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Review

# Trait-based approaches in rapidly changing ecosystems: A roadmap to the future polar oceans

Renate Degen[a,*], Magnus Aune[b], Bodil A. Bluhm[c], Camilla Cassidy[d], Monika Kędra[e], Casper Kraan[f,g], Leen Vandepitte[h], Maria Włodarska-Kowalczuk[e], Irina Zhulay[c], Paolo G. Albano[i], Julie Bremner[j,k], Jacqueline M. Grebmeier[l], Heike Link[m], Nathalie Morata[b], Marie C. Nordström[n], Mehdi Ghodrati Shojaei[o], Lauren Sutton[p], Martin Zuschin[i]

[a] Department of Limnology and Bio-Oceanography, University of Vienna, Vienna, Austria
[b] Akvaplan-niva, The Fram Centre, Hjalmar Johansens Gate 14, 9007 Tromsø, Norway
[c] Department of Arctic and Marine Biology, UiT – The Arctic University of Norway, Tromsø, Norway
[d] Ocean and Earth Science, National Oceanography Centre Southampton, University of Southampton, Southampton, UK
[e] Institute of Oceanology Polish Academy of Sciences Sopot, Poland
[f] Department of Functional Ecology, Alfred Wegener Institute Helmholtz Centre for Polar and Marine Research, Bremerhaven, Germany
[g] Helmholtz Institute for Functional Marine Biodiversity (HIFMB) at the University of Oldenburg, Oldenburg, Germany
[h] Flanders Marine Institute (VLIZ), Oostende, Belgium
[i] Department of Palaeontology, University of Vienna, Vienna, Austria
[j] Centre for Environment, Fisheries and Aquaculture Science (CEFAS), Lowestoft Laboratory, Lowestoft, United Kingdom
[k] Collaborative Centre for Sustainable Use of the Seas, University of East Anglia, Norwich, UK
[l] Chesapeake Biological Laboratory, University of Maryland Center for Environmental Science, Solomons, MD, USA
[m] Department Maritime Systems, University of Rostock, Rostock, Germany
[n] Environmental and Marine Biology, Åbo Akademi University, Turku, Finland
[o] Department of Marine Biology, Tarbiat Modares University, Noor, Mazandaran, Iran
[p] Institute of Marine Sciences, University of Alaska Fairbanks, USA

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## ABSTRACT

Polar marine regions are facing rapid changes induced by climate change, with consequences for local faunal populations, but also for overall ecosystem functioning, goods and services. Yet given the complexity of polar marine ecosystems, predicting the mode, direction and extent of these consequences remains challenging. Trait-based approaches are increasingly adopted as a tool by which to explore changes in functioning, but trait information is largely absent for the high latitudes. Some understanding of trait–function relationships can be gathered from studies at lower latitudes, but given the uniqueness of polar ecosystems it is questionable whether these relationships can be directly transferred. Here we discuss the challenges of using trait-based approaches in polar regions and present a roadmap of how to overcome them by following six interlinked steps: (1) forming an active, international research network, (2) standardizing terminology and methodology, (3) building and crosslinking trait databases, (4) conducting coordinated trait-function experiments, (5) implementing traits into models, and finally, (6) providing advice to management and stakeholders. The application of trait-based approaches in addition to traditional species-based methods will enable us to assess the effects of rapid ongoing changes on the functioning of marine polar ecosystems. Implementing our roadmap will make these approaches more easily accessible to a broad community of users and consequently aid understanding of the future polar oceans.

## 1. Introduction

Climate change is a serious threat to humanity, in particular the rapid changes observed in polar regions have global implications (Hassol, 2005; IPCC, 2014; Sunday et al., 2015). Although we have gained insights into how certain polar marine species, taxon groups and local assemblages were affected by climate change (Gutt et al., 2013; Kortsch et al., 2015; Matishov et al., 2012; Montes-Hugo et al., 2009;

**Table 1**
Glossary in alphabetic order. If terms within the explanation occur also as entries themselves, they are given in italics.

| | |
|---|---|
| Biological trait | A well-defined, measurable property of organisms, usually at the individual level and used comparatively across species (McGill et al., 2006; Reiss et al., 2009; Violle et al., 2007). Examples of frequently used biological traits in the marine realm are body size, mobility, and feeding habit |
| Biological Trait Analysis (BTA) | An approach that considers a range of *biological traits* of organisms to assess how functioning varies between assemblages (Bremner et al., 2003). Also, it may explore potential relationships between community biology and environmental characteristics, including human activities (Beauchard et al., 2017) |
| Ecosystem function | Comprises the stocks and fluxes of energy and materials in the system, and the relative stability over time (Paterson et al., 2012). Examples are primary production, nutrient cycling, or sediment stability. Absolute separation of *ecosystem functions* and *ecosystem processes* is not always possible, and in literature terms are often used synonymously (Paterson et al., 2012; Reiss et al., 2009). |
| Ecosystem functioning | The joint effects of all processes that sustain an ecosystem (Reiss et al., 2009) |
| Ecosystem goods and services | Ecosystem services are the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfil human life. They maintain biodiversity and the production of ecosystems goods such as seafood, forage, timber, biomass fuels, natural fiber, and many pharmaceuticals, industrial products, and their precursors (Daily, 1997) |
| Ecosystem process | Mostly small-scale transformation and translocation of energy and material within the ecosystem, due to physical, chemical or biological action; in sum regulating the observed level of *ecosystem functions* (Paterson et al., 2012). Examples are electron transport pathways of photosynthesis or shell formation in bivalves |
| Effect traits | Those *functional traits* that determine how an organism affects ecosystem properties (Hooper et al., 2005; Lavorel and Garnier, 2002). An example are traits related to bioturbation, which affect sediment biogeochemistry |
| Functional trait | Component of an organism's phenotype that influences *ecosystem processes* and its response to environmental factors (Naeem and Wright, 2003; Petchey and Gaston, 2006) |
| Functional diversity | The range and value of those traits that influence *ecosystem functioning* (Tilman, 2001). Functional diversity indices usually describe two broad aspects of functional diversity: (1) how much of the functional niche space is filled by the existing species (functional richness) and (2) how this space is filled (functional evenness, functional divergence/variance) (Schleuter et al., 2010; Villéger et al., 2008) |
| Fuzzy coding | A coding procedure allowing organisms to exhibit *trait categories* to different degrees, to reflect its biology, or our uncertainty of its biology (Chevenet et al., 1994; Frid et al., 2008) |
| Response traits | Those *functional traits* that determine how organisms respond to a disturbance or change in the environment (Hooper et al., 2005). An example is life span: in highly disturbed environments species with short life span and high turnover prevail |
| Trait-based approach | Here used for any framework in community ecology that considers organism traits rather than individual species, including studies that focus only on a single trait |
| Trait categories | Traits can be subdivided into categories (often also called modalities). For example, the trait 'feeding habit' can be split up into the categories deposit feeder, filter/suspension feeder, opportunist/scavenger and predator (Bremner et al., 2006b) |
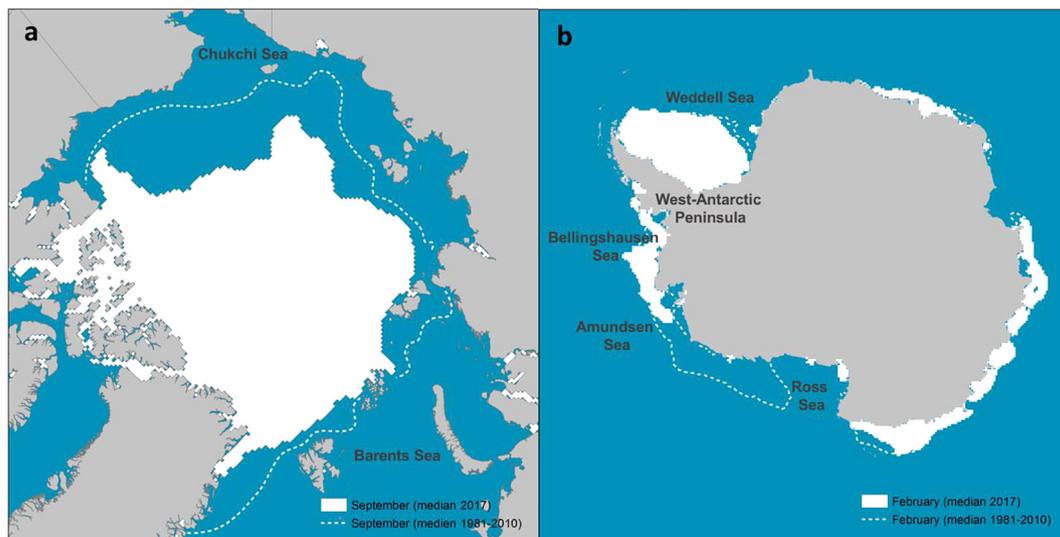


**Fig. 1.** Arctic and Antarctic study region and sea ice extent. Mean Arctic sea ice extent of September 2017 compared to the September median of 1981–2010 (a) and mean Antarctic sea ice extent of February 2017 compared to the February mean of 1981–2010 (b). Shapefiles by NSIDC (http://nsidc.org/data/; Fetterer et al. 2002).

