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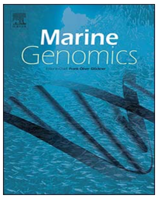

Review

Cross-disciplinarity in the advance of Antarctic ecosystem research

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ABSTRACT

The biodiversity, ecosystem services and climate variability of the Antarctic continent and the Southern Ocean are major components of the whole Earth system. Antarctic ecosystems are driven more strongly by the physical environment than many other marine and terrestrial ecosystems. As a consequence, to understand ecological functioning, cross-disciplinary studies are especially important in Antarctic research. The conceptual study presented here is based on a workshop initiated by the Research Programme Antarctic Thresholds – Ecosystem Resilience and Adaptation of the Scientific Committee on Antarctic Research, which focussed on challenges in identifying and applying cross-disciplinary approaches in the Antarctic. Novel ideas and first steps in their implementation were clustered into eight themes. These ranged from scale problems, through risk maps, and organism/ecosystem responses to multiple environmental changes and evolutionary processes. Scaling models and data across different spatial and temporal scales were identified as an overarching challenge. Approaches to bridge gaps in Antarctic research programmes included multi-disciplinary monitoring, linking biomolecular findings and simulated physical environments, as well as integrative ecological modelling. The results of advanced cross-disciplinary approaches can contribute significantly to our knowledge of Antarctic and global ecosystem functioning, the consequences of climate change, and to global assessments that ultimately benefit humankind.

1. Introduction

The Antarctic continent, including its surrounding Southern Ocean, overlying atmosphere, and its portion of the biosphere, is an integral component of the Earth system. As Antarctic ecosystems change, so do the services they provide to global ecosystems and humankind. In the context of this framework, cross-disciplinary science is essential to conducting Antarctic ecosystem research. Physical-chemical (including geological) drivers, especially ice, temperature close to or below freezing, wind and drought, are more relevant to life on the Antarctic continent and in the Southern Ocean than in many other ecosystems. In addition, important biological interactions, such as energy flux between trophic levels, are also important influences at varying scales. (Convey et al., 2014; Gutt et al., 2015). Conversely, biological activity in turn modulates the physical-chemical environment, for example through the emission of the climatically active gas dimethylsulphide (DMS) by algae (Stefels et al., 2007), by shaping marine sediments (Graf and Rosenberg, 1997), biological contributions in rock weathering and soil formation (Thomas et al., 2008) and the production of oxygen (Field et al., 1998). As a result, it is essential to (a) understand the response of the biosphere to climate change by taking into account species-specific adaptations to the specific environment, (b) estimate the proportion of endemic Antarctic biota in relation to the global biodiversity, and (c) quantify Southern Ocean contributions to global ecosystem goods and services including fishery and other natural products, biogeochemical cycling, climate regulation, oxygen production, maintenance of biodiversity and ethical benefits (Grant et al., 2013). Linking the physical and biological components of Antarctic ecosystems is also a key challenge since many parts of the Antarctic and Southern Ocean climate system are heterogeneous in space and time (Mayewski et al., 2009; Turner et al., 2009, 2014; Jones et al., 2016), but descriptions of the physical environment, and associated modelling, often differ widely from those applied to biological processes.

As a consequence, Antarctic research is at the forefront of important scientific challenges, applying holistic approaches that combine systematic assessments of key physical predictors and key biota. Antarctic interdisciplinary research also helps to provide societal benefits by delivering new technologies and projections of potential impacts of the Antarctic environment to change and the impacts of those changes on ecosystem goods and services. Challenges range from increasing the availability of quantitative information, such as increasing the number of studies and publicly available data sets, to more functional requirements such as developing new analytical tools and progressing our ability to resolve and simulate systems of greater complexity. Many of these challenges can only be tackled synergistically and need to be addressed to provide a framework for future development of research in Antarctica, and elsewhere.

The Antarctic science community has made remarkable progress over the past 20 years. However, despite some outstanding exceptions, this has largely been achieved within single disciplines. It is not only the traditional structure of how scientific research is organised and funded that encourages single-discipline approaches, but it is also the extreme Antarctic environment, including difficulty of accessing support, that has resulted in generally narrow science programmes. This has led to the current silo structure of Antarctic research. Today we can sequence genes and modify genomes, and we can remotely observe area-wide temperature, sea-ice cover and primary production including their spatial patchiness and temporal dynamics from space. This allows us to make projections, for instance, of sea-ice change for the next 100 years; we can also count penguins, seals and whales by satellites, drones, helicopters and airplanes, and we can survey marine habitats by remotely operated and autonomous vehicles. We can also conduct physiological, ecological and ‘omics’ experiments on terrestrial or marine environments, either in situ, or in the laboratory, by manipulating environmental variables. A drawback of such rapid and successful advances in single disciplines is that it leaves gaps in cross-disciplinary developments. To date, we are left with a mosaic of information that does not provide a coherent and robust picture of past, present and future Antarctic ecosystems. With access to emerging new technologies, the collaboration of Antarctic biological, geological and physical scientists provides an exciting opportunity to develop a comprehensive assessment of future ecosystem vulnerabilities and resilience. But this is only likely to happen if scientists extend their research interests beyond their discipline and are encouraged to establish true interdisciplinary collaborations. To achieve this, historical barriers dividing distinct areas of expertise need to be removed so that a new era of research targeted at systematically addressing specific cross-disciplinary questions is ushered in. Biologists need support from the climate and physical research fields (including chemistry and geology) to solve the challenges of understanding complexity of real life systems. In turn, physicists benefit from approaches that address obvious requirements of society. Large international initiatives, once sufficiently developed, could in the future provide an appropriate ‘home’ for advanced cross-disciplinary research e.g. the Southern Ocean Observing System (SOOS; Rintoul et al., 2012), the Polar Climate Predictability Initiative (PCPI; www.climate-cryosphere.org/wcrp/pcpi, last access: 20 September 2017) or ongoing Scientific Research Programmes (SRP) of the Scientific Committee on Antarctic Research (SCAR). Even more promising, would be truly cross-disciplinary SRPs to be developed in the near future.

In this sense, the 1st SCAR Antarctic and Southern Ocean Science Horizon Scan (hereinafter the SCAR Horizon Scan; Kennicutt et al., 2015, www.scar.org/horizonscanning, last access: 20 September 2017), was a key step to opening new doors. It provided discipline-clustered overarching science questions central to advancing Antarctic and Southern Ocean science over the next two decades. The biology theme "Life at the precipice" centred on processes of various biota (see also Xavier et al., 2016). However, besides nature conservation issues, the genomic, molecular and cellular basis of adaptation of organisms to their environment, was the only other biological challenge highlighted in one of the published versions (Kennicutt et al., 2014). Life in Antarctica and the Southern Ocean is always shaped by various non-biological drivers, but also modulated and propagated through biological interactions (Gutt et al., 2013a; Convey et al., 2014). Hence, the status of ecosystems can only be evaluated if environmental requirements of organisms are related to the chemical-physical constraints of their survival. The present conceptual study aims to contribute to this challenge by focussing on the urgency of cross-disciplinary approaches for the advance of Antarctic ecosystem research. The fact that assessments by organisations such as the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services (IPBES; Díaz et al., 2015) and the Intergovernmental Panel on Climate Change (IPCC, 2013) require scientifically reliable information on interactions between the biological and physical environment is clear evidence that such cross-disciplinary approaches are needed now. This information is also used for the development of future scenarios and, thus, related to socio-cultural, as well as socio-economic aspects.

The timing of such initiatives to improve inter-disciplinary approaches to Antarctic science is appropriate because the quality and quantity of spatially and temporally explicit data on the state of the Antarctic environment has increased enormously in the past few years. This refers especially to variables that are relevant as global change stressors of ecosystems, including freshwater availability, sea-ice extent, atmosphere, and ocean temperature change, and to other anthropogenic impacts, such as fishing and the introduction of non-indigenous species. Major advances have also recently been achieved in application of molecular markers to study the taxonomy, diversity and distribution of taxa. In addition, the availability of new and historic biogeographic data uploaded to repositories and made publicly available allows insights into large-scale biodiversity patterns (De Broyer et al., 2014; Terauds and Lee, 2016) and potentially to assess the role of contemporary and historical processes in shaping these patterns (Convey et al., 2008). Projections of expected future changes for single physical environmental variables, and for populations of a very few iconic Antarctic species, have been developed (e.g. Jenouvrier et al., 2009; Bracegirdle and Stephenson, 2012). In essence, enormous single-disciplinary advances happened in the past five to ten years, and included a transition to a new generation of SCAR SRPs (Bergstrom et al., 2006; Gutt et al., 2013a; Verde et al., 2016).

