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Antarctic ecosystems in transition – life between stresses and opportunities

Julian Gutt[1]*, Enrique Isla[2], José C. Xavier[3,4], Byron J. Adams[5], In-Young Ahn[6], C.-H. Christina Cheng[7], Claudia Colesie[8], Vonda J. Cummings[9], Guido di Prisco[10], Huw Griffiths[4], Ian Hawes[11], Ian Hogg[12,13], Trevor McIntyre[14], Klaus M. Meiners[15], David A. Pearce[16,4], Lloyd Peck[4], Dieter Piepenburg[1], Ryan R. Reisinger[17], Grace K. Saba[18], Irene R. Schloss[19,20,21], Camila N. Signori[22], Craig R. Smith[23], Marino Vacchi[24], Cinzia Verde[10] and Diana H. Wall[25]

[1]*Alfred Wegener Institute, Helmholtz Centre for Polar and Marine Research, Columbusstr., Bremerhaven, 27568, Germany*
[2]*Institute of Marine Sciences-CSIC, Passeig Maritim de la Barceloneta 37-49, Barcelona, 08003, Spain*
[3]*University of Coimbra, MARE - Marine and Environmental Sciences Centre, Faculty of Sciences and Technology, Coimbra, Portugal*
[4]*British Antarctic Survey, Natural Environmental Research Council, High Cross, Madingley Road, Cambridge, CB3 OET, U.K.*
[5]*Department of Biology and Monte L. Bean Museum, Brigham Young University, Provo, UT, U.S.A.*
[6]*Korea Polar Research Institute, 26 Songdomirae-ro, Yeonsu-gu, Incheon, 21990, South Korea*
[7]*Department of Evolution, Ecology and Behavior, University of Illinois, Urbana, IL, U.S.A.*
[8]*School of GeoSciences, University of Edinburgh, Alexander Crum Brown Road, Edinburgh, EH9 3FF, U.K.*
[9]*National Institute of Water and Atmosphere Research Ltd (NIWA), 301 Evans Bay Parade, Greta Point, Wellington, New Zealand*
[10]*Institute of Biosciences and BioResources (IBBR), National Research Council (CNR), Via Pietro Castellino 111, Naples, I-80131, Italy*
[11]*Coastal Marine Field Station, University of Waikato, 58 Cross Road, Tauranga, 3100, New Zealand*
[12]*School of Science, University of Waikato, Private Bag 3105, Hamilton, 3240, New Zealand*
[13]*Canadian High Antarctic Research Station, Polar Knowledge Canada, PO Box 2150, Cambridge Bay, NU, X0B 0C0, Canada*
[14]*Department of Life and Consumer Sciences, University of South Africa, Private Bag X6, Florida, 1710, South Africa*
[15]*Australian Antarctic Division, Department of Agriculture, Water and the Environment, and Australian Antarctic Program Partnership, University of Tasmania, 20 Castray Esplanade, Battery Point, TAS, 7004, Australia*
[16]*Department of Applied Sciences, Faculty of Health and Life Sciences, Northumbria University at Newcastle, Northumberland Road, Newcastle upon Tyne, NE1 8ST, U.K.*
[17]*Centre d'Etudes Biologique de Chizé, UMR 7372 du Centre National de la Recherche Scientifique - La Rochelle Université, Villiers-en-Bois, 79360, France*
[18]*Center for Ocean Observing Leadership, Department of Marine and Coastal Sciences, Rutgers University, 71 Dudley Rd., New Brunswick, NJ, 08901, U.S.A.*
[19]*Instituto Antártico Argentino, Buenos Aires, Argentina*
[20]*Centro Austral de Investigaciones Científicas, Bernardo Houssay 200, Ushuaia, Tierra del Fuego, CP V9410CAB, Argentina*
[21]*Universidad Nacional de Tierra del Fuego, Ushuaia, Tierra del Fuego, CP V9410CAB, Argentina*
[22]*Oceanographic Institute, University of São Paulo, Praça do Oceanográfico, 191, São Paulo, CEP: 05508-900, Brazil*
[23]*Department of Oceanography, University of Hawaii at Manoa, 1000 Pope Road, Honolulu, HI, 96822, U.S.A.*
[24]*Institute for the Study of the Anthropic Impacts and the Sustainability of the Marine Environment (IAS), National Research Council of Italy (CNR), Via de Marini 6, Genoa, 16149, Italy*
[25]*Department of Biology and School of Global Environmental Sustainability, Colorado State University, Fort Collins, CO, U.S.A.*

ABSTRACT

Important findings from the second decade of the 21st century on the impact of environmental change on biological processes in the Antarctic were synthesised by 26 international experts. Ten key messages emerged that have stakeholder-relevance and/or a high impact for the scientific community. They address (*i*) altered biogeochemical cycles, (*ii*) ocean

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* Address for correspondence (Tel: +49 471 4831 1333; E-mail: julian.gutt@awi.de)

acidification, (*iii*) climate change hotspots, (*iv*) unexpected dynamism in seabed-dwelling populations, (*v*) spatial range shifts, (*vi*) adaptation and thermal resilience, (*vii*) sea ice related biological fluctuations, (*viii*) pollution, (*ix*) endangered terrestrial endemism and (*x*) the discovery of unknown habitats. Most Antarctic biotas are exposed to multiple stresses and considered vulnerable to environmental change due to narrow tolerance ranges, rapid change, projected circumpolar impacts, low potential for timely genetic adaptation, and migration barriers. Important ecosystem functions, such as primary production and energy transfer between trophic levels, have already changed, and biodiversity patterns have shifted. A confidence assessment of the degree of 'scientific understanding' revealed an intermediate level for most of the more detailed sub-messages, indicating that process-oriented research has been successful in the past decade. Additional efforts are necessary, however, to achieve the level of robustness in scientific knowledge that is required to inform protection measures of the unique Antarctic terrestrial and marine ecosystems, and their contributions to global biodiversity and ecosystem services.

Key words: adaptation, benthic dynamism, biogeochemical cycles, climate change, invasion, new habitats, ocean acidification, primary production, range shifts, sea ice

CONTENTS

I. INTRODUCTION

Life in the Antarctic makes a key contribution to our knowledge of the global biosphere due to its uniqueness and connectivity to adjacent ecosystems. The observed impacts and projected risks of rapid climate change for Antarctic biotas (Rogers *et al.*, 2020) are a function of the severity of the hazards, the exposure and vulnerability of the biotas to stresses (Convey & Peck, 2019), and their capacity to adapt or escape. Research strategies are needed to assess further the uniqueness and resilience of Antarctic biotas to inform decision-makers and conservationists on regional and global priorities (Meredith *et al.*, 2019).

The findings in this synthesis focus on studies published since 2010, building upon research carried out since the beginning of the 20th century. This research included basic biological approaches (e.g. taxonomy), targeted studies on key species such as Antarctic krill *Euphausia superba* (Miller & Hampton, 1989), and ecological studies of biogeochemical cycles, including fluxes of energy to apex predators and physiological adaptations. For a broad coverage of historical results see e.g. Laws (1984), Smith (1990), Hempel (1994), and Knox (2006). Notable research into Antarctic life sciences during the past century includes the demonstration of how life, particularly fishes, evolved and adapted physiologically to the ice-cold environment (di Prisco, Maresca & Tota, 1991). Since then, the rapid development of biomolecular methods has enabled a variety of advances. New research platforms (e.g. research stations, ships) and novel instrumentation (e.g. satellites, landers, autonomous underwater vehicles, robotic floats and automated observatories) have allowed much-improved investigations of biological developments and environmental changes. While numerical and conceptual models often originated in more-accessible ecosystems, specific analytical tools have also been developed to obtain deeper insights into Antarctic-specific ecological processes. Highly focused studies of Antarctic biotas and their environments have been conducted under international initiatives, such as the Ecology of the Antarctic Sea Ice Zone (EASIZ), Evolution and Biodiversity in the Antarctic (EBA) and additional research initiatives of the Scientific Committee on Antarctic Research (SCAR) and the Scientific Committee on Oceanic Research (SCOR).

In 2010, SCAR launched the Scientific Research Programme 'Antarctic Thresholds – Ecosystem Resilience and Adaptation' (AnT-ERA) to facilitate biological process-focused research in marine, freshwater and terrestrial ecosystems facing various stressors. Since then, a vast array of results ranging from molecular to ecosystem levels has been generated. Examples, are assembled in the *Antarctic Climate Change and the Environment* report and its regular updates to Antarctic Treaty Meetings (Turner *et al.*, 2014).

This synthesis aimed to identify the most important climate-dependent findings from the past decade on biological processes in Antarctic ecosystems. These findings are synoptically synthesised into scientific messages, with associated levels of confidence. Where appropriate the findings are assembled independently for the marine, limnetic or terrestrial ecosystem from which they originate, to identify similarities and contrasts across these ecosystems. Results were considered to be 'most important' if they (*i*) were novel and could be clustered into messages with considerable relevance for the scientific community, research and funding strategies, projects and textbooks, or (*ii*) have relevance for stakeholders, such as: the Intergovernmental Panel on Climate Change (IPCC), the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES), the United Nations Decade of Ocean Science for Sustainable

Development, the Antarctic Treaty System with its nature conservation initiatives, the Commission for Environmental Protection (CEP) and the Commission on the Conservation of Antarctic Living Resources (CCAMLR). Stakeholders also include science managers, politicians, journalists, and the general public. Some of the findings reflect questions raised by the 1st Scientific Antarctic Committee on Antarctic Research Antarctic and Southern Ocean Science Horizon Scan, the implementation of which has recently been assessed (Kennicutt *et al.*, 2019).

II. MATERIALS AND METHODS

A SCAR AnT-ERA workshop held in Coimbra, Portugal, in 2019 identified 10 high-level scientific key messages (Fig. 1) on biological processes in the Southern Ocean and on the Antarctic continent, which fall into 31 more detailed sub-messages (Fig. 2). These are discussed in detail in Section III. The messages and sub-messages were developed by consensus of the 25 experts from the AnT-ERA steering committee and invited guest experts, who jointly authored this assessment and whose areas of expertise are provided as online supporting information in Appendix S1. We are aware that other groups might identify different key questions, but we attempted to include all scientific themes, groups of organisms, Antarctic regions and ecosystems. We restrict our survey to research published from 2010 onwards, other than in a few exceptional cases. While our 10 key messages are interrelated to some extent, the aggregation of focused results cannot always reflect these thematic overlaps. Only the most recent publications and only those considered to be 'most important' (for definition see above) are cited. Numerous additional valuable results have been published that are referenced in the publications mentioned herein.