Nahrgang et al., 2014; Sahade et al., 2015), we have considerably less understanding of how certain ecosystem processes, let alone overall ecosystem functioning (see Table 1 – Glossary for definitions) will be affected. A major reason for this uncertainty is that we lack knowledge of community structure-function relationships that could be related to (changing) environmental parameters in large-scale approaches (Worm et al., 2006). Animals, plants and microbes shape ecosystem functions via their collective life activities or traits; accordingly, we infer that stressor-induced changes in community structure will alter certain functions (Naeem et al., 1999). Today, polar marine communities are facing drastic changes. The Arctic is warming at twice the rate of the global average (Pachauri et al., 2014), most visibly reflected in the drastic decrease of Arctic sea ice thickness and extent within the last

decades (Comiso, 2016) (Fig. 1a). The Antarctic shows a different trend and stronger natural variability than the Arctic (Turner and Overland, 2009). This variability is reflected in the long-term decline of sea ice in the Bellingshausen Sea, and in the increase of sea ice in the adjacent Ross Sea (Stammerjohn et al., 2008). In austral spring 2016, overall Antarctic sea ice decreased at a record rate, leading to a decrease of sea ice 28% greater than the mean (Turner et al., 2017). Sea ice is the central structuring force in polar ecosystems: it serves as a habitat for a variety of taxa (Loeb et al., 1997; Moore and Huntington, 2008), while its seasonal growth and melt rhythms control the stratification of the water column and light availability, and thus the availability of nutrients and the onset of the productive season (Leu et al., 2015, 2011; Turner et al., 2009). Consequently, drastic changes in sea ice affect the

| ECOSYSTEM FUNCTIONS AND PROPERTIES | | | |
|---|---|---|---|
| **Energy & nutrient cycling** | **Secondary production** | **Stability / Vulnerability** | **Heterogeneity** |
| **Morphology** | | | |
| Body size | Body size | Body size | Body size |
| Body form | | Body form | Body form |
| Protection / Fragility | | Protection / Fragility | |
| Sociability | | Sociability | Sociability |
| **Life history** | | | |
| Reproduction | Reproduction | Reproduction | |
| Fecundity | Fecundity | Fecundity | |
| Larval development | | Larval development | |
| Dispersal / Migration | | Dispersal / Migration | |
| Life span | Life span | Life span | |
| **Behavior** | | | |
| Environmental position | | Environmental position | Environmental position |
| Living habit | | Living habit | Living habit |
| Mobility / Movement | | Mobility / Movement | |
| Feeding habit / Diet | Feeding habit / Diet | Feeding habit / Diet | Feeding habit / Diet |
| Bioturbation / Irrigation | | Bioturbation / Irrigation | Bioturbation / Irrigation |
| Ecosystem engineering | | Ecosystem engineering | Ecosystem engineering |

**Fig. 2.** Trait-function relationships based on the example of benthic invertebrates. This scheme does not claim completeness, but includes the traits and functions the authors consider most relevant in terms of benthic ecosystem functioning. See S1 for literature sources.

entire marine ecosystem, from surface waters down to the deep-sea floor (Gutt, 2001; Gutt et al., 2013; Slagstad et al., 2015). In addition, warmer water masses have been directly linked to range shifts in the distribution of some polar species and the poleward expansion of boreal species and communities (Cheung et al., 2009; Frainer et al., 2017; Mueter and Litzow, 2008; Smith et al., 2012), the latter also influenced by the increased human activity in the polar regions (Aronson et al., 2011; Renaud et al., 2015).

Traits – here defined as the life history, morphological, physiological and behavioral characteristics of species – provide a link between species and multiple ecosystem-level functions, such as oxygen, nutrient and energy fluxes (Fig. 2). Since species influence these functions via their collective traits (Naeem and Wright, 2003), such traits are termed effect traits (Hooper et al., 2005; Suding et al., 2008) (Table 1). When the relationship of traits and functions is soundly assessed we can use the collective trait pattern of a community in combination with community abundance or biomass to indicate ecosystem functioning (Bremner et al., 2006b) Fig. 2. This approach benefits studies on large spatial scales, as measuring functions at those scales is inherently difficult, and in many cases impossible. Another advantage of trait-based approaches is that early responses to changes are visible in the functional structure rather than in the taxonomic structure of a community (Gagic et al., 2015; Mouillot et al., 2013). Recent use in terrestrial ecosystems has demonstrated that trait-based methods enable generalizations of the trait diversity-functioning relationship within and between ecosystems, and aid prediction of the functional consequences of biodiversity loss (Gross et al., 2017). Accordingly, those traits showing a response to a disturbance are termed response traits (Hooper et al., 2005) (Table 1). These traits are highly relevant in assessing species thresholds and the resilience of ecosystems to change (Gutt et al., 2017) and consequently are important indicators for management and conservation (Bremner, 2008). Uses with immediate application potential for polar regions include identifying regions that are most vulnerable to changes (Diaz et al., 2013; Mouillot et al., 2013; Suding et al., 2008), detecting early conservation outcomes in marine protected areas (Coleman et al., 2015), and identifying functional hotspots (Stuart-Smith et al., 2013). Given their high invasion potential (Cheung et al., 2009), polar areas would also benefit from using trait-based approaches to assess the response of ecosystems to species invasions as done in European Seas (Hewitt et al., 2016; Weigel et al., 2016), or to assess the potential of particular species to become invasive (Cardeccia et al., 2015). Similarly, Suding et al.'s (2008) and Hewitt et al.'s (2016) application of trait-based approaches to estimate climate

change effects on ecosystem functions is highly relevant to polar regions.

The origin of trait-based approaches lies in freshwater (Southwood, 1977; Townsend and Hildrew, 1994) and terrestrial ecology (McIntyre et al., 1995; Olff et al., 1994). They are, however, used with increasing frequency in marine systems: a survey of 233 peer-reviewed studies on marine communities (S1) showed that only 5% where published prior to 2000, and after 2010 the number of publications showed an almost threefold increase despite great challenges in sampling, observation and manipulation of natural assemblages in marine ecosystems (Beauchard et al., 2017). These obstacles are particularly prevalent in polar marine systems, likely contributing to the sparsity of studies, which consider trait-function relationships in these regions. In the Arctic Ocean, only one study from the Canadian Arctic measures a function (benthic remineralization) and relates it to the functional diversity of local benthic communities (Link et al., 2013). A small number of further studies – mostly benthic and very recent – harness trait-based approaches (see overview in Fig. 3) to indicate ecosystem functions (Rand et al., 2017), explore the functional responses to human impacts and climate change (Frainer et al., 2017; Krumhansl et al., 2016; Wiedmann et al., 2014b), or relate functional observations to environmental parameters and gradients (Cochrane et al., 2012; Kokarev et al., 2017; Meyer et al., 2015). Functional diversity was estimated for Arctic zooplankton (Pomerleau et al., 2015), fish (Wiedmann et al., 2014a), and benthic meiofauna (Hasemann and Soltwedel, 2011). A majority of studies analyze the correlation of only one or two biological traits – chiefly feeding type, body size, and/or mobility – to certain environmental parameters (e.g. Grzelak et al., 2016; Pisareva et al., 2015), or use them to indicate community vulnerability (Jørgensen et al., 2015) or functional redundancy (Włodarska-Kowalczuk et al., 2012). From the Southern Ocean we are aware of four studies that included at least two traits each (Jacob et al., 2011; Potthoff et al., 2006; Smale, 2008; Valdivia et al., 2015), while a further study investigated the correlation of one trait (feeding type) and sediment parameters (Liu et al., 2015).