As a legacy of the SCAR Horizon Scan, the workshop "Interactions between Biological and Environmental Processes in the Antarctic" was initiated by the SCAR SRP Antarctic Thresholds – Ecosystem Resilience and Adaptation (AnT-ERA, www.scar.org/srp/ant-era, last access: 20 September 2017; Gutt et al., 2013a). The core aim of this workshop was to exchange novel ideas among scientists to gain an improved understanding of the focal questions generated by the SCAR Horizon Scan. In addition the participants identified challenges, which have recently been identified for other ecosystems or which refer to a global scale, e.g. by the IPCC or IPBES, but remain unanswered for the Antarctic. The first steps towards implementation of these new ideas and questions were also discussed. The workshop deliberations can serve as a basis for research proposals in a second step of project realization. In addition, underrepresented cross-disciplinary concepts that have been difficult to implement in the past were highlighted. Various developments within disciplines were also discussed, because answering cross-disciplinary questions still demands specific disciplinary knowledge (for a general illustration of this concept see Fig. 1). The overarching aim of this paper is to present the intellectual output of this brainstorming workshop with a focus on the most striking novel ideas for cross-disciplinary studies in Antarctica and the Southern Ocean.

To identify the fields most urgently requiring focus, the outcomes of the workshop were clustered into eight themes according to an informal survey among the participants. Apart from sea-ice, the themes were purposely not ecosystem-specific. The authors are aware that this clustering, necessary for the dissemination of novel ideas, is somewhat arbitrary. As a result, overlaps exist between the selected themes. Theme 1 on upscaling and downscaling is considered to cover overarching approaches, which are applicable to all other themes. Despite an attempt to cover a very broad scientific scope, the authors accept that this paper does not and cannot claim to represent a complete overview but rather the identification of leading novel research themes from, and for, the Antarctic scientific community.

The workshop was held in September 2015 at the Institute of Marine Sciences in Barcelona, Spain. Research initiatives that contributed to this conceptual study in addition to AnT-ERA are listed in the Acknowledgements.

2. Theme 1: spatio-temporal scales: upscaling and downscaling in climate change research

2.1. Background and justification

Climate change fundamentally operates over a range of spatial scales and involves multiple variables in addition to air temperature, i.e. impacts extend beyond the often-used term 'global warming'. Responses of biological systems to climate change, and more widely to all aspects of environmental variability and change, can operate over a broad range of temporal scales, from instantaneous through diurnal, seasonal, interannual and evolutionary, and spatial scales from square or cubic metres or even less in microbial systems, with distinct biological patchiness to many kilometres (Peck et al., 2006; Peck, 2011; Blois et al., 2013). Biological responses, in turn, feed back on climate so that the entire system must be viewed as multi-scale (e.g. Lavergne et al., 2010).

Multi-scale is a convenient term, but it is exceedingly challenging to

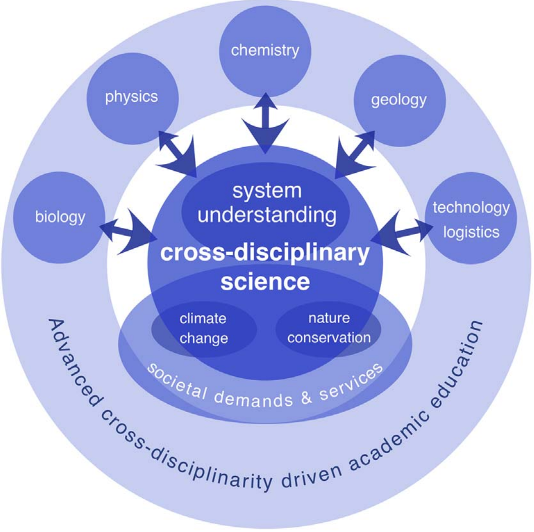

Fig. 1. Schematic overview of how to achieve advanced cross-disciplinary research. Different scientific disciplines can contribute through cross-disciplinary coordination and management to improved scientific and societal approaches. This strategy includes modern cross-disciplinary academic education.

implement especially in Antarctic ecosystem studies, for instance when assessing ecosystem functioning, functional diversity and ecosystem services. Required observations need to be carried out simultaneously at a well-defined range of scales, and modelling needs to encompass this range of scales (e.g. Ådlandsvik and Bentsen, 2007). Spatio-temporal is also a term that suggests a good understanding of the dynamics required across multiple spatial and temporal scales but, again, this is not easily achieved. The EPIC approach (Ensemble Projections Incorporating Climate model uncertainty, Fig. 2) is an example of a class of approaches that seeks to take predictions, contextualise with what is known about variability and determine implications at smaller scales (Lewis et al., 2017). The implication then is the requirement to know everything, everywhere and all the time – something patently impossible. Furthermore, making observations at high latitudes is logistically challenging. Often it is difficult to develop simultaneous spatial and temporal perspectives on a given process let alone interactions between processes (e.g. Sinclair et al., 2014). Simplistically, while the climate as a driver can be viewed as physical, it is clearly multi-factorial as it incorporates chemical and biological processes (Niiranen et al., 2013) that range across multiple scales.

This suggested effort must advance into focusing on predictive skills for targeted questions, especially around connecting different spatial scales, both upscaling from small local scales to hemispheric scales, and downscaling from global to local scales (for methods in meteorological circulation models see: Wilby and Wigley, 1997). To aid such efforts, one needs to consider (a) what are the critical scales for linking biological responses to climate (see Potter et al., 2013) and where do current knowledge gaps lie, (b) what data are needed to more effectively link biology and climate, relevant to what is to be predicted (Gutt, 2017), (c) how and what simulation tools (models) can be best used to upscale and downscale biological responses. Connecting these scales will be a necessary component of almost all aspects considering ecological change in relation to climate in Antarctica. In terms of research structure, it is useful to identify what can be produced in an overarching sense, irrespective of the ecology in question, and what needs to be process-specific.

The overarching aim of upscaling is a comprehensive and spatially explicit large-scale knowledge of ecosystem responses to environmental change. This knowledge is derived, in part, from localised data (e.g. Sinclair et al., 2014) and from information on different levels of biological organization ranging from molecules to entire ecosystems (Le Quesne and Pinnegar, 2012; Gutt et al., 2013a). Downscaling should not only be considered as the development of mono-disciplinary models with smaller grid cells or by reference to a socioecological context (IPCC, 2014) but lead to a better system understanding by focussing on interactions between selected biological and non-biological variables. This is predominantly based on detailed observational data, which are also needed to advance ecosystem modelling and projections but not including spatial variability. However, downscaling must focus on scenarios that are representative of larger components of the Antarctic environment, including the ecosystem i.e. extending approaches applied by Rickard et al. (2010) to contribute to a whole ecosystem view.

2.2. Questions

1. Projections of future changes in climate are best generated using global climate models, which generally simulate atmosphere, ocean and cryosphere changes at a coarse grid spacing (e.g., horizontal 100 km × 100 km); how efficiently (i.e., what scales can be transitioned in each step), and to what extent, can climate model outputs be usefully downscaled?
2. What key elements are missing from these large-scale climate models both structurally (e.g., ice shelves and their cavities) or with respect to parameterizations (i.e., parameterization of sub-grid-scale processes)? This approach recognises that climate projections, remote sensing and in situ observations do not always span the same spatio-temporal scales (Fig. 2).
3. How interconnected are scientific disciplines (physics, biology, chemistry, geology/sedimentology) when transitioning various scales?
4. Is upscaling the simple reverse of downscaling, and vice versa? If not, what are the fundamental differences?

2.3. First steps towards implementation

First, goals need to be defined to enable models to work sufficiently as tools to understand how change will manifest itself in biological/ecological systems. To define and then achieve these goals, a clear dialogue between observational and modelling communities needs to be established and maintained.

- Biology must be parameterized well, including definitions of key parameters, to inform cross-disciplinary models, such as important marine functional organism types (for example mobile vs. sessile, filter feeders vs. predators) or major pathways of energy flow (for example from microalgae to krill, from krill to whales, from ice algae to the benthos).
- Models from different disciplines should be embedded within each other by bridging fundamental differences in biological and physical spatio-temporal data.
- A quantified differentiation between realistic variability of the climate system (‘noise’) and scales not captured by the models (‘aliasing’) should be developed.
- Specific biophysical systems need to be identified as logical, tractable starting-points for an overall project.
- Taking a system view, minimum standards for adequately defining and describing the system should be identified. Besides ecological systems comprising biological and chemical-physical issues, this can include aspects of “system's biology” where, in particular, molecular and cell complexity is modelled to understand the functioning of organisms.
- Observational gaps and first-principle models can provide a set of tools for conducting thought experiments.

Tools that can contribute to cross-disciplinary up- and down-scaling (for example single model components, remote sensing techniques from space or applied in the ocean, long-term crawlers, Autonomous Underwater Vehicles (AUVs) and next generation genetic sequencing) are increasingly available, under development or planned (Brandt et al., 2016). There are a small number of in-depth studies at local or regional scales that provide useful examples of successful downscaling. These include studies on the relevance of sea-ice thickness for primary

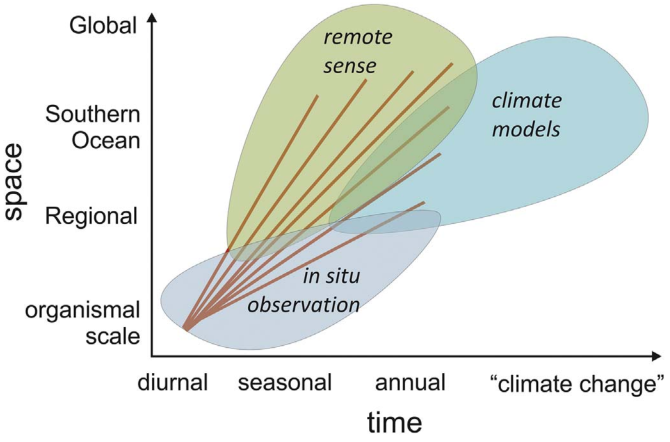

Fig. 2. Spatio-temporal perspective of research approaches to understanding multi-scale ecosystems (Stommel-type diagram). Currently climate modelling, remote sensing and in situ observations occupy distinct regions of understanding.

production and biochemical cycling (Lohrer et al., 2013); on the effects of changes in the ice-scape on benthic and pelagic biological processes and carbon sequestration in the East Antarctic (Shadwick et al., 2014); and on carbon sequestration in the Amundsen Sea (Yager et al., 2016). Due to the general relevance of the investigated phenomena these studies also demonstrate the need for spatial upscaling.

