

PERSPECTIVE

Correlative and dynamic species distribution modelling for ecological predictions in the Antarctic: a cross-disciplinary concept

Julian Gutt,¹ Damaris Zurell,² Thomas J. Bracegridle,³ William Cheung,⁴ Melody S. Clark,³ Peter Convey,³ Bruno Danis,⁵ Bruno David,⁶ Claude De Broyer,¹⁰ Guido di Prisco,⁷ Huw Griffiths,³ Rémi Laffont,⁶ Lloyd S. Peck,³ Benjamin Pierrat,⁶ Martin J. Riddle,⁸ Thomas Saucède,⁶ John Turner,³ Cinzia Verde,⁷ Zhaomin Wang³ & Volker Grimm⁹

¹ Department of Benthic-pelagic processes, Alfred Wegener Institute, Columbusstr., DE-27568 Bremerhaven, Germany

² Institute of Earth and Environmental Sciences, University of Potsdam, Karl-Liebknecht-Str. 24-25, DE-14476 Potsdam, Germany

³ British Antarctic Survey, High Cross, Madingley Road, Cambridge CB3 0ET, UK

⁴ Fisheries Centre, University of British Columbia, 2202 Main Mall Vancouver, BC, Canada

⁵ Department of Antarctic biodiversity information facility, Royal Belgian Institute of Natural Sciences, rue Vautier, 29, BE-1000 Brussels, Belgium

⁶ Biogéosciences, Laboratory 6282, Centre National de la Recherche Scientifique, Université de Bourgogne, 6 boulevard Gabriel, FR-21000 Dijon, France

⁷ Institute of Protein Biochemistry, National Research Council, Via Pietro Castellino 111, IT-80131 Naples, Italy

⁸ Australian Antarctic Division, 203 Channel Highway, Kingston, Tasmania 7050, Australia

⁹ Department of Ecological Modelling, Helmholtz Centre for Environmental Research, Permoserstr. 15, DE-04318 Leipzig, Germany

¹⁰ Department of Invertebrates, Royal Belgian Institute of Natural Sciences, rue Vautier, 29, BE-1000 Brussels, Belgium

Keywords

Environmental change; integrative modelling framework; spatially and temporally explicit modelling macroecology; biodiversity; habitat suitability models.

Correspondence

Julian Gutt, Alfred Wegener Institute, Columbusstr., DE-27568 Bremerhaven, Germany.

E-mail: julian.gutt@awi.de

Abstract

Developments of future scenarios of Antarctic ecosystems are still in their infancy, whilst predictions of the physical environment are recognized as being of global relevance and corresponding models are under continuous development. However, in the context of environmental change simulations of the future of the Antarctic biosphere are increasingly demanded by decision makers and the public, and are of fundamental scientific interest. This paper briefly reviews existing predictive models applied to Antarctic ecosystems before providing a conceptual framework for the further development of spatially and temporally explicit ecosystem models. The concept suggests how to improve approaches to relating species' habitat description to the physical environment, for which a case study on sea urchins is presented. In addition, the concept integrates existing and new ideas to consider dynamic components, particularly information on the natural history of key species, from physiological experiments and biomolecular analyses. Thereby, we identify and critically discuss gaps in knowledge and methodological limitations. These refer to process understanding of biological complexity, the need for high spatial resolution oceanographic data from the entire water column, and the use of data from biomolecular analyses in support of such ecological approaches. Our goal is to motivate the research community to contribute data and knowledge to a holistic, Antarctic-specific, macroecological framework. Such a framework will facilitate the integration of theoretical and empirical work in Antarctica, improving our mechanistic understanding of this globally influential ecoregion, and supporting actions to secure this biodiversity hotspot and its ecosystem services.

To access the supplementary material to this article please see Supplementary Files under Article Tools online.

Projections of future climate following a range of scenarios are becoming increasingly important for scientists, decision makers and the public. It has become apparent that, besides Antarctic-specific questions, integral to improved global predictions is a greater understanding of processes in the Southern Ocean, the Antarctic ice sheets and the polar atmosphere (Marshall et al. 2006; Le Quéré et al. 2007). Predictions relating to biological processes have been attempted since the 1930s, but such approaches were selective and only covered short periods, for instance in the modelling of fish population dynamics and yields (Stock et al. 2011). Nowadays, social and political demands for a healthy environment make the development of more general predictions of the impacts of climate change on ecosystems increasingly urgent. This could lead to improved understanding of the contribution of Antarctic ecosystems to global ecosystem services, such as in biological carbon sequestration (Arrigo, van Dijken & Bushinsky 2008; Arrigo, van Dijken & Long 2008; Peck, Barnes et al. 2009). In addition, concerns about the loss of biodiversity (Butchart et al. 2010) and of genetic information have practical implications, such as in the loss of potentially useful natural products, as well as the risk that some components of the full diversity of life on this planet may be lost before they have even been discovered (Ehrlich 1992). Moreover, there is increasing recognition of the conservation value and even necessity of protecting larger marine and terrestrial areas. These must now also be designed to accommodate a rapidly changing environment and to include the locations of potential future refuges and threatened habitats (Agardy 1994).

The development of long-term predictions of selected parameters of the physical environment is quite advanced. They are based on georeferenced data, although the quantity and quality of these data may vary considerably. Predictive simulation models in this realm are under continuing development, and new theoretical approaches exist. However, a comprehensive framework for an interdisciplinary model of Antarctic ecosystems under future climate change is still lacking, particularly one that can accommodate the full range of biodiversity in the region, the extreme spatial heterogeneity of species assemblages and aspects of ecosystem dynamics and biological interactions.

The aim of this paper is to propose such a framework, building on the bioregionalization approach (Grant et al. 2006) to model the composition of Antarctic marine and terrestrial ecosystems and their relationship to current and future conditions of the atmosphere, cryosphere and ocean. Antarctica provides an ideal test-bed with which to develop such an approach, encompassing ecosystems

across the range from probably the simplest on the planet, e.g., those of the inland continental frigid deserts and isolated nunataks (Freckman & Virginia 1997; Convey & McInnes 2005; Hodgson et al. 2010) to marine ecosystems that are arguably second only to tropical coral reefs in their diversity and complexity (Clarke & Johnston 2003). To be of greatest value the framework has to cover large spatial scales from, for example, the Antarctic Peninsula or Ross Sea areas up to the entire Antarctic and sub-Antarctic region. Accordingly, it must accommodate spatial and temporal heterogeneity (Gutt et al. 2010) across a wide range of scales. The framework is partly based on existing methods, tools and data. In addition, we set out to identify gaps and develop new ideas, both in terms of realistic development based on existing understanding, and more imaginative or speculative approaches. We consider means of merging correlative approaches and dynamic modelling, both of which are important to understanding ecosystem functioning and in explaining ecosystem structure. Although this general approach could be applied globally, there are important Antarctic characteristics and processes that are specific to the region. These include ozone-hole-related atmospheric processes, the ice cover of the continent and large areas of the Southern Ocean, the Antarctic Circumpolar Current, the hydrodynamic separation of cold from warmer water masses, and specific adaptations of individual species or entire biological systems to this unique environment.

With this framework, we aim to engage climatologists and biologists in contributing to a broad cross-disciplinary concept, which has important and clearly defined outcomes, including contributing to human well-being. This will significantly enhance the value of individual measurements, samples, data, experiments and calculations. This paper is also intended to inform decision makers of, for instance, the value of biogeographical databases and the necessity of improving and embracing ecological theory, which have important potential in creating a platform for practical application. These aims are in accordance with the terms of reference of the Action Group on Prediction of Changes in the Physical and Biological Environments of the Antarctic, formed by the Scientific Committee on Antarctic Research (SCAR) in 2008. The necessity of this type of integrated research has been emphasized by Turner et al. (2009); for a summary see Convey et al. (2009).

In the following sections, we briefly summarize the state-of-the-art of existing modelling approaches for spatiotemporal predictions of species distributions in general, and provide overviews of physical and biological data available from the Antarctic and of recent model

applications. We then present a route by which these often separate bodies of information can be assembled to lead the development of future Antarctic biodiversity scenarios. In this paper the term “prediction” is understood as any information relevant to describing how physical and biological habitats may appear in future, based on mathematical modelling and empirical approaches, sound scientific assumptions, and current conditions. Consequently, this term is considered here as synonymous with “projection” and “development of future scenarios”. We believe this approach is the best available for providing robust predictions relating to the ecosystems of Antarctica and the Southern Ocean, in order to make a positive contribution to and further the international debate on climate change.

Modelling species distribution: state of the art

Models of large-scale species distributions have been available for many years, and cover many biological groups across terrestrial, freshwater and marine environments although, until recently, primarily focusing on terrestrial systems (Elith & Leathwick 2009; Robinson et al. 2011). Numerous recent studies have also attempted to project 21st century species extinctions under scenarios of environmental change (Pereira et al. 2010 and references therein).

The majority of climate change impact studies rely on phenomenological, correlative approaches. Statistical species distribution models (SDMs; synonymously known as habitat suitability models, environmental envelope models, niche-theory models) fit the environmental niche of a species by relating species location data to environmental variables in order to describe the conditions under which a given species occurs. Because SDMs do not depend on detailed prior knowledge of the species concerned, and require comparatively simple, widely available occurrence data, these models currently constitute one of few practical approaches for rapid impact assessments (“screening”) for a wide range of species over large spatial scales (Elith & Leathwick 2009). Nevertheless, SDMs are increasingly questioned for climate change applications due to their correlative and static nature (Guisan & Thuiller 2005; Elith & Leathwick 2009). They assume that species are in equilibrium with their current environment, that all environmental factors limiting species’ distribution are included in the model, and that these environmental factors and any gradients therein have been adequately sampled and described. Further, they ignore factors or processes that are likely to modify species’ response to environmental change, including genetic variability, phenotypic and behavioural

plasticity, biotic interactions, migration or dispersal (Jeltsch et al. 2008; Angilletta 2009; Zurell et al. 2009; Somero 2010). One means of increasing confidence in the projections of SDMs is by employing multiple SDMs, which are based on different assumptions and methods, thereby reducing uncertainties by identifying robust predictions, or providing understanding of why the predictions of the different models are not consistent (Elith & Leathwick 2009).

Alternative approaches allow projections under non-equilibrium conditions (Thuiller et al. 2008; Zurell et al. 2009). In these, the environmental niche of a species may be depicted by ecophysiological models that incorporate mechanistic links between species’ functional traits and their environment (Kearney & Porter 2009). Such models have the promise of producing more robust predictions of the fundamental niches of different species (Helmuth 2009). The main problems with this approach lie with the lack of inclusion of information on characteristics such as dispersal mechanisms that may constrain abilities to colonize new benthic habitats and to maintain pelagic systems (Hoffmann & Murphy 2004), and of understanding of physiological resistance and adaptation rates (Somero 2010). Including such data in models may be very difficult, if not impossible in some cases (Soberón 2007) and is feasible for few species only. Spatially explicit population models can be used to model dynamic processes and could incorporate evolutionary, macroecological and physical processes as well as interactions and feedbacks (Jeltsch et al. 2008). Process-based models may also help to uncover “tipping points” in ecosystems that could lead to rapid and potentially irreversible changes (Pereira et al. 2010). However, such models usually are quite complex and therefore data-hungry, and require extensive knowledge of species’ biology and population processes. This often limits the spatial scale of such studies, the number of species included or the generality of the results obtained (Jeltsch et al. 2008) and, in particular, their predictive power (e.g., Angilletta 2009; Helmuth 2009).

Attempts have been made to develop a “minimal” solution, using SDM outputs and spatially and temporally explicit projections of habitat suitability as environmental input layers that constrain basic demographic parameters of population models that are deliberately kept simple. Applications of this approach are currently rare in a global change context, but are promising (Cheung et al. 2008; Cheung et al. 2009; Keith et al. 2008; Anderson et al. 2009; Zurell et al. 2011). Effects of large-scale environmental change patterns and processes on population dynamics, as well as the relative importance of different processes in shaping population responses, can be assessed.

Modelling Antarctic-specific species distributions and the environment: state of the art

The physical environment: modelling future scenarios

Climate models provide estimates of how the ocean, atmosphere and ice components of the physical environment may change in the future. The most comprehensive dataset of outputs from climate models available to date was compiled as part of the preparation for the fourth assessment report of the Intergovernmental Panel on Climate Change (IPCC; Solomon et al. 2007). This is the Coupled Model Intercomparison Project phase 3 (CMIP3) data set and contains output from 24 different climate models from major modelling centres around the world. A wide range of different parameters output from the climate model simulations are stored at the CMIP3 archive (<https://esg.llnl.gov:8443/home/publicHomePage.do>). These range from variables such as temperature, wind and precipitation to diagnostics such as incoming solar radiation and precipitation extremes (a full list of variable names can be found at: <https://esg.llnl.gov:8443/about/ipccTables.do>).

The IPCC's fourth assessment report (Solomon et al. 2007) models predict a consistent intensification and poleward shift of the circumpolar westerly winds over the Southern Ocean during the 21st century. This leads to an increased cyclonic wind forcing on the subpolar ocean circulation. Consequently, the westward flows in the southern limbs of the subpolar gyres become intensified in most models. However, there exist considerable discrepancies in the simulated total gyre transports, mainly due to the large uncertainties in the simulated meridional shifts of the gyre axes. These lead to uncertain predictions of the future Antarctic Circumpolar Current transport through the Drake Passage, although the maximum currents become intensified and shift poleward consistently in the majority of these models.

In addition to the projected 21st century poleward shifts in winds and ocean currents, a robust retreat of sea ice is also predicted by the IPCC's fourth assessment report models (Bracegirdle et al. 2008). The annual average total sea-ice area around Antarctica is expected to decrease by $33 \pm 9\%$ (assuming the SRESA1B emissions scenario) by the end of the century.