To verify the relevance of our key messages, the peer-reviewed literature for 2010–2020 was analysed in a standardised way by using in the *Web of Science* the key words listed in Appendix S2. The results are illustrated in Fig. 2. To document the progress of knowledge in the past decade values are also provided for period 1970–2020 in Appendix S2.

To assess the level of confidence of the sub-messages, IPCC AR5 methodology was applied (Mach *et al.*, 2017; IPBES, 2019; see Appendix S3), which categorises the quantity/quality of evidence in combination with the agreement between them as: 'limited', 'emerging', 'divergent', or 'robust'). Important results were initially proposed by experts, then discussed during the workshop or by later correspondence until agreement among all authors was reached. Principally this classification depends not only on the quality/quantity of the evidence and agreement between conclusions, but also on the wording of the message. The confidence level is higher for simple and general statements, but lower if an evidence-based message tries to capture the complexity of a system. The high-level key messages themselves were considered too general to be assessed in this way.

III. RESULTS

Of the literature resulting from our search terms predominantly referring to Antarctic biotas in transition as a response to environmental change (Morley *et al.*, 2020), 67% were published in the past 10 years. Only 33% of the papers identified were from the 1970 to 2010 period (see Appendix S2). Even for the traditional theme of 'adaptation', 56% of papers since 1970 were written between 2010 and 2020. This predominance is due to a steadily increasing knowledge on biochemical processes within single cells, often subsumed under the term 'adaptation', and a shift from qualitative to quantitative ecosystem-level analyses. It is still challenging to link these two extremes by up- and downscaling approaches to assess the variability and sensitivity of ecological functions (Gutt *et al.*, 2018; Neumann *et al.* (2019). Figure 1 shows that our 10 messages affect humans most in their connection with climate regulation, followed by nature conservation and to a lesser extent with human food provision and bioprospecting, including for medicine and lifestyle products and applications (Fig. 1). The literature survey (Fig. 2) identified topics with high societal interest and relevance, such as the responses of biotas to climate change (message 3) and short- to mid-term biogeochemical cycles (message 1), and adaptation of species to polar conditions (message 6), to be numerically best represented in the scientific literature. However, not all globally relevant or emerging themes, such as long-term carbon sequestration by benthic processes (part of message 1), ocean acidification (message 2) and pollution (message 8), have been intensively investigated in the Antarctic.

(1) Changes in the Antarctic cryosphere modify pathways of marine and terrestrial biogeochemical cycling in different ways

Antarctic ecosystems play a central role in regulating global biogeochemical cycles, particularly in the ocean, and affect the global climate system (Henley *et al.*, 2020). Changes in these functions are rapid, hampering our ability to describe and assess their outcomes fully. Cascading effects ultimately can impact processes at all ecosystem levels, determining the stability and resilience of Antarctic biotas and their interactions both on land and in the ocean.

(*a*) Anthropogenic pressures accelerate nutrient release and buildup of organic matter resulting from the melting of terrestrial and sea ice

Microbially maintained subglacial brines can be reservoirs of nutrients such as iron, and organic matter, connecting the land, including subglacial lakes, with the ocean (Hawkins *et al.*, 2014; Vick-Majors *et al.*, 2020). Similarly, land-based glaciers are a significant source of nutrients and organic matter for stream and cryolake ecosystems (Bagshaw *et al.*, 2016). Warming enhances these transport processes. The sediment fluxes that accompany nutrient transport produce additional

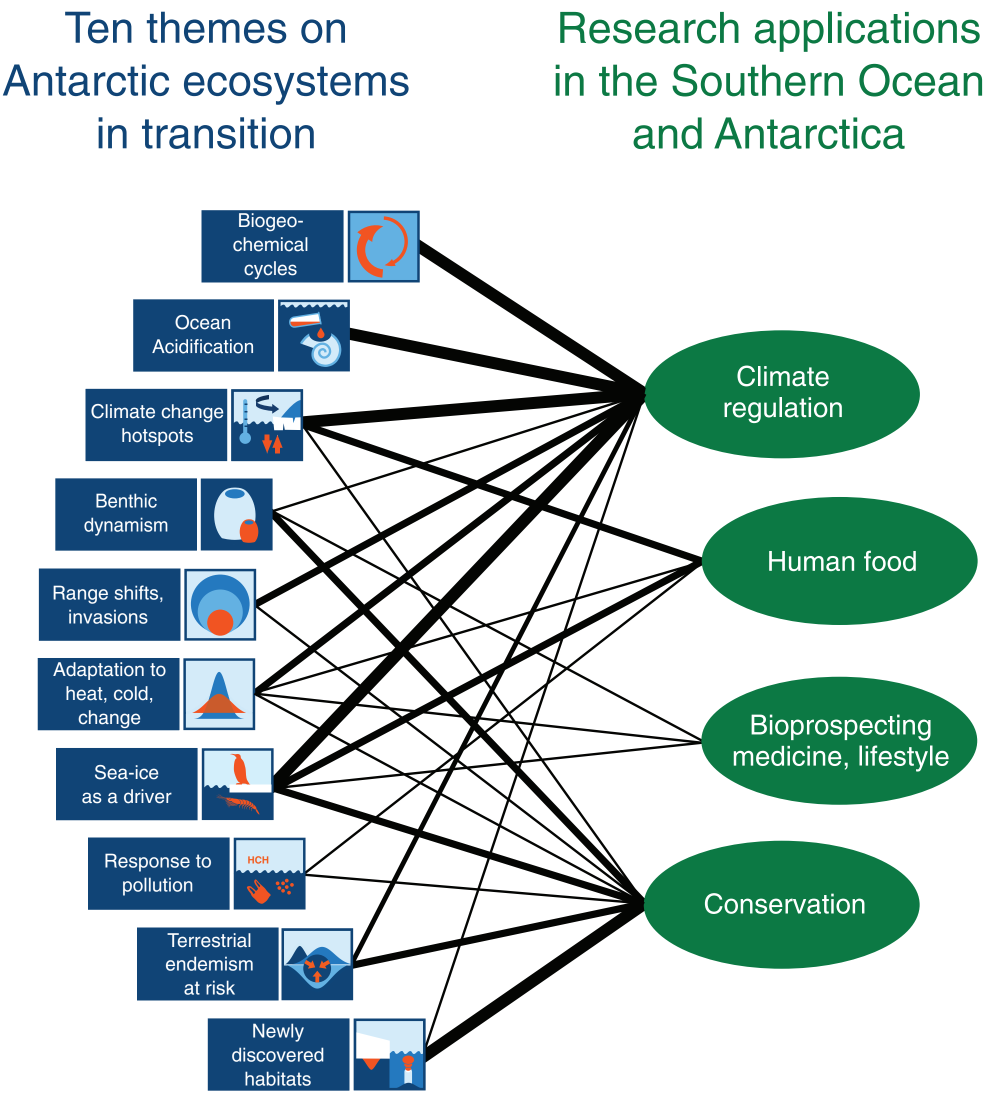


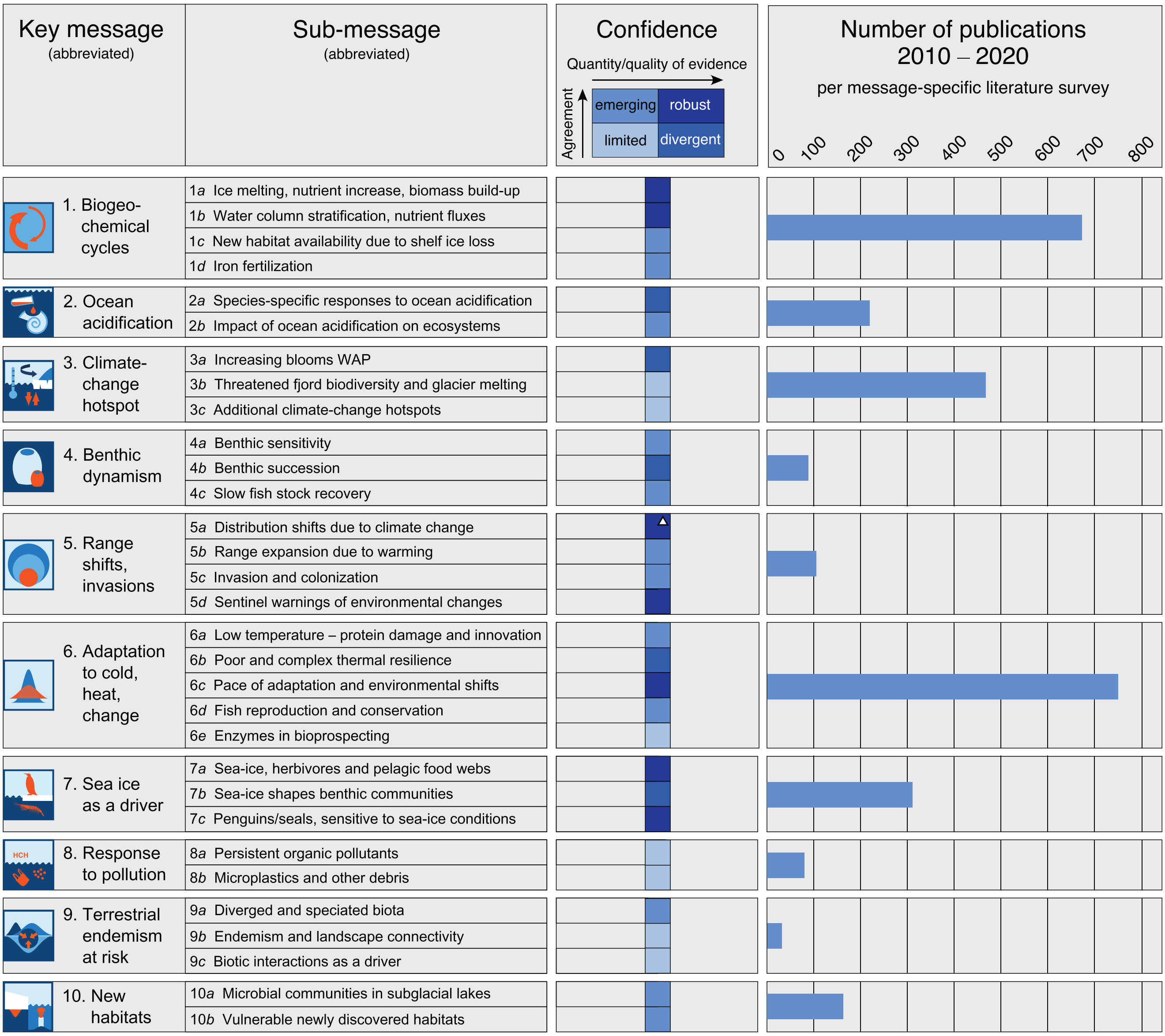
Fig 1. Relationships between 10 themes, for which we synthesized our 10 evidence-based scientific key messages (left) and fields of applied research in Antarctica and the Southern Ocean represented by ecosystem goods and services (nature's contributions to people) or related applications (right). Thicker lines indicate stronger relationships.