To briefly summarize the current status of trait-based approaches in the marine realm, there is a clear dominance of studies on benthic invertebrates and fish over other ecosystem components (see Table 2; S1). This trend is visible also in trait studies from polar regions, which additionally show a clear majority of Arctic over Southern Ocean studies. Applied methods are mostly of correlative and indicative nature, while studies that estimate functions and trait-function relationships – thus providing a foundation for the correlative approaches – are scarce. As such, we are currently limited in our ability to answer ecological

**Table 2**
Traits used in publications based on a literature survey of 233 marine trait studies from 1979 to 2018. The 323 (standardized) traits found in literature where grouped into 20 topical clusters for simplification (see S1 and S2 for details). The number of studies per ecosystem component (animals in blue, plants and phytoplankton grey) is given in brackets. Trait clusters that occurred in studies from all marine ecosystem components are indicated by white cell filling. The highest number of studies per ecosystem component is emphasized in bold, indicating the most frequently used trait cluster. The ecosystem component "Other" combines studies on mammals, birds, reptiles, biofilm and fouling communities.

| Trait cluster | Benthic invertebrate (108) | Fish (73) | Zooplankton (10) | Multi-taxon (12) | Macrophyte (6) | Phytoplankton (16) | Other (8) |
|---|---|---|---|---|---|---|---|
| Body size | 80 | **63** | **9** | 6 | **5** | 8 | **5** |
| Morphology | 48 | 18 | 3 | 3 | 5 | 4 | 3 |
| Life history | 57 | 30 | 3 | 1 | 4 | – | 2 |
| Reproduction | 56 | 23 | 5 | 3 | 3 | – | 4 |
| Dispersal | 41 | 5 | 2 | 4 | 1 | – | 1 |
| Population dynamics | 10 | 20 | 5 | 4 | 5 | 9 | 2 |
| Physiology | 11 | 15 | 2 | 6 | 3 | 14 | – |
| Environmental position | 40 | 23 | 2 | 2 | – | 1 | 1 |
| Habitat | 9 | 16 | 1 | 2 | – | 1 | 1 |
| Living habit | 42 | 2 | – | 1 | – | – | – |
| Feeding | **84** | 46 | 6 | **10** | – | 2 | 4 |
| Mobility | 68 | 10 | – | 6 | – | 1 | 2 |
| Distribution | 5 | 17 | – | 2 | 1 | – | 2 |
| Migration | 7 | 13 | 2 | 1 | – | – | 3 |
| Sociability | 16 | 18 | – | 2 | – | 1 | 4 |
| Ecosystem engineering | 9 | – | – | – | 1 | – | – |
| Bioturbation | 34 | – | – | – | – | – | – |
| Vulnerability | 25 | 2 | – | 2 | 3 | 2 | – |
| Taxonomy | 3 | 2 | – | – | – | – | 1 |
| Other | 1 | 2 | – | – | – | – | – |

questions which are of ever increasing relevance to ecosystem scientists and managers (IASC, 2016; Kennicutt et al., 2015). These include:

- How do climate induced changes affect polar marine communities, ecosystem functions, goods and services today and under future scenarios?
- How functionally redundant, and resistant to stressor effects (especially those resulting from climate change, biological invasions, and anthropogenic activity) are marine communities in polar regions?
- Which polar marine regions, ecosystems and functions are most threatened or prone to change?

Here we discuss the main challenges of the application of trait-based approaches in polar regions and provide a roadmap to overcome the current obstacles (Fig. 4). As the present paper resulted from the *Arctic Trait Workshop* (University of Vienna, December 2016) that was attended predominantly by benthic ecologists, we use Arctic benthic ecosystems as model systems by which to approach many of the specific issues we discuss. Nonetheless, the presented roadmap underpins a holistic ecosystem approach, and is applicable to all (polar) marine ecosystem components.

## 2. Challenges

### 2.1. Knowledge gaps related to logistical challenges of sampling polar regions

The two polar marine ecosystems of our planet are – despite being both shaped by low temperatures and strong seasonality in light regimes – highly dissimilar. The Arctic Ocean comprises about half mostly shallow, continental shelves, and half slopes, extensive deep sea plains and steep deep-sea ridges (Jakobsson et al., 2012) (Fig. 1a). Due to its proximity to densely populated northern landmasses, areas of the Arctic have been explored for hundreds of years. The Southern Ocean comprises mostly narrow shelves around Antarctica that are submerged deeply by the burden of the inland ice masses, and that drop off steeply towards the basins of the Atlantic, Pacific, and Indian Ocean (Fig. 1b). The exploration of the Southern Ocean started much later in history due to the harsh conditions and remote location, far off the nearest human populations (Howkins, 2016). Technological advancement and improved accessibility (in the Arctic, due to declining sea ice cover) have

facilitated larger sampling campaigns in recent decades, and global efforts like the Census of Marine Life (McIntyre, 2010) that included an Arctic and Antarctic census improved our knowledge of polar biodiversity. Most campaigns have, however, focused on shallow, easy to reach and seasonally ice-free shelf ecosystems (Deal et al., 2014; Sakshaug et al., 2009) including areas of commercial interest. For the Antarctic, the regions with longest history of scientific exploration are the islands of the Scotia Sea, the West Antarctic Peninsula, the Eastern Weddell Sea, and the Ross Sea (Griffiths, 2010; Hamel and Mercier, 1995). Given the high cost of polar exploration, in several other regions – such as the Arctic basins, and Antarctic regions including the Amundsen Sea and the shelves covered by floating ice shelves – our knowledge on species biology and, especially, ecology remains limited (De Broyer et al., 2014; Griffiths, 2010; Kędra et al., 2015). Systematic monitoring programs provide ongoing quantitative time-series in certain areas, however gaps in pre-impact baselines hinder assessment of the magnitude and speed of change in large regions (Wassmann et al., 2011).

### 2.2. Lack of trait information

Apart from the general lack of biological information from some polar regions, huge knowledge gaps exist when it comes to ecological characteristics or traits of polar species, which form the basic input to all types of trait-based approaches (Fig. 3, Beauchard et al., 2017). Even information about fundamental traits is sometimes hard to find, such as body size, despite authors acknowledging it to be among the most important and interlinked traits (Costello et al., 2015; Norkko et al., 2013). This lack of accessible trait information is not a problem restricted to the polar regions. For example, a study quantifying data availability for the demersal fauna of the United Kingdom reveals that information about eight fundamental traits (body size, diet, feeding method, reproductive timing, fecundity, larval dispersal, adult dispersal, longevity) was available for only 9% of the benthic community in that study (Tyler et al., 2012). The authors noted that body size was the best documented trait (data available for 80% of species), while data on fecundity was especially scarce (data available for only 19% of species). Publications that provide such ecological information are usually often cited clearly stating their high value to the scientific community. A notable example is the study of polychaete feeding guilds on family level by Fauchald and Jumars (1979) which is currently cited > 1300 times (Web of Science, accessed December 4, 2017).

## 2.3. Paucity of established trait-function relationships

A basic requirement when using traits to indicate ecosystem functioning is sound knowledge of trait-function relationships. To date experiments that quantitatively explore specific trait-function relationships in the marine realm are quite rare (but see Lohrer et al., 2005; Michaud et al., 2006, 2005; Norkko et al., 2013; Thrush et al., 2017), and even less data are available to build correlative approaches in polar marine regions (Link et al., 2013). Indeed, those experimental studies which do exist have often only limited explanatory power as they are: 1) conducted in the lab or on small scales the field, 2) include only a few species, and/or 3) usually focus only on a single ecosystem function (Stachowicz et al., 2007). By contrast, real world ecosystems are species rich, and species usually contribute to more than one function, while the overall ecosystem functioning is sustained by multiple processes across multiple spatial and temporal scales (Reiss et al., 2009). This complexity is emphasized in a recent study by Thrush et al. (2017) that nested holistic Biodiversity-Ecosystem functioning (B-EF) experiments into a natural landscape (an extensive intertidal flat). Their results clearly showed that the community-function relationship was not always linear or stable, but could change with changes in either the ecological landscape or the environmental drivers.

