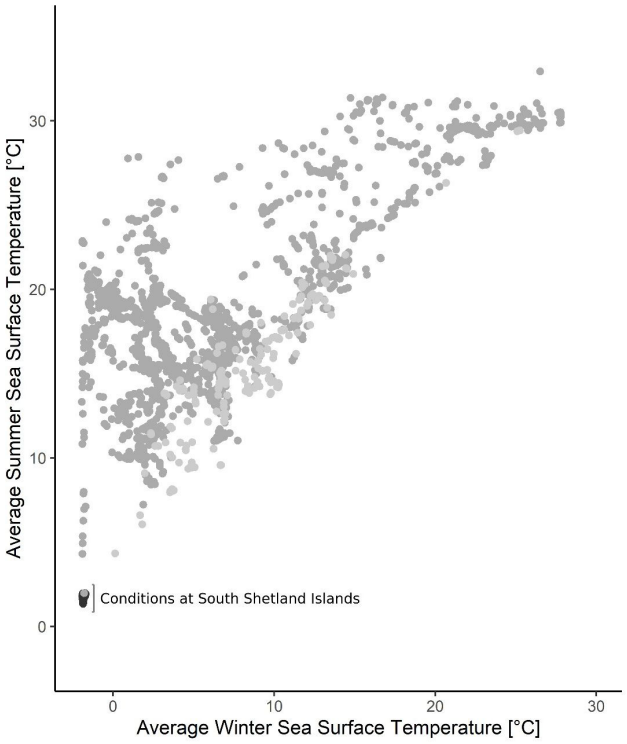

Figure 5. Winter and summer sea surface temperatures at pre-Antarctic and Antarctic occurrence sites of all species. Dark grey = species of category I (cosmopolitan & amphiequatorial), light grey = species of categories II (Pacific coast of North America) and III (Southern Hemisphere), black = conditions at Antarctic sites (South Shetland Islands). The dark grey dot within the range of the Antarctic sites belongs to *Petalonia fascia*.

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. fascia*, 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. fascia* 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 (Van den Hoek 1982, Lüning 1990, Peters and Breeman 1993). 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. fascia*. 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; Spreen et al. 2008) 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 (Junker et al. 2016) 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 (Guisan et al. 2014). 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 (Lüning 1990). 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 (Fraser et al. 2018). 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 (Laeseke et al. 2020). Under this assumption, correlative ENMs are predestined to be incomplete and to underestimate suitable ranges of southern

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://seaice.uni-bremen.de/start/ (Spreen et al. 2008). For each day, a pixel with concentration ≥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.