3. Theme 2: risk maps and ecoregions

3.1. Background and justification

Our current understanding of Antarctic biodiversity has been catalysed by the growing discovery of its rich ecological diversity and complex biogeography (Convey et al., 2008, 2014; Gutt et al., 2013b; Chown et al., 2015; Terauds and Lee, 2016). In parallel, projections to 2100 suggest faster rates of change with higher amplitude of physical changes than previously experienced (Bracegirdle and Stephenson, 2012; IPCC, 2013). This includes, in particular, changes in melt-water flux, ocean and atmospheric circulation, sea-ice extent and thickness, stratospheric ozone concentrations, and CO_2 fluxes, as well as changes in the frequency and strength of patterns of change such as the El Niño - Southern Oscillation, the Southern Annular Mode and the Pacific Decadal Oscillation. Despite significant uncertainties that remain, it is apparent that in addition to currently-observed changes, projected changes in the physical environment will have a considerable effect on the distribution of organisms due to geographical shifts and disappearance of suitable habitats, and on ecosystem functioning.

Ecoregions are strongly cohesive and recognizable areas determined by unique biological assemblages and abiotic (climatic) environments, delimited with distinct but dynamic boundaries (Spalding et al., 2007; Koubbi et al., 2010; Bailey, 2014). They include habitat suitability, i.e., maps reporting current availability of optimal conditions for species and communities. Risk maps constitute essential tools for conservation planning by designating Antarctic Specially Protected Areas (ASPAs) and Marine Protected Areas (MPAs); see also discussion in Chown et al. (2017) and Coetzee et al. (2017) about the rational requirement for area protection in Antarctica as part of applying conservation 'best practice'. Risk maps also provide a baseline for establishing key sites for environmental monitoring, assessing ecosystem vulnerabilities, and predicting the consequences of future scenarios on biodiversity (Constable et al., 2014; Gutt et al., 2015). Ecoregions can be used as operational areas on which ecological scenarios of highest risk of biodiversity loss and functional shifts can be formulated to produce risk maps (i.e. maps forecasting areas where changes are more likely to occur) and to provide current baselines as reference points for climate changes, to assess human impacts on the continent (Chown et al., 2012b). Species and community distributional data suitable to produce such maps are still scarce. However, for some study sites and in some case studies, the quality of data enables such assessments and models (e.g. Nkem et al., 2006; Pinkerton et al., 2010). Initiatives such as the OBIS-ENV-DATA pilot project, established to combine biological, physical and chemical data sets within the same repository, are a major step forward in this direction (De Pooter et al., 2017), being similar to the approach of the research programme Antarctic Near-shore and Terrestrial Observing System (ANTOS; www.scar.org/ssg/life-sciences/antos, last access: 20 September 2017). The US Long Term Ecological Research Sites of the McMurdo Dry Valleys (terrestrial) and Palmer Station on the Antarctic Peninsula (marine), and the French Long Term Ecological Research PROTEKER observatory at the Kerguelen Islands, are examples of long-term field observations of physical processes and ecosystem change.

The long-term objective of this theme is to produce risk maps. They must cover biologically relevant scales and derive from field observations. This can reach the scale of the entire Antarctic continent and the Southern Ocean using airborne and satellite remote sensing techniques. The overarching aim is to define at-risk ecoregions in order to provide the best possible scientific basis to protect unique, vulnerable and valuable ecosystems in Antarctica and the Southern Ocean.

3.2. Questions

1. What are the most important anthropogenic (climate change, pollution, overexploitation) and natural impacts for current species distribution and regional biodiversity?
2. Where are the locations expected to be most impacted by future anthropogenic and natural changes and how do these correlate with hot and cold-spots in vulnerability to environmental changes?
3. Which non-linear changes and thresholds will have a critical impact on biophysical/biological processes, for instance, changes in liquid water availability and increased ecosystem connectivity on land as a result of increased glacial melt and changes in precipitation?
4. What is the regional risk for the introduction of non-native species and their likely impacts on natural ecosystems, i.e., increase in access, exceeding thresholds in survivable conditions for endemic species, development of suitable conditions for non-native species, human traffic, as well as atmospheric transport?
5. To what extent does environmental change alter the effectiveness of dispersal mechanisms, source/sink dynamics and the potential for both native and non-native species to spread through e.g., aeolian and oceanic currents and processes?
6. When did current trends of change commence and are there signs of acceleration?

3.3. First steps towards implementation

A first step towards understanding the impact of physical changes on life in Antarctica would be high-resolution temporal observations of ecosystem drivers. These are to be measured within a monitoring network able to help refine models to quantify and deal with expected uncertainties. Recent efforts by PAGES (PAGES 2ka Consortium, 2013) to develop regional reconstructions of changes in temperature (Stenni et al., 2017) and snow accumulation over the past 2000 years (Thomas et al., 2017) are useful efforts to identify climatic regions and to assess their current trends in view of the recent climate variability. Such networks should be established further particularly in rapidly changing regions such as the Antarctic Peninsula and, for comparative purposes, in regions expected to remain stable, for example in the East Antarctic. To quantify the likely impacts based on currently-available information and models, it will be important to develop and apply new metrics and evaluation tools such as the Earth System Model Evaluation Tool (ESMValTool; Davin et al., 2016).

A stronger collaboration of biologists, physical oceanographers and climate modellers will allow us to more robustly identify key regions and locations that are vulnerable to future change including improved abilities to map biological communities, determine species ranges, and physiological vulnerabilities or robustness. These could serve as the foci of intensive comparisons between modelling and observations to fill in data gaps. Once this monitoring network is established, it will be possible to develop benchmarks and to understand sensitivity to thresholds for species and communities, for example in terms of temperature and food supply, that are likely to face environmental changes in the future. Up- and downscaling (see Theme 1) is likely to play an important role in this approach. Emphasis should be placed on estimating when and where rapid and especially non-linear changes will occur, as this could lead to identification of biologically relevant thresholds or ecological tipping points (Nielsen and Wall, 2013; Fountain et al., 2016). This task can only be achieved by establishing an internationally cooperative and geographically comprehensive and robust monitoring system to produce a reference baseline and understanding relevant to ecological processes in this context.

4. Theme 3: organism responses, resilience and thresholds

4.1. Background and justification

Understanding the impacts of Antarctic climate change on marine and terrestrial organisms ultimately depends on understanding the specific tolerance of species to changes in their current environment. To define where and when organisms will first experience conditions that threaten their future persistence therefore requires intimate knowledge of species traits and their tolerances. However, in broad terms, organisms that have high specificity for habitats and, thus, low resilience to change in specific properties, e.g. sea-ice, or other environmental demands such as a specific food preference, will likely be the 'losers' of anthropogenic change. By contrast, species endowed with the adequate physiological plasticity and/or being able to count on adaptive evolution may be 'winners' in future climates, although they may not be able to compete with non-native species in the longer term.

According to Schofield et al. (2010), the conservation and management of polar marine populations (Simmonds and Isaac, 2007) requires an elucidation of the causes and impacts of marine ecosystem changes. These studies will only succeed if they can accommodate the concepts of time-dependent species modifications by natural selection (microevolution) and phenotypic plasticity. Species and ecosystems may undergo sudden shocks in response to external changes that approach their thresholds or tipping points. When environmental changes exceed a threshold or tipping point, life, ranging from a single cell to ecosystems, may rearrange and reach an alternative stable state (Sheffer et al., 2001; Nielsen and Wall, 2013).

Besides altered food availability, temperature variability may be a major factor in dictating responses, especially of Antarctic organisms, to environmental change. For example, terrestrial plants exposed to seasonal temperature variations exhibit higher physiological plasticity than Antarctic fish, which are exposed to year-round relatively stable temperatures. For terrestrial organisms liquid water availability is recognised as the main driver of biodiversity processes in the Antarctic (Convey et al., 2014).

The objective of this theme is to highlight the fact that knowledge on species-specific traits and environmental requirements is essential for most, if not all, approaches to assess the thresholds and responses of species, as well as the resilience of ecosystems to environmental change.

4.2. Questions

1. When and where are environmental changes in Antarctica and the Southern Ocean projected to surpass natural variability of the climate system (for the methodological challenge see question 1 of Theme 4); when and where will such changes exceed tolerance limits of key species?
2. To what extent and under which conditions can potential biological responses and tipping points be reliably extrapolated from the fossil record, genetics, and physiology?
3. To what extent can functional groups/key species be used to develop useful/informative system models, and can these models predict the impacts of environmental change?
4. What are the likely range shifts in existing species and where will non-native species become established under future environmental conditions, e.g. due to changes in vectors such as currents, winds, frontal zones, ice shelves, running water, permafrost, humans, sea-ice extent?
5. What are the most urgent interfaces where physiologists and geneticists, in particular, must work together with physical scientists to ensure that information generated is equally relevant across disciplines and as ecologically relevant as possible?