## 2.4. Are polar traits and processes different?

It is unclear whether trait-function relationships determined at lower latitudes are valid also at high latitudes. Polar ecosystems are unique in several respects (e.g. very low temperatures, strong seasonality in light and productivity), and polar species are often highly adapted to life in small physiological ranges and extreme environmental conditions (Peck et al., 2004). Thus, their response to stressors like temperature increase may strongly differ in comparison to their relatives in temperate regions. For example, Sainte-Marie (1991) and Węsławski and Legeżyńska (2002) suggested gammaridean amphipods might express intraspecific variability in reproductive traits (e.g. number of broods, life-span) along latitudinal gradients. Decreasing growth rates have been documented for a single sea urchin species with decreasing temperature along a latitudinal gradient (64–77° N) in Greenland (Blicher et al., 2007). For widely distributed species with ranges extending into subarctic/subantarctic or even temperate regions, trait information mostly originates from those lower latitudes. Trait approaches at lower latitudes commonly assume that traits of the same species stay constant across a wider geographical range, enabling large scale assessments or comparison of community functioning among different regions (Bernhardt-Römermann et al., 2011; Bolam and Eggleton, 2014; Bremner et al., 2006b). However, there is evidence that species in polar regions might have developed certain adaptations that influence their trait expression, including slow growth, high longevity, high lipid content or production of anti-freeze agents (Margesin and Schinner, 1999; Pörtner and Playle, 1998). Such considerations advise against the use of information from lower latitude trait literature and further restrict the pool of available trait data.

## 2.5. Choice of traits and terminology

Table 2 shows the most commonly used traits per ecosystem component in the marine realm, based on a literature survey (S1, S2). The number of traits and trait categories (Table 1) used in marine studies varies from 5 or less (e.g. (de Juan et al., 2007) to > 50 (Doxa et al., 2016). While a number of traits are common to many trait-based studies and across ecosystem components (see Table 2), the diversity of language which surrounds them grows as trait-based studies are adopted more widely. Across literature, traits are named and defined in a myriad of contrasting ways that act to lessen their applicability and ease of use

(Kremer et al., 2017; Violle et al., 2007) (S1). Non-standardized and even contradictory trait definitions prevent authors from readily comparing their findings (Costello et al., 2015). Alternatively, imprecise trait definitions or classifications could mean information is mishandled and wrongly incorporated. Issues are likely to be particularly complex during broad-scale studies investigating ecosystem management strategies or consequences of change. For example, traits such as 'body size' are likely to be interpreted differently when not clearly defined depending on the preconceptions of the author, and the morphology of the species in question. Practices may work well within a scientific field or research group, or where the appropriate terminology is apparent for a given taxa, but become 'lost in translation' when considered across multiple data sources. This variety limits the potential to generalize findings across studies or compare patterns across spatial and temporal scales (Carmona et al., 2016; Costello et al., 2015).

## 2.6. Past and current climate changes

Studies are needed that directly relate environmental change to responses in ecosystem functions in polar regions, as has previously been explored in terrestrial (Diaz and Cabido, 1997; Lavorel and Garnier, 2002) and freshwater ecosystems (Bonada et al., 2007; Maasri and Gelhaus, 2012). A number of polar studies have succeeded in documenting climate change effects on certain species, taxon groups, local assemblages (Gutt et al., 2013; Kortsch et al., 2015, 2012; Matishov et al., 2012; Sahade et al., 2015) or larger-scale community properties like biodiversity (Michel et al., 2012; Wesławski et al., 2011). So far, only one recent study on Arctic fish tackled how these changes affect the communities' trait pattern and consequently ecosystem function as a whole (Frainer et al., 2017). Frainer et al. (2017) detected that the recent warming period in the Barents Sea triggered a rapid shift from an Arctic fish community characterized by small-sized bottom-dwelling benthivores, towards a boreal fish community characterized by the traits large body size, longer lifespan and piscivory. This phenomenon – also known as the borealization of Arctic fish communities (Fossheim et al., 2015) – has the potential to reconfigure Arctic food webs and affect ecosystem functioning in the region. Given this scarcity of studies, there is currently not a sufficient basis from which generalizations can be drawn. The same holds true for past ecosystem changes: few studies from lower latitudes use fossil trait data to estimate how past climate change affected ecosystem functions (and ecosystem services) in order to contextualize contemporary observations (e.g. Caswell and Frid, 2013; Frid and Caswell, 2016), and even fewer focus on the past and present of the polar regions in this context. Vemeij and Roopnarine (2008) refer to trans-Arctic invasions that occurred during the warm mid-Pliocene epoch and predict a resumed spreading from the Pacific through the Bering Strait into a warmer Arctic Ocean and eventually into the temperate North Atlantic. The adding of Pacific-derived fast-growing and large bodied mollusk species to the Arctic and North Atlantic species pool might affect the regional food webs and ecosystem functions (Vermeij, 1991; Vermeij and Roopnarine, 2008). Bonn et al. (1998) used biogenic opal as proxy for paleo-productivity and observed a glacial/interglacial pattern with high productivity during peak warm stages with reduced sea ice coverage back to 400 ka.

## 3. Roadmap

Here we present a roadmap consisting of six steps to address the identified challenges. The aim is to facilitate the successful application of trait-based approaches on various spatial and temporal scales, and to assess trait and functional patterns in order to understand current and predict future ecosystem functioning in rapidly changing polar marine

systems. Recommendations regarding each step of the roadmap are summarized in Fig. 4.

Step 1: International network

Much knowledge of species traits is unavailable in the published literature, and is instead dispersed among individual scientists' personal observations and unpublished notes. The formation of a comprehensive, international network of experts (biologists/ecologists from all specializations, ocean surface to seafloor, taxonomists, physiologists, museum curators, technicians) is thus indispensable to integrating expert knowledge and to covering the entire polar regions. Any such network should reach internationally. We suggest an editorial board be formed that is interlinked with the World Register of Marine Species platform WoRMS (WoRMS Editorial Board, 2017), today's largest standardized and expert-curated marine species inventory (Horton et al., 2017; Vandepitte et al., 2018). Such a board is necessary to organize the network, identify traits experts for particular taxonomic groups, regions, or methods, and document where relevant trait sources such as voucher collections or video material are deposited. Recommendations on standardized protocols for field and laboratory work could be made available for download. The network could also promote the integration of traits data into ongoing Arctic and Antarctic monitoring programs (see also Step 2), including the Circumpolar Biodiversity Monitoring Program (CBMP, http://www.caff.is/monitoring) in the Arctic and the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) Ecosystem Monitoring Program (CEMP) (Agnew, 1997; https://www.ccamlr.org/en/science/ccamlr-ecosystem-monitoring-program-cemp) in the Antarctic.

Step 2: Trait terminology and methodology

Application of trait-based approaches in the polar regions is a relatively recent development (S1). Though a drawback in many ways, this offers an opportunity to promote standardized trait definitions and best practices before the plethora of approaches seen in other regions also inundates the polar regions. While acknowledging that approaches are case specific, unification of the following aspects will allow enhanced comparability and extrapolation of results.

2.1. Choice of traits and terminology

While the choice of traits is driven by a given research question, a comprehensive list of traits and their categories needs to be developed for polar regions using standardized terminology. In the currently developed traits data base linked to WoRMS, Costello et al. (2015) have proposed a prioritized list of 10 traits (taxonomic identity, environment, geography, depth, substratum, mobility, skeleton, diet, body size and reproduction), which resulted from a study on the availability and use of traits, both in literature and existing database, and consultation of experts. Here, we focus solely on biological traits, i.e. such that comprise morphological, physiological, life history and behavioral traits of organisms. For taxonomic traits, we refer to specific platforms like the World Register of Marine Species (WoRMS Editorial Board, 2017; http://www.marinespecies.org/), Integrated Taxonomic Information System (ITIS; www.itis.gov), and for biogeographic information to Global Biodiversity Information System (GBIF; http://www.gbif.org/) or Ocean Biogeographic Information System (OBIS; http://www.iobis.org). Within WoRMS, registration of trait data requires that one should easily be able to apply a trait to any given taxon (Costello et al., 2015). More specific research questions however may require the use of additional taxon or ecosystem specific traits. Clarity and standardization of trait terminology should be a foremost priority, in order to facilitate meta-analysis or comparison of results. Successful communication platforms should be developed to ensure this

standardization process. An example of how such a platform can be organized is given in Costello et al. (2015).