consequences: in lakes, pulsed sediment flux can lead to short-term turbidity, initially resulting in decreased photosynthetically active radiation and net primary production, followed by increases in both variables (Obryk *et al.*, 2016). Marine benthic biomass is expected to increase due to enhanced export of carbon to the sea-bed (Jones *et al.*, 2013) and to contribute to carbon sequestration as a negative feedback of climate change feedback (Barnes, 2017). In the open ocean, the numbers of icebergs increase when calving rates from glaciers and iceshelves rise due to atmospheric and ocean warming. These changes affect the stimulation of primary production, especially through fertilisation (Wu & Hou, 2017), with consequences for food webs, but also create phytoplankton losses due to complex hydrodynamic and biogeochemical processes (Vernet *et al.*, 2011), creating another negative feedback from climate change (Hopwood *et al.*, 2019).

Due to warming of the Antarctic Peninsula, blooms of green snow algae strongly influenced by marine nutrient inputs are expected to shrink in some areas, due to ice melt, and to expand in others, especially close to bird and seal colonies, resulting in a net increase in biomass and, thus, to act as a significant carbon sink (Gray *et al.*, 2020).

(*b*) Climate-induced breakdown in sea and freshwater ice coverage, and changes in ocean-circulation patterns modify stratification of water columns; primary production is expected to increase, while carbon and nutrient fluxes will be altered

Climate change effects, including increased freshwater inputs, strengthen shallow marine water-column stratification, stimulating the production of large-cell diatoms and the haptophyte *Phaeocystis antarctica* (Kaufman *et al.*, 2017;



△ divergent for krill, salps, and vegetation of the WAP region; emerging for poorly investigated species.

Fig 2. Scientific key messages/themes, sub-messages (left, abbreviated) with assessment of 'confidence' of the sub-messages [centre; after Mach *et al.* (2017) and IPBES (2019)] and number of scientific publications per key message over the period 2010–2020 resulting from the literature survey (right; for search terms see Appendix S2). WAP, West Antarctic Peninsula.

Höfer *et al.*, 2019), but also the growth of other small flagellates (Mendes *et al.*, 2018). In contrast to most other oceans, intense nutrient trapping is expected due to warming in the Southern Ocean (Moore *et al.*, 2018). This process will increase total marine net primary production, which will also be enhanced by increased light from shorter sea ice-cover periods (Moreau *et al.*, 2015). As a consequence, increasing CO_2 uptake could occur, especially along the West Antarctic Peninsula (WAP) (Brown *et al.*, 2019). Models project, especially for highly productive areas such as the Ross Sea and WAP, that increased rates of remineralisation (Henley *et al.*, 2018) support pelagic ecosystem function (Petrou *et al.*, 2016). Furthermore they increase the amount of food available to krill and salps and through them, albeit to different extents, support higher trophic levels (Flores *et al.*, 2012; Henschke *et al.*, 2016) and further remineralisation (Plum, Hillebrand & Moorthi, 2020). However, nutrient upwelling could be reduced, with negative impacts on phytoplankton growth. A projected increase in westerly winds (positive Southern Annular Mode in combination with the long-term Amundsen Sea Low) would regionally promote upwelling of nutrient-rich waters, compensating the shallowing of mixed-layer depths and increased stratification (Deppeler & Davidson, 2017). Planktonic production is expected to increase anthropogenic CO_2 uptake with ongoing climate change due to a decreasing buffering capacity of the ocean (Hauck & Völker, 2015). Models have also predicted that Southern Ocean primary production and related ecosystem functions will maintain high oxygen concentrations in adjacent surface waters (Keller *et al.*, 2016). In freshwater inland water bodies, perennial ice covers have profound impacts on primary producers (Sutherland, Howard-Williams & Hawes, 2020), and a shift to seasonal ice cover will gradually break down highly stratified water columns, leading to increased primary production and other, as yet unknown, consequences for ecosystem processes (Obryk, Doran & Priscu, 2019).

(*c*) Mass loss of inland and shelf ice leads to increases in habitat availability and suitability

Glacial retreat increases the available ground for slow colonisation in maritime terrestrial systems, which can result in local increases in biomass and productivity (Favero-Longo *et al.*, 2012). Indirect impacts of inland ice melt on habitat are mediated through increased meltwater production. Resulting expansions of stream volume and wetted soil area, and lake level rise in the endorheic lakes common in much of Antarctica, will enhance habitat area and/or quality. For increasing terrestrial connectivity, through increased streamflow, see Section III.9*c*. In marine ecosystems, ice shelf collapses expand suitable habitat for plankton blooms (Bertolin & Schloss, 2009), depositing fresh organic matter onto the sea floor, which represents a new biological ('blue') carbon uptake in the Southern Ocean water column (Peck *et al.*, 2010) and suitable territory for benthos (Gutt *et al.*, 2011; Sañé *et al.*, 2012). However, evidence is still insufficient regarding whether the sea-bed accumulates enough organic matter to act as a long-term carbon sink (Isla & DeMaster, 2018).

(*d*) Anthropogenic iron fertilisation of pelagic systems seems inefficient in sequestering carbon dioxide

Studies on iron limitation combined with ocean acidification (e.g. Hoppe *et al.*, 2017), especially for high-nutrient low-chlorophyll pelagic systems, have been used to assess carbon cycling and sequestration. In a more applied approach, an iron-fertilisation experiment, north of the polar front in the Atlantic sector of the Southern Ocean showed significant changes in pelagic community composition and ecological functions. However, it found no enhanced export of organic matter from surface waters to deeper layers (Laglera *et al.*, 2017), even though signals in the deep sea generally mirrored processes in the euphotic layer. Upwelling meant that a calculated 66% of remineralised carbon reaching 1000 m depth was re-exposed to the atmosphere after only 38 years (Robinson *et al.*, 2014). Iron fertilisation can even reduce natural deep-ocean CO_2 storage (Salter *et al.*, 2014).

(2) **Ocean acidification potentially stresses vulnerable Antarctic key biotas**

Ocean acidification (OA) is another anthropogenic climate-related stressor affecting marine species, with ocean uptake of atmospheric CO_2 reducing carbonate concentrations and pH. Models project a rapid shallowing of the water depths below which carbonate dissolution will occur in almost the entire Southern Ocean that will affect calcifying and non-calcifying life forms. Thus, OA may become one of the most serious pressures on marine organisms and ecosystems.

(*a*) Species respond specifically to ocean acidification; some can potentially acclimatise

Responses of primary producers (including growth and photosynthesis) to simulated OA vary among species and with duration of exposure, ranging from positive to negative. The dominant phytoplankton species, the haptophyte *Phaeocystis antarctica*, is more tolerant to OA than the abundant diatoms *Chaetoceros debilis* and *Fragilariopsis kerguelensis* (Trimborn *et al.*, 2017). This may have feedbacks to climate, as *Phaeocystis* is a source of dimethyl sulfide, modifying cloud properties and cooling air temperatures. Responses of key Antarctic invertebrate species parallel those in non-polar regions, with early life-history stages being generally more vulnerable. For example, development and/or carbonate structures of young Antarctic krill, echinoderms and molluscs may be disrupted (e.g. Bylenga, Cummings & Ryan, 2017), and the hatching success and suitable habitat of krill is projected to decrease (Kawaguchi *et al.*, 2013). Across a range of species, adult life stages show effects of exposure to end-century pH levels [e.g. on survival, shell dissolution, reproductive development; Manno *et al.*, 2017; Dell'Acqua *et al.*, 2019)]. Other species/stages are not adversely affected, including adult Antarctic krill (Ericson *et al.*, 2018). Negative effects are observed only in association with increased temperatures (e.g. development of Antarctic dragonfish (*Gymnodraco acuticeps*); Flynn *et al.*, 2015), and warming may have stronger effects than acidification (e.g. in some notothenioid fishes; Enzor, Hunter & Place, 2017). Longer-term studies reveal the potential for compensatory responses to OA: polar brachiopods produce a thicker shell in response to dissolution of the outer layer (Cross, Harper & Peck, 2019). Among the meiofauna, foraminiferans are expected generally to suffer from OA, especially where shallowing of the calcite compensation depth is predicted, whilst nematodes seem to be more robust and show species-specific responses (Ingels *et al.*, 2012).

(*b*) Communities respond differently to ocean acidification, with ecosystem implications depending on the response of ecological key species

Direct investigations of rates of change associated with OA (Negrete-García *et al.*, 2019) and community-level responses are rare. Short-term (~2 week) studies of coastal Antarctic systems have revealed reductions in primary production and increases in bacterial activity (e.g. Deppeler *et al.*, 2018). Under-sea-ice microalgal communities showed only modest productivity increases and no change in biomass or composition (Cummings *et al.*, 2019). In a three-month *in situ* experiment, benthic diatoms changed their photo-tactile vertical migration behaviour, affecting their photo-physiology and net production (Black *et al.*, 2019). However, crustacean grazer assemblages remained unaffected after 1 month at end-century OA conditions (Schram *et al.*, 2016).

Predictions of ecosystem-level changes require knowledge of which species and functional groups will be, and will not be, impacted by acidification (in combination with other stressors), and particularly their long-term ability to adapt to these changes.