4.3. First steps towards implementation

Modern distribution patterns of a wide range of Antarctic organisms can be assessed with varying degrees of confidence from existing biodiversity databases, such as www.biodiversity.aq (last access 20 September 2017). Through collaboration with oceanographers, chemists, sea-ice scientists, geologists, glaciologists and modellers, distribution patterns can in principle be mapped against environmental datasets (where these exist) to define the realised environmental envelope of single species and communities. Additional information on the physiological and ecological limits of an organism or tissue can be obtained through genetics, advanced biomolecular methods, such as transcriptomics (e.g., Sadowsky et al., 2016), and implemented in ecological concepts, models and biogeographical projections (Kearney and Porter, 2009; Chevin et al., 2010; Pörtner and Gutt, 2016). All these approaches could usefully include comparative studies along gradients in terrestrial, limnetic and marine systems, such as between fjords of the Antarctic Peninsula and northwards to the South Shetland and South Orkney Islands and to the sub-Antarctic. Physical models of predicted environmental change should be used to target those regions that will reach predicted thresholds first, so that monitoring programmes can be established to detect non-linear changes in populations, including the establishment of non-native species (see also Theme 2). Environmental variability and change at biologically-relevant scales needs to be identified and tracked (e.g. through ANTOS-type programmes), to accurately advise biological, physical, and Earth science studies. System models will need to include features such as cascade effects, food webs, changes to ecosystem function and services, points of no return, new stable/equilibrium states, highly resilient versus non-resilient assemblages and evolution.

To understand which organisms are likely to be impacted, where thresholds may be crossed, and where the consequences of change are likely to be strongest, the upper and lower tolerance limits controlling organism distribution are to be defined. For example, geographic ranges have been analysed for selected species using existing database records (see Barnes et al., 2009); a next step would be to take known species ranges and plot these against oceanographic, chemical and physical properties to develop more accurate descriptions of species environmental requirements/tolerances. In parallel, the ecophysiology of ecological key species must be studied because knowing only their current distribution without further system understanding is obviously not sufficient to model their future distribution. Environmental envelope modelling, such as illustrated in a preliminary way in the study of Hughes et al. (2013) assessing the potential current limits to the distribution of the maritime Antarctic non-native terrestrial midge *Eretmoptera murphyi*, illustrate the potential utility of geographic range modelling both under current and future climate scenarios. One of the biggest challenges is to integrate biomolecular data into ecological distribution models (Gutt et al., 2012).

Only a collective and a cooperative effort from coordinated and cross-disciplinary research groups in conducting large-scale meta-studies will encompass the sources and bias of variability (time and space scale), helping to achieve a suitable breadth of knowledge and avoid the risk of under- or overestimating the impact of climate change on biodiversity.

5. Theme 4: ecosystem response to natural climate variability and anthropogenic change: studying the response to multiple stressors

5.1. Background and justification

Ecosystems are almost always shaped by multiple environmental parameters, and in the Antarctic similar to the Arctic Ocean and permafrost-influenced ecosystems, physical drivers such as sea-ice, seasonality and low temperature seem to be more relevant than in other ecosystems, e.g. tropical rainforests and coral reefs. Only rarely it is easy to identify the most important driver, e.g. water availability for terrestrial vegetation. Pelagic species such as pteropods, coccolithophorids, and foraminiferans for instance, are exposed to increasing carbonate undersaturation due to ocean acidification (OA), which is driven by atmospheric CO_2 concentration, pressure and temperature (Orr et al., 2005). Since under OA marine organisms need more energy to maintain their calcium-based shells and skeletons (Manno et al., 2007, Moy et al., 2009), OA is never the problem alone; it is always influenced by temperature, pressure and food/nutrient availability. For Antarctic benthic species on the deeper continental shelf, such as bryozoans, corals, echinoderms, and sponges, it is not possible to identify only one or two major natural drivers. Relationships to depth for instance, may relate to associated changes in temperature, pressure, dissolved oxygen, food availability and depth of iceberg scour. Climate change and its impacts on ecosystems not only include temperature increases but is a phenomenon comprising temperature, wind, quality and quantity of precipitation, and is related to the ozone hole causing increased UV-B radiation. In addition to natural and indirect anthropogenic drivers such as climate change and OA, all the aforementioned ecosystems are or have been exposed to direct anthropogenic impacts, such as whaling and fishing, local pollution, invasion of non-native species, soundscape changes and terrestrial habitat loss (Tin et al., 2009).

Timescales associated with complex ecological processes briefly described above range from nanoseconds (cellular processes) to millions of years and longer (species evolution). When studying the effects of long-term trends and variability in climate on ecosystems, scaling climate change projections to biologically relevant temporal and spatial scales is challenging. Quantifying the extent to which changes in climate push Antarctic ecosystems beyond the natural variability (e.g. daily to seasonal variation) to which they have adapted (Fig. 3) requires a combined physical and biological perspective. Although increases in temperature or changes in water availability may be important drivers of Antarctic ecosystems (Convey et al., 2014), exposure to novel climates could have much greater impacts. To predict the potential impacts of climate change it is therefore necessary to assess the severity of such events of the past and present beyond intrinsic variability. For the physical Antarctic climate system, the Amundsen Sea Low is the most variable region of the global atmosphere, which must be taken into account when considering potential future envelopes of change in the physical system (Hawkins et al., 2016). Long-term sampling can determine the 'baseline variability', but this is limited in the extent to which it can inform projections of anthropogenic climate change.

The objective of this theme is to find solutions to disentangle cause-effect relationships, and multiple global change stressors. The real challenge therefore, is to identify intrinsic and extrinsic biotic responses using statistical methods, which permit the design of hypothesis-driven multiple-stressor experiments as well as provide adequate parameterization in global ocean-climate models.

5.2. Questions

1. What methods are available to detect trends beyond natural variability in climate time series (for effects on key species see question 1 for Theme 3)?
2. To what extent does past climate variability moderate species' responses to anthropogenic climate change?
3. How can outputs from projections from Earth System Models be tailored to match the spatial and temporal scales required to understand biological system responses?
4. How can statistical models be used to design robust multiple global-change stressor experiments?
5. What is the real contribution of biological CO_2 uptake of the Southern Ocean to the global CO_2 budget and what is its variability in space and time, in the present and future?

5.3. First steps towards implementation

To better assess Antarctic ecosystem responses to climate change, large ensembles of climate model simulations are required (Stock et al., 2010). They allow better quantification of future climate envelopes (Fig. 3) and the definition of ranges of stress, which must then be applied at ecologically relevant temporal and spatial scales. As they are now just becoming available, such simulations provide novel research opportunities, for example, the Large Ensemble Community Project (Kay et al., 2015). Changes in ecosystems may then potentially feedback on the climate system, whereby changes in ecosystems affect local environment attributes such as ocean turbidity (which then affects absorption of solar radiation in the water column and resultant ocean temperature change) and the carbon cycle (which affects ocean CO_2 uptake and pH). This requires (a) better communication between the biology and climate physics communities, and (b) techniques that provide two-way connections between climate models and ecosystems at the relevant spatial and temporal scales (Murphy et al., 2012; Potter et al., 2013). Semi-empirical models can help to identify which variables, i.e. environmental factors, are most relevant to determine the response of the biological system to changes in key climate variables, and thereby contribute to better understanding of cause-effect relationships.

6. Theme 5: interactions between biological and climate processes - Antarctic top predators and food webs

6.1. Background and justification

Ecosystem processes occurring in the vast expanses of the Southern Ocean, including under the sea-ice and ice shelves, remain difficult to examine with conventional methods (e.g. surveys from research ships, remote sensing). However, this region is regularly visited by a wide

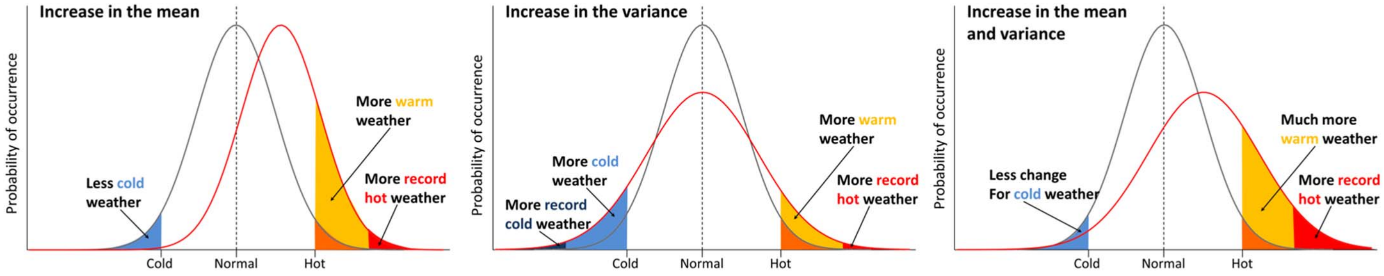

Fig. 3. Environmental shifts and response of species occurrence. A change in climate at any location can be considered as a shift in the probability density function (PDF) of the climate variable of interest, such as temperature, a change in the width of the PDF, or some combination of both. While a shift in the PDF to higher temperatures may be small (∼1 °C), the increase in the number of days when maximum temperatures exceed some threshold can be a factor or 2 or 3 larger. The proportional change in 'physiological time' or 'day degrees' above a given threshold (often 0 °C) can be considerably greater, which is part of the reason for the expectation of large responses in polar (especially terrestrial) biota. Since biological systems are more likely to respond to the severity, duration and frequency of extreme events, attention must be paid to the tails of the distributions of climate states when considering biological responses to climate change.