Figure 1 shows the predicted ocean temperature changes over the 21st century (Turner et al. 2009). Regardless of season, temperatures become warmer throughout the water column, with the warming being intensified near the surface, particularly at mid-latitudes and in the subtropics. Along the continental margin,

ocean temperature changes, 21st century (Feb., Mar., Apr.)
zonal mean cross-section

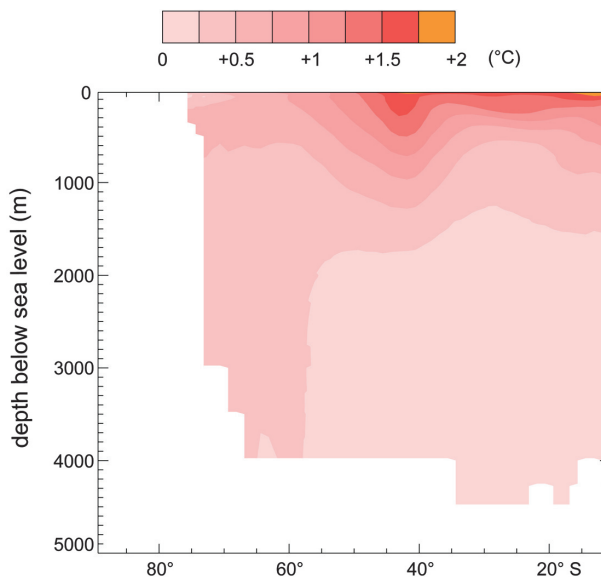


Fig. 1 Southern Ocean temperature changes over the 21st century, defined as the means over the last decade minus the means over the first decade for the late austral summer season (February, March, April).

bottom waters are predicted to warm by around 0.25°C , or up to 0.5°C at depths of 200 to 500 m. The largest surface warming is seen to the north of the Antarctic Circumpolar Current, partly caused by the poleward shifting of the westerly jet. In the Southern Ocean, the surface warming is weaker, which is partly related to the large heat storage by the ocean, and is partly due to the enhanced northward Ekman drift associated with the intensified westerlies.

Unfortunately, the carbon cycle has not yet been represented in the CMIP3 simulations, impairing predictions of biologically important variables such as pH. However, climate model simulations including the carbon cycle have been requested as part of preparation for the next IPCC assessment report. A new climate model database is currently being compiled for this (CMIP5) for which biogeochemical parameters are being requested (see http://cmip-pcmdi.llnl.gov/cmip5/output_req.html?submenuheader=2). An alternative source of biogeochemical data from climate models is the Ocean Carbon Model Intercomparison Project Phase 2 (OCMIP-2) data set (Orr et al. 2005; see also www1.whoi.edu/mzweb/ocmip_ipsl.html).

There remain some caveats associated with the use of data from global climate models. In particular, the horizontal grid size of the climate models used for CMIP3 is typically about 200 km for the atmosphere and 150 km for the ocean component, so that the details

of land and bathymetric features on a smaller spatial scales are not resolved.

The ecosystems and their susceptibility

The huge pelagic system of the Antarctic is very much driven by the seasonal advance and retreat of sea ice. Primary production is limited by micronutrients rather than by nutrients. Communities within and north of the sea-ice zone are aligned in latitudinal bands from the continent to the Antarctic Polar Front, with copepods, krill and salps being the key organisms (from south to north) shaping other components of the pelagic system such as warm-blooded animals (see, e.g., Brierley & Thomas 2002; Smetacek & Nicol 2005; Barnes & Clarke 2011). The speciose benthos can be separated into shelf and deep-sea communities, with both being increasingly but still poorly sampled. The shelf benthos shows an obvious spatial heterogeneity at all spatial scales, ranging from habitats being extremely helle (e.g., in sponge communities), to those that are extremely poor (e.g., under the ice shelf). They are driven by a variety of environmental factors such as sea ice, food supply, and iceberg scouring, but are not influenced to the same extent by sediment characteristics as is seen in other shelf areas (Gutt 2000, 2007 and references therein; Gutt & Starmans 2001; Cummings et al. 2006; Barnes & Conlan 2007; Barnes & Peck 2008). Fish can obviously be classified according to the temperature of their habitat, with *Notothenia* species predominating west of the Antarctic Peninsula and a higher proportion of icefish and representatives of other families at higher latitudes. Whilst the most demersal shelf species belong to the suborder Notothenioidei and occupy a broad variety of niches, *Pleuragramma antarcticum* is the only true Antarctic high-latitude pelagic fish (Kock 1992).

The most serious changes in the Antarctic marine ecosystem (for review see Turner et al. 2009; Brandt & Gutt 2011) are expected for biological processes related to the sea ice, not least because some changes have already been observed and are ongoing, affecting processes such as primary production, krill recruitment and population dynamics of penguins (McClintock et al. 2008; Montes-Hugo et al. 2009; McClintock et al. 2010). Direct effects of temperature increase and acidification are also likely at both the regional and global scale. It is as yet unclear whether the response in these pelagic and benthic systems will be limited to a biogeographical shift of ecologically key species and entire communities, especially along the Antarctic Polar Front, or whether changes in ecosystem functioning at all latitudes will result. At a local scale dramatic changes in environmental

conditions and obvious impacts to the life in coastal waters happen on both sides of the Antarctic Peninsula, where ice shelves collapse.

On land, changes in three physical environmental variables are of direct importance to terrestrial biota and their responses—the thermal environment, the availability and amount of liquid water, and the radiation environment. Plainly, changes in these variables may also be associated with others of biological significance, for instance with desiccation influencing salinity or nutrient availability in soils or freshwaters, or with cloud cover influencing radiation environment and hence primary production (see Convey 2006, 2010 for review). To date the most rapid changes in the first two variables are apparent along the Antarctic Peninsula/Scotia Arc, in general with warming, increased precipitation, and longer periods of temperatures permitting liquid water in the environment (Convey et al. 2009; Turner et al. 2009). Where this direction of change occurs, biological responses are rapid and positive, allowing increased production, growth, population size and local dispersal/colonization (Fowbert & Smith 1994; Convey & Smith 2006). However, the precise detail of environmental changes at local scale is obviously important and may lead to positive or negative consequences for biota at specific locations. This has been demonstrated for instance in the Victoria Land Dry Valleys, where population declines have been seen in terrestrial invertebrates associated with multi-year but still short-term local cooling trends (Doran et al. 2002), and changes in relative population abundances of soil nematodes with different water environment requirements as a result of an exceptional thawing and flooding event (Barrett et al. 2008; Nielsen et al. 2011). Some freshwater ecosystems appear particularly sensitive to and strong indicators of climatic changes, magnifying the rates of change and response seen in the adjacent terrestrial environment (Quayle et al. 2002; Quayle et al. 2003; Vincent & Laybourn-Parry 2008).

Clearly these generalizations inevitably hide specific instances where reverse environmental trends occur, e.g., local cooling over a period of years as reported in the Dry Valleys by Doran et al. (2002). Synergies between variables can also lead to negative results. For instance, both field ecophysiological data (Convey et al. 2003) and the results of controlled environmental manipulation experiments (Convey et al. 2002) are consistent with warming leading to increased desiccation stress being experienced by terrestrial arthropods, hypothesized to indicate that warming has a greater effect on evaporation of water than on making liquid water available (e.g., through increased snowmelt) in the studied systems.

Impacts of exposure to increased UV-B radiation linked with the ozone hole are negative in a different manner in marine, freshwater and terrestrial habitats, relating to the costs of protection and damage repair, and their ramifications through the food chain (see, e.g., Karsten et al. 2009).

Biogeographical and environmental data

An increasing number of georeferenced environmental data are becoming available for both terrestrial and marine Antarctic ecosystems. They potentially contribute to the definition of suitable habitats and prediction of the spatial occurrence of single (key) species, assemblages or functional groups. For the marine ecosystem a total of 39 abiotic factors have been assessed during a Census of Antarctic Marine Life/SCAR–Marine Biodiversity Information Network (SCAR–MarBIN) workshop, held in Villefranche-sur-Mer, France, in May 2010 to determine which of these could have a significant effect on the distribution of benthic and pelagic organisms of the Antarctic margin and the Southern Ocean (Supplementary Table S1). Detailed descriptions of these data sets will be made available as metadata records in the Global Change Master Directory (<http://gcmd.gsfc.nasa.gov/>). The data itself will be posted on SCAR–MarBIN's geoserver, as open access geographic information system layers.

There is currently no Antarctic-wide terrestrial parallel for this programme of work. At the smaller, but still ambitious, scale of the Ross Sea region, the New Zealand Terrestrial Antarctic Biocomplexity Survey (<http://nztabs.ictar.aq/mission.php>) is currently obtaining data in order to build a biocomplexity model linking biodiversity, landscape and environmental factors. This programme has the stated aim of being able to identify the biological or environmental factors that drive terrestrial biocomplexity at any chosen location in the Ross Sea region of Antarctica.

Biological data documenting local-scale occurrence are available for a variety of species, systematic or functional groups of organisms. For the marine biota most of this information is accessible via SCAR–MarBIN (recently renamed Antarctic Biodiversity Information Facility [ANTABif]), the regional Ocean Biogeographic Information System node for the Antarctic (www.scarmarbin.be; www.biodiversity.aq), while terrestrial biodiversity data are also available through the SCAR database held at the Australian Antarctic Division (<http://data.aad.gov.au/aadc/biodiversity/>). This biogeographic information is constantly being extended and updated with data from recent projects and by the input of historical data

sets (De Broyer & Danis 2010; Gutt et al. 2010). This compilation of data provides, for the first time, a truly synoptic circumpolar view, even if it has some limitations such as a lack of “confirmed absence” records and few abundance data. In principle, biological data with a more process-oriented relevance, such as biomass, productivity, and metabolic rate measures could also be included in these databases, although this is not currently the case. Although there are many publications documenting genetic or physiological adaptations to the Antarctic environment (e.g., Peck et al. 2005; Hennion et al. 2006; Peck et al. 2006; Chen et al. 2008; Russo et al. 2010; Patarnello et al. 2011), to date there are no databases of Antarctic “omics” or physiological capacities which could be allied to biogeographic patterns and data-mined for modelling purposes.

Existing biological models

Currently available studies aimed at characterizing Antarctic marine habitats by using physical, chemical and biological parameters have used a bioregionalization approach (Grant et al. 2006). Here, mainly non-biological parameters were classified into clusters representing similar environmental conditions, primarily with reference to open water but also with some application to the sea-floor. A partly analogous “environmental domains” analysis has been carried out in the Antarctic terrestrial environment (Morgan et al. 2007). However this is based purely on physical environmental parameters, and linking the regions produced with biological communities is complicated by the strong historical/evolutionary regionalization now becoming apparent in the Antarctic terrestrial biota. Regions defined by contemporary environmental features often do not match biogeographical distributions whose boundaries are indicative of far more ancient processes (Convey et al. 2008).

More sophisticated approaches using, for example, correlative species distribution models, although still rare, are beginning to be published, as illustrated below.

The distribution of echinoids in the Southern Ocean, known from more than 3500 occurrence data (for data repository see David et al. 2005), make a computation of a distribution model for two species, *Ctenocidaris perrieri* and *Amphipneustes lorioli*, possible. They belong to two phylogenetically distant, ecologically contrasting families, Cidaridae and Schizasteridae, which are widespread over the Antarctic continental shelf (David et al. 2005; Supplementary Table S2). An SDM was constructed using a GIS (ArcGIS version 9.3) and MaxEnt (version 3.3.2) for assessing species distributions from presence-data (for details see Dudik et al. 2004; Phillips et al. 2006).

The technique aims at evaluating the target probability distribution, i.e., the real probability distribution of a species over the whole study area. Among the set of environmental data, 10 variables assumed to be ecologically significant to echinoids were selected (Supplementary Table S1). These variables were checked for pairwise Spearman correlations of less than 0.85. The evaluation of the model was based on 10-fold-cross-validation, and the predictive performance of the model was tested as its ability to predict a “test subsample” from a “training subsample”.

The results obtained for the two species were similar (Figs. 2, 3), although indicating a slightly more southern distribution of *Amphipneustes lorioli*. The modelled and observed distributions are in very good agreement as judged by the area under the Receiver Operation Characteristic curve, also known as AUC (Swets 1988). The AUC values obtained for *Ctenocidaris perrieri* and *A. lorioli* were 0.984 and 0.987, respectively, where a value of 1 represents the best possible fit. Depth, sea-ice

coverage and sea surface temperature (Supplementary Table S1) showed the highest contribution values, explaining a total of 89% to 90% of the potential distribution of each species.