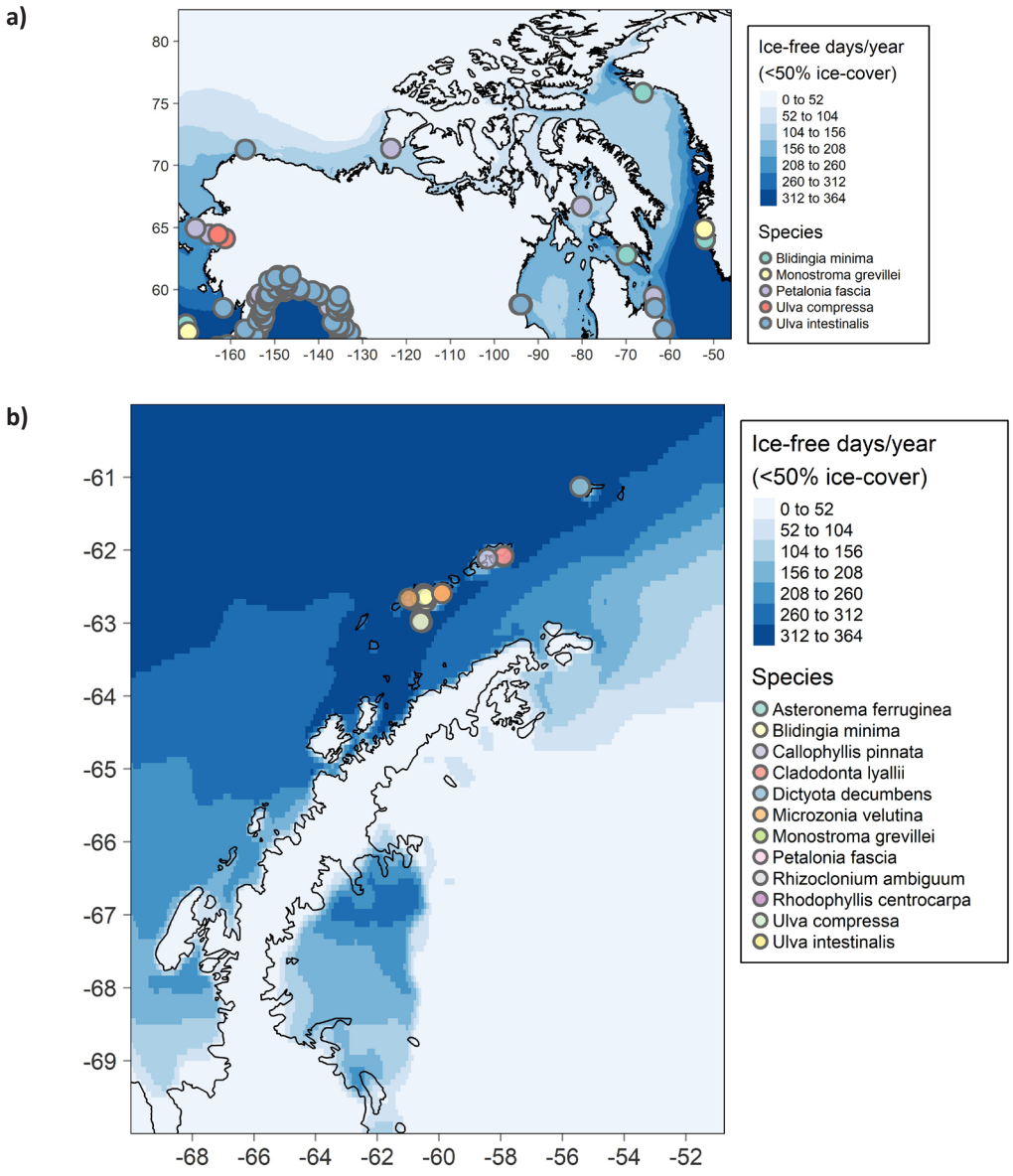

Figure 6. Comparison of ice-prevalence in the North American Arctic (a) and at the South Shetland Islands (b). Data were averaged over the years 2003 – 2014, except for the year 2011. Data source: https://seaice.uni-bremen.de/start/ (Spreen et al. 2008).

species in the climatically non-matching habitats of Antarctica (Peterson 2005, Araújo and Peterson 2012, Guisan et al. 2014).

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. Cárdenas et al. (2020) 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, Avila et al. (2020) 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. membranaceae* 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 (Wiencke and Clayton 2002) and Wiencke et al. (2014) 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 (Wiencke et al. 2014, Oliveira et al. 2020), 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 (Fraser et al. 2018, McCarthy et al. 2019, Avila et al. 2020) 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, Hariot 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 (Lüning 1990, Peterson et al. 1999, Losos 2008, Warren et al. 2008). 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 (Yañez-Arenas et al. 2020). 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 (Peterson et al. 1999). Further, experimentally tested temperature tolerances could inform about fundamental niches in a mechanistic approach (Kearney and Porter 2009). Experimentally-tested temperature tolerances are available for many species in the literature (e.g. tom Dieck 1993). 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 (Liesner et al. 2020). 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 (Lüning 1990). 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 (Chown et al. 2012).

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 (Braun and Gossmann 2002, Zacher et al. 2009, Fraser et al. 2018). Therefore, the invasion risk of Antarctica should not be underestimated (Hughes et al. 2020) 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. McCarthy et al. 2019). 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 Bi 772/17-1.