range of species that cover most of the uncharted volume of the Southern Ocean: from penguins and albatrosses to seals and cetaceans; from the continental shelf through the deep-sea to the northernmost limits (and beyond) of the Southern Ocean. With the advent of animal-embarked data-recording technology (bio-logging, Ropert-Coudert and Wilson, 2005), these foraging animals have been turned into living probes, scouting the environment and delivering not only biological information on their ecology, but also a wealth of physical information on parts of the Antarctic environment that are still poorly studied. As an illustration of this, CTD profiles obtained by data recorders attached to elephant seals (*Mirounga leonina*) are achieving more than simply complementing those given by Argo floats: they are doubling the dataset (Roquet et al., 2014). In this domain, prospects for future cross-disciplinary studies (e.g. bridging biology, oceanography, engineering, physics) are booming as the type of data that can be acquired by animal-embarked technology benefits from progression in, for example, the mobile phone industry. New sensors measuring dissolved oxygen, bioluminescence, sea-ice thickness or acoustic signals, among other variables, are set to help physical oceanographers, biochemists, plankton biologists and trophic ecologists to address the questions below. Cameras attached to the heads of seals and penguins provide direct insights in their feeding behaviour and food preferences, as well as additional information on under ice-shelf habitats, e.g. isopods living attached to the ice subsurface.

The overarching scientific aim of combining biological and physical methods and approaches is to identify the major drivers of top predator populations, the position and functioning of regions of ecological importance, and to predict their development under climate change. A mechanistic understanding of the biophysical processes controlling trophic chains in the Southern Ocean is needed for assessing the impact of climate change scenarios – which are expressed in terms of physical changes - to marine populations. In turn, this knowledge should support the deployment of conservation actions, like the establishment of marine protected areas.

6.2. Questions

1. What are the biotic and abiotic mechanisms controlling energy and biomass flow from primary producers to top predators at various temporal and spatial scales, and how will these change according to shifts in the physical environment? What are the spatio-temporal scales and key locations associated with these mechanisms?
2. How can dynamic multi-scale food-web models such as end-to-end models be constructed that include physical and biological data, as well as threats (human impacts, pollution, fisheries)?
3. What is happening under the sea-ice and ice shelves? Which new sensors are needed to understand physical and biological processes in habitats that are beyond the reach of traditional methods?
4. What are the key biophysical mechanisms through which climate change will impact marine ecosystems?

6.3. First steps towards implementation

In this context, the assembling of a network to maximize usage of chemical/physical/biological, multi-scale data collected by top predators, and their integration, is a priority. An additional goal of such a network should be to maintain a state-of-the-art survey of progress in observational technologies so as to inform users of animal-embarked devices from the physical and biological sciences of the latest trends in sensor development. Continuity is particularly important in these years, in which the anthropogenic signal of climate change is emerging. Effects of historic and recent exploitation and over-exploitation of living resources, such as whales, seals, fish and krill must be considered in modern studies of top-predator ecology. Enhanced collaboration between research disciplines should be favoured through the organization of dedicated programmes/surveys that integrate a wide range of expertise, as well as cross-disciplinary fora that emphasize data sharing. Finally, urgent questions on the current state and future of the well-being of Antarctic top predators demands the integration of the data obtained from modern sensor development and use by advanced modelling techniques, including the simulation of the dynamics of trophic interactions. In terms of scales, satellite observations are now opening a new frontier, allowing for the first time mapping of the environment at a scale that approaches the resolution of animal telemetry. Thanks to Synthetic Aperture Radar and visible imaging and SWATH bathymetry, the details of complex seascapes like the ice margin and seafloor topography are now accessible. In the open ocean, activities such as the Surface Water and Ocean Topography mission will soon provide fine-scale details of ocean circulation, making it possible to reconstruct the physical context at the resolution of the behavioural switches of marine predators.

7. Theme 6: impact of changing ice sheet dynamics on circumpolar, nearshore, and off-shore environments

7.1. Background and justification

Anthropogenic pressure on the global climate is forcing the Antarctic ice shelves and glaciers to retreat and consequently modify the coastal and continental shelf ecosystems. For example, phytoplankton blooms in recently opened water areas and the subsequent downward fluxes of fresh organic matter set conditions for the benthic recolonization of the seabed (Bertolin and Schloss, 2009; Sañé et al., 2011). Glacier melt run-off releases sediment and nutrients into the water column, which can both stimulate and hamper photosynthesis and also affect benthic life (e.g., clogging, burying) (Grange and Smith, 2013; Sahade et al., 2015). Massive icebergs calving from ice shelves can scour the sea floor to several hundred metres in depth and remove benthic life from it on their way, but also stimulate or hamper life, especially primary production, in the pelagic realm (Arrigo et al., 2002; Gutt et al., 2011, 2013c; Vernet et al., 2012). At the same time, melting glaciers and receding ice fronts may result in the exposure of new ice-free land as well as intertidal zones, in turn supporting terrestrial and limnetic ecosystem development.

The developmental trajectories of these new ecosystems obviously depend on a multitude of factors. These include the bioavailability of nutrients, the connectivity with existing ecosystems affecting colonization dynamics, microclimatic conditions and biotic interactions, such as soil formation processes and nutrient remineralisation by microbes (Domack et al., 2005). The effect of physical and chemical parameters on these newly emerged ecosystems is also expected to vary through time (Sañé et al., 2013; Sahade et al., 2015). For example, liquid water may become increasingly available in a particular region due to direct meltwater input from retreating glaciers, while conditions may become drier over longer timescales when the ice front further retreats and local sources of water become exhausted. Many of these processes have been occurring more extensively in recent decades (e.g. Favero-Longo et al., 2012) and open the opportunity to study them for the first time in the history of science.

With a trend of increasing ice shelf disintegration and glacial retreat, other discrete regime shifts in coastal waters are expected over the coming decades. The direction of these regime shifts may change in a second phase thereafter (for conceptual models see Sheffer et al., 2001). Their impacts on terrestrial, near-shore and off-shore ecosystems must be identified and addressed and their effect and the direction in which they may change in the future must be anticipated. Such studies can also incorporate large field experiments aimed at assessing the general resilience or vulnerability of Antarctic ecosystems.

7.2. Questions

1. What is/was the effect of ice-shelf collapse, glacier retreat and

iceberg scouring in the past, present and future on benthic marine, intertidal and terrestrial biodiversity and nutrient cycles, including factors such as biological storage, release, sequestration, and remineralization of nutrients over space and time, including the devastation of benthic assemblages through iceberg scour, and fast-ice occurrence?
2. What is the contribution of nutrients (e.g. iron fertilization) from icebergs and wind from exposed land surfaces to local and regional primary production in a changing pelagic environment?
3. How do fjord/coastal ecosystem drivers (e.g. meltwater and glacial sediment inputs, light regime) and ecological responses change along the Western Antarctic Peninsula (WAP) and other regions with obvious climate gradients?
4. What are the timescales and dynamics (continuous versus episodic, local versus regional) of climate shifts around the Antarctic continent, and how will these shifts be reflected in under-ice shelf, fjord and sea-ice shaped ecosystems?
5. Which Holocene ice shelf and sea-ice processes, and their biological responses, are mirrored by sediment characteristics, which, in turn, affect (other) biological processes, especially at the sea floor?
6. How will glacier-retreat affect the appearance of more connected habitats, and shape the diversity of terrestrial and limnetic ecosystems, and what will be the short- and longer-term effects of changing physical, chemical and (micro-) climatic conditions on these ecosystems and their functioning?
7. How important are microbial biofilms in the recolonization of ice-devastated benthic habitats and what is the role of early-life history in the recruitment of invaders?