(3) Physical processes in the atmosphere force rapid ecosystem changes in climate change hotspots

Biological responses to warming and related physical processes over the last 50 years along the WAP (listed in Table 1) indicate what other Antarctic marine and terrestrial ecosystems may experience with predicted large-scale climate change under similar forcing variables. Important changes in the biology of krill species (Euphausiacea) and their competitors and predators are described in Section III.3*b*.

(*a*) Algal blooms are increasing along the West Antarctic Peninsula (WAP)

Phytoplankton dynamics along the WAP respond to sea ice-mediated changes in the water column. Years of higher winter ice extent and duration, reduced winds, and increased water-column stability favour high summer phytoplankton biomass (Venables, Clarke & Meredith, 2013; Saba *et al.*, 2014; Schloss *et al.*, 2014). Moreover, ice type (fast, grease, pack or brash ice), temperature and water column properties contribute to phytoplankton composition and cell size structure of early summer blooms with small cryptophytes in relatively warm water and larger diatoms under prolonged summer stratification combined with wind-induced mixing (Biggs *et al.*, 2019). A 40% increase in primary production in a sampling area off the northern WAP between 1997 and 2010 was associated with longer production seasons due to sea ice retreat and ocean warming (Moreau *et al.*, 2015); however, there are regional disparities that have reversed in the past decade. In the northern offshore WAP region, years of low winter sea ice and a relatively deep mixed layer observed between 1995 and 2006 correlated with lower phytoplankton biomass and a shift towards small size-dominated microbial plankton (Montes-Hugo *et al.*, 2009). Observations since 2010 revealed increases in phytoplankton biomass in the northern WAP that are above the long-term average (Schofield *et al.*, 2017) and a decrease in average biomass with deepening mixed-layer depths in southern inshore WAP sites (Kim *et al.*, 2018). Future projections indicate that primary production (along with nitrate consumption) will increase further in this area. In this case, iron additions from melting in glacial environments may allow complete nitrate depletion in some coastal waters, which is currently rarely observed (Höfer *et al.*, 2019).

Microbes such as eukaryotic phototrophs and prokaryotic photoheterotrophs, chemoheterotrophs and aerobic anoxygenic phototrophs characterise spring and summer microbial communities, whereas winter communities harbour a higher proportion of archaeal and bacterial chemolithoautotrophs (Grzymski *et al.*, 2012; Luria *et al.*, 2016). Kim & Ducklow (2016) suggested an increasingly important role of marine heterotrophic bacteria in future warmer coastal WAP food webs. The role of viruses in microbial processes and ecosystem functions remain understudied in the Southern Ocean, although this information is critical to predicting future changes in microbial dynamics.

Table 1. Changes in distribution and abundance of key pelagic organisms along the West Antarctic Peninsula (WAP), and the key message sections in which they are described

Distribution and abundance of key organisms along the WAP	Message
Antarctic krill (*Euphausia superba*) aggregate in fjords	3*b*
Hotspots of post-larval Antarctic krill abundance have shifted southwards	5*a*
Increase in the abundance of the non-ice-dependent *Thysanoessa macrura* krill in the northern WAP region and of ice-dependent crystal krill (*E. crystallorophias*) in the south	5*b*
Salp and pteropod summer abundances are inversely related to abundance of Antarctic krill	7*a*
Large reductions in the distribution of ice-dependent Antarctic silverfish (*Pleuragramma antarctica*) have occurred on the WAP shelf	5*a*
Adélie penguins (*Pygoscelis adéliae*) have declined in the northern but increased in the southern WAP	5*d*
Sub-polar penguin species (chinstrap, *P. antarctica*; gentoo, *P. papua*) have increased in the northern WAP	5*b*
Strong correlations between pelagic chlorophyll biomass, krill recruitment, and penguin foraging demonstrate tight trophic coupling in the WAP coastal ocean	7*a*

(*b*) Marine biological hotspots in fjords experience ecosystem changes due to warming-induced glacier melt and retreat

Atmospheric warming and increased incursions of warm Circumpolar Deep Water onto the continental shelf have caused rapid retreat of fjord tidewater glaciers at the WAP (Cook *et al.*, 2016).

In Potter Cove on King George/25 de Mayo Island (KGI), benthic structure shifted markedly from dominance by ascidians towards a mixed community comprising e.g. sea-pens, sponges, bivalves, sea anemones and ophiuroids, resulting from increased sedimentation rates following glacier retreat (Sahade *et al.*, 2015). By contrast, newly ice-free seabed has sustained explosive growth of obviously sedimentation-tolerant ascidians (Lagger *et al.*, 2018). In the adjacent Marian Cove, megazoobenthic assemblages changed with distance from the retreating glacier front, suggesting that physical disturbance is a major process shaping benthic communities (Moon *et al.*, 2015), and some benthic diatoms (e.g. *Paralia* sp.) reported rarely in previous studies showed an intense and persistent bloom from which herbivorous and filter-feeding consumers benefited (Ha *et al.*, 2019). The observed processes in the two KGI fjords allow the conclusion that climate-induced glacial retreat will alter ecosystem structure and functioning in additional fjords along the WAP, including those that have experienced little glacial retreat so far (see e.g. Lundesgaard *et al.*, 2020).

Fjords in the WAP region are also known as local hotspots of biodiversity (Pabis, Sicinski & Krymarys, 2011), with e.g. two million tons of Antarctic krill and >300 feeding humpback whales *Megaptera novaeangliae* (Nowacek *et al.*, 2011) observed in single fjords, and up to 38-fold higher megafaunal abundances compared to the adjacent continental shelf (Grange & Smith, 2013).

(*c*) Additional hotspots of climate change impact are to be expected in the future or exist already at a local scale

A significant decrease in late-summer sea ice concentration is projected for the Bellingshausen and Amundsen Seas as a consequence of geographically extending climate change (Meredith *et al.*, 2019). Similar consequences to those already experienced for decades by the WAP region (see Section III.3*a*), must be expected also for these currently cooler sectors of the Southern Ocean, since they have similar pelagic and benthic systems. A southward shift of the Antarctic Circumpolar Current remains controversial (Cristofari *et al.*, 2018; Meijers *et al.*, 2019). If it reaches >4 km per decade (Yang *et al.*, 2020), it will have a crucial impact on the entire pelagic system (Cheung *et al.*, 2009), with cascading effects on higher tropic levels (see also Section III.5*a*) due to shifts in the steep gradient in sea-surface temperature. Bokhorst, Convey & Aerts (2019) found that terrestrial biodiversity hotspots are often related to penguin and seal excrement, which creates conditions adequate for local and potentially invasive plants to establish. When seasonal ice cover is reduced in lakes, exposing open water, variations in the precipitation–evaporation balance can increase desiccation and salinisation, and the lakes will become important hotspots of climate change impacts on biodiversity (Verleyen *et al.*, 2012).

(4) Benthic communities exhibit unexpected dynamism – from explosive growth to mass mortality

Until recently, Southern Ocean benthic systems were described as characterised by long-term stability and slow biological processes. Novel evidence demands a paradigm shift towards populations and community dynamics ranging from 'slow–stable' in a global context to 'fast–variable' compared to the majority of the Antarctic benthos, with profound implications for their resilience or vulnerability.

(*a*) Some benthic near-shore populations are sensitive to complex environmental forcing

In McMurdo Sound (Ross Sea), the glass sponges *Anoxycalyx joubini* and *Rossella nuda* showed virtually no growth over a 10-year observation interval (Dayton *et al.*, 2013, 2016). They were mostly >2 m tall, some were killed by the predatory starfish *Acodontaster conspicuous* with no subsequent recruitment. While artificial substrates deployed in the 1970s were not significantly colonised by epifauna until 1989, they were found in 2010 to be totally covered by *A. joubini* and other sponges, some of which had grown to 50 cm in diameter. They continued growing until 2015, when most specimens died due to amphipod infestation, predation or sedimentation. These unexpectedly strong population dynamics in an environment that is both very cold (at nearly −2°C) and very stable in temperature were only weakly correlated with shifts in phytoplankton productivity driven by the calving of a massive nearby iceberg. While such dramatic changes were not observed for sponges on natural substrates, similar population shifts of echinoderms and bivalves were clearly attributable to the alteration of the marine production regime affected by regional iceberg and sea ice dynamics (Dayton *et al.*, 2019; Kim, Hammerstrom & Dayton, 2019*b*). In addition, sea ice cover duration and thickness as well as snow cover, all related to climate change, were important large-scale variables in explaining the diversity and functional traits of coastal benthic communities in this area (Cummings *et al.*, 2018). In laboratory experiments, demosponge species exhibited extreme phenotypic plasticity in metabolic physiology, with differences in metabolism among species being greater than seasonal changes (Morley *et al.*, 2016), a finding that contributes considerably to our understanding of high benthic dynamism. See Section III.3*b* for climate change impacts on the WAP benthos.

(*b*) Benthic recolonisation after sea ice and iceberg disturbance fosters mass occurrence of pioneer species

Twelve years after the Larsen A ice shelf disintegrated in the western Weddell Sea, recruits of the glass sponge *Rossella* cf. *villosa* dominated the newly exposed seabed (Gutt *et al.*, 2011). Dense aggregations of holothurians indicated unusually successful recruitment. Ophiuroid assemblages shifted from suspension- to deposit-feeder dominance. Abundant ascidian species disappeared, whilst formerly rare species doubled in abundance. Typical macrobenthic deep-sea species, assumed to characterise the sub-ice shelf benthos, may vanish when conditions turn to Southern Ocean shelf 'normality' (Gutt *et al.*, 2013; Segelken-Voigt *et al.*, 2016). These shifts are most likely caused by changes in food availability driven by ice shelf disintegration, current patterns, unpredictable sea ice dynamics (Cape *et al.*, 2014) and prey–predator interactions. Meiofaunal communities generally responded more slowly to change, still resembling those of food-limited deep-sea habitats 5 years after the Larsen B ice shelf disintegration (Rose *et al.*, 2014). However, two nematode genera were found to be rapid colonisers (Raes, Rose & Vanreusel, 2010).

After local devastation of the benthos due to anchor ice uplift in McMurdo Sound, the demosponge *Homaxinella balfourensis* recruited immediately and grew rapidly (Dayton *et al.*, 2016). Sponges of this genus were also abundant near the terminus of tidewater glaciers in the Ross Sea and in iceberg scours in the Weddell Sea (Gutt *et al.*, 2011). The demosponge *Stylocordyla chupachups*, gorgonians such as *Primnoisis* sp. and *Ainigmaptilon antarcticus*, as well as the hydrozoans *Corymorpha* spp. and *Oswaldella antarctica*, are further examples of pioneer species. The patchwork of dynamic stages of recolonisation increase regional beta-diversity (Turner *et al.*, 2014).