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

Araújo, M.B. & Peterson, A.T. (2012) Uses and misuses of bioclimatic envelope modeling. Ecology, 93, 1527-1539. https://doi.org/10.1890/11-1930.1

Assis, J., Tyberghein, L., Bosch, S., Verbruggen, H., Serrão, E.A. & De Clerck, O. (2017) Bio-ORACLE v2.0: extending marine data layers for bioclimatic modelling. Global Ecology and Biogeography, 27, 277-284. https://doi.org/10.1111/geb.12693

Atwater, D. Z., Ervine, C. & Barney, J. N. (2018) Climatic niche shifts are common in introduced plants. Nature Ecology and Evolution, 2, 34-43. https://doi.org/10.1038/s41559-017-0396-z

Avila, C., Angulo-Preckler, C., Martín-Martín, R.P., Figuerola, B., Griffiths, H.J. & Waller, C.L. (2020) Invasive marine species discovered on non–native kelp rafts in the warmest Antarctic island. Scientific Reports, 10, 1639. https://doi.org/10.1038/s41598-020-58561-y

Barnes, D.K., Walters, A. & Gonçalves, L. (2010) Macroplastics at sea around Antarctica. Marine Environmental Research, 70, 250-252. https://doi.org/10.1016/j.marenvres.2010.05.006

Becker, S., Walter, B. & Bischof, K. (2009) Freezing tolerance and photosynthetic performance of polar seaweeds at low temperatures. Botanica Marina, 52, 609-616. https://doi.org/10.1515/BOT.2009.079

Bergstrom, D.M., Lucieer, A., Kiefer, K., Wasley, J., Belbin, L., Pedersen, T.K. & Chown, S.L. (2009) Indirect effects of invasive species removal devastate World Heritage Island. Journal of Applied Ecology, 46, 73-81. https://doi.org/10.1111/j.1365-2664.2008.01601.x

Bivand, R., Keitt, T. & Rowlingson, B. (2020). rgdal: bindings for the 'Geospatial' Data Abstraction Library. Available at: https://cran.r-project.org/web/packages/rgdal/index.html

Bolton, J., Oyieke, H. & Gwada, P. (2007) The seaweeds of Kenya: checklist, history of seaweed study, coastal environment, and analysis of seaweed diversity and biogeography. South African Journal of Botany, 73, 76-88. https://doi.org/10.1016/j.sajb.2006.08.006

Braun, M. & Gossmann, H. (2002) Glacial Changes in the Areas of Admiralty Bay and Potter Cove, King George Island, Maritime Antarctica. In: Geoecology of Antarctic Ice-Free Coastal Landscapes. Ecological Studies (Analysis and Synthesis) (ed. by L. Beyer and M. Bölter), pp. 75-89. Springer, Berlin, Heidelberg. https://doi.org/10.1007/978-3-642-56318-8_6

Broennimann, O., Treier, U.A., Müller-Schärer, H., Thuiller, W., Peterson, A. & Guisan, A. (2007) Evidence of climatic niche shift during biological invasion. Ecology Letters, 10, 701-709. https://doi.org/10.1111/j.1461-0248.2007.01060.x

Cárdenas, L., Leclerc, J.-C., Bruning, P., et al. (2020) First mussel settlement observed in Antarctica reveals the potential for future invasions.

Scientific Reports, 10, 5552. https://doi.org/10.1038/s41598-020-62340-0

Casas, G., Scrosati, R. & Piriz, M.L. (2004) The invasive kelp Undaria pinnatifida (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biological Invasions, 6, 411-416. https://doi.org/10.1023/B:BINV.0000041555.29305.41

Chapuis, J.-L., Frenot, Y. & Lebouvier, M. (2004) Recovery of native plant communities after eradication of rabbits from the subantarctic Kerguelen Islands, and influence of climate change. Biological Conservation, 117, 167-179. https://doi.org/10.1016/S0006-3207(03)00290-8

Chown, S.L., Clarke, A., Fraser, C.I., Cary, S.C., Moon, K.L. & McGeoch, M.A. (2015) The changing form of Antarctic biodiversity. Nature, 522, 431-438. https://doi.org/10.1038/nature14505

Chown, S.L., Huiskes, A.H., Gremmen, N.J., et al. (2012) Continent-wide risk assessment for the establishment of nonindigenous species in Antarctica. Proceedings of the National Academy of Sciences USA, 109, 4938-4943. https://doi.org/10.1073/pnas.1119787109