7.3. First steps towards implementation

Improved approaches of upscaling (see Theme 1) have to be applied because glacier and ice-shelf disintegration is a local phenomenon but the expected impact is regional. It is important also to apply downscaling techniques, for instance to understand the consequences of higher turbidity for pelagic and benthic organisms and to date significant sediment layers. Emphasis has to be placed onto the dynamics of cryosphere-ocean interactions (e.g., ice-shelf and marine ice sheet collapse) and ice-sheet processes (e.g., rapid melting, glacial erosion, pulsed iceberg inputs) to be studied through modelling and observational surveys (Scambos et al., 2003) as well as documentation of past changes (Scherer et al., 1998, 2016). This particularly refers to biologically relevant changes, such as water mass characteristics, rather than the recently emphasized physical changes, such as sea-level increase. Cross-disciplinary studies can be supported by more sedimentological results acting as archives for recent processes in the water column, such as transitions from sub-ice shelf to sea-ice ecosystems in response to climate forcing (Sañé et al., 2013). Better dating of Antarctic marine sediments will have wider benefits than simply for studies focussing on ice-related habitats. Biological studies under areas of permanent ice (sea ice and ice shelves) provide a technical challenge but are broadly significant. Currently-available technology, such as autonomous underwater vehicles and crawlers, can provide valuable, previously almost non-existent, information across broader scales and with higher spatial resolution than that obtained through drilling cores. Good results might also be achieved when remotely operated vehicles are deployed through drill holes. The application of swarms of autonomous probes using collective intelligence might solve the problem of obtaining results that are representative for large areas. This is especially important since these areas are highly relevant to understanding ecosystem functioning, including feedback processes between life in the ocean, the cryosphere and the atmosphere. Modelling and long-term observations of ice dynamics and the relationship to climate forcing (applying ecologically relevant spatial and temporal scales) will improve predictions of the impact of the behaviour of ice bodies on marine ecosystems. A better understanding of environmental and biological processes induced by small-scale upwelling around marine glacier termini and around grounded as well as floating icebergs will allow the assessment of some still fragmentary knowledge on polar-specific ecological processes. Terrestrially relevant information can be obtained from long-term observations, in combination with space-for-time substitution approaches, in which glacier fore fields can be used to study the short- and longer-term effects of receding glaciers on the interplay between biological processes and nutrient and carbon dynamics in soils, wetlands and lake ecosystems.

8. Theme 7: sea-ice ocean and sea-ice atmosphere boundary layers - impact of changes on primary production and other biological processes

8.1. Background and justification

In general, trends over recent decades in Antarctic sea-ice distribution contrast dramatically with what is happening in the Arctic. While Arctic sea-ice extent has been reaching record lows, satellite data have shown that sea-ice extent had been increasing around Antarctica since the satellite era started in 1979, with the extent exceeding 2×10^7 km^2 for the first time in 2014. In 2016/17, however, the recent unprecedented Antarctic austral springtime retreat (Turner et al., 2017) highlights the possibility of a switch to future declines in sea ice extent. However, there are large mid-term regional differences, with slight increases in the Ross Sea area and off East Antarctica and extensively declining ice cover in the Bellingshausen/Amundsen Seas (Comiso et al., 2017). Variation in sea-ice cover may be associated with large-scale atmosphere-ocean features like the Southern Annular Mode and the El Niño–Southern Oscillation (Kwok et al., 2016), identified by the decline in ice cover during 2015 and 2016. Currently, the majority of simulations conducted as part of the Coupled Model Intercomparison Projects (CMIP) indicate ice-extent trends that are the opposite of those that are currently happening. The reasons for this are difficult to identify and could simply be a consequence of different timings in natural ocean cycles. Irrespective of the ultimate explanation, the model-observation differences appear to be associated with inability to reproduce observed trends in surface temperature in the ice-covered and surrounding regions (Comiso et al., 2017).

The ecology and productivity of the Southern Ocean are strongly influenced by the sea-ice cover (Smith and Comiso, 2008). Sea ice causes the replacement of surface water through vertical mixing during the growth period when dense water is formed, becomes submerged and is replaced by nutrient-rich water from below. During ice retreat, the melt-water forms a stable surface layer that is exposed to abundant sunlight and becomes an ideal platform for photosynthesis. With algal biomasses 1000 times higher than pelagic levels, sea-ice forms a rich support for higher trophic levels. It seeds pelagic blooms and the high sedimentation rates of ice algae fuel benthic communities (Riebesell et al., 1991; Isla et al., 2009). Hence, sea-ice-associated communities also form the basis of the Antarctic marine food web. Reductions in the extent and timing of sea-ice around the WAP since 1979 have been associated with phytoplankton community spatial shifts (Montes-Hugo et al., 2009) and with shifts from a krill-dominated to a salp-dominated community (Atkinson et al., 2004). Such changes may have important cascading effects on higher trophic levels (Schofield et al., 2010; see also Theme 5; for a general application of end-to-end and, alternatively, population concepts see Steele and Gifford, 2010).

Sea-ice biogeochemistry is a new and growing scientific discipline. Due to its large heterogeneity in time and space, sea-ice is a difficult medium to study and from which to construct a generalized view of state parameters, let alone of quantitative process rates. Sea-ice is an important mediator in the carbon cycle, driving carbon exchange from atmosphere to ocean and vice versa due to extreme and specific physical, chemical and biological processes in the ice matrix (Vancoppenolle et al., 2013). Sea-ice also contributes to the dynamics of other climate-relevant gases, such as dimethyl sulfide (Tison et al., 2010) and halocarbons, and to the oxidative capacity of the cold Antarctic atmosphere (Simpson et al., 2007). Many processes are still unknown and may be very different across long regional gradients, making it a challenge to advance our understanding of the system. Close collaboration between field scientists and modellers is needed to advance this field of research forward (Steiner et al., 2016).

Given the above, sea-ice as a habitat and driver is highlighted here because (a) sea-ice biogeochemistry potentially contributes to the global C-cycle and is fundamentally important for the Antarctic marine foodweb, (b) this highly relevant issue was not identified in the questions of the SCAR Horizon Scan, (c) sea-ice – primary production relationships are not yet well understood.

8.2. Questions

1. What methods are available to model movement of sea-ice on a bay-scale? How can these models/results feed climate models?
2. Can physical modellers help with predicting small-scale features like leads, ridges, first-year ice versus multi-year ice, floe drift and polynya development?
3. Which are the important predictors of climate gas fluxes and heat exchange between ocean, sea-ice and atmosphere?
4. How can information on historical shifts in sea-ice extent be improved (e.g. through sediment records or time-series of pelagic species biomass) to match with ongoing changes detected from satellite data and model simulations of periods further back in time?
5. What is the contribution of sea-ice to the global C-cycle in general and specifically to Southern Ocean biology?
6. What happens to coastal and offshore blooms when ice disappears?
7. What is the role of ice-shelf cavities on sea-ice growth and under-ice habitat structure? How will this change when ocean water warms?

8.3. First steps towards implementation

Since seasonality is perhaps the most important characteristic of Antarctic sea-ice, year-round studies are needed to understand the high temporal variability of biogeochemical processes and feedbacks with climate. Modellers should become involved in the development of such field experiments at an early stage, so as to collect field data that can be directly implemented in models. The challenge will be to develop a set of tools useful for future projections on the impact of sea-ice on the regional carbon/primary production cycle. This can be done by using scenarios of both rapid sea-ice melt-back and more stable sea-ice cover in coupled models, thereby taking account of the uncertainty in future projections (models project significant melt, observations so far indicate only regional melt).

Improvements can be made through small-scale modelling of ice movement, formation and melting by combining weather data with sea-ice extent. To resolve small-scale features in sea-ice relevant to gas- and heat-exchange processes, statistical distribution models need to be developed from satellite data that can then be extrapolated to the regional scale. In order to improve modelling of biogeochemical cycles in sea-ice and the coupling between sea-ice and ocean, benthos as well as atmosphere, there is an urgent need for more studies of inter-annual variability using time series of biogeochemical parameters.

9. Theme 8: evolution of biota in relation to glaciation history, marine and terrestrial glacial refugia, trans-Antarctic seaways and connectivity

9.1. Background and justification

Antarctic biota are a reservoir for evolutionary novelty, including adaptations to a unique environment following natural selection over millions of years in response to past climate changes and tectonic events (Clarke and Crame, 1989; Poulin et al., 2002; Convey et al., 2008, 2009; Strugnell et al., 2008; Fraser et al., 2012; Wilson et al., 2013). The break-up of Gondwana led to the geographic isolation of the continent, the formation of the Southern Ocean and in particular the Antarctic Circumpolar Current, and accelerated the development of continental-scale Antarctic ice sheets (e.g. Zachos et al., 2001). Over time, repeated glacial-interglacial cycles have resulted in a wide range of environmental conditions as well as changes in the connectivity among habitats. These include the formation of seaways (e.g. between the Ross and the Weddell Seas; Barnes and Hillenbrand, 2010, Strugnell et al., 2012), large fluctuations in sea level, periods of higher discharge of freshwater and icebergs into the Southern Ocean, increased liquid water availability in terrestrial regions, and a higher surface area of ice-free habitats during warm periods (De Conto and Pollard, 2016). During glacial maxima, both marine and terrestrial (including limnetic and microbial) biota appear to have survived in glacial refugia (Convey et al., 2008, 2009; Vyverman et al., 2010; Allcock et al., 2011; Fraser et al., 2012), as revealed by both recent molecular studies (see Allcock and Strugnell, 2012 for review) and classical biogeographic analyses (Terauds and Lee, 2016) although the nature and locations of these refugia are still poorly understood (Pugh and Convey, 2008; Lyons et al., 2016). Most terrestrial habitats are extremely isolated. Potential refugia locations are poorly localised at anything less than regional scale, although in some areas there is evidence for refugia in volcanic and other geothermal areas (Fraser et al., 2014). Marine habitats seem to be more connected, although dispersal limitation between regions appears to be present for example of Southern Ocean octopods of tropic clown fish (Strugnell et al., 2012; Pinsky et al., 2017), but can vary even between closely related species (Strugnell et al., 2017). Biogeographic and phylogeographic patterns are often in conflict due to the presence of cryptic species, or a poor understanding of taxonomy (e.g. Díaz et al., 2011; Brasier et al., 2016), so generalities of distributions are not yet well-understood. Thus, historical processes have left a clear imprint on the contemporary diversity and distribution of biota in Antarctica and resulted in a high incidence of endemism, geographic structuring of populations, evolution in isolation, and clear bioregionalization patterns even at small spatial scales in both multicellular and microbial organisms (Convey et al., 2014). Moreover, this particular evolutionary history has also led to biological differences between habitats in Antarctica and comparable counterparts in the Arctic (Fraser et al., 2012; Pointing et al., 2015). Changes in the permafrost, active layer, freshwater availability and groundwater circulation have important connections with ecosystem processes. Old permafrost can be an interesting repository of microbes including pathogens (Drancourt and Raoult, 2005), metabolic products and biodiversity (Gilichinsky et al., 2007). The effect of viable microbes stored in permafrost and becoming active again on contemporary ecosystems is largely unknown. Biological comparison of taxa inhabiting the two polar regions pinpoints the differences in evolutionary histories between the two systems. As a result, for instance, Arctic fish have higher biodiversity (Mecklenburg et al., 2011).