(*c*) Demersal fish stocks recover only very slowly from commercial fishery

Commercial bottom trawling in the Southern Ocean between the 1960s and 1990 led to a substantial depletion of the target and by-catch nototheniid rockcod and icefish species. The recovery time of these populations has been estimated to last 2–3 decades because of slow growth and low fecundity. A more recent study indicated that even this estimate was too optimistic, because the fish habitats around the South Shetland Islands are also severely impacted by rapid climate change (Marschoff *et al.*, 2012; Barrera-Oro, Marschoff & Ainley, 2017).

(5) **Range shifts, expansions, contractions and invasions are driven by environmental changes and human impacts**

Distribution shifts have been observed and predicted for a variety of Antarctic species. They are driven by changing climate (in marine and terrestrial habitats) and/or human introductions (mainly in terrestrial habitats). Human movements and declining ocean barriers enhance connectivity of the Antarctic to the rest of the world, facilitating biological invasions. Warmer temperatures boost species' range expansions, threatening adapted local specialists.

(*a*) Species geographical distributions are moving rapidly with changing environments

Consistent, long-term distribution shifts are occurring in the Southern Ocean, with warming resulting in poleward shifts in many species. For example, in response to the strengthening and southward shift of westerly winds, the foraging range of wandering albatross (*Diomedea exulans*) shifted southwards (Weimerskirch *et al.*, 2012). However, the direction and extent of range shifts vary among species. Some albatrosses and petrels shifted southwards from the 1990s to 2000s, but white-chinned petrels (*Porcellaria aequinoctialis*) occurred further north (Péron *et al.*, 2010). Of seven Southern Ocean seabird species, the foraging ranges of four are projected to contract in the north, instead of shifting polewards (Krüger *et al.*, 2018). Historical hotspots of post-larval Antarctic krill abundance have moved southwards from the Southwest Atlantic Sector to the WAP shelf system over the past 90 years. Sharp decreases in juveniles and new recruitment since the 1970s are attributed to increased temperatures and winds, and a reduction in sea ice (Atkinson *et al.*, 2019). Krill habitat quality is projected to continue to shift southwards and impact phenology due to warming and changes in phytoplankton biomass (Veytia *et al.*, 2020), subsequently impacting the foraging habitats of their predators, such as crabeater seals (Hückstädt *et al.*, 2020). On the WAP shelf, a large reduction in the distribution of a key sea ice dependent species, the Antarctic silverfish (*Pleuragramma antarctica*), suggests a local population collapse (Parker *et al.*, 2015). Ninety per cent of lanternfish (Myctophidae) species are also predicted to shift polewards (Freer *et al.*, 2019). Terrestrial nematodes, tardigrades, and rotifers are wind-dispersed across vast geographical space whereas springtails (Collembola) generally disperse long distances *via* open waterways. Climate-driven changes that lead to increased frequency and magnitude of extreme wind and meltwater events will likely expand the geographic range of cosmopolitan taxa. Similarly, the geographic ranges of more endemic species are predicted to contract concomitant with landscape-scale changes in habitat suitability (Adams *et al.*, 2014).

Increasing temperatures alone are not predicted to result in wholesale extinction or invasion of Antarctic life, but 79% of Antarctic endemic sea-floor invertebrate species (down to 1000 m) are projected to face reductions of habitats charcterised by suitable temperature conditions. The 963 species with ranges that cross the Polar Front were projected either to lose (53.5%) or to gain (46.5%) potential habitat (Griffiths, Meijers & Bracegirdle, 2017). King penguin (*Aptenodytes patagonicus*) colonies are predicted to disappear or decline in most of the sub-Antarctic, but new colonies may appear as the winter sea ice disappears (Cristofari *et al.*, 2018). Models for baleen whale populations generally predict declines, as the abundances of their prey decrease due to warming, but impacts vary among populations. If whales adapt their migratory behaviour, some species (e.g. minke whales, *Balaenoptera bonaerensis*) may benefit from changing conditions, while others (e.g. southern right whales, *Eubalaena australis*) will decline (Tulloch *et al.*, 2019). For contraction of species found under disintegrating ice shelves and the expansion of the 'normal' shelf fauna into such areas, see Section III.4*b*.

(*b*) Species expand their ranges in a warming Antarctic – faster, greener, and more competitive

Range expansion is most obvious in the terrestrial realm where habitat availability is predicted to increase by ~25% by the end of the 21st century (Lee *et al.*, 2017). Deglaciated terrains can be colonised rapidly, supporting an increased diversity and abundance of bacteria, lichens and bryophytes (Favero-Longo *et al.*, 2012). In particular, taxa with wider ecological response amplitudes are predicted to thrive, with evidence available for hypoliths (Le *et al.*, 2016) and soil microbial communities. A general trend emerges that warmer temperatures boost terrestrial ecosystem productivity. Between 1991 and 2002, with increasing temperature, four out of six monitored lichen species increased their growth rates by 124% (Sancho, Pintado & Green, 2019). Moss growth rates have quadrupled over the past approximately 50 years (Amesbury *et al.*, 2017), and also the two Antarctic native vascular plants *Colobanthus quitensis* and especially *Deschampsia antarctica* proliferated.

Such changes can cause drastic shifts in terrestrial populations because locally adapted species may have evolved life-history trade-offs that result in decreased resilience. Endemic lichen species have shown little to no potential to acclimatise (Colesie *et al.*, 2018) and for Antarctic tardigrades, changes in soil hydrology can modify physical constraints and alter their abundance (Andriuzzi *et al.*, 2018).

In the marine realm, range expansions of various zooplankton species are linked to differences in sea ice changes with warming. From 1993 to 2013, the abundance of non-ice-dependent krill *Thysanoessa macrura* increased in coastal and shelf waters of the northern WAP region, while the abundance of sea ice-dependent crystal krill *Euphausia crystallorophias* increased in the south (Steinberg *et al.*, 2015). Furthermore, sub-polar penguin species, including chinstrap (*Pygoscelis antarctica*) and gentoo (*P. papua*), increased in abundance in the northern WAP region as Adélie penguins (*P. adéliae*) have declined (Ducklow *et al.*, 2013). Range expansions of king crabs (*Neolithodes yaldwyni*) with reproductively viable populations were recently reported in the Palmer Deep and on the WAP slope (C.R. Smith *et al.*, 2012*b*; Griffiths *et al.*, 2013).

(*c*) A warming Antarctica enhances prospects for invaders and colonisation

In the terrestrial realm, humans have introduced non-native organisms, including the grass species *Poa annua*. While the two native vascular plants have been shown to be capable of withstanding competition for space, this might change with climate warming (Cavieres *et al.*, 2018). The flightless chironomid midge *Eretmoptera murphyi* was introduced to Signy Island in the 1960s, accelerating nutrient cycling and potentially outcompeting in the future the indigenous and endemic chironomid *Belgica antarctica*, highlighting the importance of biosecurity measures (Bartlett *et al.*, 2020).

The occurrence of invasive species has been most evident at sites with high human visitation frequency. Monitoring programs have detected high levels of non-native species (e.g. 233 individuals from 14 orders) around Scott Base (Newman *et al.*, 2018). However, clear evidence of an impact of invasive taxa at highly visited sites is missing (Velasco-Castrillón, Hawes & Stevens, 2018). Antarctica is currently unsuitable for most of the globally invasive terrestrial species; however, areas of the Antarctic Peninsula are predicted to become suitable for up to six of these species within the 21st century (Duffy *et al.*, 2017).

In the marine realm, four non-native invertebrates (crustacean, bryozoan, ascidian, cnidarian) and one cryptogenic kelp have been recorded (McCarthy *et al.*, 2019). Antarctica is not as physically isolated as previously thought. Newly identified mechanisms for colonisation include rafting on kelp or passive transport in surface waters, as eddies and storms move southwards across the Polar Front (Fraser *et al.*, 2018). The risk of human-introduced invasive species is linked to ship activity, with approximately 180 vessels and 500+ voyages into Antarctic waters annually (McCarthy *et al.*, 2019).

(*d*) Sentinel species and communities warn of environmental changes

Long-term observations of selected species can be valuable indicators of change. The use of lichens as biomonitors for warming is increasing, especially on the sub-Antarctic islands (Sancho *et al.*, 2019), and mosses are used as proxies for coastal climate change in the regionally drying East Antarctica (Robinson *et al.*, 2018).

In the ocean, extreme sea-surface temperature events decrease population growth in black-browed albatrosses (*Thalassarche melanophris*; Pardo *et al.*, 2017), making them valuable sentinels. Food stress caused by climate change increased the heterozygosity of breeding Antarctic fur seal (*Arctocephalus gazella*) females by 8.5% per generation over the last two decades (Forcada & Hoffman, 2014). Southern elephant seals (*Mirounga leonina*) produce pups of poorer condition in years with lower ocean productivity within their foraging ranges (Oosthuizen *et al.*, 2015). In the WAP, precipitous declines (80% since the mid-1970s) of Adélie penguins in the north and increases in the south (Ducklow *et al.*, 2013) have been attributed to differences in Antarctic krill availability and recruitment (Trivelpiece *et al.*, 2011) and changes in sea ice, precipitation and snowmelt (Cimino *et al.*, 2016). A geographic shift of areas of ecological significance based on aggregations of various top predators has been projected, which has relevance for future conservation and protection measures (Hindell *et al.*, 2020). New ways of using marine top predators as sentinels for trends in environmental conditions are emerging. For example, the adiposity of humpback whale blubber is a proxy of sea ice conditions in the preceding year (Bengtson Nash *et al.*, 2018).

'Ecosystem Essential Ocean Variables' represent a complex combination of biological traits and ecologically relevant physico-chemical variables related to biological functional groups (Constable *et al.*, 2016). They can be used as sentinels of changing environmental conditions, including single ecosystem components such as marine benthic communities, since they complement world-wide initiatives such as the Long-Term Ecological Research (LTER) network. Specifically, bivalve shells and fish otoliths can record environmental signals such as changing sea ice dynamics and temperature over their lifetimes (Trevisiol *et al.*, 2013).