Chwedorzewska, K.J. (2008) Poa annua L. in Antarctic: searching for the source of introduction. Polar Biology, 31, 263-268. https://doi.org/10.1007/s00300-007-0353-4

Clarke, A., Barnes, D.K. & Hodgson, D.A. (2005) How isolated is Antarctica? Trends in Ecology and Evolution, 20, 1-3. https://doi.org/10.1016/j.tree.2004.10.004

Clayton, M., Wiencke, C. & Klöser, H. (1997) New records of temperate and sub-Antarctic marine benthic macroalgae from Antarctica. Polar biology, 17, 141-149. https://doi.org/10.1007/s003000050116

Convey, P. & Peck, L.S. (2019) Antarctic environmental change and biological responses. Science Advances, 5, eaaz0888. https://doi.org/10.1126/sciadv.aaz0888

Davison, I.R., Dudgeon, S. & Ruan, H.-M. (1989) The effect of freezing on seaweed photosynthesis. Marine Ecology Progress Series, 58, 123-131.

Fitzpatrick, M.C., Weltzin, J.F., Sanders, N.J. & Dunn, R.R. (2007) The biogeography of prediction error: why does the introduced range of the fire ant over-predict its native range? Global Ecology and Biogeography, 16, 24-33. https://doi.org/10.1111/j.1466-8238.2006.00258.x

Fraser, C.I., Morrison, A.K., Hogg, A.M., Macaya, E.C., van Sebille, E., Ryan, P.G., Padovan, A., Jack, C., Valdivia, N. & Waters, J.M. (2018) Antarctica's ecological isolation will be broken by storm-driven dispersal and warming. Nature Climate Change, 8, 704-708. https://doi.org/10.1038/s41558-018-0209-7

Frenot, Y., Chown, S.L., Whinam, J., Selkirk, P.M., Convey, P., Skotnicki, M. & Bergstrom, D.M. (2005) Biological invasions in the Antarctic: extent, impacts and implications. Biological Reviews, 80, 45-72. https://doi.org/10.1017/S1464793104006542

Gallardo, T., Pérez-Ruzafa, I., Flores-Moya, A. & Conde, F. (1999) New collections of benthic marine algae from Livingston and Deception Islands (South Shetland Islands) and Trinity Island (Bransfield Strait) Antarctica. Botanica Marina, 42, 61-69.

GBIF (2020) The Global Biodiversity Information Facility: What is GBIF? Available at: https://www.gbif.org/what-is-gbif

GEBCO Bathymetric Compilation Group (2019) The GEBCO_2019 Grid - a continuous terrain model of the global oceans and land. British Oceanographic Data Centre, National Oceanography Centre, NERC, UK. https://doi.org/10.5285/836f016a-33be-6ddc-e053-6c86abc0788e

Guiry, M.D. & Guiry, G.M. (2020) AlgaeBase. World-wide electronic publication, National University of Ireland, Galway. Available at: https://www.algaebase.org

Guisan, A. & Thuiller, W. (2005) Predicting species distribution: offering more than simple habitat models. Ecology Letters, 8, 993-1009. https://doi.org/10.1111/j.1461-0248.2005.00792.x

Guisan, A., Petitpierre, B., Broennimann, O., Daehler, C. & Kueffer, C. (2014) Unifying niche shift studies: insights from biological invasions. Trends in Ecology and Evolution, 29, 260-269. https://doi.org/10.1016/j.tree.2014.02.009

Hijmans, R.J. (2020). raster: Geographic data analysis and modeling. Available at: https://cran.r-project.org/web/packages/raster/index.html

Hill, M. P., Gallardo, B., & Terblanche, J. S. (2017) A global assessment of climatic niche shifts and human influence in insect invasions. Global

Ecology and Biogeography, 26, 679-689. https://doi.org/10.1111/geb.12578

Hughes, K.A. & Convey, P. (2012) Determining the native/non-native status of newly discovered terrestrial and freshwater species in Antarctica – Current knowledge, methodology and management action. Journal of Environmental Management, 93, 52-66. https://doi.org/10.1016/j.jenvman.2011.08.017