Despite this unique biological constellation, it is becoming increasingly evident that the human influence on biological colonization into and within Antarctica is already high and is only likely to increase in the future, challenging the governance and environmental management mechanisms of the Antarctic Treaty System (Frenot et al., 2005; Tin et al., 2009; Chown et al., 2012a, 2017; Convey et al., 2012; Hughes et al., 2015; Coetzee et al., 2017). Robust knowledge of the evolutionary background of recent life in the Southern Ocean and Antarctica is essential to assess its contribution to global biodiversity and ecosystem functioning and to provide reliable estimates of the consequences of projected anthropogenic climate change and other environmental changes.

9.2. Questions

1. What strategies allowed biota to persist during glacial cycles, where and when did glacial refugia exist?
2. Does any generality exist in these processes between marine, terrestrial and limnetic systems or between large groups of organisms, or are they all unique?
3. Is it possible to reliably predict (remotely) where suitable habitats exist today, and how will these habitats change under climate-change scenarios and in which direction, towards higher or lower complexity?
4. How connected are regions at present and have they been in the past in terms of both colonization and also other biological processes and ecosystem functions (e.g., nutrient flows between and among terrestrial and marine ecosystems), what mechanisms connect them and on what timescales?
5. Under which environmental conditions will regionally extinct species/taxa re-colonize?
6. Will new species appear for the first time in Antarctica and the Southern Ocean and what will future colonization processes be?
7. What is the genetic diversity of Antarctic organisms and can improved constraints on the timing of key evolutionary events be generated and, resulting from this, insights into the long-term drivers of taxa distribution provided?

9.3. First steps towards implementation

There is a particular need for improved spatial coverage of biodiversity surveys and for molecular phylogenies across more taxonomic groups, including links to non-Antarctic regions and taxa, and to sample under-represented areas (e.g. sub-ice environments). This can only be achieved by increased sample and data exchange between national programmes and individual scientists. Substantial advances in biogeographic understanding with an evolutionary background, however, will involve correlating biodiversity distribution, occurrence of ecological key species and communities as well as ecosystem functions with evolutionary physical drivers. The integration of bioinformatics and taxonomic skills will facilitate (a) the combination of classical approaches and state-of-the-art molecular techniques to reveal cryptic species diversity and (b) large-scale barcoding initiatives of taxa based on molecular markers. These biodiversity assessments should be interlinked with climate modelling, and physical and geosciences, including programmes aimed at monitoring environmental properties as part of large-scale networks, which will enable disentanglement of the drivers of present-day diversity patterns. There is thus a particular need for developing finer-resolution glaciological, oceanographic, paleogeographic, atmospheric/climate reconstructions and models to study biological processes at biologically relevant scales. These multidisciplinary programmes are required to achieve congruence between geological and molecular and fossil-based estimates of evolutionary events, including adaptive radiations, range expansions and contraction colonization events and regional extinctions.

10. Discussion

Most ecosystems on the Antarctic continent and in the Southern Ocean are unique, and vary greatly in their connectivity to other ecosystems on the planet (Frenot et al., 2005; Clarke et al., 2005). However, they all are exposed to the high spatial and temporal variability of the physical climate environment. The complexity of these relationships is illustrated below as a schematic (Fig. 4) and the potential for focused research on these interactions, or aspects of them, is apparent (Gutt, 2017). The connection between Antarctic biological and non-biological systems can be divided into the exposure of biota to environmental impact and the response of life at all levels of organization to it (Turner et al., 2009), which contributes significantly to the functioning of the entire Earth system (Grant et al., 2013). Thus, knowledge about Antarctic ecosystem functions arising from question-based research is essential to understand these unique ecosystems in a global context (di Prisco et al., 2012).

The aim of this conceptual study, built on the impetus provided by the SCAR Horizon Scan, was to identify new science directions focussing across disciplines, resulting in a variety of questions, and to suggest the first steps towards their implementation. Most of the themes presented herein are polar/Antarctic specific but a few can also be applied to any biological system independent of global region or specific environmental conditions, for instance the up- and downscaling challenges (Theme 1). Similarly, important non-Antarctic approaches and methods exist, such as in the fast developing fields of genomic and biomolecular research and modelling/downscaling approaches (Wilby and Wigley, 1997; Flint and Flint, 2012), that are still underrepresented in Antarctic research. The Antarctic community can benefit from the exchange of ideas with non-Antarctic scientists and the application of such methods if these are embedded in an Antarctic-relevant research programme (Kennicutt et al., 2016).

In this discussion overarching challenges are identified to allow a certain generality to be developed across the questions from the different themes. This type of clustering could provide an extended basis

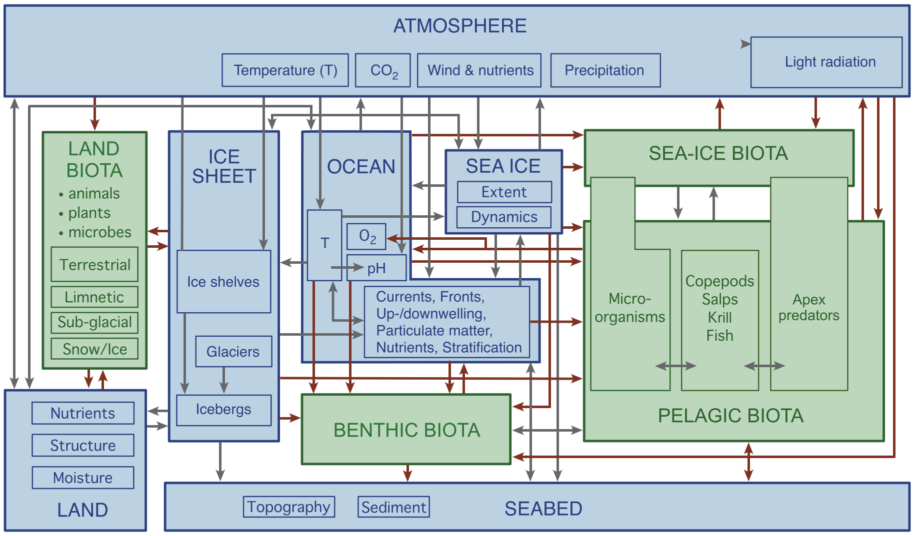

Fig. 4. Interactions between the chemical-physical environment and biota. This generalized and simplified schematic focuses on the main components of Antarctic ecosystems and their interactions, including with the non-living environment. Blue boxes represent physical-chemical conditions/variables, green boxes the biota. Interactions between living and non-living components are shown by red arrows. Changed after Gutt et al. (2015).

for science managers and scientists to plan the realization of novel approaches.

(A) Cross-disciplinary bridging of methodological incompatibilities between physical and biological sciences, with respect to scales, is urgently needed (see e.g. Potter et al., 2013). In an ecosystem research approach both disciplines have the common aim to provide an Antarctic-wide system understanding and to provide reliable results, which are representative of larger areas, extended periods, or scientific phenomena, for instance the formation of deep water or biological CO_2 uptake (see for example Kennicutt et al., 2015). If the desired Antarctic-wide geographical cover is not achievable directly, it may instead be feasible through remote-sensing approaches or the application of upscaling methods. All disciplines also require detailed insights into system processes (Gutt et al., 2015), where downscaling approaches help. Despite this common ground, biological and non-biological disciplines often differ in important details. The following requirements are therefore suggested: (1) a conformity of spatial and temporal scales and resolution at which data are to be acquired and which should serve for up- and downscaling approaches. Biological approaches generally demand a priori higher spatial and temporal resolution than physical approaches, for instance intermediate to small-scale krill swarming behaviour is highly relevant (see e.g. Nowacek et al., 2011); knowledge is also required of short-term and rare extreme events, which can erase sessile benthic assemblages in a short period of time, and are hardly traceable by physical scientists or biologists (Peck et al., 2006). (2) Biological data should be implemented in interdisciplinary cause-and-effect relationships because biological phenomena depend on the physical environment. Physical oceanographic information of biological relevance, for instance changes in up- and down-welling, must be traced back to their source, in this case changes in wind regimes, to make spatial and temporal predictions possible. Temperature increase throughout the entire water column can be the consequence of horizontal and vertical shifts of water masses and also directly of atmospheric warming (Gutt et al., 2015). Changes in ocean pH follow increased atmospheric CO_2 levels in a complex cause and effect relationship (Orr et al., 2005). Biologists also need specific information from the sediments, groundwater and soil, including age and biogeochemical characteristics, in order to explain recruitment processes and optimum or limiting conditions for all life stages of benthic, terrestrial or limnetic organisms. Less frequently, for instance in the case of biological production of climate-related gases, the situation is reversed. Biologists must provide estimates of the uptake of CO_2 and production of climate gases mostly by marine primary producers in order to improve regional and global climate models (Kennicutt et al., 2014). Such knowledge is essential for future projections including both the response of organisms, communities and ecosystems to environmental change and the effects of life on the atmosphere and ocean.