(6) Survival and resilience of species depend on their adaptation and acclimation potential

Abilities to respond to changing Antarctic environments vary among organisms, shaped by distinctive selective pressures they experienced in their respective habitats during their evolutionary history. Marine waters hover chronically around −1.9°C, just above the freezing point of sea water, while terrestrial temperatures fluctuate widely seasonally, even daily, reaching vastly lower extremes. Marine ectotherms have adapted to remain active in pervasive constant cold, while terrestrial organisms have adapted to quiescent tolerance of prolonged aridity and frozen habitats, and to burst into growth during a finite window of more clement conditions. Knowledge of the complexity of adaptations of organisms to polar conditions is crucial to infer which species will become winners or losers in response to climate change, and to predict resilience, tipping points and impacts on ecosystem services.

(*a*) Feeling the cold – low temperatures damage proteins and constrain organismal performance but may also drive protein functional innovation

(i) Marine systems. Cold can prevent proteins from forming properly. With Southern Ocean temperatures at or near freezing point year-round, Antarctic notothenioid fishes are the most cold stenothermal marine vertebrates globally (Verde, Parisi & di Prisco, 2006), and are found to sustain high levels of protein damage. The repair machinery responsible for recycling improperly formed or damaged proteins in their cells runs 2–5 times faster than in lower latitude species (Todgham, Crombie & Hofmann, 2017). At the organism level, growth, embryonic development and post-prandial processes are 3–10 times slower than the expected effects of low temperature in Antarctic species, a consequence of problems in producing proteins at low temperatures (Peck, 2018). Cellular proteins and membrane lipids can be damaged by the high oxygen concentrations in cold water. Neuroglobin and cytoglobin were discovered in Antarctic fishes, including the haemoglobin-less channichthyid species, suggesting the evolution of functional innovations to mitigate such oxidative damage. Under experimental conditions, neuroglobin showed oxygen-related functions but its precise role in protection from damage remains unknown (Cuypers *et al.*, 2017, Giordano *et al.*, 2020).

(ii) Terrestrial systems. For Antarctic terrestrial organisms, shifts in the frequency of soil freeze–thaw cycles represent a physiological challenge. Small, poikilothermic animals with limited mobility – such as *Scottnema lindsayae*, the dominant nematode in Taylor Valley, Dry Valleys, East Antarctica – experienced population shifts with an increased frequency of soil freeze–thaw cycles between 1999 and 2001. Fewer juveniles reached maturity, and reduced reproductive success ultimately had the potential to impact population size (Knox *et al.*, 2016; T.E. Smith *et al.*, 2012). Similarly, for Antarctic mosses (Bramley-Alves *et al.*, 2014) and lichens, ice encapsulation at subfreezing temperatures can have detrimental effects (Bjerke, 2011), even if some of the isolated symbiotic photobionts exhibit high cryoresistance (Hájek *et al.*, 2012).

(*b*) Feeling the heat – Antarctic species are vulnerable to change; their thermal resilience is poor, complex and variable

(i) Marine systems. Ocean warming is a key climate change stressor. New research has tested the thermal resilience of Antarctic marine species. At the organismal level, species generally require 2–15 times as long as temperate species to acclimate to warming (Peck, 2018). Their long-term limits are about 2–3°C above ambient temperature, similar to species of the thermally stable tropics, compared to 6–9°C for temperate species (Peck *et al.*, 2014). Some experiments show significant plasticity in early-life stages (Suckling *et al.*, 2015), and no single cellular or physiological mechanism sets the thermal limits, because different species fail for different reasons (M.S. Clark *et al.*, 2017*b*). Recently, the first long-term (two-year) field experiment showed that 1°C warming doubled growth rates in most species, and community structure changed dramatically (Ashton *et al.*, 2017). At 2°C warming, growth was not faster, or even was slower, species had not acclimated, and there were stress responses and indicators of cell death (Clark *et al.*, 2019).

At the cellular level, brain lipid membranes are especially vulnerable to heat, and neuronal impairment is the first impact of acute heat stress. While broadly stenothermal, Antarctic fishes vary in acute thermal tolerance, e.g. brain synaptic membrane fluidity varies among species (Biederman *et al.*, 2019), with the more thermal-tolerant fish being least fluid. In short-term thermal acclimation, homeoviscous (i.e. maintenance of optimal fluidity) responses also vary among species, with membrane lipid remodelling occurring in one but not in a related sympatric species (Malekar *et al.*, 2018).

Recent comparative studies on thermal responses showed that for Antarctic fish, differences exist among latitudes and species within and across regions. This complexity is evident even for only a small number of studied species, in terms of Critical Thermal Maximum as a measure for thermal tolerance (Beers & Sidell, 2011), in terms of cellular transcriptional response to warm acclimation (Huth & Place, 2016), or to acute heat stress (Bilyk, Vargas-Chacoff & Cheng, 2018). Furthermore, analyses of the X-ray structure of haemoglobin of *Eleginops maclovinus* demonstrate that mechanisms underlying ATP regulation and the Root effect are diverse between sub- and high-latitude Antarctic notothenioids (Coppola *et al.*, 2012). This finding suggests that the distinct evolutionary history of each lineage may have influenced the extant genotype and adaptive potential to future change.

(ii) Terrestrial systems. Many Antarctic terrestrial biotas, in contrast to most marine organisms, have broad environmental tolerances allowing them to survive wide temperature fluctuations, including sub-Antarctic caterpillars, microarthropods and nematodes, all of which can cope with increased and/or variable temperatures (e.g. Everatt *et al.*, 2013). Furthermore, McGaughran *et al.* (2010) showed that the metabolic rate of the springtail *Cryptopygus antarcticus traveia* on Marion Island was strongly correlated with microclimate, suggesting physiological differentiation at the molecular level. Metabolic rate, through its influence on energy assimilation, significantly affects life-history trait evolution and on Marion Island the differences in microclimate appear to promote plasticity in springtail metabolic responses. Similarly, Chown, Haupt & Sinclair (2016) showed that fluctuating temperatures had a minor influence on caterpillar metabolic rate, again indicating plasticity to microhabitat variation. For Antarctic vegetation, thermal resilience is complex. For instance, a study of Antarctic lichens indicted that symbiosis integrity is highly imbalanced with changes in frequency and magnitude of warming events (Colesie *et al.*, 2018).

(*c*) Feeling climate change – can genetic adaptations keep pace with environmental shifts?

Climate change and other environmental shifts will likely favour species with short generation times (e.g. bacteria), which can rapidly alter their genetic make-up and adapt (Verde *et al.*, 2016), and, thus, reduce the impact on ecosystem processes. Many terrestrial and marine invertebrates and vertebrates, vascular plants, as well as microbes, both prokaryotes and eukaryotes are also exposed to environmental shifts. In groups with long generation times, the time needed for genetic adaptation might be too long to allow adaption to change (Peck, 2011).

The two main mechanisms effecting genetic change are mutation and gene flow within and among populations. Most Antarctic species may be poor in this respect under rapid environmental change, due to long generation times, slow growth rates, and large (hence fewer) eggs, all of which reduce rates of production and fixation of novel genetic material in populations (Peck, 2018). To assess capacity for adaptive potential, entry points include whole-genome sequencing, tests of functional responses to stress to evaluate adaptive plasticity, and estimation of genetic variability in populations to gauge survival potential. Only a handful of Antarctic marine vertebrate genomes have been sequenced and analysed to date: for two penguins (Li *et al.*, 2014) and five notothenioid fishes (Shin *et al.*, 2014; Bargelloni *et al.*, 2019; Chen *et al.*, 2019; Kim *et al.*, 2019*a*). One of these studies compared the genomes (and transcriptomes) of the high-latitude cold-adapted Antarctic toothfish (*Dissostichus mawsoni*) and a basal non-Antarctic and closest sister species, which never experienced the same selective pressure, to identify Antarctic-specific adaptations (Chen *et al.*, 2019). These include co-opted genes for intracellular freeze resistance, expansion of specific gene families that combat oxidative stress, a rapid amplification of transposable elements potentially related to speciation, and shifts in genetic and developmental programs enabling secondary pelagicism and niche expansion.

(*d*) Brood care and nesting of Antarctic fish call for modified management and conservation strategies

Since 2010, the use of cameras has revealed important ecological and ethological attributes of Antarctic fishes, especially in terms of reproductive strategies. We now know that nesting and parental care of embryos is typical, as observed in at least two dozen notothenioid species, including icefishes (Ferrando *et al.*, 2014), dragonfishes (La Mesa *et al.*, 2019), plunderfishes (Jones & Near, 2012) and nototheniids (Eastman *et al.*, 2013). As these species cover most Antarctic fish families, nesting and parental care are likely their prevailing strategies. The keystone species, the Antarctic silverfish utilises the sub sea ice platelet layer as a nursery ground (Vacchi, Pisano & Ghigliotti, 2017). In addition, for the Antarctic toothfish *Dissostichus mawsoni*, areas and timing of reproduction, as well as the pelagic nature of the eggs, have been discovered (Parker *et al.*, 2019). This new knowledge is key for improving conservation and management strategies of Antarctic marine living resources.

(*e*) Bioprospecting is still in its infancy but enzymes seem to be most promising

The systematic search for bioactive metabolites (bioprospecting) in the Antarctic focusses on marine benthic invertebrates, krill species, fishes, microorganisms, fungi and plants. Such metabolites can be used as scaffolds for biotechnological applications in medicine (e.g. for anticancer, anti-inflammatory, and antibacterial applications, and cardiovascular disease prevention), as well as in the development of lifestyle products, cryopreservation, and environmental technologies (Tripathi *et al.*, 2018). Currently, enzymes seem to be most promising (Bruno *et al.*, 2019). Nevertheless, despite the Southern Ocean being considered "a prolific resource of bioactive chemicals" (Núñez-Pons & Avila, 2015, p. 1127), market-ready products are still rare. An example for genetic engineering is the introduction of the *DaCBF7* gene isolated from Antarctic hairgrass (*Deschampsia antarctica*) into rice cultivar, resulting in increased low-temperature tolerance (Byun *et al.*, 2015). A breakthrough for the use of antifreeze glycoproteins, e.g. in medicine and food technology, is yet to come.

