Biodiversity colonisation of the Arctic under climate change: impacts on land, sea and people

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Author's Declaration

The material contained within this thesis has not previously been submitted for a degree at Durham University or any other university. The research reported within this thesis has been conducted by the author unless indicated otherwise.

Chapter 5 has now been published as:

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The author contributions were as follows: ERG, ABB, TDE conceptualized the study, with input from SGW. ERG and ABB conducted formal data analysis and visualization, wrote the original draft, reviewed and edited the manuscript. TDE and SGW provided supervision and validation of results, reviewed, and edited the manuscript.

Elizabeth Gillie

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Abstract

Climate change is driving a redistribution of species worldwide. The Arctic is a particularly vulnerable ecosystem which is affected by climate change at a much greater rate than the rest of the world. Both terrestrial and marine systems are under pressures of climate-driven species range shifts, and it is imperative to understand how these ecosystems and communities may change in the future. Despite the magnitude of changes, the Arctic remains relatively understudied and the consequences of novel species shifting into the Arctic remain relatively unknown. By addressing these critical knowledge gaps, this thesis offers comprehensive insights into the impacts of climate-driven species redistribution on terrestrial and marine ecosystems in the Arctic, alongside its repercussions for people. Using species distribution models (SDMs), I find a high potential for novel species assemblages to emerge in the Arctic, particularly in the high and low Arctic which are the northernmost Arctic regions situated above 75° and between 75°-65° North, respectively. I show, however, that species' dispersal abilities and habitat availability limit range shifts, constraining the capacity of terrestrial species to track suitable climate. Marine ecosystems exhibit significant variations in species responses to climate change, with projections indicating over 50% losses of marine fish and mammal species by 2100 from the Greenland Sea, Norwegian Sea and Barents Sea regions in the Arctic. Additional indicators of biodiversity change, such as functional and phylogenetic diversity, provide nuanced insights into the impacts of range-shifting species on Arctic communities. I project increases in functional diversity driven by the influx of novel species with traits distinct from those of current Arctic communities, potentially reshaping community structure and function. Despite significant increases in novel colonists, I find significant implications from concurrent losses of native Arctic species. These losses disrupt ecosystem functioning and emphasise the importance of considering both species gains and losses in biodiversity assessments. Then, by combining SDMs and food-web models, I explore the emergence of novel ecosystems in the North Water Polynya, one of the most productive ocean ecosystems in the world. I find that incoming species decrease energy transfer to higher trophic levels, suggesting climate change could completely disrupt a marine Arctic food web. Finally, I find that climate change disproportionately impacts local Arctic communities, with effects on their livelihoods and cultural identities being far greater than the effects experienced at national or international levels, as their lives are deeply intwined with native species. While novel species may offer new trade opportunities, especially of marine fish, the loss of native species may outweigh these gains, particularly in terrestrial systems. Together, my results from this thesis significantly advance our understanding of the impacts of biodiversity colonisation in the Arctic on land, sea and people. This thesis highlights the urgency of adopting future-oriented conservation approaches to safeguard Arctic biodiversity in the future, support resilient ecosystems, and address the multifaceted challenges posed by ongoing environmental change. Engaging stakeholders, including local communities, scientists, policymakers and industry representatives, in collaborative research and decision-making processes will be crucial to ensuring the relevance and effectiveness of conservation and management efforts in the Arctic.