An example model from the circumpolar pelagic realm addresses *Oithona similis*, a very abundant copepod in the Southern Ocean (Pinkerton et al. 2010). A multispecies approach has recently been applied to mesopelagic fish for a smaller area in the Dumont d’Urville Sea off East Antarctica at approximately 140°E (Koubbi et al. 2010). A rare example of the application of an Antarctic-specific predictive biological approach is that predicting a dramatic decline of an Emperor penguin (*Aptenodytes forsteri*) colony related to large-scale and long-term changes in sea-ice extent (Jenouvrier et al. 2009)

An individual-based model, Simulation Model of Benthic Antarctic Assemblages (SIMBAA; Potthoff 2006), developed to contribute to the understanding of the Antarctic marine benthic ecosystem functioning, uses a completely different approach. It is based on

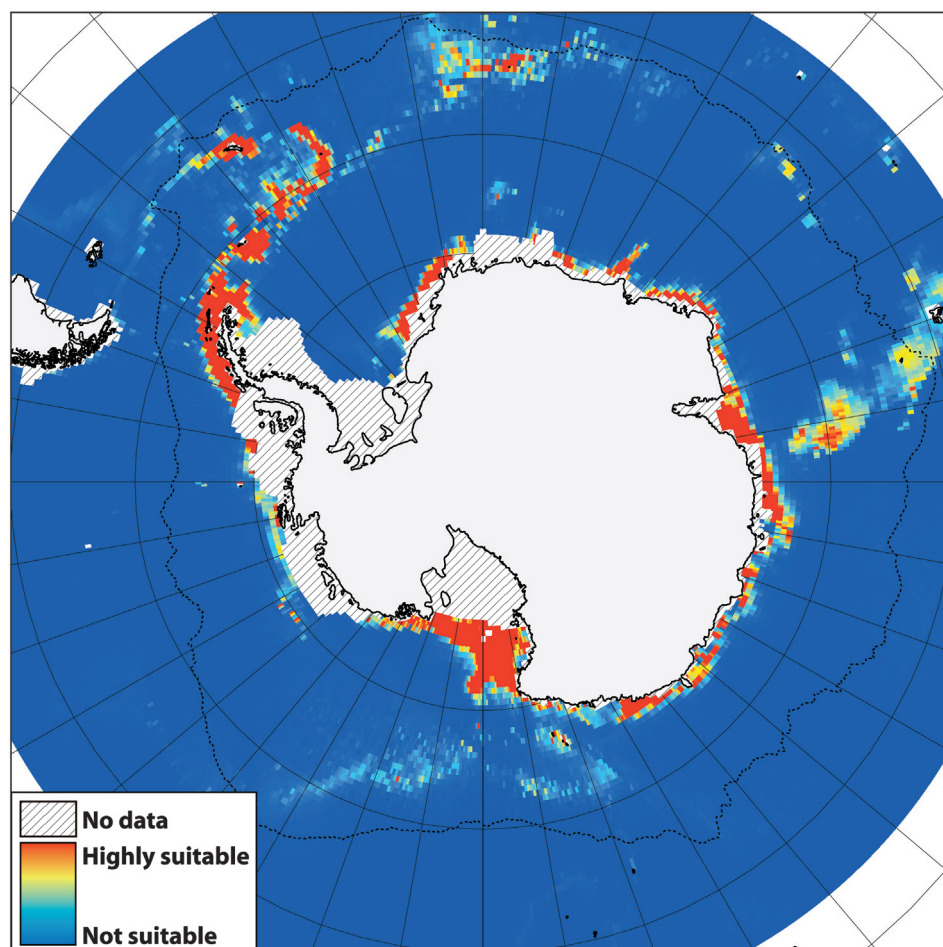


Fig. 2 Map of habitat suitability (probability of occurrence) for *Ctenocidaris perrieri* generated by maximum entropy modelling (MaxEnt).

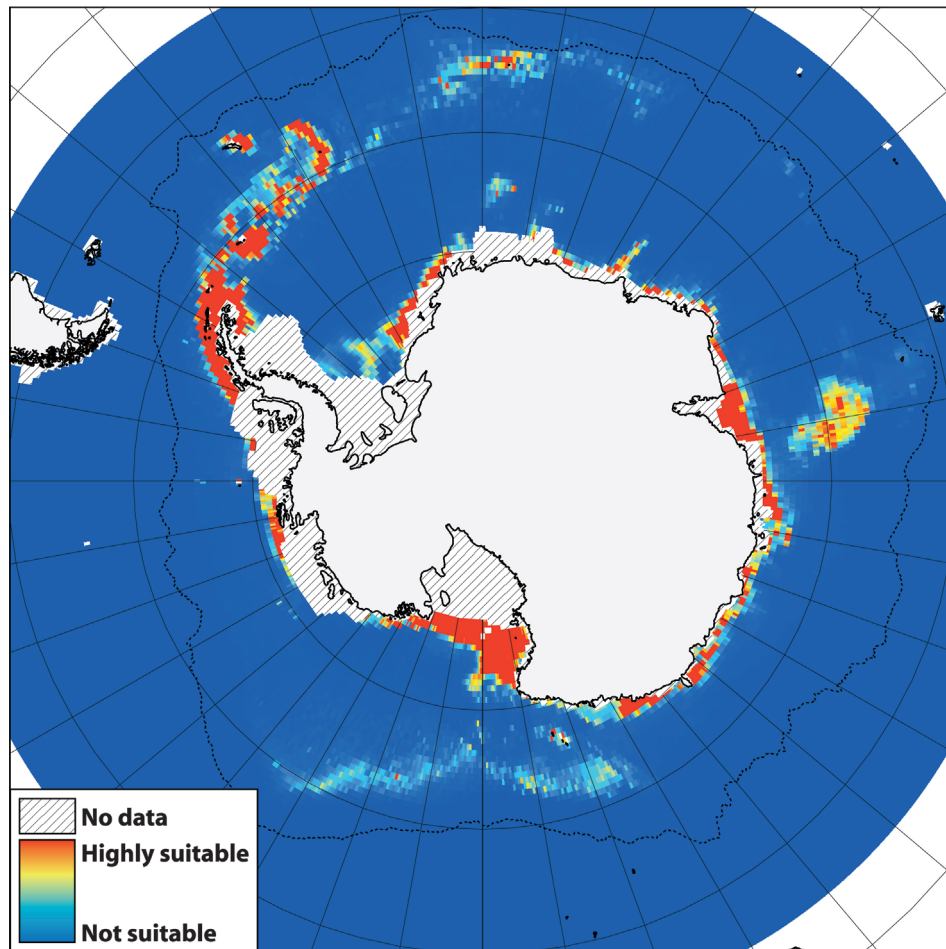


Fig. 3 Map of habitat suitability (probability of occurrence) for *Amphipneustes lorioli* generated by maximum entropy modelling (MaxEnt).

representing generic ecological guilds that respond to changing environmental parameters. Their fitness depends on modifiable functional traits describing reproduction, dispersal, growth, and mortality in combination with lottery competition (Chesson & Warner 1981) during recruitment. The development of single guilds and community structure is determined by a locally variable carrying capacity of the grid cells, by larval dispersal driven by ocean currents and by disturbances due to grounding icebergs causing local mortality. The model's outputs stressed that patchy dispersal supported the coexistence of sessile species even at short distances (Potthoff, Johst & Gutt 2006; Potthoff, Johst, Gutt et al. 2006). A similar but less complex model confirmed the Intermediate-Disturbance Hypothesis (Connell 1978) with regard to iceberg disturbance and benthic biodiversity (Fig. 4; Johst et al. 2006).

The first spatially explicit and dynamic distribution model was developed for a total of 1066 fish and invertebrate species distributed over the entire world's

ocean (Cheung et al. 2008; Cheung et al. 2009). This dynamic bioclimate envelope model goes beyond niche habitat modelling and attempts to incorporate more mechanistic relationships between ocean–atmospheric changes and the biology and biogeography of marine species. It was developed to study the potential effects of climate change on marine biodiversity. Physiological preferences to environmental conditions were inferred from the relationship between the spatially predicted actual distribution of the species and environmental variables, including sea surface and bottom temperature, salinity, sea-ice extent, upwelling strength and association to specific habitat types (e.g., seamounts). The model then simulated changes in relative abundance within $0.5^\circ \times 0.5^\circ$ cells under projected changes in oceanographic conditions based on a spatially explicit population dynamic model. Specifically, population dynamics were driven by changes in carrying capacity of each cell (a function of its suitability as a habitat for the species concerned), and changes in recruitment and migration

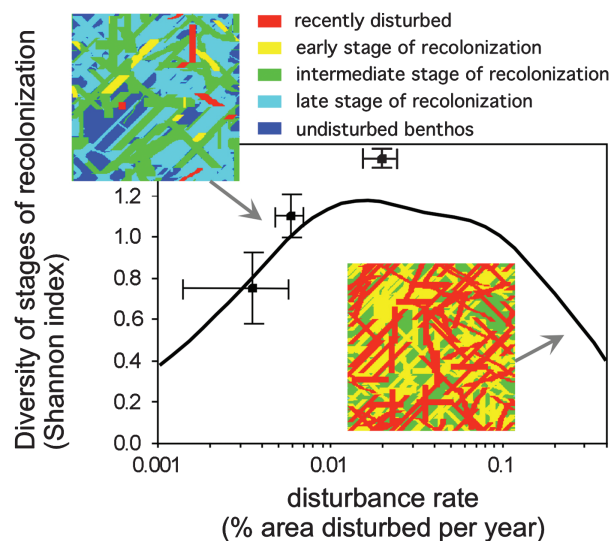


Fig. 4 An analytical model simulating the effect of the intensity of disturbance by grounding icebergs (x axis) on the diversity of benthic successional stages (y axis). The disturbance intensity covers intensities ranging from very rare and low to extremely high values. Squares with error bars indicate empirical data, the site with greatest Shannon index being an “iceberg cemetery” with unusually high disturbance rates, and the two other locations being representative for larger shelf areas between 100 and 300 m depth. Curve and empirical data redrawn from Johst et al. (2006); the recolonization patterns are based on unpublished data.

based on larval dispersal along ocean currents and adult migration. The model projected that, under the SRES A1B and B1 scenarios predicted from the National Oceanic and Atmospheric Administration’s GFDL CM2.1, distributions of fish and invertebrates would shift polewards, resulting in high rates of species invasion in the Arctic and the Southern Ocean. Local extinction events were concentrated in the tropics, semi-enclosed seas and sub-polar regions. A species-specific version of this model predicts that the Antarctic toothfish (*Dissostichus mawsoni*), a commercially exploited species, will become largely reduced because it cannot extend its southern limit in response to warming (Cheung et al. 2008).

While Antarctic marine habitats exhibit relatively high thermal stability, terrestrial habitats experience extreme environmental variations (Peck et al. 2006). The challenge of identifying and modelling species’ responses in the Antarctic terrestrial environment is therefore rather different. Terrestrial invertebrates and plants have been the focus of a body of ecophysiological research studying their environmental tolerance that has developed over many years. For general introductions to the literature across various taxa see, e.g., Longton (1988), Sømme (1995), Hennion et al. (2006), Peck et al. (2006) and Denlinger & Lee (2010). As is often the case, a relatively

small number of species have been the subject of the most detailed analyses, effectively becoming “example” taxa (Chown & Convey 2007) and comprehensive spatially explicit models are still missing. Terrestrial microarthropods have provided a particular focus for study, with the springtail *Cryptopygus antarcticus*, oribatid mite *Alaskozetes antarcticus* and dipteran *Belgica antarctica* being the subject of the majority of studies in the maritime Antarctic (Block 1990; Block & Convey 1995; Elnitsky et al. 2008; Lopez-Martinez et al. 2009; Burns et al. 2010; Teets et al. 2011). In the continental Antarctic, similar studies have largely been limited to Victoria Land, where the springtail *Gomphiocephalus hodgsoni* (McGaughan, Convey et al. 2010), and the nematodes *Panagrolaimus davidi*, *Scottinema lindsayae* and *Eudorylaimus antarcticus* (Wharton 2003; Nielsen et al. 2011) have received most attention. From these we extrapolate to conclude that terrestrial biota are well-adapted to survive the considerable range of variation in environmental conditions that is typical in their Antarctic habitats. Judged from currently available century-scale climate scenarios, we expect generally moderated physical environmental constraints on land (although note again the caveat discussed above, that at local scale the combinations of changes may also result in more severe constraints), and hence that predicted changes are well within the tolerances of the native species. Therefore, in circumstances where warming (i.e., increased thermal energy availability) is experienced in combination with an increase or at least no change in water stress, native biota are expected to benefit in terms of increased growth rates and biomass, population sizes and extent, and through local colonization of newly available areas of ice-free habitat, see Convey (2010, 2011) and Nielsen et al. (2011) for review. Manipulation experiments (Day et al. 1999; Smith 2001; Convey & Wynn-Williams 2002; but see Kennedy 1995 and Bokhorst et al. 2011 for caveats on methodological weaknesses) and limited field observations (Fowbert & Smith 1994; Parnikoza et al. 2009) tend to support this observation, with native species and communities responding positively to the major predicted changes of increased temperature and water availability, as these relax current constraints on biological processes and activities.

Therefore, the major challenge for terrestrial Antarctic ecosystems may lie in predicting the impacts of “incoming” species, rather than the failure of native ones per se (Convey 2011). While there is reasonable knowledge of actual distributions of “example” taxa, more generally there are many gaps in available survey data across all terrestrial faunal and floral groups, compounded by a lack of up to date or authoritative taxonomic evaluation

(e.g., Adams et al. 2006; Chown & Convey 2007). More recently, studies of molecular phylogeography have started to become available, however these are again currently limited to a small number of target taxa (e.g., McGaughan, Toricelli et al. 2010; Mortimer et al. 2011).

At small physical scale, usually for a single location, some studies have attempted to link observed native and non-native terrestrial species distributions and physical environmental data (Usher & Booth 1984; Freckman & Virginia 1997; Sinclair et al. 2006; Lee et al. 2009; Davies et al. 2011), while Lee & Chown (2009) have also done this for an invasive slug species on sub-Antarctic Marion Island. In studies of Antarctic plants, broad descriptions of vegetation types and ecological associations are also implicitly or explicitly linked with general descriptions or assumptions about linked environmental features (e.g., Smith 1972; Longton 1988; Gremmen & Smith 2008). However, such studies are yet to be placed into a larger scale and more predictive modelling framework. Furthermore, in the context of modelling possible future distribution changes it must also be taken into account that, unlike the generally inter-connected structure of the Antarctic marine environment, terrestrial ecosystems are effectively restricted to normally tiny “islands” of habitat (contributing only 0.34% of the total area of the continent, or in total about 44 000 km²). Hence, terrestrial biota are not uniformly distributed across habitats within a geographical extent defined by their environmental tolerance envelope but are rather isolated on physical scales up to hundreds of km from either the “next” population of the same species, or the next available area of habitat for colonization.

Given the scale of physical isolation of most islands of Antarctic terrestrial habitat, models that attempt to overcome this type of constraint therefore also require incorporation of information that is currently not available relating to dispersal and colonization mechanisms, frequencies and routes. A further complication is the recently described considerable and ancient biogeographical regionalization within the terrestrial biota of Antarctica (Convey et al. 2008; Vyverman et al. 2010), which highlights that the various elements within Antarctica have been (and still are) strongly isolated from each other, presumably by physical barriers, over very long periods of time. The ancient biogeographical signal within Antarctica requires incorporation in model development, in order to overcome the problem that, for many if not most taxa, any attempt to describe a simple “environmental envelope” will not take into account of these boundaries and will therefore inevitably incorporate areas of different regions, even though the taxa

concerned do not occur across these boundaries. An example of this is that the majority of mites and spring-tails (the dominant and largest terrestrial invertebrates in the Antarctic) currently known from the maritime Antarctic, as well as smaller groups such as nematodes, tardigrades and rotifers, would face no apparent change in ecological or physiological stress in terrestrial habitats of the coastal continental Antarctic, or vice versa, i.e., could live there if transplanted. Yet, at species level, there is no overlap in the current faunas in the majority of these groups between the two regions (see, e.g., Andr assy 1998; Convey et al. 2008).