2.2. Sources of trait information

A diversified, holistic approach is appropriate when it comes to compiling traits information. Many biological traits can be readily assessed during sampling. These include morphological traits, e.g. body size/length/weight and body form. In situ imaging and diver-based observations may identify some behavioral traits (e.g. sociability, activity, environmental position), as well as feeding and movement traits (Balazy et al., 2014; Hewitt et al., 2014) (Supplementary data). Other traits can be derived from biochemical analysis. Traits defining trophic roles can be assessed from stable isotopes ($\delta^{15}N$, $\delta^{13}C$), fatty acids and other chemical markers (e.g. Fry, 2006; Kelly and Scheibling, 2012). Traits related to energy-storage can be derived from lipid and caloric content analysis (Falk-Petersen et al., 2009). Radionuclides ($^{210}Pb$, $^{234}Th$ and other) have been used as particle tracers to assess sediment reworking rates (bioturbation) by benthic organisms (Maire et al., 2008). Stable isotopes can be also used to inform on the migratory habits of pelagic fish (Trueman et al., 2012).

Museum or other voucher collections are of high value especially when containing specimens that are rare or from remote polar regions. Accordingly, a list of relevant collections together with the contact details of responsible authorities/persons should be added to the joint management system. It is noteworthy, however, that museum collections may be biased towards "exceptional" individuals (e.g. particularly large specimens), and organisms preserved in ethanol and formalin experience shrinkage or body deformations (Cunningham et al., 2000). When physical samples are unavailable, the common approach to build up a traits collection is by performing a literature survey of articles relating to either individual traits or groups of traits of species or taxon groups. Often trait information is recorded in grey literature not accessible to the general public, like internal reports, descriptions in museum libraries, ship protocols or lab notes (Vanden Berghe et al., 2009). Such grey literature should be added to a joint database managed via the network (Step 1, Step 3).

Time- and cost-saving needs fueled the search for surrogate methods in biodiversity assessments. In benthic studies for example, lowering the taxonomic resolution of taxonomic identification to family level or choosing a certain representative taxon gave similar results to those obtained based on all taxa in detecting the effects of natural and anthropogenic disturbance on benthic diversity and distribution patterns (Włodarska-Kowalczuk and Kędra 2007). The search for similar surrogate methods in trait and functional diversity assessment may be needed for the > 7000 known marine animal and plant species in the Arctic (CAFF, 2013) and > 8800 in the Antarctic (Griffiths, 2010) (e.g. to provide cost-effective monitoring tools), but only after a thorough assessment of the effect of lowering the functional resolution.

2.3. Trait data analysis

Trait-based approaches in the marine realm are diverse and range from the assessment of ecological indices, such as various measures of functional diversity (Laliberté and Legendre, 2010; Mason and Mouillot, 2013; Petchey and Gaston, 2002; Schleuter et al., 2010) and the development of ecological indicators (Beauchard et al., 2017), to more complex methods, often summarized under the term biological trait analysis (BTA) (Bremner et al., 2006b). A BTA enables scientists to explore the relationship between species or community trait patterns and environmental characteristics (or stressors) (Beauchard et al., 2017) (Fig. 3). The choice of which trait-based method and subsequent equation, multivariate statistic or model to use (see overview in Fig. 3) depends very much on the respective research question and environment, and thus cannot be discussed here in detail (excellent overviews
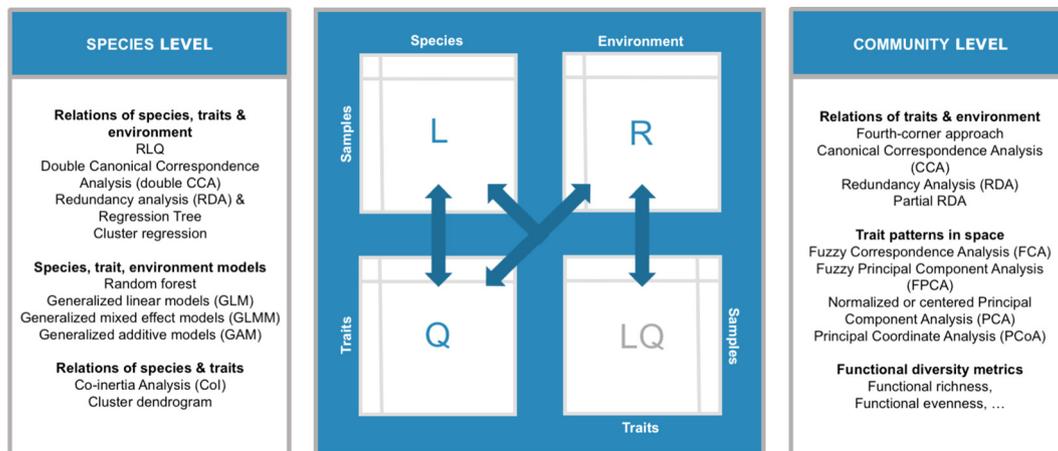
**Fig. 3.** Trait-based approaches use a set of up to three matrices: 1) the species per station matrix (L table) using presence/absence, abundance or biomass data of species per sample/station, 2) the traits per species matrix (fuzzy coded or otherwise) (Q table), and 3) the environmental or stressor data matrix (R table). Out of 1) and 2) the abundance or biomass weighted traits matrix can be constructed (LQ table). Common analysis tools used in trait studies are listed left (species level approaches) and right (community level approaches) of the conceptual model. Species level approaches are performed on the separate L and Q, or L, Q, and R tables and allow to gain information on species level, while community level approaches are performed on the LQ table; here the entire community is analyzed and findings can no longer be traced back to single species. Double arrows indicate which matrices can get analyzed together (see Kleyer et al., 2012; Beauchard et al., 2017 for methodical details).

are given in Kleyer et al., 2012 and Beauchard et al., 2017). The required data structure underlying all methods however comprises the construction of several data matrices, and here some standardizations appear useful. The degree to which a species expresses a trait category can be indicated in the 'traits per species' matrix (or Q table, Fig. 3) via a coding procedure. The fuzzy coding procedure (Chevenet et al., 1994) offers a pathway from descriptive words to a common code enabling analysis of diverse kinds of biological information derived from a variety of sources (e.g. samples, literature, personal observations). Fuzzy codes found in the literature range from 0–3 (Bremner et al., 2006b), 0–4 (Tillin et al., 2006), and 0–6 (Chevenet et al., 1994). We promote the use of the 0–3 coding scheme as it is the most commonly used, and provides a compromise between binary codes and many not clearly delineated graduations. Including code matrices as supplements to publications enables comparisons and aids the use of consistent coding (Bremner et al., 2006b; Kokarev et al., 2017; Santoul et al., 2005).

### 2.4. Sensitivity analyses

The analysis of how uncertainties in input data affect the output of a mathematical model is a central aspect of any model evaluation. In trait-based approaches on the other hand, a formalized sensitivity analysis is not a standard procedure. Several authors do, however, point out uncertainties potentially affecting the outcome of the respective trait study and suggest ways of addressing this issue. This includes the type and number of traits or functional groups used (Bremner et al., 2006b; Guillemot et al., 2011; Thrush et al., 2017), the weighting of traits (Elleouet et al., 2014), the number of traits not measured "on site" (Borgy et al., 2017), and generally incomplete trait information (Májeková et al., 2016; Tyler et al., 2012). Regarding the fuzzy coding of traits, the degree of subjectivity of scientists and the consequent potential differences of fuzzy codes is a concern that is not yet studied. To get a first insight we conducted a small experiment among participants of the Arctic traits workshop (University of Vienna, December 2016). Participants coded 27 trait categories (belonging to six traits) of three common Arctic benthic invertebrates (the bivalve *Macoma calcarea,* the brittle star *Ophiura sarsii,* and the amphipod *Anonyx nugax*), the final matrices were compared. We found that 83% of the coding was identical, while 17% were different in at least one category per trait. We assume that the differences result from a combination of the fact that

most of the participants were new to the use of fuzzy codes, and partly not experts for the chosen taxa. The exchange of trait information and fuzzy codes via publications and databases along with explicit guidelines on how to code will improve the consensus (see Step 3).