Chapter 1

General Introduction

1.1 Introduction

Climate change is occurring at an unprecedented rate across the globe. Global average surface temperatures in the period 2001-2020 have increased by 1.1°C from the baseline 1850-1900 (IPCC, 2023). Globally, 2023 was the warmest year on record since 1850, 1.46°C above the pre-industrial baseline (1850-1900) (IPCC, 2023) and, as a result, for the first time ever, ten years in a row exceeded 1°C above the baseline (ECMWF, 2023). The consequences of such global warming are far-reaching. Since 1979, Arctic sea-ice minimum and maximum extents have decreased at a rate of between 3.5-4.1% per decade (IPCC, 2014), and between 2011-2020 sea ice reached its all-time minimum since 1850 (IPCC, 2021). Global sea level rose by an average of 0.19 m from 1901 to 2010, and the rate of sea-level rise since the mid-19th century has been higher than at any point during the previous two millennia (IPCC 2014). The increase in anthropogenic greenhouse gas (GHG) emissions is extremely likely to be the driver of observed climate warming since the mid-1900s (IPCC, 2014; Notz & Stroeve, 2016). To project potential trajectories of future climatic change, the IPCC first developed Representative Concentration Pathways (RCPs) and subsequently developed the complementary Shared Socioeconomic Pathways (SSPs) (van Vuuren et al., 2017). The RCPs comprise four scenarios based on global emission trajectories, used to make projections of how concentrations of GHG emissions will change up to 2100 because of anthropogenic activities. These were later updated by the SSPs offering five future pathways, exploring broader narratives of future change and including socioeconomic aspects such as population, education and economic growth. Climate projections show that, even under the sustainability-focused lowest emissions scenario (SSP1-2.9), global mean surface temperatures will increase by 3°C to 3.5°C by 2100 (Bauer et al., 2017). For a high-growth, energy intensive emissions scenario (SSP5-8.5), warming of 4.7°C to 5.1°C is predicted (Bauer et al., 2017). To understand the impact of these changes on both biodiversity and humanity, it is imperative to consider the changing interactions between climate, human and natural systems.

Anthropogenic climate change is already threatening biodiversity across much of the world (Román-Palacios & Wiens, 2020). Global studies have shown that many species, across both terrestrial (Harvey et al., 2023; Rees et al., 2020; Stephens et al., 2016) and marine systems (Edgar et al., 2023; Free et al., 2019; Moore et al., 2018; Poloczanska et al., 2016), are already being affected by climate change (Díaz et al., 2019; Isbell et al., 2023). Under scenarios of climatic change, increasing rates of species extinctions (Jones & Cheung, 2015; Thomas et al., 2004; Toussaint et al., 2021), changes in species' abundance (Edgar et al., 2023), and changes to community structure (Stewart et al., 2022; Voskamp et al., 2021) have been forecast. Contemporary climatic change has also been linked to habitat alteration and degradation (Powers & Jetz, 2019), changes to species' distributions (Hällfors et al., 2024; Scheffers & Pecl, 2019), biome shifts (Powers & Jetz, 2019), and changes in phenology (Pendleton et al., 2022; Visser & Both, 2005). However, significant knowledge gaps remain regarding the long-term adaptive capacity of many species, the resilience of ecosystems to compounded stressors, and the cascading effects of biodiversity changes on ecosystem services and human well-being. It is vital to understand how natural systems are responding to climate change and to assess the consequences for ecosystem function and human societies. Providing policymakers and conservation management with reliable assessments of change and their impacts is a vital, ongoing challenge in ecological research.

In the following section, I briefly discuss how species are responding to recent climate change, including changes in species' distributions and biotic interactions. I then focus on the Arctic, examining why this region is especially vulnerable to climate change, with particular focus on biodiversity colonisation in terrestrial and marine systems. I then discuss the wider implications of biodiversity colonisation in the Arctic for ecological communities and the ecosystem services provided to human societies. Following this, I give a brief overview of the modelling approaches used to assess the impacts of climate change on species' distributions, the considerable knowledge gaps associated with these methods, and the various approaches that can help fill these knowledge gaps. Finally, I outline the aims of this thesis.