While the focus of this paper is on predicting biological responses associated with systematic climatic change, this last point also further highlights that other “direct” human impacts may act in synergy with climate. Perhaps highest amongst these is that of human-assisted movement of biota both into Antarctic terrestrial and marine ecosystems from elsewhere, and, especially on land, between the different regions within Antarctica (Frenot et al. 2005; Hughes & Convey 2010). Indeed, inspection of the establishment of non-indigenous species currently known particularly from the sub-Antarctic islands strongly suggests that these may have considerably greater impacts on native species and ecosystems than any that are likely to arise as a consequence of climatic change over the same period (Convey 2011). In this context, a more applied approach utilized on a specific sub-Antarctic island to the prediction of biological change is to model the response of communities to the suppression of invasive species (Raymond et al. 2011).

Proposed integrative framework for the Antarctic

Broad-scale screening and dynamic predictions

Biodiversity scenarios for the Antarctic can be derived in different steps of increasing complexity. Pragmatically, we should start with simple models and, perhaps more importantly, choose an approach that can be supported with data. Correlative (static) approaches are useful for broad-scale screening purposes. Calculations of potentially suitable habitat identify combinations of environmental parameters which best explain contemporary occurrence of selected species, systematic or functional groups, or entire ecological assemblages for which sufficient information is available (Cheung et al. 2008; Cheung et al. 2009). Thus, it allows investigation of the main environmental forces shaping the niches of species and groups of species. The larger the geographic areas considered are, the smaller the expected errors due to

undersampling of single cells and the better will be the calculations representing regional or global diversity. Conclusions will substantially contribute to an improved and holistic understanding of Antarctic ecosystem functioning. Applications in a global change context will provide rapid assessments of potential changes in suitable habitats, as many examples from global terrestrial biogeography have underscored (see Pereira et al. 2010).

This static approach can then be complemented by predictions of dynamic outcomes that incorporate demographic processes. Such models typically require a greater level of biological knowledge and data than are currently available. However, in the preceding section we have described the outcomes of some models that incorporate demographic processes (Potthoff 2006; Cheung et al. 2008; Cheung et al. 2009; Jenouvrier et al. 2009). These exemplify how even limited biological knowledge can be utilized to inform dynamic population models for large numbers of species, for example by supplementing known process parameters with those obtained from allometric relationships (e.g., maximum growth rates inferred from body size). Spatially explicit dynamic population models allow for qualitative analyses of local and regional population viability and for assessing alternative management scenarios. Approaches such as those used by Potthoff (2006) can be applied to functional types, trophic guilds or keystone species. In a further step, it would be straightforward to relate such generic models to more realistic sea- or landscapes, especially in terms of coastline, current patterns and topography.

Incorporating “first principles”

Dynamic distribution models, which incorporate simple models of population dynamics, are more flexible than purely correlative models, which assume constant species–environment relationships but may still be limited because they are based on demographic parameters that are valid only for those environmental conditions under which these parameters were observed. Predicting the response of species distributions to future climate scenarios will, however, very likely include unprecedented environmental conditions, for which no data exist. To solve this problem, modelling the response of organisms to their environment has to be based on “first principles”, i.e., ecophysiological or behavioural mechanisms. In such models, demographic parameters are no longer imposed, but emerge from individual-level processes (Grimm & Railsback 2005).

For example, a later version of the model developed by Cheung et al. (2008) further examines the interactions between changes in ocean biogeochemistry (acidity and

dissolved oxygen level, phytoplankton community structure) and species’ biogeography by incorporating an explicit ecophysiological component into the model. This model simulates changes in metabolic rates according to temperature and ocean chemistry, and predicts their effects on body size, reproduction, and growth and natural mortality rates of the studied species (Cheung et al. 2011). Changes in life history characteristics then affect the species’ population dynamics that determine its predicted distributions. For example, applying the model to 120 species of exploited demersal fishes and invertebrates in the north-east Atlantic, this study showed that ocean acidification and changes in oxygen content may reduce species’ growth performance, increase the rate of range shift, and lower the estimated catch potentials. This highlights the potential sensitivity of marine biodiversity to ocean acidification and reduced dissolved oxygen. A more general conclusion is that we need to distinguish carefully between imposed and emerging demographic responses of species to their environment. Basing models on first principles requires more effort than simpler approaches but is rewarded by higher flexibility and more reliable predictions; see also, for populations in other types of ecosystems, Railsback & Harvey (2002) and Goss-Custard et al. (2006). Focusing on first principles is also a trend in macroecology, where recently “macro-physiology” has been suggested as a new focus area (Gaston et al. 2009; Chown et al. 2010). It will be interesting to relate these approaches to mechanistic models based on first principles, but it should be noted that the rationale of macroecology is completely different from mechanistic modelling in that it focuses on statistical correlations instead of causal relationships.

Incorporating adaptation and genetic information

A key element in producing better predictive models is the need to include improved understanding of populations that are stressed by changing environments. However, whilst ecological observations can record shifts in species ranges and regime changes associated with climate change events (Drinkwater 2009), these are a posteriori observations. Currently, besides ecological methods, physiological and biochemical criteria are available to answer questions on population level fitness, relatedness, genetic diversity and geneflow. All these population-specific characteristics potentially influence extinction or survival probabilities in a changing environment.

A better understanding of long-term adaptations to the environment can be achieved through phylogenetic

screening across the whole genome for the presence of multiple genes indicative of stress. Within a macroecological context, we are now able to formulate experiments which correlate the capacity to cope with changes and survival characteristics with genome tags. Such adaptations are widespread and not restricted to isolated populations, such as gigantism (Chapelle & Peck 1999), lack of haemoglobin (e.g., di Prisco et al. 2002; Cheng et al. 2009), increased muscle-fibre diameter (Johnston 2003), the lack of production of a heat-shock response (Hoffmann et al. 2000; Clark et al. 2008; Clark & Peck 2009), and the development of antifreeze glycoproteins (deVries 1988). These examples are specifically marine and a wide range of genes that respond to temperature stress has now been identified and may be valuable in future (Thorne et al. 2010; Truebano et al. 2010). However, the amount of molecular work on terrestrial species is increasing with a concentration on understanding freezing and desiccation resistance in the arthropods *Cryptopygus antarcticus* (Burns et al. 2010) and *Belgica antarctica* (Lopez-Martinez et al. 2009) and the nematode *Plectus murrayi* (Adhikari et al. 2009; Adhikari et al. 2010). The examples above (both marine and terrestrial) are largely concerned with either single gene studies or at most 2000 transcripts. However, Next Generation sequencing technologies promise to expand our genetic repertoire immensely with recent studies generating around 20 000 transcripts for both the Antarctic clam (*Laternula elliptica*) and krill (*Euphausia superba*) as public resources (Clark et al. 2010; Clark et al. 2011).

To provide a priori predictions, we need to understand whether organisms/species can survive long enough in any given habitat that is challenged by change until they adapt via microevolution (see below). Recently, it has been shown that short-term laboratory experiments have value in predicting physiological limits (e.g., Pörtner & Knust 2007; Peck, Clark et al. 2009). Results are currently available from a range of species, but are far from covering all ecologically key species. We can start to link these with data on species longevity, reproduction, and life histories. However, further data are required from both physiological and behavioural experiments, ground-truthed by comparison with field observations (e.g., Morley, Tan et al. 2009). Long-term studies are also vital as they document inter-annual variability and often highlight the long-term cycles intrinsic in polar environments (Grange et al. 2004; Bowden et al. 2009).

This is an area where the application of new “omics” technologies could significantly improve our predictive abilities. In addition to genomics, proteomics encompasses approaches to analyse the molecular structure and

functioning of a complete set of proteins, and transcriptomics shows which genes are transcribed (i.e., genetic activity). A corresponding molecular screening can, for example, determine accurately the temperatures at which a species starts to experience cellular stress, which may impact whole animal health (Truebano et al. 2010). By combining the transcriptomics and proteomics approaches, we can understand how organisms translate the effects of a changing environment into molecular and biochemical responses. Extreme sensitivities for whole organisms are relatively easy to describe, such as in the brittle star *Ophionotus victoriae* (Peck, Clark et al. 2009). However, acclimation to +4°C or higher, such as among the sea star *Odontaster validus* (Peck et al. 2008) and notothenioid fishes (e.g., Bilyk & deVries 2010) are more difficult to characterize as this requires detailed understanding of life history traits such as growth, metabolism, reproduction and recruitment, coupled to competitive and abiotic interactions. Data presented by Chen et al. (2008) suggest that evolution in the cold has produced genomic expansions and/or upregulations of specific protein-gene families, many of which are involved in the antioxidant function. These may produce increased vulnerabilities *via* decreased capacities to cope or reduced cellular energetic buffering. In the terrestrial field, the latter is of particular interest as there are clear energetic trade-offs required in such a highly variable environment, the animals are often subjected to sudden freezing events and multiple freeze/thaw events as well as seasonal cooling and over-wintering (Michaud et al. 2008; Lopez-Martinez et al. 2009; Adhikari et al. 2010; Teets et al. 2011). These have started to provide interesting data on stress-specific biochemical pathways with indications that, at least in *Belgica antarctica*, some of these pathways may be shared between responses to different stresses (Michaud et al. 2008). These data enable the relative costs of survival to be determined under the different environmental regimes, a prerequisite for understanding responses to climate change (Teets et al. 2011). They are also required to enable an understanding of the success of invasive species, a more pressing issue in the terrestrial field than the marine (Worland 2010).

Antarctic notothenioid fish also provide an example of the relevance of spatially explicit data in studies of trade-offs, since they show geographically patchy acclimation abilities at the physiological and molecular level, for instance, in comparison between the Antarctic Peninsula and Ross Sea (Bilyk & deVries 2010). Such spatial heterogeneity, traditionally described as physiological races, might explain some of the differences between field observations and physiological experiments on the temperature tolerance of the fish *Pagothenia borchgrevinki*,

which are otherwise contradictory due to unknown reasons (Franklin & Seebacher 2009).

Genomic studies will also help us to understand microevolution and its underlying mechanisms. Again, this has been described in model species and such processes must surely operate in Antarctic species, albeit at a slower rate. Novel genomics techniques, such as restriction site-associated DNA (RAD) tags (Baird et al. 2008) are revolutionizing traditional phylogenetic studies, allowing rates of gene evolution to be assessed. Given the rate of sea water warming along the Antarctic Peninsula, and the limitations of adaptation rates that are given by the cold Antarctic marine environment (slow growth, longevity, deferred maturity, etc.), it is key to understand how effective microevolution is at realistic timescales in producing new gene complements in populations which are under environmental stress. Studying the genetic structure and responses of populations in regions where change is greatest (currently, the Antarctic Peninsula) compared to those areas where temperatures are largely unchanged (such as the Bellingshausen, Weddell and Ross seas) could potentially provide indicators of adaptation abilities and how they have been altered by recent change.

Antarctic studies are a long way behind those of laboratory model species, where susceptibility and resistance can be linked to genetic traits, heritability and range limitations (see, e.g., Hoffman et al. 2010). However, development and exploitation of a similar array of genetic analysis tools has the potential to identify vulnerable species, the loss of which would cause marked imbalance at the ecosystem level. In this case we will be able not only to model possible biogeographic shifts but also significant *in situ* changes in the ecosystems. Specific physiological acclimatization seems to be linked to specific habitats and microevolution might accelerate in areas under environmental stress, whilst no selective pressure is expected in environmentally stable areas. Both phenomena are valuable to be simulated focusing on mechanisms to maintain or, if new competitive interactions occur, diminish species occurrence. These mechanisms would also produce feedback effects on microevolution that would be difficult to predict without a mechanistic approach. The examples mentioned above show that selected results from physiological and biomolecular studies are *a priori* relevant for future predictive models due to their spatially and temporally explicit nature. If implemented in such models their general relevance to predict the structure and functioning of future Antarctic ecosystems could also be assessed and confirmed.

Refining environmental parameters

All biological forecasts rely on the availability of relevant environmental parameters in global change scenarios. Therefore, we can consider (1) environmental parameters for which future scenarios exist, for instance sea-ice, air and sea-water temperatures, or pH in the ocean, (2) parameters that are expected to be stable over the period of extrapolation, such as bathymetric features, and (3) assumptions for parameters expected to change but for which no predictions exist, such as the intensity of iceberg scouring or flux of phytodetritus through the water column.

The average predictions made by the IPCC are of limited value for biological models, because organisms may be (differentially) more vulnerable than expected to fine-scale spatial and temporal niche-specific temperatures, and subject to the effects of both biotic and abiotic factors (Helmuth 2009). For example, for many species sea surface temperatures as predicted by climate models may not be ecologically meaningful. Species such as bivalve molluscs, that are known to exist in the benthic shallows of the Antarctic Peninsula (67°S, annual temperature at 15 m water depth in the range between -2°C and $+1^{\circ}\text{C}$), are only present in deeper water near South Georgia (54°S, average temperature 1.2°C) as the annual shallow water is between -1°C and $+4^{\circ}\text{C}$, with upper summer limits beyond their known physiological coping capacity (Morley, Hirse et al. 2009; Morley et al. 2010). Hence presence/absence could be directly correlated with water temperature. For future ecological predictions it is therefore important to understand and quantify the physical parameters in three dimensions (see Turner et al. 2009).

We know that also highly dynamic and spatially patchy physical and biological processes and interactions shape life in Antarctic ecosystems. For example, the recruitment of krill depends very much on the existence of sea ice during the late austral winter, particularly in the south-west Atlantic sector of the Southern Ocean (Atkinson et al. 2004). Further, the distribution, at least at local scale, of sessile benthic species may be most strongly influenced by single extreme events, such as occasional upwelling of warm water masses or of physical disturbance through iceberg scour, which occur rarely and are of very short duration (Gutt 2006). Such features may therefore require a high temporal resolution of the environmental predictions used in models, especially if the important extreme events are of ephemeral nature. Such variability of environmental parameters not only plays an important role in predictions but also in improved definition of contemporary potentially suitable habitats, because a modified and extended analysis

would provide refined information on organism tolerance (and the limits thereof) to environmental variability (Zimmermann et al. 2009).