### Step 3: Trait databases

As traits are already being documented within several (not region specific) databases [e.g. FishBase www.fishbase.org, polytraits (Faulwetter et al., 2014), or the trait database for marine copepods (Brun et al., 2017)] it is key to look for collaboration opportunities with these initiatives, thereby avoiding duplication of effort. Accordingly, a large number of traits in the WoRMS traits portal (http://www.marinespecies.org/traits/index.php) are sourced from these databases that are focused on certain taxonomic groups. The traits compilation currently being tackled by the WoRMS Data Management Team and the Editorial Board is grouped at higher taxonomic level as much as possible, thereby lessening the workload. The use of 'generalistic' traits, here such that are applicable across ecosystem components (Table 2), enables analyses across marine realms and large biogeographical scales. This represents a potential for investigating mechanistic relationships between ecological function and the physical environment. The use of such traits also allows more holistic investigations of function that encapsulate several ecological groups, such as invertebrates, fish and mammals (something that has been seldom attempted in marine studies to date). More specific traits – as may be desirable for polar taxa - can be added. For example, the maximum sediment burrowing depth is highly relevant for benthic (polar) ecosystem functions, but does not apply to pelagic taxa. Under these circumstances these pelagic taxa must not be excluded from analysis, but are merely scored a '0' for that respective trait, indicating that it is not expressed (see Step 2).

Several options exist regarding the way in which trait information is stored in databases, specifically as text information or coded. The Arctic Traits Database (Degen et al. unpublished; www.univie.ac.at/arctictraits), a trait platform for Arctic benthic taxa, provides both text and fuzzy codes by species for direct download and import into relevant analysis software. The advantage of this approach is that researchers who are less trained in fuzzy coding can also perform rapid trait analyses. This goal is supported by the additional provision of manuals and R-code. Also, detailed records of the information from which the fuzzy codes were sourced are provided to ensure data

traceability and reproducibility, and potential revision of codes in the event of new findings. In general, quality assurance for all data repositories should aspire to be of the same rigor as that of printed publications (Costello and Berghe, 2006). A best practice example is the Polytraits database (http://polytraits.lifewatchgreece.eu), where every trait is referenced, often by directly quoting the exact literature passage which has led to the coding of the information (Faulwetter et al., 2014).

In addition to trait information, a BTA requires presence/absence, abundance, or biomass data by location, as well as environmental data. Tools have already been developed through the EMODnet Biology Project (http://www.emodnet-biology.eu/toolbox/), allowing to query a selection of traits in combination with taxonomic and distribution data (Costello et al., 2015).

### Step 4: Trait-function relationships

In order to apply trait-based approaches to study ecosystem functioning in the rapidly changing polar regions, it is crucial that sound links between polar community traits and functions are established. Substantial understanding of trait–function relationships could be gathered from experimental approaches at lower latitudes (Lohrer et al., 2005; Michaud et al., 2006, 2005; Norkko et al., 2013; Thrush et al., 2017), but we must question whether these relationships can be directly transferred to polar functions. We consequently recommend performing a series of experimental and observational approaches in contrasting ecosystems and several polar regions. Most naturally, experimental approaches in polar regions should be performed in well studied regions (e.g. coastal shelf or fjords), and/or where regular monitoring is carried out, and a large volume of species and environmental information is already available. In the planning phase of experiments, a critical step is to define the traits that are relevant for the ecosystem function(s) of interest (Lepš et al., 2006). Given the uncertainty of which traits are the appropriate ones to select, we follow Lepš et al. (2006) and suggest treating the final choice as a hypothesis that needs to be tested. Once trait-function relationships are identified, the use of these particular traits in future studies and their inclusion in trait databases should be encouraged. Not only the traits but also the functions investigated need to be chosen a priori. While some traits are intimately linked to particular functions ("hard" traits), others serve only as indirect indicators ("soft" traits) (Petchey and Gaston, 2006). Functional diversity should be included among the functional parameters (along single and multiple traits and functional groups), as it explains variation in ecosystem functions (Cadotte et al., 2011). The use of thresholds was successfully used to identify if overall functioning was sustained in disturbance experiments (Gamfeldt et al., 2008; Thrush et al., 2017, 2014). Below we list four types of studies that we suggest be carried out in polar regions:

#### 4.1. Lab and microcosm experiments

The relation and effect of single and multiple traits of polar species to specific ecosystem functions can be assessed in laboratory or microcosm experiments. Communities (or subsets of these), selected based on their expression of certain traits (see e.g. Braeckman et al., 2010; Mermillod-Blondin et al., 2004; Norling et al., 2007), can be exposed to different environmental conditions (e.g. varying temperatures, varying food input). Fluctuations in functions are then measured in order to provide important baseline information on trait-function relationships and on potential thresholds of functions (Thrush et al., 2014). The microcosm experiment by Braeckman et al. (2010), as one specific example, showed a pronounced influence of the trait bioirrigation on benthic respiration, nutrient release, and denitrification, compared to the trait biodiffusion. The traits (and the species expressing them) that explain most of the effects in lab and microcosm studies should be clearly identified so they can be further analyzed, manipulated, and quantified in field studies.

#### 4.2. Field experiments

While most challenging, field experiments offer important trait-function relationships previously identified in lab experiments to be analyzed under real-world conditions. Complex community interactions resulting in complementarity (i.e. when a mixture of species outperforms all monocultures) necessitate multiple aspects of the total community response (function) to be considered simultaneously (multifunctionality) or integrated into a multivariate index of ecosystem performance (Gross et al., 2017; Stachowicz et al., 2007). As an example, Thrush et al. (2014) manipulated light, nutrient concentrations and species densities in a coastal sandflat (Manukau Harbour, New Zealand) and detected a changed interaction network between biogeochemical fluxes, productivity, and macrofauna, once potential thresholds were crossed. Coordinated experiments on different community components could be performed in different regions of the Arctic to provide the basis for a 'functional atlas'. For example, functional traits response to experimentally disturbed seafloor on different spatial scales can provide insight into the recovery processes of communities and associated functions exposed to various stressors and along stressor gradients (Lohrer et al., 2015, 2010; Snelgrove et al., 2014). We support the recommendation by Gamfeldt et al. (2015) that future studies should explicitly consider also manipulations of species density in order to disentangle density-dependent population processes and diversity effects.

#### 4.3. Observational studies

Observational studies are empirical and do not involve manipulative experimentation (Thrush and Lohrer, 2012). Examples are descriptions of trait patterns in space and time, correlative studies of traits and functions, or broad-scale hypothesis tests of patterns and relationships (all part of approaches shown in Fig. 3) which may result from observational field studies designed for the question or from data mining. The advantage of such studies is that they can – contrary to field experiments – rather easily be performed on large spatial scales, given the ecological information is available. A disadvantage, however, is that the conclusions drawn are based on statistical correlations and not causality, thus underlying mechanisms might remain unknown. We, therefor, recommend to perform observational studies including those significant traits and functional groups that were previously identified in field and lab experiments from polar regions, to validate the outcomes of the experiments on a larger scale and, in turn, to generate new hypotheses and trait-function relationships.

#### 4.4. Integrative approaches

Although a generally positive effect of higher (functional) diversity on ecosystem functioning is assumed (Hooper et al., 2005; Stachowicz et al., 2007), experimental findings are often contradictory and the relevance and generality of many experimentally determined B-EF relationships are questioned. We assume that the same will hold true for the outcome of trait-function experiments in polar regions (see Link et al., 2013). Accordingly, Srivastava and Vellend (2005) highlight the need for rigorous and integrative science if general principles are to be found. Following Thrush and Lohrer (2012), integration can for example be achieved by testing predictions based on theory or small-scale experiments with broad-scale observational studies. Regarding our topic this suggests a meta-analysis of field and lab experiments from polar regions (and lower latitudes), the identification of the significant trait-function relationships, and a correlative study of these traits and functions on larger, up to pan-Arctic scales.