Hughes, K.A., Pertierra, L.R., Molina-Montenegro, M.A. & Convey, P. (2015) Biological invasions in terrestrial Antarctica: what is the current status and can we respond? Biodiversity and Conservation, 24, 1031-1055. https://doi.org/10.1007/s10531-015-0896-6

Hughes, K.A., Pescott, O.L., Peyton, J., et al. (2020) Invasive non-native species likely to threaten biodiversity and ecosystems in the Antarctic Peninsula region. Global Change Biology, 26, 2702-2716. https://doi.org/10.1111/gcb.14938

Hutchinson, G.E. (1957) Concluding remarks. Cold Spring Harbor Symposia on Quantitative Biology, 22, 415-427.

Jiménez-Valverde, A., Peterson, A.T., Soberón, J., Overton, J., Aragón, P. & Lobo, J.M. (2011) Use of niche models in invasive species risk assessments. Biological invasions, 13, 2785-2797. https://doi.org/10.1007/s10530-011-9963-4

Junker, R.R., Kuppler, J., Bathke, A.C., Schreyer, M.L. & Trutschnig, W. (2016) Dynamic range boxes–a robust nonparametric approach to quantify size and overlap of n-dimensional hypervolumes. Methods in Ecology and Evolution, 7, 1503-1513. https://doi.org/10.1111/2041-210X.12611

Kearney, M. & Porter, W. (2009) Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. Ecology letters, 12, 334-350. https://doi.org/10.1111/j.1461-0248.2008.01277.x

Laeseke, P., Martínez, B., Mansilla, A. & Bischof, K. (2020) Future range dynamics of the red alga *Capreolia implexa* in native and invaded regions: contrasting predictions from species distribution models versus physiological knowledge. Biological Invasions, 1-14. https://doi.org/10.1007/s10530-019-02186-4

Lauzeral, C., Leprieur, F., Beauchard, O., Duron, Q., Oberdorff, T. & Brosse, S. (2011) Identifying climatic niche shifts using coarse-grained occurrence data: a test with non-native freshwater fish. Global Ecology and Biogeography, 20, 407-414. https://doi.org/10.1111/j.1466-8238.2010.00611.x

Leung, B., Lodge, D.M., Finnoff, D., Shogren, J.F., Lewis, M.A. & Lamberti, G. (2002) An ounce of prevention or a pound of cure: bioeconomic risk analysis of invasive species. Proceedings of the Royal Society of London B, 269, 2407-2413. https://doi.org/10.1098/rspb.2002.2179

Liesner, D., Fouqueau, L., Valero, M., Roleda, M.Y., Pearson, G.A., Bischof, K., Valentin, K. & Bartsch, I. (2020) Heat stress responses and population genetics of the kelp *Laminaria digitata* (Phaeophyceae) across latitudes reveal differentiation among North Atlantic populations. Ecology and Evolution, 10, 9144-9177. https://doi.org/10.1002/ece3.6569

Losos, J.B. (2008) Phylogenetic niche conservatism, phylogenetic signal and the relationship between phylogenetic relatedness and ecological similarity among species. Ecology Letters, 11, 995-1003. https://doi.org/10.1111/j.1461-0248.2008.01229.x

Lowe S., Browne M., Boudjelas S. & De Poorter M. (2000) 100 of the world's worst invasive alien species: a selection from the global invasive species database. Published by The Invasive Species Specialist Group (ISSG), a specialist group of the Species Survival Commission (SSC) of the World Conservation Union (IUCN), 12pp. First published as special lift-out in Aliens 12, December 2000. Updated and reprinted version: November 2004.

Lüning, K. (1990) Seaweeds: their environment, biogeography, and ecophysiology. Thieme. Stuttgart, New York.