Many climate models predict an increase in the frequency of extreme events. In the context of the Antarctic marine environment examples include the collapse of large ice sheets and greater iceberg activity, as well as increased sedimentation and fresh-water runoff (Barnes & Conlan 2007; Brandt & Gutt 2011). Whilst the effects of these may be relatively local, they may change core populations with wider ranging consequences. There is a clear need to link more effectively information on reduction in sea ice, glacial erosion and iceberg activity with chlorophyll measurements (both satellite and actual). Loss of ice sheets creates “new” areas of open water, which can then contribute to primary productivity, providing a negative feedback on the climate system (Peck et al. 2010; Gutt et al. 2011). Loss of sea ice can impact not only on the seasonal availability of open water and primary production (Arrigo & Thomas 2004), but also on certain life history stages of macro-invertebrates (Atkinson et al. 2004), with consequences for the food web. In addition, primary production is expected to increase as a result of increased nutrient upwelling (Arrigo, van Dijken & Bushinsky et al. 2008). Drifting icebergs have been shown to increase local primary productivity (Schwarz & Schodlok 2009), whilst grounded icebergs can obviously cause the opposite effect (Arrigo et al. 2002). Icebergs scouring the sea-floor have locally drastic effects on benthic communities (see Peck et al. 1999; Lee et al. 2001; Brown et al. 2004), but the patchwork of stages of succession after such events increases regional diversity (Gutt & Piepenburg 2003). Our ability to track icebergs is becoming increasingly sophisticated (Silva & Grant 2005; Tournadre et al. 2008). Given examples of both greater and locally reduced likelihood of iceberg disturbance, these data should be used in combination with climate prediction models to further develop models such as those of Potthoff (2006), Potthoff, Johst & Gutt (2006), Potthoff, Johst, Gutt et al. (2006) and Johst et al. (2006), briefly described above.

A fundamental advance in biological predictions could be achieved through the use of higher spatial resolution than the current 0.5° by 0.5° to 3° by 3° cells (which also have variable area due to the influence of latitude) used in most Southern Ocean scale analyses and general circulation models. Many biological processes and their spatial variability are specific for a spatial scale of 1 km or (much) less rather than the ca. 200 km used in the majority of global climate models. However, most global scale climate models do not necessarily increase local accuracy with finer scale analyses. Local variability is

often driven by local processes that are independent of regional or global climate change. However, if biological data are sampled in a patchy way, they may not be suitable for fine-scale analysis due to high variation in sampling effort across cells. In both the Southern Ocean and on land in Antarctica some larger regions are known to be better sampled than others, while hotspots of regional climate change exist (Turner et al. 2009). For such regions the use of a finer scale model to predict local changes in biodiversity would be a major step forward. Regional climate models are increasingly being used to better represent smaller-scale features, such as the mountains of the Antarctic Peninsula, which have a dramatic influence on surrounding wind, temperature and precipitation patterns. These models are run with horizontal grid sizes in the range of 1 to 100 km. An important caveat is that large uncertainty still remains in regional model predictions, the main source of which is the global climate models within which they are nested.

The resolution of available sea-surface data collected remotely, such as temperature and primary productivity, increases with each generation of satellite technology. However, other data, which are only collected in situ, such as sea-floor temperature, are impossible to obtain at the same spatial resolution. Approaches that provide data otherwise impossible or difficult to obtain include biologging—the mounting of sensors on large animals—or the deployment of floats, gliders, crawlers and autonomous operated vehicles. The data resolution required depends upon the nature of the question being answered and the associated errors and uncertainties. An example of macroecological features which demand higher spatial resolution is given by oceanic gyres of only a few kilometres diameter, because they can significantly shape the composition of planktonic assemblages within a larger region, along with further impacts to other trophic levels. An analogous example is given by krill swarms extending in length to between 10 m and > 1 km (Tarling et al. 2009). Benthic patterns range in size, depending features of interest, from as little as a few metres to description of a relatively homogeneous circumpolar faunistic province (Gutt et al. 2010).

Validation

If models are to provide a basis for political decision-making, confidence in predictions needs to be high. Validation of climate impact predictions is therefore crucial, though at the same time inherently difficult as the future is unknown. A largely theoretical approach to validation of climate impact predictions is presented by Zurell and co-workers (Zurell et al. 2009; Zurell et al.

2010). These authors use virtual data generated by a mechanistic model to investigate the effects of transient dynamics as well as ecological properties and processes on the prediction accuracy of correlative species distribution models. A more applied way of independently testing the predictive ability of models across time is to use retrospective data, for example from fossil records (Pearman et al. 2008). Some responses of Antarctic biological systems to environmental changes have been inferred from palaeo-ecological samples and their analyses, and from studies over recent decades linked with contemporary changes. Examples include changes in krill, penguins and phytoplankton in areas experiencing sea-ice reduction (Barbraud & Weimerskirch 2001; Atkinson et al. 2004; Ducklow et al. 2007; Montes-Hugo et al. 2009). Further, observed 20th century distribution shifts can provide validation (Araújo et al. 2005; Willis et al. 2009). If our model is initiated with a pre-industrial scenario in a relatively predictable and stable environment, *in silico* predictions for contemporary scenarios can be calculated and compared with the *in situ* results from field surveys. Analogous “ground-truthing” will become important if contemporary scenarios are used as the initial point, with model results then being compared with results from future field surveys. This approach appears promising, especially among sensitive functional groups of organisms or in specific areas with, for instance, clearly reduced sea ice or at the shifting polar frontal system. Such “ground-truthing” can help to narrow the otherwise wide scope of potential options for future ecological developments.

Challenges

Measurements of some oceanographic and atmospheric physical parameters, which contribute most to climate processes, are carried out regularly by remote sensing techniques, which cover large areas and have a relatively high spatial resolution. In addition, manned and unmanned ground stations provide locally detailed data. Our ability to predict such parameters is reasonably well advanced. In biology such synoptic approaches are limited to parameters amenable to remote sensing approaches, such as chlorophyll measurement at the sea surface, or to the description of bird and mammal movements through satellite tracking. Remote-sensing technologies also have the potential to measure features such as vegetation extent, although this is yet to be applied widely to the Antarctic (but see Fretwell et al. 2011). Measurements of biological, chemical and some physical parameters in the water column at high spatial and temporal resolution will remain scarce until new

techniques are developed or existing modern approaches widely applied. However, ongoing single measurements and biodiversity surveys focusing on specific areas and systematic groups can help to overcome current limitations, especially in the bioregionalization approach where information gaps are overcome using interpolation techniques. Data on benthic topography and sedimentological parameters, such as surface grain size, are very patchily distributed but, since it can be reasonably assumed that these are stable over long periods, each new survey contributes to a continuous improvement in the Antarctic-wide picture. The situation is similar for territorial and sedentary organisms such as benthic animals and their assemblages, or vegetation and its associated fauna, as long as they are not (yet) affected by unusual environmental changes such as the climate change already seen along the Antarctic Peninsula or by direct anthropogenic disturbance, such as the historical and recent exploitation of marine mammals and fisheries (Montes-Hugo et al. 2009; Trathan & Reid 2009). In such cases it is doubtful whether the approach described above can reconstruct the pre-disturbance conditions, required to generate a starting point for model modifications having different foci.

A further limitation that cannot be ignored within an intermediate temporal scale arises from biological complexity. It is important in biodiversity studies to know the sampling effort at each site, and this is especially so in Antarctica. Understanding of patchiness of distributions is still generally poor, and even the “presence/absence” classification may be interpreted erroneously due to lack of sampling effort, leaving “presence” alone as the lowest common denominator within comprehensive biodiversity data sets. Where abundance data have been estimated in previous surveys, such as for some specific species (e.g., krill), this could be proposed as a future standard for all biogeographical biodiversity surveys. A major advantage of the inclusion of abundance data is that the most basic but important additional information of absence (=zero abundance) can improve the approach considerably. In addition, abundance in general may be a parameter in community structure, which responds first to environmental change well before species become locally, regionally or globally extinct. On the other hand, the inclusion of abundance makes predictive ecological climate models less robust to changes in population size being independent of climate change processes. A compromise could be to use abundance classes, providing some robustness against methodological errors. One potential method to correct species richness values for sampling effort is to calculate the residuals of the regression of the number of species on

the number of samples from defined areas with higher residuals indicating higher than average species richness (Clarke et al. 2007, for examples see also Gutt et al. 2010). There is optimism that, in future, rapid analyses of metagenomes will increase the efficiency of species determinations by orders of magnitudes. However, this technique will only be applicable to ecological studies if the corresponding information for most known species is available in genetic libraries.

Dynamic distribution models based on “first principles” as described above are also not without challenges. They need to be carefully designed, tested, and analysed to avoid unnecessary complexity, which could obstruct understanding and thereby render the model useless. One strategy for avoiding overly complex models is “pattern-oriented modelling”, where model structure is tied to a limited number of key patterns observed in the real system to be modelled (Grimm & Railsback 2005; Grimm et al. 2005).

Implementation and conclusions

Even if a relatively poor systematic and spatial coverage of Antarctic biological data and of some ecologically relevant parameters remain the largest challenges in the foreseeable future, we cannot wait to develop powerful predictive ecological models. There is a pressing demand for biological predictions from decision makers and society in general because of their implications in terms of ecosystem services. Examples of their need are clear in the ongoing exploitation of natural resources including genetic information, the protection of devastated, threatened or sensitive habitats by Marine Protected Areas, Vulnerable Marine Ecosystems and Antarctic Specially Protected Areas, and the contribution of biological systems in compensating for or accelerating global change processes, especially in the context of the Southern Ocean acting as a major biological CO₂ sink (Arrigo, van Dijken & Long 2008). A predictive framework as proposed above would affect political decisions on how these problems are tackled or ignored. Due to its high levels of endemism, Antarctic fauna and flora make an important contribution to global biodiversity. Furthermore, ecologically key Antarctic species provide the main food source for some globally distributed species, such as some whales, fish and birds.

The importance of bi-polar approaches is increasingly recognized in the international research community, including SCAR and International Arctic Science Committee, as the geographic differences between the two regions are differently reflected in global change, and hence in adaptive responses (di Prisco & Verde 2006;

Verde et al. 2008). The framework described above is especially designed for the Antarctic. However, despite the obvious differences in physical environmental and biological characteristics, it could relatively easily also apply to the Arctic because general principles, such as decreasing duration and extent of sea-ice cover, with major impact on primary production and higher trophic levels, as well as the direct effects of oceanic warming, are similar. Due to the spatially explicit nature of this concept, the principle difference between both polar regions in the potential for range shifts along latitudinal gradients can also be easily considered.

These are good reasons to bring skilful modellers together with specialists providing all relevant biological and environmental data. While accepting that, in their initial phase, the predictive power of such models is not high, if seriously developed they will contribute to a considerably improved understanding of complex systems, in our case of Antarctic ecosystems under climate change stress, and to increasing robustness. The outcomes of the approach described here will also inform other models focusing on possible biosphere–cryosphere–atmosphere–hydrosphere feedback effects and, thus, contribute to improving and extending predictions based on future IPCC scenarios.

Acknowledgements

This paper is a contribution to the project Antarctic Species Flocks of the French National Research Agency and to the project Biodiversity of Antarctic Amphipod Crustaceans II of the Belgian Policy Science Office. This paper is a major output of SCAR’s Action Group on Prediction of Changes in the Physical and Biological Environments of the Antarctic.

References

- Adams B., Bardgett R.D., Ayres E., Wall D.H., Aislabie J., Bamforth S., Bargagli R., Cary C., Cavacini P., Connell L., Convey P., Fell J., Frati E., Hogg I., Newsham N., O’Donnell A., Russell N., Seppelt R. & Stevens M.I. 2006. Diversity and distribution of Victoria Land biota. *Soil Biology and Biochemistry* 38, 3003–3018.
- Adhikari B.N., Wall D.H. & Adams B.J. 2009. Desiccation survival in an Antarctic nematode: molecular analysis using expressed sequenced tags. *Bmc Genomics* 10, 18.
- Adhikari B.N., Wall D.H. & Adams B.J. 2010. Effect of slow desiccation and freezing on gene transcription and stress survival of an Antarctic nematode. *Journal of Experimental Biology* 213, 1803–1812.