1.1.1 Species' responses to climate change

Increasing evidence suggests that species are already responding to climate change (Isbell et al., 2023; Pecl et al., 2017). Climate change is causing changes in the timing of seasonal events such as migration, insect emergence, flowering of plants and breeding (Burrows et al., 2011; Kharouba et al., 2018; Marrot et al., 2018; Poloczanska et al., 2016). Parmesan and Yohe (2003) carried out one of the first comprehensive analyses of over 1,700 species to summarise evidence of biological impacts of climate change. In their quantitative assessment of phenological data from 677 species from six taxa, 62% showed trends towards spring advancement whilst only 9% demonstrated delayed phenology (Parmesan & Yohe, 2003). Of those that shifted, 87% were in the direction expected from climate change. Climate change also drives changes in the availability and location of suitable habitat, causing changes in species distributions (Lenoir et al., 2020; Lenoir & Svenning, 2015). Both elevational and latitudinal shifts in species' ranges have been recorded across various taxa (Loarie et al., 2009), and more recent assessments show even greater range changes than previously thought (Chen et al., 2011; Lenoir et al., 2020; Pinsky et al., 2013). Species do not respond uniformly and, as a result, changes in community dynamics and composition have been documented for species including butterflies (Menéndez et al., 2006), plants (Bertrand et al., 2011) and birds (Devictor et al., 2008).

Not all species will be affected by climate change in the same way. Understanding how species respond to climate change requires consideration of a species' inherent vulnerability (Foden et al., 2013; Pacifici et al., 2015). Vulnerability has three components: exposure, sensitivity and adaptive capacity (Dawson et al., 2011). Species have greater exposure to climate change in locations undergoing greater rates or magnitudes of warming, sea-level rise and other extreme events. Sensitivity depends on life-history traits and habitat preferences; sensitive species will undergo significant population changes and declines in survival or fecundity even under the smallest changes in climate. Finally, if a species can persist by tracking suitable climate, they have a higher adaptive ability. Species' vulnerability thus depends on specific factors such as life-history traits, genetic diversity, colonisation ability, and phenotypic plasticity. For example, species with certain life-history traits, such as long generation times or limited dispersal abilities, will be less capable of recovery after environmental change or disturbance. Species with specialist diets are likely to be more adversely affected by climate change and generalists more likely to persist, causing functional homogenization in communities (Davey et al., 2012; Warren et al., 2001).

1.1.1.1 Range shifts

Anthropogenic climate change is driving a redistribution of the Earth's species (Pecl et al., 2017). Species across terrestrial, marine and freshwater ecosystems are already altering their ranges in response to changing climatic conditions (Chen et al., 2011; Lenoir & Svenning, 2015; Poloczanska et al., 2013). Both latitudinal and elevational shifts have been recorded for a variety of taxa with this effect being predicted to intensify into the future (Pecl et al., 2017). In a quantitative assessment of range and abundance data from 893 species, Parmesan and Yohe (2003) found that 434 species have changed in either range or abundance. Of these, 80% shifted in accordance with climate change. Their meta-analysis further detected an average poleward or elevational range shift of 6.1 km (or m upward) per decade. More recently however, evidence suggests this original estimate may be conservative. Although they only focused on terrestrial species, Chen et al. (2011) reported range shift rates two to three times higher: a median rate of latitude shift of 16.9 km per decade and elevational shift of 11 m per decade. More recent findings have found shifts are more conservative, whereby European birds have shifted their ranges at a rate of 2.4km per decade (Howard et al., 2023). Species tracking shifting climate may not be moving at a fast enough rate to track climate change (Devictor et al., 2008). One of the first global studies of climate change impacts in the marine realm was undertaken by Cheung et al. (2009). They projected future range shifts of species to investigate climate change impacts on global marine biodiversity and predicted a mean poleward range shift of 600 km and 223 km for pelagic and demersal species respectively by 2050. Though they incorporated population dynamics and dispersal abilities into their models, there were significant uncertainties in distribution data and dispersal parameters. Projections of biodiversity changes on more local, regional scales and in most sensitive areas should provide a more accurate picture of likely impacts. Regardless of their limitations, these studies imply greater projected responses of species than previously thought. It is unsurprising that studies report varying responses to climate change as the magnitude of changes depends on the taxa being studied, the geographical scale and area of focus, and even the specific population. Marine species are largely expected to track isotherm migration rates to maintain thermal niches, and so how sensitive a species is to climate change and how much their range might shift depends on the velocities of change in specific regions (Ackerly et al., 2010; Loarie et al., 2009). Lenoir et al. (2020) found that poleward shifts of species were six times faster in oceans than those on land, further finding marine species track isotherm shifts far better than terrestrial species. This could explain the larger rates of range shifts for marine species (Burrows et al., 2011; Cheung et al., 2009), largely because there are fewer human disturbances blocking range shifts in the ocean and fewer constraints to dispersal and colonisation in open oceans (Poloczanska et al., 2013). In addition, in the tropics, marine species are living in environments closer to their upper thermal limits because sea temperatures are the highest, so are more likely to shift faster with rising sea surface temperatures (Pinsky et al., 2019). There is a growing need to understand the consequences of such changes for ecosystem functioning and dynamics, conservation management and human societies (Bonebrake et al., 2018).