### Step 5: Modelling

Given the scarcity of trait-based research in polar regions, modelling

approaches that incorporate multiple traits are equally rare. A prerequisite to large-scale modelling studies are data of sufficient geographical coverage, which are extremely difficult to obtain in many polar regions, as well as trait information on largely unknown taxonomic units. Access to sufficient data would enable the application of species distribution models (SDM), which are commonly used tools to study the distribution of species and support conservation measures (Guisan et al., 2013; Reiss et al., 2015; Wittmann et al., 2016). Two different frameworks exist to model species distribution patterns and take into account the traits of species during analysis, i.e. 4th-corner models and joint SDM (Brown et al., 2014; Pollock et al., 2012; Warton et al., 2015). The advanced model-based approach to the fourth-corner problem suggested by Brown et al. (2014) allows to develop a predictive model for species abundance, as a response to traits and environmental variables. Joint SDM are model-based hierarchical (Bayesian) approaches that assess the strength and direction of trait-environment relationships, allow model-selection procedures, and facilitate prediction to new scenarios while propagating data uncertainty (Ovaskainen et al., 2017; Warton et al., 2015). For example, it would be possible to assess which traits are most associated with particular environments and determine their fate if these environments decline or even disappear. In their study on geographic range shifts in an ocean-warming hotspot Sunday et al. (2015) used multi-model averaging of mixed-effects linear models (GLMM) with maximum likelihood estimation to test the effect of species traits on shifts in poleward range boundaries. Their study showed that including traits more than doubled the variation explained than if climate velocity alone was used as predictor. GLMMs were also used by Lefcheck and Duffy (2015) and showed that functional diversity predicted ecosystem functioning better than species richness. Predictive models can be used to assess ecosystem functioning in future scenarios, e.g. when traits and functions are included into ecosystem models (Queirós et al., 2015b). Another relevant method are generalized additive models (GAM), which have the advantage of allowing the assessment of non-linear relationships without fitting arbitrarily selected functions (Valdivia et al., 2015; Wood, 2006). Valdivia et al. (2015) used GAMs to test for an effect of environmental gradients (distance to glacier and water depth) on the functional richness of a subtidal community in the Western Antarctic peninsula. Gross et al. (2017) promote a new modelling approach to assess trait distributions on global or at between-ecosystem scales, i.e. models that include skewness-kurtosis of trait-abundance distributions. These models have a higher predictive power of multifunctionality, as they enable generalizations across ecosystems and prediction of the functional effect of biodiversity loss. However, although the prediction of multifunctionality would be of highest interest in the polar regions, to our knowledge these approaches have not been applied there yet, nor in the marine realm in general.

Size is often regarded as a 'master' or 'key' trait of an organism as it may determine its functioning in terms of physiology, trophic strategies, life-histories and interactions with abiotic and biotic elements of the ecosystem (Andersen et al., 2016; Brose et al., 2016). At the community level, size spectrum models (based on size as a basic descriptor of community components, ignoring species identity or other traits characteristics) have been employed, for example to estimate consumer biomass, productivity or predict the changes in community structure through time (Blanchard et al., 2017; Brose et al., 2016). In the Arctic, size spectra have been described for pelagic (Basedow et al., 2010; Forest et al., 2012; Trudnowska et al., 2014) and benthic communities (Górska and Włodarska-Kowalczuk, 2017). Recently, a need to include additional functional traits into size-based ecosystem models has been raised, especially in systems where not all processes are size-based (like the energy flow through the detritus-based food webs in benthos, Blanchard et al. 2017). For example, a study assessing the number of dimensions (trait-axes) that determine whether individuals of different species interact (trophically, antagonistically, or mutualistically) found that models accounting for only a small number of traits already

dramatically improve understanding of the structure of ecological networks (Eklöf et al., 2013).

Step 6: Management and conservation

One of the motivations for applying trait-based approaches in the rapidly changing polar regions is that new insight and information are needed to advise management and conservation efforts (Aarnio et al., 2011; Bremner, 2008; Doxa et al., 2016). Consequently, traits are now included among those "ecosystem Essential Ocean Variables" (eEOVs) recommended to address the dynamics and change in Southern Ocean ecosystems (Constable et al., 2016). In the Arctic, currently eleven Ecologically and Biologically Significant Areas (EBSAs) are defined after seven criteria: 1) uniqueness or rarity, 2) special importance for life history stages of species, 3) importance for threatened, endangered or declining species and/or habitats, 4) vulnerability, fragility, sensitivity, or slow recovery, 5) biological productivity, 6) biological diversity, and 7) naturalness (CBD, 2014). Recent studies have shown that trait approaches provide new means to define these marine areas of interest, as they can identify functional hotspots and vulnerable regions (Stuart-Smith et al., 2013) and assist in the boundary setting of MPAs (Bremner et al., 2006a; Frid et al., 2008). BTAs were successfully applied to assist in the formulation of conservation objectives, e.g. by testing fisheries effects on ecosystem function (Cooper et al., 2008; Koutsidi et al., 2016). In addition, trait-based approaches were applied in the monitoring of already defined MPAs. A study by Coleman et al. (2015) comparing different types of MPAs showed that functional traits can elucidate early conservation outcomes, while traditional multi-metric diversity indices were not able to distinguish between the differently treated habitats. Recently, the very promising approach to integrate traits and functional diversity into ecosystem models was launched (Queirós et al., 2015a; see also Step 5). Such models provide a holistic view of ecosystems and the opportunity to assess the impacts of conservation and management as they enable us to project possible states of future marine ecosystems.

Several legislative agreements require management schemes to directly address the functioning of ecosystems (Frid et al., 2008). The European Marine Strategy Framework Directive (MSFD), for example, has the objective to "enable the integrity, structure and functioning of ecosystems to be maintained or, where appropriate, restored" (Article 13/5) (EU, 2008). Article 11 states further that coordinated monitoring programs for the ongoing assessment of the environmental status – accounting for the structure and functioning of marine waters – should be established. There are already several studies from other realms where trait approaches were successfully used in that field, mainly in terrestrial (de Bello et al., 2010; Tilman et al., 2014), but also marine habitats (Claudet et al., 2010; Violle et al., 2014). However, to date, there are only few multivariate applications of biological traits to support environmental policies in the marine realm (Beauchard et al., 2017; Brind 'amour et al., 2016; Frid et al., 2008). In order to advise marine management, recent studies stress the importance of trait-based approaches for reliable indicator development to assess environmental health or status and to detect tipping points or regime shifts (Beauchard et al., 2017; Pedersen et al., 2017). Still, these studies also highlight obstacles related to missing ecological understanding on trait-function relationships and the inherent difficulties related to large scale approaches, points we have discussed in the previous paragraphs.