- Agardy M.T. 1994. Advances in marine conservation: the role of marine protected areas. *Trends in Ecology and Evolution* 9, 267–270.
- Anderson B., Akçakaya H., Araújo M., Fordham D., Martinez-Meyer E., Thuiller W. & Brook B. 2009. Dynamics of range margins for metapopulations under climate change. *Proceedings of the Royal Society of London B* 276, 1415–1420.
- Anderson J.B., Shipp S.S., Lowe A.L., Wellner J.S. & Mosola A.B. 2002. The Antarctic Ice Sheet during the Last Glacial Maximum and its subsequent retreat history: a review. *Quaternary Science Reviews* 21, 49–70.
- Andrássy I. 1998. Nematodes in the sixth continent. *Journal of Nematode Morphology and Systematics* 1, 107–187.
- Angilletta M.J. 2009. *Thermal adaptation: a theoretical and empirical synthesis*. Oxford: Oxford University Press.
- Antonov J.I., Seidov D., Boyer T.P., Locarnini, R.A., Mishonov A.V., Garcia H.E., Baranova O.K., Zweng M.M. & Johnson D.R. 2010. *World Ocean atlas 2009. Vol. 2. Salinity*. Washington, DC: US Government Printing Office.
- Araújo M.B., Pearson R.G., Thuillers W. & Erhard M. 2005. Validation of species-climate impact models under climate change. *Global Change Biology* 11, 1504–1513.
- Arrigo K.R. & Thomas D.N. 2004. Large-scale importance of sea ice biology in the Southern Ocean. *Antarctic Science* 16, 471–486.
- Arrigo K.R., van Dijken G.L., Ainley D.G., Fahnestock M.A. & Markus T. 2002. Ecological impact of a large Antarctic iceberg. *Geophysical Research Letters* 29, article no. 1104, doi 10.1029/2001GL014160.
- Arrigo K.R., van Dijken G.L. & Bushinsky S. 2008. Primary production in the Southern Ocean, 1997–2006. *Journal of Geophysical Research—Oceans* 113, C08004, doi 10.1029/2007JC004551.
- Arrigo K.R., van Dijken G.L. & Long M. 2008. Coastal Southern Ocean: a strong anthropogenic CO₂ sink. *Geophysical Research Letters* 35, L21602, doi 10.29/2008GL035624.
- Atkinson A., Siegel V., Pakhomov E. & Rothery P. 2004. Long-term decline in krill stock and increase in salps within the Southern Ocean. *Nature* 432, 100–103.
- Baird N.A., Etter P.D., Atwood T.S., Currey M.C., Shiver A.L., Lewis Z.A., Selker E.U., Cresko W.A. & Johnson E.A. 2008. Rapid SNP discovery and genetic mapping using sequenced RAD markers. *PLoS One* 3, e3376, doi 10.1371/journal.pone.0003376.
- Barbraud C. & Weimerskirch H. 2001. Emperor penguins and climate change. *Nature* 411, 183–185.
- Barnes D.K.A. & Clarke A. 2011. Antarctic marine biology. *Current Biology* 21, R451–457, doi 10.1016/j.cub.2011.04.012.
- Barnes D.K.A. & Peck L.S. 2008. Vulnerability of Antarctic shelf biodiversity to predicted regional warming. *Climate Research* 37, 149–163.
- Barnes D.K.A. & Conlan K.E. 2007. Disturbance, colonization and development of Antarctic benthic communities. *Philosophical Transactions of the Royal Society B* 362, 11–38.
- Barrett J.E., Virginia R.A., Wall D.H., Doran P.T., Fountain A.G., Welch K.A. & Lyons W.B. 2008. Persistent effects of a discrete warming event on a polar desert ecosystem. *Global Change Biology* 14, 2249–2261.
- Bilyk K.T. & DeVries A.L. 2010. Heat tolerance and its plasticity in Antarctic fishes. *Comparative Biochemistry and Physiology Part A* 158, 382–390.
- Block W. 1990. Cold tolerance of insects and other arthropods. *Philosophical Transactions of the Royal Society B* 326, 613–633.
- Block W. & Convey P. 1995. The biology, life cycle and ecophysiology of the Antarctic mite *Alaskozetes antarcticus* (Michael). *Journal of Zoology* 236, 431–449.
- Bokhorst S., Huiskes A., Convey P., Sinclair B.J., Lebouvier M., van de Vijver B. & Wall D.H. 2011. Microclimate impacts of passive warming methods in Antarctica: implications for climate change studies. *Polar Biology* 34, 1421–1435.
- Bowden D.A., Clarke A. & Peck L.S. 2009. Seasonal variation in the diversity and abundance of pelagic larvae of Antarctic benthic marine invertebrates. *Marine Biology* 156, 2033–2047.
- Bracegirdle T.J., Connolly W.M. & Turner J. 2008. Antarctic climate change over the twenty first century. *Journal of Geophysical Research—Atmospheres* 113, D03103, doi 10.1029/2007JD008933.
- Brandt A. & Gutt J. 2011. Biodiversity of a unique environment: the Southern Ocean benthos shaped and threatened by climate change. In F.E. Zachos & J.C. Habel (eds.): *Biodiversity hotspots: distribution and protection of conservation priority areas*. Pp. 503–521. Heidelberg: Springer.
- Brierley A.S. & Thomas D.N. 2002. On the ecology of Southern Ocean pack ice. *Advances in Marine Biology* 43, 171–278.
- Brown K.M., Fraser K.P.P., Barnes D.K.A. & Peck L.S. 2004. Links between the structure of an Antarctic shallow-water community and ice-scour frequency. *Oecologia* 141, 121–129.
- Burns G., Thorne M.A.S., Hillyard G., Clark M.S., Convey P. & Worland M.R. 2010. Gene expression associated with changes in cold tolerance levels of the Antarctic springtail. *Cryptopygus antarcticus*. *Insect Molecular Biology* 19, 113–120.
- Burrough P.A. & McDonnell R.A. 1998. *Principles of geographical information systems*. New York: Oxford University Press.
- Butchart S.H.M., Walpole M., Collen B., van Strien A., Scharlemann J.P.W., Almond R.E.A., Baillie J.E.M., Bomhard B., Brown C., Bruno J., Carpenter K.E., Carr G.M., Chanson J., Chenery A.M., Csirke J., Davidson N.C., Dentener F., Foster M., Galli A., Galloway J.N., Genovesi P., Gregory R.D., Hockings M., Kapos V., Lamarque J.-F., Leverington F., Loh J., McGeoch M.A., McRae L., Minasyan A., Hernández Morcillo M., Oldfield T.E.E., Pauly D., Quader S., Revenga C., Sauer J.R., Skolnik B., Spear D., Stanwell-Smith D., Stuart S.N., Symes A., Tierney M., Tyrrell T.D., Vié J.-C. & Watson R. 2010. Global biodiversity: indicators of recent declines. *Science* 328, 1164–1168.
- Chapelle G. & Peck L.S. 1999. Polar gigantism dictated by oxygen availability. *Nature* 399, 114–115.
- Chen Z.Z., Cheng C.H.C., Zhang J.F., Cao L.X., Chen L., Zhou L.H., Jin Y.D., Ye H., Deng C., Dai Z.H., Xu Q.H., Hu P., Sun S.H., Shen Y. & Chen L.B. 2008. Transcriptomic and genomic evolution under constant cold in Antarctic

- notothenioid fish. *Proceedings of the National Academy of Sciences of the United States of America* 105, 12944–12949.
- Cheng C.H., di Prisco G. & Verde C. 2009. Cold-adapted Antarctic fish: the discovery of neuroglobin in the dominant suborder Notothenioidei. *Gene* 433, 100–101.
- Chesson P.L. & Warner R.R. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117, 923–943.
- Cheung W.W.L., Close C., Kearney K., Lam V., Sarmiento J., Watson R. & Pauly D. 2009. Projections of global marine biodiversity impacts under climate change scenarios. *Fish and Fisheries* 10, 235–251.
- Cheung W.W.L., Dunne J., Sarmiento J.L. & Pauly D. 2011. Integrating ecophysiology and plankton dynamics into projected changes in maximum fisheries catch potential under climate change in the Northeast Atlantic. *ICES Journal of Marine Science* 68, 1008–1018.
- Cheung W.W.L., Lam V. & Pauly D. 2008. *Modelling present and climate-shifted distributions of marine fishes and invertebrates. Fisheries Centre Research Reports* 16(3). Vancouver: The Fisheries Centre, University of British Columbia.
- Chown S.L. & Convey P. 2007. Spatial and temporal variability across life's hierarchies in the terrestrial Antarctic. *Philosophical Transactions of the Royal Society B* 362, 2307–2331.
- Chown S.L., Hoffmann A.A., Kristensen T.N., Angilletta M.J. Jr., Stenseth N.C. & Pertoldi C. 2010. Adapting to climate change: a perspective from evolutionary physiology. *Climate Research* 43, 3–15.
- Clark M.S., Fraser K.P.P. & Peck L.S. 2008. Lack of an HSP70 heat shock response in two Antarctic marine invertebrates. *Polar Biology* 31, 1059–1065.
- Clark M.S. & Peck L.S. 2009. HSP70 heat shock proteins and environmental stress in Antarctic marine organisms: a mini-review. *Marine Genomics* 2, 11–18.
- Clark M.S., Thorne M.A.S., Toullec J.Y., Meng Y., Guan L.L., Peck L.S. & Moore S. 2011. Antarctic krill 454 pyrosequencing reveals chaperone and stress transcriptome. *Plos One* 6, e15919, doi 10.1371/journal.pone.0015919.
- Clark M.S., Thorne M.A.S., Vieira F.A., Cardoso J.C., Power D.M. & Peck L.S. 2010. Insights into shell deposition in the Antarctic bivalve *Laternula elliptica*: gene discovery in the mantle transcriptome using 454 pyrosequencing. *Bmc Genomics* 11, 14.
- Clarke A., Griffiths H.J., Barnes D.K.A., Meredith M.P. & Grant S.M. 2009. Spatial variation in seabed temperatures in the Southern Ocean: implications for benthic ecology and biogeography. *Journal of Geophysical Research—Biogeosciences* 114, G03003, doi 10.1029/2008JG000886.
- Clarke A., Griffiths H.I., Linse K., Barnes D.K.A. & Crame A. 2007. How well do we know the Antarctic marine fauna? A preliminary study of macroecological and biogeographical patterns in Southern Ocean gastropod and bivalve molluscs. *Diversity and Distribution* 13, 620–632.
- Clarke A. & Johnston N.M. 2003. Antarctic marine benthic diversity. *Oceanography and Marine Biology: an Annual Review* 41, 47–114.
- Connell J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Convey P. 2006. Antarctic climate change and its influences on terrestrial ecosystems. In D.M. Bergstrom et al. (eds.): *Trends in Antarctic terrestrial and limnetic ecosystems: Antarctica as a global indicator*. Dordrecht: Springer.
- Convey P. 2010. Terrestrial biodiversity in Antarctica—recent advances and future challenges. *Polar Science* 4, 135–147.
- Convey P. 2011. Antarctic terrestrial biodiversity in a changing world. *Polar Biology* 34, 1629–1641.
- Convey P., Bindschadler R.A., di Prisco G., Fahrbach E., Gutt J., Hodgson D.A., Mayewski P., Summerhayes C.P. & Turner J. 2009. Antarctic climate change and the environment. *Antarctic Science* 21, 541–563.
- Convey P., Block W. & Peat H.J. 2003. Soil arthropods as indicators of water stress in Antarctic terrestrial habitats? *Global Change Biology* 9, 1718–1730.
- Convey P., Gibson J., Hillenbrand C.-D., Hodgson D.A., Pugh P.J.A., Smellie J.L. & Stevens M.I. 2008. Antarctic terrestrial life—challenging the history of the frozen continent? *Biological Reviews* 83, 103–117.
- Convey P. & McInnes S.J. 2005. Exceptional tardigrade-dominated ecosystems in Ellsworth Land, Antarctica. *Ecology* 86, 519–527.
- Convey P., Pugh P.J.A., Jackson C., Murray A.W., Ruhland C.T., Xiong F.S. & Day T.A. 2002. Response of Antarctic terrestrial arthropods to long-term climate manipulations. *Ecology* 83, 3130–3140.
- Convey P. & Smith R.I.L. 2006. Responses of terrestrial Antarctic ecosystems to climate change. *Plant Ecology* 182, 1–10.
- Convey P. & Wynn-Williams D.D. 2002. Antarctic soil nematode response to artificial climate amelioration. *European Journal of Soil Biology* 38, 255–259.
- Cummings V.J., Thrush S.F., Norkko A., Andrew N.L., Hewitt J.E., Funnell G.A. & Schwarz A.-M. 2006. Accounting for local scale variability in benthos: implications for future assessments of latitudinal trends in the coastal Ross Sea. *Antarctic Science* 18, 633–644.
- David B., Choné T., Festeau A., Mooi R. & De Ridder C. 2005. Biodiversity of Antarctic echinoids: a comprehensive and interactive database. *Scientia Marina* 69, 201–203.
- Davies K.F., Melbourne B.A., McClenahan J.L. & Tuff T. 2011. Statistical models for monitoring and predicting effects of climate change and invasion on the free-living insects and a spider from sub-Antarctic Heard Island. *Polar Biology* 34, 119–125.
- Day T.A., Ruhland C.T., Grobe C.W. & Xiong F. 1999. Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. *Oecologia* 119, 24–35.
- De Broyer C. & Danis B. 2011. How many species in the Southern Ocean? Towards a dynamic inventory of the Antarctic marine biodiversity. *Deep-Sea Research Part II* 58, 5–17.
- Denlinger D.L. & Lee R.E. 2010. *Low temperature biology of insects*. Cambridge: Cambridge University Press.