(7) Marine organisms, their life cycles and trophic interactions, are intrinsically linked to changing sea ice dynamics

Net overall Antarctic sea ice extent abruptly and unexpectedly plummeted to an unprecedented record minimum in 2016 and has remained below its long-term climatological average ever since (Reid *et al.*, 2020). Models project a 25% decrease by 2100 (Maksym, 2019). Given the tight relationships between sea ice, and pelagic and benthic food webs, including higher trophic levels, projected changes in sea ice extent, volume, seasonality and properties (e.g. thickness) are expected to have significant ecological ramifications for all Southern Ocean biotas.

(*a*) Tight relationships between sea ice, primary producers and marine herbivores suggest that changes in sea ice will have major impacts on pelagic food webs

Sea ice provides a substrate for ice-algal communities, which serve as an important food source for pelagic herbivores when food in the water column is scarce, and provides protection from predators (Meyer *et al.*, 2017). Pteropods, copepods and young Antarctic krill overwinter under the sea ice, where ice algae provide a crucial food source to sustain energy reserves (Johnson *et al.*, 2019). For the pack-ice zone in the northern Weddell Sea, a high dependency of herbivores, e.g. overwintering ice-associated copepods and larval Antarctic krill, on ice-algal carbon has been found (Kohlbach *et al.*, 2018). Off East Antarctica, larval Antarctic krill fed primarily on ice algae (O'Brien *et al.*, 2011), but showed dietary plasticity between years with different sea ice conditions (Jia *et al.*, 2016).

Sea ice is also important in priming spring phytoplankton blooms, which are strongly correlated with Antarctic krill recruitment and penguin foraging (Saba *et al.*, 2014), and in regulating zooplankton community composition. Anomalous years of high salp and pteropod summer abundance were correlated with warmer sea-surface temperatures and less sea ice in the spring, and inversely related to abundance anomalies of Antarctic krill that dominate in summers following higher winter ice extent (Steinberg *et al.*, 2015). Habitat suitability models also showed a close association of squid species with sea ice (Xavier *et al.*, 2016*b*).

(*b*) Sea ice controls benthic community composition and function

Direct links have been established between sea ice conditions, pelagic primary productivity and, subsequently, coastal benthic communities (e.g. Cummings *et al.*, 2018). Persistent, multi-year sea ice can result in decreased *in situ* primary production, through its influence on light availability, with consequences for diversity and abundance of primary consumers. Changes in phytoplankton (size class structure) under thicker, multi-year, land-fast sea ice with reduced under-ice light affected benthic invertebrate abundance by altering the quality of food (Kim *et al.*, 2019*a*). At a site with multi-year sea ice, the quantity and quality of benthic algal detritus was lower relative to that at a site with thinner, annually formed ice (Lohrer, Cummings & Thrush, 2013). A decrease in duration of sea ice cover, and the associated increased light and reduced sedimentation, resulted in a regime shift from an invertebrate- to an algal-dominated community (G.F. Clark *et al.*, 2017*a*). On the deeper shelf, the dominance of the polychaete *Aurospio foodbancsia* covaried with pack ice duration, while other species exhibited non-linear or only small responses (C.R. Smith *et al.*, 2012*a*). A simulated benthic community on the deeper shelf and slope did not show major changes under increased primary production resulting from sea ice loss (Jansen *et al.*, 2020).

Although future land-fast ice characteristics are difficult to predict, there will undoubtedly be changes in composition and function of coastal benthic communities in a warming world. Encouragingly, plasticity of feeding modes and generality of functional traits may confer resilience to sea ice-associated productivity changes (Cummings *et al.*, 2018; Wing *et al.*, 2018), with functionally diverse communities likely to store more carbon in a reduced sea ice environment (Barnes & Sands, 2017). Hints for benthic biomass decrease and composition shifts in a high-latitude area, assumed to be caused by sea ice increase, are provided by Pineda-Metz, Gerdes & Richter (2020). It this long-term study the relatively large area of investigation was characterised by high faunistic patchiness as well as high sea ice variability and different methodological approaches were applied.

(*c*) Not too much, and not too little – penguin and seal populations are sensitive to local variation in sea ice conditions

Sea ice characteristics influence the foraging and breeding success of ice-obligate vertebrates in a non-linear fashion, whereby thresholds in sea ice concentration and extent are evident. For example, Adélie penguin breeding success is affected by icescape conditions. Deviations from optimal sea ice concentrations result in increased foraging effort by adults and reduced breeding success (Le Guen *et al.*, 2018). Persistence of sea ice throughout chick-provisioning periods in the absence of polynyas, in combination with anomalous precipitation and changes in sea ice firmness, explain massive breeding failures (Ropert-Coudert *et al.*, 2018). Population growth rates of emperor penguins (*Aptenodytes forsteri*) are maximised at intermediate sea ice concentrations (Jenouvrier *et al.*, 2012). Indeed, rapid emperor penguin population changes have already been observed in relation to changing sea ice conditions (Fretwell & Trathan, 2019), and 80% of all populations are projected to be nearly extinct by 2100 under the business-as-usual IPCC scenario, whilst 91% will survive under the 1.5°C Paris Agreement goal (Jenouvrier *et al.*, 2020). Ice-obligate seals (e.g. Weddell seals, *Leptonychotes weddellii*) are seemingly less affected by short-term icescape perturbations, but more frequent disruptions, such as iceberg events causing large sea ice extent, may result in long-term negative population effects (Chambert, Rotella & Garrott, 2012).

These results suggest that sea ice requirements by seals and penguins are complex, and that many ice-dependent populations rely on intermediate sea ice concentrations for successful breeding. Therefore, not only do projected long-term sea ice declines threaten ice-obligate breeding seal and penguin species, but shorter-term local increases and decreases of sea ice stress these populations by increasing travel distances of adults and altering the distribution of suitable foraging patches. For climate-induced range expansion and contraction, see Section III.5*b*.

(8) Anthropogenic pollution and the responses of biota remain under-surveyed in Antarctic ecosystems

Anthropogenic pollutants in marine and terrestrial environments, especially novel waste products such as macro- and microplastics, persistent organic pollutants (POPs) and heavy metals, increasingly attract scientific interest and the attention of decision makers. Although currently insufficient, knowledge on the impacts of such pollutants on biotas is essential for informing both Antarctic Treaty policy and national legislation to prevent ecosystem damage.

(*a*) Pollutants accumulate in ecosystems and impact top predators

The Antarctic is an environmental sink for anthropogenic bio-accumulative POPs and heavy metals, reaching atmospheric, marine (from sea surface to the deep sea) and terrestrial environments (Isla, Pérez-Albaladejo & Porte, 2018). Biomagnification of toxic polychlorinated biphenyls (PCBs) has been reported across marine foodwebs. Studies on top predators, such as skua species and wandering albatross, showed that increasing POPs and trace metals contributed to a decrease in long-term reproductive performance, but did not affect survival rate or long-term breeding success in south polar skuas (*Catharacta maccormicki*; Goutte *et al.*, 2018). Fish and squid show a decreasing trend for at least partly anthropogenic Hg levels that are bioaccumulated in the food chain (Cipro *et al.*, 2018; Seco *et al.*, 2019). The biological impacts, however, are still unknown.

A first Environmental Risk Assessment for soil biotas on King George Island showed different responses, from neutral to negative, for bacteria, cladocerans, microalgae, and macrophytes to contamination of toxic trace elements (Pereira *et al.*, 2017). Pesticides and other legacy chlorinated hydrocarbons are detectable in different vegetation types as well as soils along the Antarctic Peninsula (Cabrerizo *et al.*, 2012).

(*b*) Plastics occur in the environment and in organisms but profound impact studies are lacking

Macroplastics have rarely been quantified in the Antarctic (e.g. Waller *et al.*, 2017) and little is known about the response of biotas. Entanglements by plastic packaging bands and other waste have been recorded over a 25-year time series in 1033 Antarctic fur seals, mainly juveniles (44%; Waluda & Staniland, 2013). Quantities of plastic debris items (>5 mm) regurgitated after ingestion by grey-headed (*Thalassarche chrysostoma*) and black-browed albatrosses in and around their nests at Bird Island (South Georgia) increased significantly from near zero between 1994 and 2019. The number of items per breeding pair varied by an order of magnitude across three albatross species, including the wandering albatross and the southern giant petrel (*Macronectes giganteus*; Phillips & Waluda, 2020). Long-lines lost during fishing activities between 2008 and 2017 reached an estimated total length of 12555 km in the areas monitored by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR Secretariat, 2018).

Microplastics comprised of fibres and fragments have already been detected in coastal sediments, water, sea ice (Munari *et al.*, 2017; Kelly *et al.*, 2020) and top predators. For example, they were present in 20% of the diet of penguins (Bessa *et al.*, 2019). Microplastics were absent in some offshore water and sediment samples (Kuklinski *et al.*, 2019; Barnes, Walters & Goncalves, 2010) but found at other sites (Isobe *et al.*, 2017). Laboratory studies demonstrated the potential for Antarctic krill to ingest microplastic particles (Dawson *et al.*, 2018), our knowledge on *in situ* accumulation of microplastics in tissues of Antarctic organisms is extremely poor. The title *Plastics everywhere…* of the publication of the first evidence for plastic fragments ingested by the collembolan *Cryptopygus antarcticus* emphasised that plastics have even entered the Antarctic terrestrial food web, and, thus, the most remote region on earth (Bergami *et al.*, 2020).

(9) Continental biotas are highly endemic and at risk from climate change

Isolation of terrestrial and limnetic habitats by glaciers and coastal ice sheets as well as topographic barriers has resulted in local populations with high levels of genetic distinctiveness. Increased connectivity and/or dispersal of individuals among habitats as a consequence of warming and human activity will potentially disrupt co-adapted gene complexes developed over millions of years. These findings need to be considered in biosecurity strategies.

(*a*) Terrestrial and limnetic populations have genetically diverged and speciated

A high degree of endemism among Antarctic terrestrial and limnetic invertebrates has been hypothesised for decades. Recent genetic advances have confirmed this speculation and identified endemism in a wide range of organisms, including groups once thought to be globally distributed, such as diatoms (Souffreau *et al.*, 2013; Kociolek *et al.*, 2017), cyanobacteria (Jung *et al.*, 2019), lichens (Jones *et al.*, 2015) and rotifers (Velasco-Castrillón *et al.*, 2014; Iakovenko *et al.*, 2015). Further, it has become increasingly clear that terrestrial and limnetic habitats support taxa that have survived multiple glacial cycles over millions of years. Many taxa have undergone evolutionary radiations on the continent, specifically springtails (Collins *et al.*, 2020), including in locations not previously considered refugial, such as the Antarctic Peninsula for *Schistidium* moss species (Biersma *et al.*, 2018).