## 4. Conclusions and outlook

Trait-based approaches are valuable tools to study the effects of rapid climate change and associated anthropogenic stressors on ecosystem structure and functions in the world's oceans, to predict future scenarios, and to advise decision makers on the required steps for sound ecological management. However, polar regions and ecosystems are unique and pose scientific challenges – divergent from those in
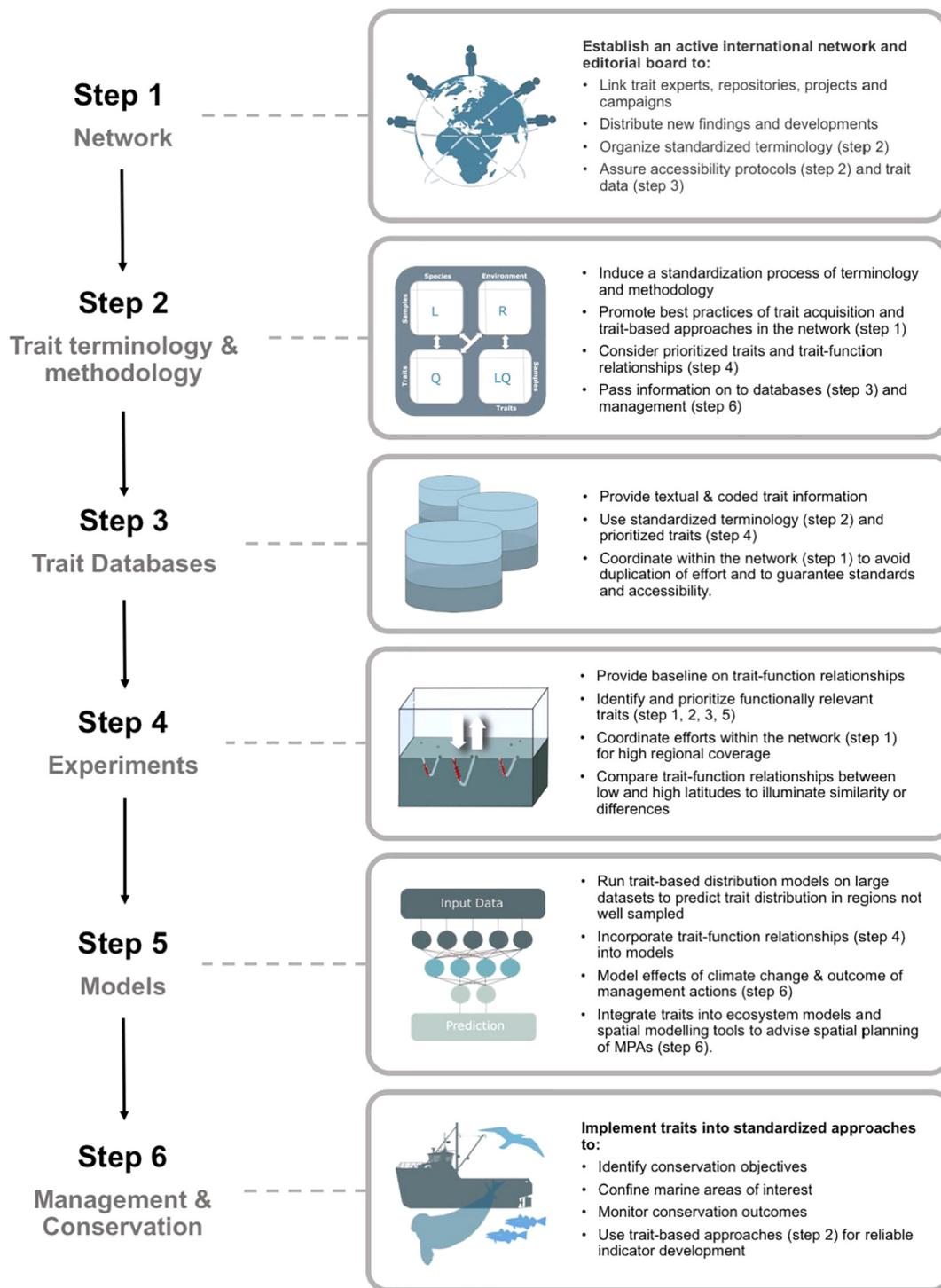
**Step 1**
**Network**

Establish an active international network and editorial board to:
- Link trait experts, repositories, projects and campaigns
- Distribute new findings and developments
- Organize standardized terminology (step 2)
- Assure accessibility protocols (step 2) and trait data (step 3)

**Step 2**
**Trait terminology & methodology**

- Induce a standardization process of terminology and methodology
- Promote best practices of trait acquisition and trait-based approaches in the network (step 1)
- Consider prioritized traits and trait-function relationships (step 4)
- Pass information on to databases (step 3) and management (step 6)

**Step 3**
**Trait Databases**

- Provide textual & coded trait information
- Use standardized terminology (step 2) and prioritized traits (step 4)
- Coordinate within the network (step 1) to avoid duplication of effort and to guarantee standards and accessibility.

**Step 4**
**Experiments**

- Provide baseline on trait-function relationships
- Identify and prioritize functionally relevant traits (step 1, 2, 3, 5)
- Coordinate efforts within the network (step 1) for high regional coverage
- Compare trait-function relationships between low and high latitudes to illuminate similarity or differences

**Step 5**
**Models**

- Run trait-based distribution models on large datasets to predict trait distribution in regions not well sampled
- Incorporate trait-function relationships (step 4) into models
- Model effects of climate change & outcome of management actions (step 6)
- Integrate traits into ecosystem models and spatial modelling tools to advise spatial planning of MPAs (step 6).

**Step 6**
**Management & Conservation**

Implement traits into standardized approaches to:
- Identify conservation objectives
- Confine marine areas of interest
- Monitor conservation outcomes
- Use trait-based approaches (step 2) for reliable indicator development

**Fig. 4.** The six steps of the proposed roadmap and concrete recommendations regarding the successful use of trait-based approaches in the rapidly changing polar ecosystems. The nestedness of the roadmap is indicated by the number of the respective working step in brackets.

temperate regions – to those aiming to apply trait-based approaches. Most of these challenges concern basic requirements that demand community consensus before any actual methodical approach can be taken. These essential basics comprise trait information of polar taxa, standardized trait terminology and methodology, and knowledge on polar trait-function relationships. In the present paper, we reviewed the existing challenges thoroughly and suggest a six-step roadmap to overcome these obstacles and progress forward (Fig. 4). This roadmap comprises the building of a strong and active international and interdisciplinary network (Step 1), capable of defining basic trait

terminology and best practice assessments (Step 2) that will lead to harmonized, well-structured and easy accessible trait databases (Step 3) and coordinated experimental approaches (Step 4). These first four steps provide the essential baseline for trait-based and modelling approaches (Step 5) on large spatial and temporal scales, appropriate to tackle the pressing questions related to climate change and to predict future scenarios. This new insight then can be used to give sound advice to decision makers and marine conservation (Step 6). Given the complexity and speed of changes that polar ecosystems, and especially those in the Arctic, are facing it might seem illusory to keep pace by following

such an apparently long and nested working process. But what are the alternatives? Isolated research projects and small-scale approaches will not be able to answer the urgent questions related to climate change, inherently a multifaceted and large-scale phenomenon. Nor are they appropriate to satisfy the need of decision makers to consider, prepare for and potentially mitigate future scenarios. Several initiatives included in this roadmap (e.g. the WoRMS traits portal) are already ongoing, while others (e.g. the Arctic Traits Database) are in progress. With joined forces and commitment of the international research community to permanent exchange and coordinated initiatives all steps of this roadmap can be tackled.

A fact we noted during the work on this paper – and that was also highlighted in Beauchard et al. (2017) – is a clear predominance of benthic trait studies in the marine realm, and – with exception of fish – less focus on pelagic ecosystems (Table 2). As climate change effects are not restricted to only one compartment, and coupling between the pelagic and benthic realm is particularly tight and thus crucial in the polar regions, we encourage more holistic ecosystem approaches, including traits of multiple species across the entire marine system. There is no technical limitation to a trait-based approach, even in broad extents when combining algae, invertebrates, fish, mammals, and birds as long as every trait is measurable or possible to code in all organisms (Dolédec and Statzner, 1994; Foden et al., 2013). Our literature review showed that several traits are used across all ecosystem components (Table 2, S1). Additionally, climate change effects do not stop at the shorelines, terrestrial ecosystems might be included in the joint trait efforts. The existing Register of Antarctic Marine Species (RAMS) (De Broyer and Danis, 2011) has recently decided to broaden its scope and to also include the non-marine species from the Antarctic Region and a number of their relevant traits (the register will then become RAS: Register of Antarctic Species) (WoRMS Editorial Board 2017).

As we demonstrated with many examples from current literature, trait-based approaches provide the most insight when used in addition to species based methods in marine community ecology. Ongoing efforts to harmonize terminology and methodology, methodical improvements via use and promotion of sensitivity analyses, and the easy access to trait information, best practices, manuals and scripts (see also Step 1, 2 and 3 of our roadmap) will make these methods more easily accessible to a broader community of users within the scientific community. Joint trait initiatives, workshops and outcomes like this perspectives paper will aid to their further promotion, potentially making them standard practice in marine ecology in the future.

## Conflict of interest

None.

## Acknowledgements

Authors' Contributions

All the authors (except MN) attended the Arctic Traits Workshop in Vienna in December 2016 (organized by RD) and outlined the manuscript via their contributions during the workshop. MA, BB, CC, MK, CK, LV, MWK and IZ contributed substantially to its writing and editing and are thus ordered right behind the lead author RD (in alphabetic order).

Other authors are listed alphabetically thereafter. RD performed the literature review and prepared the tables and figures, IZ prepared Supplementary data.

## Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolind.2018.04.050.

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