Lynch, H., Crosbie, K., Fagan, W. & Naveen, R. (2010) Spatial patterns of tour ship traffic in the Antarctic Peninsula region. Antarctic Science, 22, 123-130. https://doi.org/10.1017/S0954102009990654

McCarthy, A.H., Peck, L.S., Hughes, K.A. & Aldridge, D.C. (2019) Antarctica: the final frontier for marine biological invasions. Global Change Biology, 25, 2221-2241. https://doi.org/10.1111/gcb.14600

McGeoch, M.A., Shaw, J.D., Terauds, A., Lee, J.E. & Chown, S.L. (2015) Monitoring biological

invasion across the broader Antarctic: a baseline and indicator framework. Global Environmental Change, 32, 108-125. https://doi.org/10.1016/j.gloenvcha.2014.12.012

Medley, K.A. (2010) Niche shifts during the global invasion of the Asian tiger mosquito Aedes albopictus Skuse (Culicidae), revealed by reciprocal distribution models. Global Ecology and Biogeography, 19, 122-133. https://doi.org/10.1111/j.1466-8238.2009.00497.x

Navarro, N.P., Huovinen, P. & Gómez, I. (2019) Photosynthetic characteristics of geographically disjunct seaweeds: a case study on the early life stages of Antarctic and Subantarctic species. Progress in Oceanography, 174, 28-36. https://doi.org/10.1016/j.pocean.2018.11.001

Nyberg, C. D., & Wallentinus, I. (2005) Can species traits be used to predict marine macroalgal introductions? Biological Invasions, 7, 265-279. https://doi.org/10.1007/s10530-004-0738-z

Oliveira, M.C., Pellizzari, F.M., Medeiros, A., & Yokoya, N.S. (2020) Diversity of Antarctic seaweeds. In: Antarctic seaweeds: diversity, adaptation and ecosystem services (ed. by I. Gómez and P. Huovinen), pp. 23-42. Springer, Cham. https://doi.org/10.1007/978-3-030-39448-6_2

Papenfuss, G.F. (1964) Catalogue and bibliography of Antarctic and sub-Antarctic benthic marine algae. Antarctic Research Series, 1, 1 - 76.

Pellizzari, F., Silva, M., Silva, E., Medeiros, A., Oliveira, M., Yokoya, N., Pupo, D., Rosa, L. & Colepicolo, P. (2017) Diversity and spatial distribution of seaweeds in the South Shetland Islands, Antarctica: an updated database for environmental monitoring under climate change scenarios. Polar Biology, 40, 1671-1685. https://doi.org/10.1007/s00300-017-2092-5

Pellizzari, F., Rosa, L.H. & Yokoya, N.S. (2020) Biogeography of antarctic seaweeds facing climate changes. In: Antarctic seaweeds: diversity, adaptation and ecosystem services (ed. by I. Gómez and P. Huovinen). Springer, Cham. https://doi.org/10.1007/978-3-030-39448-6_5

Peters, A.F. & Breeman, A. (1993) Temperature tolerance and latitudinal range of brown algae from temperate Pacific South America. Marine Biology, 115, 143-150. https://doi.org/10.1007/BF00349396

Peterson, A.T. (2005) Predicting potential geographic distributions of invading species. Current Science Bangalore, 89, 9.

Peterson, A.T., Soberón, J. & Sánchez-Cordero, V. (1999) Conservatism of ecological niches in evolutionary time. Science, 285, 1265-1267. https://doi.org/10.1126/science.285.5431.1265

Petitpierre, B., Kueffer, C., Broennimann, O., Randin, C., Daehler, C. & Guisan, A. (2012) Climatic niche shifts are rare among terrestrial plant invaders. Science, 335, 1344-1348. https://doi.org/10.1126/science.1215933

Qiao, H., Peterson, A. T., Campbell, L. P., Soberón, J., Ji, L., & Escobar, L. E. (2016). NicheA: creating virtual species and ecological niches in multivariate environmental scenarios. Ecography, 39(8), 805-813. https://doi.org/10.1111/ecog.01961

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Raffo, M.P., Eyras, M.C. & Iribarne, O.O. (2009) The invasion of Undaria pinnatifida to a Macrocystis pyrifera kelp in Patagonia (Argentina, south-west Atlantic). Journal of the Marine Biological Association of the United Kingdom, 89, 1571-1580. https://doi.org/10.1017/S002531540900071X

Ricker, R.W. (1987) Taxonomy and biogeography of Macquarie Island seaweeds. British Museum (Natural History). London, UK.