- DeVries A.L. 1988. The role of antifreeze glycopeptides and peptides in the freezing avoidance of Antarctic fishes. *Comparative Biochemistry and Physiology Part B* 90, 611–621.
- di Prisco G., Cocca E., Parker S.K. & Detrich III H.W. 2002. Tracking the evolutionary loss of hemoglobin expression by the white-blooded Antarctic icefishes. *Gene* 295, 185–191.
- di Prisco G. & Verde C. 2006. Predicting the impacts of climate change on the evolutionary adaptations of polar fish. *Reviews in Environmental Science and Biotechnology* 5, 309–321.
- Doran P.T., Prisco J.C., Lyons W.B., Walsh J.E., Fountain A.G., McKnight D.M., Moorhead D.L., Virginia R.A., Wall D.H., Clow G.D., Fritsen C.H., McKay C.P. & Parsons A.N. 2002. Antarctic climate cooling and terrestrial ecosystem response. *Nature* 415, 517–520.
- Drinkwater K. 2009. Comparison of the response of Atlantic cod (*Gadus morhua*) in the high-latitude regions of the North Atlantic during the warm periods of the 1920s–1960s and the 1990s–2000s. *Deep-Sea Research Part II* 56, 2087–2096.
- Ducklow H.W., Baker K., Martinson D.G., Quetin L.B., Ross R.M., Smith R.C., Stammerjohan S.E., Vernet M. & Fraser W. 2007. Marine pelagic ecosystems: the West Antarctic Peninsula. *Philosophical Transactions of the Royal Society B* 362, 67–94.
- Dudik M., Phillips S.J. & Schapire R.E. 2004. Performance guarantees for regularized maximum entropy density estimation. In J. Shawe-Taylor & Y. Singer (eds.): *Learning theory. 17th Annual Conference on Learning Theory COLT 2004. Banff, Canada, July 2004*. Pp. 655–662. New York: Springer.
- Ehrlich P.R. 1992. Population biology of checkerspot butterflies and the preservation of global biodiversity. *Oikos* 63, 6–12.
- Elith J. & Leathwick J.R. 2009. Species distribution models: ecological explanation and prediction across space and time. *Annual Review of Ecology, Evolution and Systematics* 40, 677–697.
- Elnitsky M.A., Benoit J.B., Denlinger D.L. & Lee R.E. 2008. Desiccation tolerance and drought acclimation in the Antarctic collembolan *Cryptopygus antarcticus*. *Journal of Insect Physiology* 54, 1432–1439.
- Fowbert J.A. & Smith R.I.L. 1994. Rapid population increases in native vascular plants in the Argentine Islands, Antarctic Peninsula. *Arctic and Alpine Research* 26, 290–296.
- Franklin C.E. & Seebacher F. 2009. Adapting to climate change. *Science* 323, 876.
- Freckman D.W. & Virginia R.A. 1997. Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. *Ecology* 78, 363–369.
- Frenot Y., Chown S.L., Whinam J., Selkirk P., Convey P., Skotnicki M. & Bergstrom D. 2005. Biological invasions in the Antarctic: extent, impacts and implications. *Biological Reviews* 80, 45–72.
- Fretwell P.T., Convey P., Fleming A.F., Peat H.J. & Hughes K.A. 2011. Detecting and mapping vegetation distribution on the Antarctic Peninsula from remote sensing data. *Polar Biology* 34, 273–281.
- Gaston K.J., Chown S.L., Calosi P., Bernardo J., Bilton D.T., Clarke A., Clusella-Trullas S., Ghalambor C.K., Konarzewski M., Peck L.S., Portner W.P., Pörtner H.-O., Rezende E.L., Schulte P.M., Spicer J.I., Stillmann J.H., Terblanche J.S. & van Keulen M. 2009. Macrophysiology: a conceptual reunification. *American Naturalist* 174, 595–612.
- Goss-Custard J.D., Burton N.H.K., Clark N.A., Ferns P.N., McGrorty S., Reading C., Rehfisch M.M., Stillman R.A., Townend I., West A.D. & Worrall D.H. 2006. Test of a behavior-based individual-based model: response of shore-bird mortality to habitat loss. *Ecological Applications* 16, 2215–2222.
- Grange L., Tyler P.A., Peck L.S. & Cornelius N. 2004. Long-term interannual cycles of the gametogenic ecology of the Antarctic brittle star *Ophionotus victoriae*. *Marine Ecology Progress Series* 278, 141–155.
- Grant S., Constable A., Raymond B. & Doust S. 2006. *Bioregionalisation of the Southern Ocean: report of experts workshop, Hobart, September 2006*. WWF-Australia, Antarctic Climate and Ecosystems Cooperative Research Centre. Sydney: WWF-Australia.
- Gremmen N.J.M. & Smith V.R. 2008. Terrestrial vegetation and dynamics. In S.L. Chown & P.W. Froneman (eds.): *The Prince Edward Islands. Land-sea interactions in a changing ecosystem*. Stellenbosch: SUN Press.
- Grimm V. & Railsback S.F. 2005. *Individual-based modeling and ecology*. Princeton: Princeton University Press.
- Grimm V., Revilla E., Berger U., Jeltsch F., Mooij W.M., Railsback S.F., Thulke H.-H., Weiner J., Wiegand T. & DeAngelis D.L. 2005. Pattern-oriented modeling of agent-based complex systems: lessons from ecology. *Science* 310, 987–991.
- Guisan A. & Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. *Ecology Letters* 8, 993–1009.
- Gutt J. 2000. Some “driving forces” structuring communities of the sublittoral Antarctic macrobenthos. *Antarctic Science* 12, 297–313.
- Gutt J. 2006. Coexistence of macro-zoobenthic species on the Antarctic shelf: An attempt to link ecological theory and results. *Deep-Sea Research Part II* 53, 1009–1028.
- Gutt J. 2007. Antarctic macro-zoobenthic communities: a review and a classification. *Antarctic Science* 19, 165–182.
- Gutt J., Barratt I., Domack E., d’Udekem d’Acoz C., Dimmler W., Grémare A., Heilmayer O., Isla E., Janussen D., Jorgensen E., Kock K.-H., Lehnert L.S., López-González P., Langner S., Linse K., Manjón-Cabeza M.E., Meißner M., Montiel A., Raes M., Robert H., Rose A., Sañé Schepisi E., Saucède T., Scheidat M., Schenke H.-W., Seiler J. & Smith C. 2011. Biodiversity change after climate-induced ice-shelf collapse in the Antarctic. *Deep-Sea Research Part II* 58, 74–83.
- Gutt J., Hosie G. & Stoddart M. 2010. Marine life in the Antarctic. In A.D. McIntyre (ed.): *Life in the world’s oceans: diversity, distribution, and abundance*. Pp. 203–220. Oxford: Wiley-Blackwell.

- Gutt J. & Piepenburg D. 2003. Scale-dependent impact on diversity of Antarctic benthos caused by grounding of icebergs. *Marine Ecology Progress Series* 253, 77–83.
- Gutt J. & Starman A. 2001. Quantification of iceberg impact and benthic recolonisation patterns in the Weddell Sea (Antarctica). *Polar Biology* 24, 615–619.
- Helmuth B. 2009. From cells to coastlines: how can we use physiology to forecast the impacts of climate change? *Journal of Experimental Biology* 212, 753–760.
- Hennion F., Huiskes A., Robinson S. & Convey P. 2006. Physiological traits of organisms in a changing environment. In D.M. Bergstrom et al. (eds.): *Trends in Antarctic terrestrial and limnetic ecosystems: Antarctica as a global indicator*. Pp. 129–159. Dordrecht: Springer.
- Hodgson D., Convey P., Verleyen E., Vyverman W., McInnes S., Sands S., Fernández-Carazo R. & Wilmotte A. 2010. Observations on the limnology and biology of the Dufek Massif, Transantarctic Mountains 82° South. *Polar Science* 4, 197–214.
- Hofmann E.E. & Murphy E. 2004. Advection, krill, and Antarctic marine ecosystems. *Antarctic Science* 16, 487–499.
- Hoffman J.I., Peck L.S., Hillyard G., Zieritz A. & Clark M.S. 2010. No evidence for genetic differentiation between Antarctic limpet *Nacella concinna* morphotypes. *Marine Biology* 157, 765–778.
- Hofmann G.E., Buckley B.A., Airaksinen S., Keen J.E. & Somero G.N. 2000. Heat-shock protein expression is absent in the Antarctic fish *Trematomus bernacchii* (family Nototheniidae). *Journal of Experimental Biology* 203, 2331–2339.
- Hughes K.A. & Convey P. 2010. The protection of Antarctic terrestrial ecosystems from inter and intra-continental transfer of non-indigenous species by human activities: a review of current systems and practices. *Global Environmental Change—Human and Policy Dimensions* 20, 96–112.
- Jeltsch F., Moloney K.A., Schurr F.M., Köchy M. & Schwager M. 2008. The state of plant population modelling in light of environmental change. *Perspectives in Plant Ecology, Evolution and Systematics* 9, 171–189.
- Jenouvrier S., Caswell H., Barbraud C., Holland M., Stroeve J. & Weimerskirch H. 2009. Demographic models and IPCC climate projects predict the decline of an emperor penguin population. *Proceedings of the National Academy of Sciences*, 44–1847.
- Johnston I.A. 2003. Muscle metabolism and growth in Antarctic fishes (suborder Notothenioidei): evolution in a cold environment. *Comparative Biochemistry and Physiology B* 136, 701–713.
- Johst K., Gutt J., Wissel C. & Grimm V. 2006. Diversity and disturbances in the Antarctic megabenthos: feasible versus theoretical disturbance ranges. *Ecosystems* 9, 1145–1155.
- Karsten U., Wulff A., Roleda M.Y., Müller R., Steinhoff F.S., Fredersdorf J. & Wiencke C. 2009. Physiological response of polar benthic algae to ultraviolet radiation. *Botanica Marina* 52, 639–654.
- Kearney M. & Porter W. 2009. Mechanistic niche modelling: combining physiological and spatial data to predict species' ranges. *Ecology Letters* 12, 334–350.
- Keith D.A., Akçakaya H.R., Thuiller W., Midgley G.F., Pearson R.G., Phillips S.J., Regan H.M., Araújo M.B. & Rebelo T.G. 2008. Predicting extinction risks under climate change: coupling stochastic population models with dynamic bioclimatic habitat models. *Biology Letters* 4, 560–563.
- Kennedy A.D. 1995. Simulated climate change: are passive greenhouses a valid microcosm for testing the biological effects of environmental perturbations? *Global Change Biology* 1, 29–42.
- Kock K.-H. 1992. *Antarctic fish and fisheries*. Cambridge: Cambridge University Press.
- Koubbi P., Moteki M., Duhamel G., Goarant A., Hulley P.-A., O'Driscoll R., Ishimaru T., Pruvost P., Tavernier E. & Hosie G. 2010. Ecoregionalization in myctophid fish in the Indian sector of the Southern Ocean: results from generalized dissimilarity models. *Deep-Sea Research Part II* 58, 170–180.
- Lee J.E. & Chown S.L. 2009. Breaching the dispersal barrier to invasion: quantification and management. *Ecological Applications* 19, 1944–1959.
- Lee J.E., Janion C., Marais E., Jansen van Vuuren B. & Chown S.L. 2009. Physiological tolerances account for range limits and abundance structure in an invasive slug. *Proceedings of the Royal Society of London B* 276, 1459–1468.
- Lee H.J., Vanhove S., Peck L.S. & Vincx M. 2001. Recolonisation of meiofauna after catastrophic iceberg scouring in shallow Antarctic sediments. *Polar Biology* 24, 918–925.
- Le Quéré C., Rödenbeck C., Buitenhuis E.T., Conway T.J., Langenfelds R., Gomez A., Labuschagne C., Ramonet M., Nakazawa T., Metzl N., Gillett N. & Heimann M. 2007. Saturation of the Southern Ocean CO₂ sink due to recent climate change. *Science* 316, 1735–1738.
- Longton R.E. 1988. *The biology of polar bryophytes and lichens*. Cambridge: Cambridge University Press.
- Lopez-Martinez G., Benoit J.B., Rinehart J.P., Elnitsky M.A., Lee R.E. & Denlinger D.L. 2009. Dehydration, rehydration, and overhydration alter patterns of gene expression in the Antarctic midge, *Belgica antarctica*. *Journal of Comparative Physiology B* 179, 481–491.
- Marshall G.J., Orr A., van Lipzig N.P.M. & King J.C. 2006. The impact of a changing Southern Hemisphere Annular Mode on Antarctic Peninsula summer temperatures. *Journal of Climate* 19, 5388–5404.
- McClintock J., Ducklow H. & Fraser W. 2008. Ecological responses to climate change on the Antarctic Peninsula. *American Scientist* 96, 302–310.
- McClintock J.B., Silva-Rodriguez P. & Fraser W.R. 2010. Southerly breeding in gentoo penguins for the eastern Antarctic Peninsula: further evidence for unprecedented climate-change. *Antarctic Science* 22, 285–286.
- McCoy F.W. 1991. Southern Ocean sediments: circum-Antarctic to 30°S. In D.E. Hayes (ed.): *Marine geological and geophysical atlas of the circum-Antarctic to 30°S*. Pp. 37–46. Washington, DC: American Geophysical Union.
- McGaughran A., Convey P., Redding G.P. & Stevens M.I. 2010a. Temporal and spatial metabolic rate variation in the Antarctic springtail *Gomphiocephalus hodgsoni*. *Journal of Insect Physiology* 56, 57–64.