(B) Other complex questions centre around learning from the past to understand the present and predict the future. This refers to the research on the molecular and physiological adaptation of organisms to stable or changing environmental conditions (Theme 3) and on attempts to correlate large-scale geotectonic and climate events with evolutionary processes (Clarke and Crame, 1989; Theme 8). Firstly, fundamental differences between understanding biological processes and correspondingly driven cross-disciplinary and physical as well as geological approaches are to be recognised. For instance, adaptations over the past 25×10^6 years are key to understanding lethal temperature thresholds that have existed until the present day (Peck et al., 2006). If this threshold was exceeded even for a short period of time at any point on this long time axis, the individual, population or even species may have become extinct. Knowledge of physical events that happened a few million years ago can improve our understanding of the present environment but -in contrast to biological adaptation- the weather of today is independent of the past climate at, say 1×10^6 years ago. As a consequence, studies linking long-term environmental and biological processes demand especially detailed knowledge, for instance on the timing of geotectonic events that happened a long time ago to answer large-scale biogeographic questions on the relationships between isolation and speciation. Also important in this context is robust knowledge of the pace and amplitude of natural paleoclimate variability in order to assess tolerance limits of species in today's changing climate and the potential of microevolution to cope with such changes. Finally, high-resolution records of the recent past (i.e. the past 200 to 2000 years) allow us to determine when observed trends started, what the amplitude of change/variability is that the modern ecosystem has experienced and thus survived, and whether the current change is accelerating.

(C) A main driver of the intensification of cross-disciplinary approaches must be the pressing demand of developing future scenarios for ecosystems. Projections for cryo-pelagic systems including marine primary production, are unimaginable without large-scale and detailed knowledge of sea-ice dynamics (Arrigo and Thomas, 2004). The development of benthic communities can only be predicted if physical impacts on these systems can also be predicted (see for example Cummings et al., 2006; Gutt, 2007; Sañé et al., 2012; Griffiths et al., 2017). In this context, important factors can include patterns and trends of iceberg disturbance, altered sea-ice conditions or changes in turbidity associated with terrestrial runoff. As a consequence of the latter, light attenuation, primary production and food availability in shallow water are affected. General linkages between atmospheric and biological traits are well known, such as the influence of precipitation or wind regimes on terrestrial ecosystem components. If such relationships are non-linear, as most are, detailed knowledge on physical/chemical and biological interactions is essential for understanding them and in quantifying future projected change. This refers especially to the role of the Southern Ocean as a biological source or sink of CO_2.

(D) Another major prerequisite to encourage cross-disciplinary cooperation is to highlight its added value for scientific and applied purposes. The value of cross-disciplinary approaches lie in bringing different disciplines together and tackling questions and challenges that cannot be answered through single-disciplinary approaches. Such interactions often demand compromises within each respective discipline. Notwithstanding the value and progress of fundamental single-disciplinary research, a broader system understanding is demanded by society. Marine ecosystem goods and services (Grant et al., 2013) play an increasing role especially in the IPBES and also in the IPCC assessments. The value of terrestrial ecosystem protection in Antarctica is well recognised although yet to be properly achieved (Chown et al., 2017). First large-scale success for the Southern Ocean South of 60°S were the designations of the South Orkney Islands and Ross Sea Marine Protected Areas by the Commission for the Conservation of Antarctic Marine Living Resources, following smaller predecessors of marine Antarctic Specially Protected Areas and Vulnerable Marine Ecosystems. Further progress in this direction is expected from the Antarctic Treaty System and its Committee for Environmental Protection supported with independent scientific expertise through SCAR and its SRPs.

(E) The necessity of comparative studies, an approach which is not generally novel but remains rare in Antarctic research, is particularly important, especially in a cross-disciplinary context. Useful comparisons can be made between ecosystem functioning in areas subject to intensive versus little environmental change, shallow water versus deep-sea regions, and terrestrial coastal areas of deglaciation versus near-shore marine systems under the same stress regime. Antarctic-Arctic polar comparisons are generally beneficial in the context of understanding ecosystem functioning especially under climate change stress, for instance in the framework of the International Polar Year - Evolution and Biodiversity in the Antarctic programme Team-Fish (Christiansen, 2012). The fastest environmental changes on Earth, accompanied by sea-ice decline, are occurring in the Arctic and at the WAP. Predictions from the cross-disciplinary comparative approach can help in answering questions on response of polar marine organisms, for instance type and extent of new species distributions (Barnes et al., 2009), the relationship between primary production and climate (Constable et al., 2014) and the capacity to develop resilience to ongoing global warming and phenotypic plasticity (Chevin et al., 2010). This seems to be especially valuable when predictions for one system, for instance the Arctic, can be ground-truthed through monitoring programmes for reliability and then, after necessary modification be applied to the Antarctic. A polar comparison would also considerably improve assessment of the potential of adaptation as a result of evolution under two quite different polar scenarios.

(F) Monitoring or long-term observations provide the basis for comparisons between significant ecological changes and background variability in time and support especially Themes 2, 3 and 8; especially important is the integration of biological with atmospheric, glaciological, oceanographic, and geological measurements.

The SCAR Horizon Scan (Kennicutt et al., 2014, 2015) was the major catalyst leading to the brain-storming approach of the 2015 Barcelona workshop. The outcomes of both initiatives show a certain overlap but also differences. Most SCAR Horizon Scan questions were dominated by a single traditional discipline, whilst our approach attempt to build bridges between disciplines. Scale issues, considered either as a scientifically challenging approach or methodological problem to be solved, are highlighted in this study. Compared to the SCAR Horizon Scan, various aspects of sea-ice research are well represented by the ‘Barcelona’ questions. Considerable overlap exists between both studies in climate-change-relevant themes, whilst questions focussing on climate-change-independent ecosystem functioning are more strongly represented in this study. An attempt was also made herein to provide ideas on how to answer questions, and meet requirements by intergovernmental panels and platforms. While the SCAR Horizon Scan (Kennicutt et al., 2015) and especially the Council of Managers of National Antarctic Programs (COMNAP, Kennicutt et al., 2016) emphasized technological challenges, below we make also some general recommendations about developments in science strategies that could strengthen cross-disciplinary research in Antarctica.

The progress of cross-disciplinary development is largely a matter of science structural management (Fig. 1). This includes alignment of the scientist's ‘attitude’, funding strategies that genuinely engage with cross-disciplinary proposals, logistic organization, especially in the less accessible Antarctic areas, and the recognition and adoption of the most valuable approaches concurrent with discarding outdated traditions. Most of the techniques required for advanced cross-disciplinary studies already exist. They are often expensive and some are under (continual) development often driven by single-disciplinary projects, such as drilling through ice shelves for physical oceanography purposes or deep-sea sampling (Brandt et al., 2016). Other technologies, such as biomolecular methods, are developed beyond the communities of Antarctic researchers but must be adapted to the specific polar conditions. Society, which also drives research budgets, increasingly demands detailed and open information, which can arise only from cross-disciplinary cooperation. Thus, the conditions for working in synergy with holistic approaches are currently favourable for expanding such research effort, which must be further developed along with advances in highly specialized fields of research. Within the science community, good question-driven science management will be a key for the success of more advanced cross-disciplinary studies. Major progress towards such visions may be catalysed by a better implementation of a whole-system vision in academic education, introducing more cross-disciplinary university courses and even academic degrees.

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Contributions to the manuscript

Julian Gutt and Enrique Isla developed the general concept, including introduction and conclusion; all other authors contributed. In addition, G. E. Bodeker, N. G. Wilson, T. Bracegridle, R. Cavanagh and P. Convey contributed to significant linguistic improvements. The following authors (abbreviated by first and surnames) contributed substantially to the specific Themes: Theme 1: CS, JG, PC; Theme 2: NB, SS, ALK, DHW, TS; Theme 3: AP, CV, HJG, GdP, UNN, VC; Theme 4: AEM, CRS, GEB, IRS, JG, ST, TJB, UNN; Theme 5: JCX, YR-C; Theme 6: DDM, EI, EV, IRS, JG; Theme 7: AEM, GdP, JCC, JMS, JS, NGW, RDC, RS, TJB, VC; Theme 8: EV, SO, PC, JS, NGW, SS, DDM, JL-M.

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