Ruiz, G.M., Carlton, J.T., Grosholz, E.D. & Hines, A.H. (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. American Zoologist, 37, 621-632. https://doi.org/10.1093/icb/37.6.621

Spreen, G., Kaleschke, L., & Heygster, G. (2008) Sea ice remote sensing using AMSR-E 89-GHz channels. Journal of Geophysical Research: Oceans. 113. https://doi.org/10.1029/2005JC003384

Tennekes, M. (2018) tmap: Thematic maps in R. Journal of Statistical Software, 84, 1-39. https://doi.org/10.18637/jss.v084.i06

tom Dieck, I. (1993) Temperature tolerance and survival in darkness of kelp gametophytes (Laminariales, Phaeophyta): ecological and biogeographical implications. Marine Ecology Progress Series, 100, 253-253.

Van den Hoek, C. (1982) Phytogeographic distribution groups of benthic marine algae in the North Atlantic Ocean. A review of experimental evidence from life history studies. Helgoländer Meeresuntersuchungen, 35, 153. https://doi.org/10.1007/BF01997551

Vilà, M., Basnou, C., Pyšek, P., Josefsson, M., Genovesi, P., Gollasch, S., Nentwig, W., Olenin, S., Roques, A. & Roy, D. (2010) How well do we understand the impacts of alien species on ecosystem services? A pan-European, cross-taxa assessment. Frontiers in Ecology and the Environment, 8, 135-144. https://doi.org/10.1890/080083

Warren, D.L., Glor, R.E. & Turelli, M. (2008) Environmental niche equivalency versus conservatism: quantitative approaches to niche evolution. Evolution, 62, 2868-2883. https://doi.org/10.1111/j.1558-5646.2008.00482.x

Wickham, H. (2016). ggplot2: Elegant graphics for data analysis. Springer-Verlag, New York.

Wiencke, C. & Clayton, M.N. (2002) Antarctic seaweeds. ARG Gantner Verlag Ruggell, Lichtenstein.

Wiencke, C., Amsler, C. & Clayton, M. (2014) Chapter 5.1 Macroalgae. In: Biogeographic atlas of the Southern Ocean (ed. by C. De Broyer, P. Koubbi, H.J. Griffiths, B. Raymond, C. d' Udekem d'Acoz, et al.), pp. 66-73. Scientific Committee on Antarctic Research, Cambridge.

Williams, S.L. & Smith, J.E. (2007) A global review of the distribution, taxonomy, and impacts of introduced seaweeds. Annual Review of Ecology, Evolution, and Systematics, 38, 327-359. https://doi.org/10.1146/annurev.ecolsys.38.091206.095543

Wotton, D.M., O'Brien, C., Stuart, M.D. & Fergus, D.J. (2004) Eradication success down under: heat treatment of a sunken trawler to kill the invasive seaweed *Undaria pinnatifida*. Marine Pollution Bulletin, 49, 844-849. https://doi.org/10.1016/j.marpolbul.2004.05.001

Yañez-Arenas, C., Martín, G., Osorio-Olvera, L., Escobar-Luján, J., Castaño-Quintero, S., Chiappa-Carrara, X. & Martínez-Meyer, E. (2020) The abundant niche-centroid hypothesis: key points about unfilled niches and the potential use of supraspecfic modeling units. Biodiversity Informatics, 15, 92-102. https://doi.org/10.17161/bi.v15i2.13218

Yoneshigue-Valentin, Y., Silva, I.B., Fujii, M.T., et al. (2013) Marine macroalgal diversity in Admiralty Bay, King George Island, South Shetlands Islands, Antarctica. Annual Activity Report, 140-148. http://dx.doi.org/10.4322/apa.2014.112

Zacher, K., Rautenberger, R., Hanelt, D., Wulff, A. & Wiencke, C. (2009) The abiotic environment of polar marine benthic algae. Botanica Marina, 52, 483-490. https://doi.org/10.1515/BOT.2009.082

Submitted: 15 November 2020
First decision: 14 January 2021
Accepted: 29 June 2021

Edited by Regan Early and Robert J. Whittaker