1.2 The Arctic

The Arctic is a vast and remote region encircling the northernmost parts of the Earth. Defined by unique climatic and ecological characteristics, it spans areas where the average temperature of the warmest month remains below 10°C (Stonehouse, 1989). The region is often delineated by the Arctic Circle (66°33′N latitude), though its ecological and climatic boundaries extend further based on vegetation zones, permafrost extent, and oceanographic features.

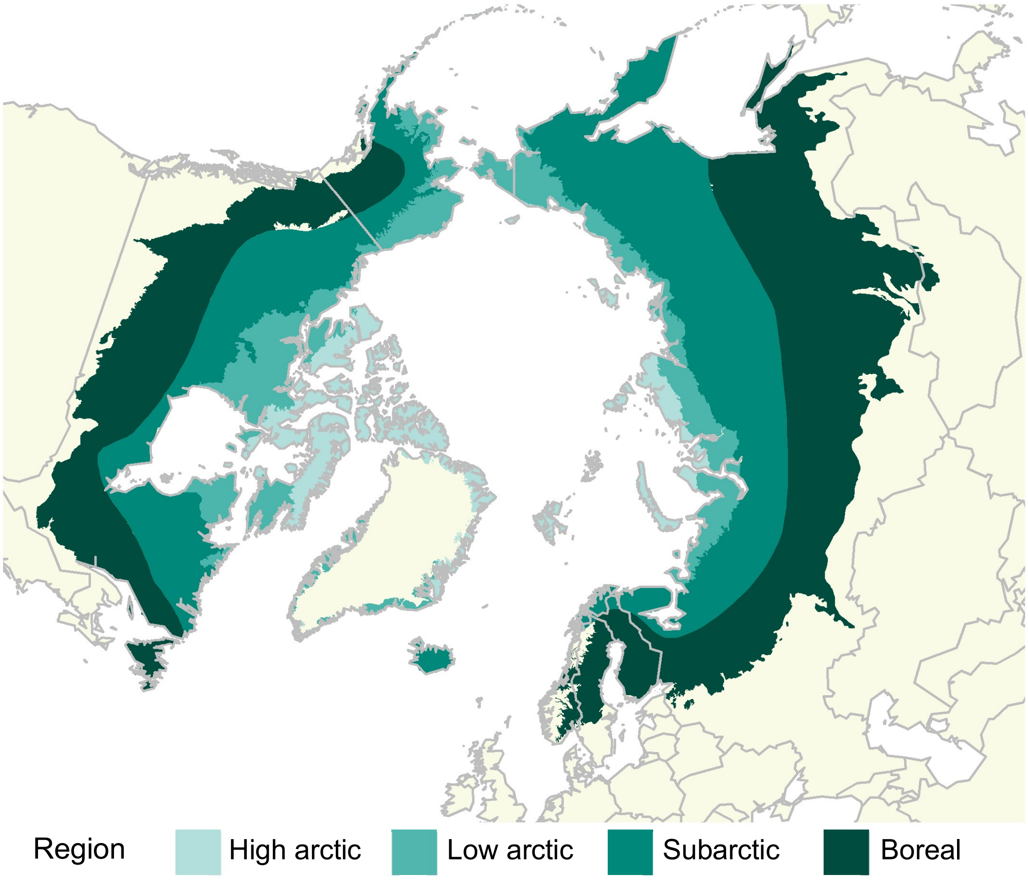

Figure 1.1. Arctic and subarctic regions. Polygons for High, Low and subarctic were from the Conservation of Arctic Flora and Fauna (CAFF) /Arctic Boundary Assessment GeoNetwork catalogue (CAFF 2019), as defined by the Circumpolar Arctic Vegetation Mapping Project - Bioclimatic subzones (CAVM Team 2003) and the Arctic Biodiversity Assessment (ABA). Boreal region from WWFs Terrestrial Ecoregions of the World (Olson et al. 2001), and was cropped to exclude the subarctic using ArcGIS Pro v2.8.6.

The Arctic can be divided into distinct zones based on vegetation and geography. The Arctic proper, the most northerly area, consists of the high and low Arctic (Figure 1.1). The high Arctic is characterised by polar deserts with sparse vegetation, while the low Arctic is dominated by tundra, a biome with mosses, lichens and grasses adapted to short growing seasons and permafrost (Peterson, 2014). South of the Arctic proper lies the subarctic, a transitional zone composed of a mix of tundra, barren land and northern boreal forest (Figure 1.1). Further south, the boreal forest (Figure 1.1), or Taiga, forms the world's largest terrestrial biome and is dominated by conifer forest (Haila, 1994). The Arctic proper, subarctic and boreal forest are situated at the northernmost part of the Holarctic which is a biogeographical zone comprising all non-tropical habitats found across the continents in the Northern hemisphere.

1.3 Climate change in the Arctic