(*b*) Distribution patterns are driven by landscape isolation combined with species-specific dispersal abilities

Geographic scales of isolation are influenced by dispersal abilities. Species that are suited to airborne dispersal, such as nematodes, can show broad-scale patterns of diversity (Adams *et al.*, 2014). Other taxa, including some springtails and copepods, have low dispersal capacity and remain genetically isolated with small distribution ranges (<10 km; Bennett *et al.*, 2016; Karanovic *et al.*, 2014 due to geomorphological barriers such as glaciers and ice sheets (Carapelli, Leo & Frati, 2017).

(*c*) Antarctica's warming will increase landscape connectivity and biotic interactions

In contrast to today's habitat fragmentation by inland ice and topographic dispersal barriers, the Pliocene was a period of relatively high habitat connectivity. Currently, the world is heading for similar conditions to the Pliocene with high CO_2 concentrations and rising temperatures. Increased habitat connectivity, also present during interglacial periods, enhances dispersal (Lee *et al.*, 2017) and reduces local endemism by mixing genetically distinct populations. The distribution and abundance of continental taxa was previously thought to be driven primarily by abiotic drivers (Hogg *et al.*, 2006). However, biotic interactions between different nematode species or fungi and cyanobacteria are now known also to shape such communities (Caruso *et al.*, 2019; Lee *et al.*, 2019). As a consequence of increased connectivity, interactions such as resource competition among species may develop, more suitable habitats may become available, and novel niches and/or habitats for invasive species may be created (Hughes *et al.*, 2019; Lee *et al.*, 2017).

(10) Recently discovered assemblages are driven by particular environmental conditions

Recently discovered habitats extend our knowledge of evolutionary and ecological processes in the Antarctic and contribute to global assessments of biodiversity and ecosystem functioning.

(*a*) Subglacial lakes contain active and functionally diverse microbial communities

Nearly 4000 operational taxonomic units of Bacteria and Archaea have been identified on the basis of 16 s subunit DNA sequences from water and sediments recovered from subglacial Lake Whillans (Christner *et al.*, 2014). Various metabolic groups have been detected that comprise relatives of species known to use reduced N, S or Fe and CH_4 as energy sources. Chemosynthetic carbon-fixation pathways appear to underpin their community metabolism (Achberger *et al.*, 2016; Purcell *et al.*, 2014).

New results from other subglacial lakes, believed to have persisted in near isolation for hundreds of thousands of years (Bulat, 2015) and to contain unique organisms, await widespread application of clean-drilling techniques. While changing climate does not pose immediate threats to these ecosystems, they remain vulnerable to risks of contamination if rigorous drilling protocols are not sustained (Mikucki *et al.*, 2016).

(*b*) Rare new habitats are vulnerable to environmental changes due to their uniqueness

The sea anemone *Edwardsiella andrillae* and antarcturid isopods use the underside of ice shelves as their habitat (Daly, Rack & Zook, 2013; Bornemann *et al.*, 2016). Scientific questions arising from these discoveries include whether the sea anemone is endemic to the ice subsurface, how the isopods colonised this habitat and whether these populations mix genetically with benthic relatives of the assumed same species.

Hydrothermal and geothermal habitats are hotspots of unique biotas. Chemosynthetic marine assemblages living at hot hydrothermal vents on the East Scotia Ridge are dominated by the yeti crab (*Kiwa tyleri*), stalked barnacles, limpets, peltospiroid gastropods, anemones, and a sea star (Linse *et al.*, 2019), and constitute a new vent-fauna province. Below the former Larsen B ice shelf, a low-activity seep (Niemann *et al.*, 2009) with a seep-specific nematode fauna (Hauquier *et al.*, 2011) was observed and analysed, while a small patch of bacteria occurred on the sediment at a different location (Gutt *et al.*, 2011). In the Ross Sea at 10 m water depth a bacterial mat, based on a hydrogen sulfide and methane seep was discovered, and may have an impact on greenhouse gas emission from marine methane reservoirs (Thurber, Seabrook & Welsh, 2020). On land, geothermally active regions allow species to survive in isolation on ice-free land or in sub-ice caves, from which recolonisation of the rest of the continent could have taken place (Fraser *et al.*, 2014). The hot fumarolic soils on Mount Erebus are home to cosmopolitan thermophiles, endemic archaea and bacteria (Herbold *et al.*, 2014). On Deception Island, bacterial and archaeal taxa are reported from a wide range of environmental conditions (Bendia *et al.*, 2018).

Unusually dense aggregations of hydrocorals occur regionally on the upper continental slope off East Antarctica (Post *et al.*, 2010). The East Antarctic Admiralty and Scott Seamounts have unique benthic biodiversities that represent different colonisation histories. They comprise stalked crinoids (Hyocrinidae), brachiopods, and suspension-feeding ophiuroids (*Ophiocamax*), as well as a high abundance of predators, including lithodid crabs, regular sea urchins, and sea stars (Bowden *et al.*, 2011). The sea floor below floating ice shelves, e.g. Larsen A and B as well as Amery, is colonised by deep-sea life forms and a sparse shelf fauna that mostly depend on an advected food supply (Gutt *et al.*, 2011; Post *et al.*, 2011).

IV. CONCLUSIONS

(1) This literature survey demonstrated the substantial progress in research around our 10 key messages on

Antarctic ecosystems under stress and how important most themes behind these messages are. However, there is a clear need for further study in many of these themes to underpin socially relevant opinion-forming, decisions and actions.

(2) A clear conclusion from the 10 key messages discussed herein is that life in the Southern Ocean and Antarctica is highly sensitive to environmental changes. We conclude that the greatest anthropogenic threat to Antarctic ecosystems is – and will be in the future – climate change. This judgment differs from the conclusions of the IPBES *Global Assessment* (IPBES, 2019), which considered exploitation to represent the greatest risk for global marine and terrestrial ecosystems. This difference is due to the currently low economic importance of exploitable Antarctic resources, as well as the little land and ocean use.

(3) Although Antarctic terrestrial and marine ecosystems are sometimes regarded as relatively homogeneous, the responses of Antarctic biotas to environmental changes vary considerably across regions, habitats, ecosystems, communities and organisms, even at the intra- and extracellular level. The highly diverse environmental demands and position in the food web will determine whether species become losers or winners in response to predicted circumpolar warming (Morley, Barnes & Dunn, 2019).

(4) Intermediate levels of confidence, defined along axes of quality/quantity of evidence and agreement among publications, were assigned to the majority of our sub-messages (Fig. 2). However, the classification of only seven of our 31 detailed sub-messages as 'robust' shows that a sound scientific basis for decisions on the management and protection of Antarctic ecosystems is not yet fully established. Antarctic biological variability, complexity and uniqueness resulting from non-linear processes at all levels of biological organisation from molecules to ecosystems remain poorly understood. In addition, the rarity of year-round and multi-year monitoring and circumpolar-scale observations limits our understanding of past, present and future biological processes.

(5) Analyses of the impact of multiple stressors (e.g. warming, oxygen depletion and CO_2 increase; Gutt *et al.*, 2015) are 'emerging' challenges for many of the 10 key messages (Pörtner & Gutt, 2016). The most difficult complex to unravel will be cause–effect relationships on multiple pathways, which cascade *via* bottom-up or top-down interactions through trophic levels, e.g. from phytoplankton to sediment communities, where carbon is sustainably sequestered, or from primary producers to top predators (Constable *et al.*, 2016).

(6) Changes observed along the Antarctic Peninsula may be harbingers for the future of the entire continent. On land, ecosystem functions such as productivity may increase, while marine organisms adapted to high-latitude conditions may suffer because southward escape is blocked by the continent (Griffiths, Meijers & Bracegirdle, 2017). Elevated CO_2 uptake through increased primary production and eventually higher productivity at exploitable trophic levels may superficially be seen as favourable. Conversely, biodiversity loss and possible negative feedbacks resulting in reduced long-term CO_2 sequestration, are not yet predictable with any accuracy. Obtaining a more comprehensive inventory of organisms and communities to help answer such questions may now be possible with advances in environmental DNA analyses (Cowart, Murphy & Cheng, 2018), particularly in pelagic systems, and seabed-imaging methods in benthic habitats.

(7) This synthesis showed that comparisons across ecosystems, e.g. among marine, limnetic and terrestrial or among different groups of organisms, are useful with regard to adaptation or range shifts. Detailing similarities and fundamental differences between two systems can provide added value in understanding the origin, structure and functioning of the systems under study.

(8) The uniqueness and rarity of biotas in the small terrestrial, ice-free areas of Antarctica justifies their protection. The Southern Ocean makes a remarkable contribution to global biodiversity and ecosystem services (nature's contributions to people) under increasing anthropogenic stress (Chown & Brooks, 2019). Protection and conservation strategies should consider that Antarctic biotas and their functioning are more connected to the rest of the world than previously understood.

(9) Pollution in both marine and terrestrial Antarctic habitats has recently attracted particular attention, especially regarding microplastics. Quantification of the impacts of pollutants and the responses of different biotas, especially of key species, is needed to develop efficient management strategies. This emerging field demonstrates the need for flexibility in research strategies to react rapidly to new threats and unexpected findings, further developing links between science and policy (Hughes *et al.*, 2018)

(10) The development of novel concepts in Antarctic science (Xavier *et al.*, 2016*a*) demands the implementation of question-driven research programs, ideally collaborative and integrative, while avoiding potentially negative effects of competition for research resources or the maintenance of traditions. To address the big challenges, a balance is necessary between applied approaches, e.g. solving climate-, conservation- and ecosystem-management problems, and academic freedom to carry out fundamental research, which in turn informs applied approaches.

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VII. Supporting information

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. List of authors with their expertise, on which the synthesis was built.

Appendix S2. Search terms for key messages used in the literature survey in *Web of Science* including numbers of publications 1970–2020 and 2010–2020; results from 4 September 2020.

Appendix S3. Scheme showing how the confidence of the scientific sub-messages was assessed following the IPCC AR5 and IPBES methodology (Mach *et al.*, 2017; IPBES, 2019).

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