- McGaughran A., Toricelli G., Caramelli A., Frati F., Stevens M.I., Convey P. & Hogg I.D. 2010. Contrasting phylogeographic patterns for springtails reflect different evolutionary histories between the Antarctic Peninsula and continental Antarctica. *Journal of Biogeography* 37, 103–119.
- Michaud M.R., Benoit J.B., Lopez-Martinez G., Elnitsky M.A., Lee R.E. & Denlinger D.L. 2008. Metabolomics reveals unique and shared metabolic changes in response to heat shock, freezing and desiccation in the Antarctic midge, Belgica Antarctica. *Journal of Insect Physiology* 54, 645–655.
- Montes-Hugo M., Doney S.C., Ducklow H.W., Fraser W., Martinson D., Stammerjohan S.E. & Schofield O. 2009. Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science* 323, 1470–1473.
- Morgan F., Barker G., Briggs C., Price R. & Keys H. 2007. *Environmental domains of Antarctica. Version 2.0. Final report. Landcare Research Contract Report LC0708/055*. Auckland: Landcare Research, New Zealand Ltd.
- Morley S.A., Griffiths H.J., Barnes D.K.A. & Peck L.S. 2010. South Georgia: a key location for linking physiological capacity to distributional changes in response to climate change. *Antarctic Science* 22, 774–781.
- Morley S.A., Hirse T., Pörtner H.-O. & Peck L.S. 2009. Geographical variation in thermal tolerance within Southern Ocean marine ectotherms. *Comparative Biochemistry and Physiology A* 153, 154–161.
- Morley S.A., Tan K.S., Day R.W., Martin S.M., Pörtner H.O. & Peck L.S. 2009. Thermal dependency of burrowing in three species within the bivalve genus *Laternula*: a latitudinal comparison. *Marine Biology* 156, 1977–1984.
- Mortimer E., Jansen van Vuuren B., Lee J.E., Marshall D.J., Convey P., Daniels S.R. & Chown S.L. 2011. Mite dispersal among the Southern Ocean Islands and Antarctica before the last glacial maximum. *Proceedings of the Royal Society of London B* 278, 1247–1255.
- Nielsen U.N., Wall D.H., Adams B.J. & Virginia R.A. 2011. Antarctic nematode communities: observed and predicted responses to climate change. *Polar Biology*, 1701–1711.
- Orr J.C., Fabry V.J., Aumont O., Bopp L., Doney S.C., Feely R.A., Gnanadesikan A., Gruber N., Ishida A., Joos F., Key R.M., Lindsay K., Maier-Reimer E., Matear R., Monfray P., Mouchet A., Najjar R.G., Plattner G.K., Rodgers K.B., Sabine C.L., Sarmiento J.L., Schlitzer R., Slater R.D., Totterdell I.J., Weirig M.F., Yamanaka Y. & Yool A. 2005. Anthropogenic ocean acidification over the twenty-first century and its impact on calcifying organisms. *Nature* 437, 681–686.
- Parnikoza I., Convey P., Dykyy I., Trokhymets V., Milinevsky G., Tyschenko O., Inozemetsva D. & Kozeretka I. 2009. Current status of the Antarctic herb tundra formation in the Central Argentine Islands. *Global Change Biology* 15, 1685–1693.
- Patarnello T., Verde C., di Prisco G., Bargelloni L. & Zane L. 2011. How will fish that evolved at constant sub-zero temperatures cope with global warming? Notothenioids as a case study. *BioEssays* 33, 260–268.
- Pearman P.B., Randin C.F., Broennimann O., Vittoz P., Van der Knaap W.O., Engler R., Lay G.L., Zimmermann N.E. & Guisan A. 2008. Prediction of plant species distributions across six millennia. *Ecology Letters* 11, 357–369.
- Peck L.S., Brockington S., Vanhove S. & Beghyn M. 1999. Community recovery following catastrophic iceberg impacts in a soft-sediment shallow-water site at Signy Island, Antarctica. *Marine Ecology Progress Series* 186, 1–8.
- Peck L.S., Clark M.S., Clarke A., Cockell C.S., Convey P., Detrich H.W.III, Fraser K.P.P., Johnston I.A., Methe B.A., Murray A.E., Römisch K. & Rogers A.D. 2005. Prospects for genomic research in Antarctica. *Polar Biology* 28, 351–365.
- Peck L.S., Convey P. & Barnes D.K.A. 2006. Environmental constraints on life histories in Antarctic ecosystems: tempos, timings and predictability. *Biological Reviews* 81, 75–109.
- Peck L.S., Webb K.E., Clark M.S., Miller A. & Hill T. 2008. Temperature limits to activity, feeding and metabolism in the Antarctic starfish *Odontaster validus*. *Marine Ecology Progress Series* 381, 181–189.
- Peck L.S., Barnes D.K.A., Cook J., Fleming A.H. & Clarke A. 2009. Negative feedback in the cold: ice retreat produces new carbon sinks in Antarctica. *Global Change Biology* 16, 2614–2623.
- Peck L.S., Barnes D.K.A., Cook A.J., Fleming A.H. & Clarke A. 2010. Negative feedback in the cold: ice retreat produces new carbon sinks in Antarctica. *Global Change Biology* 16, 2614–2623.
- Peck L.S., Clark M.S., Morley S.A., Massey A. & Rossetti H. 2009. Animal temperature limits and ecological relevance: effects of size, activity and rates of change. *Functional Ecology* 23, 248–256.
- Pereira H.M., Leadley P.W., Proença V., Alkemade R., Scharlemann J.P.W., Fernandez-Manjarrés J.F., Araújo M.B., Balvanera P., Biggs R., Cheung W.W.L., Chini L., Cooper H.D., Gilman E.L., Guénette S., Hurtt G.C., Huntington H.P., Mace G.M., Oberdorff T., Revenga C., Rodrigues P., Scholes R.J., Sumaila U.R. & Walpole M. 2010. Scenarios for global biodiversity in the 21st Century. *Science* 330, 1496–1501.
- Phillips S.J., Anderson R.P. & Schapire R.E. 2006. Maximum entropy modeling of species geographic distributions. *Ecological Modelling* 190, 231–259.
- Pinkerton M.H., Smith A.N.H., Raymond B., Hosie G.W., Sharp B., Leathwick J.R. & Bradford-Grieve J.M. 2010. Spatial and seasonal distribution of adult *Oithona similis* in the Southern Ocean: predictions using boosted regression trees. *Deep-Sea Research Part I* 57, 469–485.
- Pörtner H.-O. & Knust R. 2007. Climate change affects marine fishes through the oxygen limitation of thermal tolerance. *Science* 315, 95–97.
- Potthoff M. 2006. *The role of disturbance for the Antarctic benthos—a simulation study*. PhD thesis, Carl von Ossietzky Universität, Oldenburg.
- Potthoff M., Johst K. & Gutt J. 2006. How to survive as a pioneer species in the Antarctic benthos: minimum dispersal distance as a function of lifetime and disturbance. *Polar Biology* 29, 543–551.
- Potthoff M., Johst K., Gutt J. & Wissel C. 2006. Clumped dispersal and species coexistence. *Ecological Modelling* 198, 247–254.

- Quayle W.C., Convey P., Peck L.S., Ellis-Evans J.C., Butler H.G. & Peat H.J. 2003. Ecological responses of maritime Antarctic lakes to regional climate change. In E. Domack et al. (eds.): *Antarctic Peninsula climate variability: historical and palaeoenvironmental perspectives*. Pp. 341–347. Washington, DC: American Geophysical Union.
- Quayle W.C., Peck L.S., Peat H., Ellis-Evans J.C. & Harrigan P.R. 2002. Extreme responses to climate change in Antarctic lakes. *Science* 295, 645.
- Railsback S.F. & Harvey B.C. 2002. Analysis of habitat-selection rules using an individual-based model. *Ecology* 83, 1817–1830.
- Raymond B., McInnes J., Dambacher J.M., Way S. & Bergstrom D.M. 2011. Quantitative modelling of invasive species eradication on Subantarctic Macquarie Island. *Journal of Applied Ecology* 48, 181–191.
- Robinson L.M., Elith J., Hobday A.J., Pearson R.G., Kendall B.E., Possingham H.P. & Richardson A.J. 2011. Pushing the limits in marine species distribution modelling: lessons from the land present challenges and opportunities. *Global Ecology and Biogeography* 20, 789–802.
- Russo R., Giordano D., Riccio A., di Prisco G. & Verde C. 2010. Cold-adapted bacteria and the globin case study in the Antarctic bacterium *Pseudoalteromonas haloplanktis* TAC125. *Marine Genomics* 3, 125–131.
- Schenke H.W., Dijkstra S., Niederjasper H., Hinze H., Hoppmann B. & Schöne T. 1998. The new bathymetric charts of the Weddell Sea: AWI BCWS. In S.S. Jacobs & R.F. Weiss (eds.): *Ocean, ice, and atmosphere: interactions at the Antarctic continental margin*. Pp. 371–380. Washington, DC: American Geophysical Union.
- Schwarz J.N. & Schodlok M.P. 2009. Impact of drifting icebergs on surface phytoplankton biomass in the Southern Ocean: ocean colour remote sensing and in situ iceberg tracking. *Deep-Sea Research Part I* 56, 1727–1741.
- Silva T.A.M. & Grant R.B. 2005. Computer-based identification and tracking of Antarctic icebergs in SAR images. *Remote Sensing of Environment* 94, 287–297.
- Sinclair B.J., Terblanche J.S., Scott M.B., Blatch G.L., Klok C.J. & Chown S.L. 2006. Environmental physiology of three species of Collembola at Cape Hallett, North Victoria Land, Antarctica. *Journal of Insect Physiology* 52, 29–50.
- Smetacek V. & Nicol S. 2005. Polar ocean ecosystems in a changing world. *Nature* 437, 362–368.
- Smith R.I.L. 1972. *Vegetation of the South Orkney Islands with particular reference to Signy Island*. *British Antarctic Survey Scientific Reports* 68. London: British Antarctic Survey.
- Smith R.I.L. 2001. Plant colonization response to climate change in the Antarctic. *Folia Facultatis Scientiarum Naturalium Universitatis Masarykianae Brunensis, Geographia* 25, 19–33.
- Smith W.H.F. & Sandwell D.T. 1997. Global seafloor topography from satellite altimetry and ship depth soundings. *Science* 277, 1957–1962.
- Soberón J. 2007. Grinnellian and Eltonian niches and geographic distributions of species. *Ecology Letters* 10, 1115–1123.
- Sokolov S. & Rintoul S.R. 2009. Circumpolar structure and distribution of the Antarctic Circumpolar Current fronts: 1. Mean circumpolar paths. *Journal of Geophysical Research—Oceans* 114, C11018, doi 10.1029/2008JC005108.
- Solomon S., Qin D., Manning M., Chen Z., Marquis M., Averyt K.B., Tignor M. & Miller H.L. Jr. (eds.) 2007. *Climate change 2007. The physical science basis: contribution of Working Group I to the fourth assessment report of the Intergovernmental Panel on Climate Change*. Cambridge: Cambridge University Press.
- Somero G.N. 2010. The physiology of climate change: how potentials for acclimatization and genetic adaptation will determine 'winners' and 'losers'. *Journal of Experimental Biology* 213, 912–920.
- Somme L. 1995. *Invertebrates in hot and cold environments*. Berlin: Springer.
- Spreen G., Kaleschke L. & Heygster G. 2008. Sea ice remote sensing using AMSR-E 89 GHz channels. *Journal of Geophysical Research—Oceans* 113, C02S03, doi 10.1029/2005JC003384.
- Stock C.A., Alexander M.A., Bond N.A., Brander K., Cheung W.W.L., Curchitser E.N., Delworth T.L., Dunne J.P., Griffies S.M., Haltuch M.A., Hare J.A., Hollowed A.B., Lehodey P., Levin S.A., Link J.S., Rose K.A., Rykaczewski R.R., Sarmiento J.L., Stouffer R.J., Schwing F.B., Vecchi G.A. & Werner F.E. 2011. On the use of IPCC-class models to assess the impact of climate on living marine resources. *Progress in Oceanography* 8, 1–27.
- Swets J.A. 1988. Measuring the accuracy of diagnostic systems. *Science* 240, 1285–1293.
- Tarling G.A., Klevjer T., Fielding S., Watkins J., Atkinson A., Murphy E., Korb R., Whitehouse M. & Leaper R. 2009. Variability and predictability of Antarctic krill swarm structure. *Deep-Sea Research Part I* 56, 1994–2012.
- Teets N.M., Kawarasaki Y., Lee R.E. & Denlinger D.L. 2011. Survival and energetic costs of repeated cold exposure in the Antarctic midge, *Belgica antarctica*: a comparison between frozen and supercooled larvae. *Journal of Experimental Biology* 214, 806–814.
- Thorne M.A.S., Burns G., Fraser K.P.P., Hillyard G. & Clark M.S. 2010. Transcription profiling of acute temperature stress in the Antarctic plunderfish *Harpagifer antarcticus*. *Marine Genomics* 3, 35–44.
- Thuiller W., Albert C., Araújo M.B., Berry P.M., Cabeza M., Guisan A., Hickler T., Midgley G.F., Paterson J., Schurr F.M., Sykes M.T. & Zimmermann N.E. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* 9, 137–152.
- Tournadre J., Whitmer K. & Girard-Ardhuin F. 2008. Iceberg detection in open water by altimeter waveform analysis. *Journal of Geophysical Research—Oceans* 113, C08040, doi 10.1029/2007JC004587.
- Trathan P.N. & Reid K. 2009. Exploitation of the marine ecosystem in the sub-Antarctic: historical impacts and current consequences. *Papers and Proceedings of the Royal Society of Tasmania* 143, 9–14.

- Truebano M., Burns G., Thorne M.A.S., Hillyard G., Peck L.S., Skibinski D.O.F. & Clark M.S. 2010. Transcriptional response to heat stress in the Antarctic bivalve *Latemula elliptica*. *Journal of Experimental Marine Biology and Ecology* 391, 65–72.
- Turner J., Bindschadler R., Convey P., di Prisco G., Fahrbach E., Gutt J., Hodgson D., Mayewsky P. & Summerhayes C. 2009. *Antarctic climate change and the environment*. Cambridge: Scientific Committee on Antarctic Research and Scott Polar Research Institute.
- Usher M.B. & Booth R.G. 1984. Arthropod communities in a maritime Antarctic moss-turf habitat: three-dimensional distribution of mites and Collembola. *Journal of Animal Ecology* 53, 427–441.
- Verde C., Vergara A., Mazzarella L. & di Prisco G. 2008. The hemoglobins of fishes living at polar latitudes—current knowledge on structural adaptations in a changing environment. *Current Protein & Peptide Science* 9, 578–590.
- Vincent W.F. & Laybourn-Parry J. 2008. *Polar lakes and rivers—limnology of Arctic and Antarctic aquatic ecosystems*. Oxford: Oxford University Press.
- Vyverman W., Verleyen E., Wilmotte A., Hodgson D.A., Willem A., Peeters K., Van de Vijver B., De Wever A., Leliaert F. & Sabbe K. 2010. Evidence for widespread endemism among Antarctic micro-organisms. *Polar Science* 4, 103–113.
- Wharton D.A. 2003. The environmental physiology of Antarctic terrestrial nematodes: A review. *Journal of Comparative Physiology B* 173, 621–628.
- Willis S.G., Thomas C.D., Hill J.K., Collingham Y.C., Telfer M.G., Fox R. & Huntley B. 2009. Dynamic distribution modelling: predicting the present from the past. *Ecography* 32, 5–12.
- Worland M.R. 2010. Eretmoptera murphyi: pre-adapted to survive a colder climate. *Physiological Entomology* 35, 140–147.
- Zimmermann N.E., Yoccoz N.G., Thomas C., Edwards J., Meier E.S., Thuiller W., Guisan A., Schmatz D.R. & Pearman P.B. 2009. Climatic extremes improve predictions of spatial patterns of tree species. *Proceedings of the National Academy of Sciences of the United States of America* 106, 19723–19728.
- Zurell D., Berger U., Cabral J.S., Jeltsch F., Meynard C.N., Münkemüller T., Nehrbass N., Pagel J., Reineking B., Schröder B. & Grimm V. 2010. The virtual ecologist approach: simulating data and observers. *Oikos* 119, 622–635.
- Zurell D., Grimm V., Rossmann E., Zbinden N., Zimmermann N.E. & Schröder B. 2011. Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps. *Ecography*, doi 10.1111/j.1600-0587.201.07200.x
- Zurell D., Jeltsch F., Dormann C.F. & Schröder B. 2009. Static species distribution models in dynamically changing systems: how good can predictions really be? *Ecography* 32, 733–744.