Arctic ecosystems are particularly vulnerable to ongoing climatic and environmental change. The current warming in the Arctic (here being considered as all areas above 66'33°N latitude) is occurring at two to four times the rate of the global average (Overland et al., 2019). The average land-surface air temperature in the region between 2018 and 2019 was the second warmest on record. Snow cover extent has decreased steadily from 1981-2019 by 3.4% and 15.2% per decade in May and June respectively (Mudryk et al., 2019). Snow depth and density across the Arctic has decreased by more than 10% since 1981 (Mudryk et al., 2019). Arctic sea ice is undergoing rapid change; not only declining but also becoming increasingly unstable as older sea ice declines and younger sea ice dominates, with the latter being thinner and more prone to melting (Kwok, 2018; Lindsay & Schweiger, 2015; Moore et al., 2019). Evidence suggests a linear trend between sea-ice loss and anthropogenic CO_2 emissions (Serreze & Stroeve, 2015), indicating a sensitivity of 3.0 ± 0.3 m^2 sea-ice area loss per metric ton of CO_2 emissions across the period 1953-2015 (Notz & Stroeve, 2016). Despite the magnitude of changes compared to other regions, the Arctic remains relatively understudied particularly regarding its biodiversity and ecosystem responses to climate change. Future climate change and the adverse effects already being observed have created a growing urgency to improve our understanding.

Continued warming and decreasing sea ice are impacting Arctic ecosystems and communities. Ecological consequences consistent with recent environmental changes have already been observed across the Arctic. Here, I present some examples of these recently recorded changes. Plant growing seasons are lengthening, as ice is melting earlier and phenologies are changing. Warming spring temperatures in the Arctic are causing a trophic mismatch between reindeer and forage availability. Post and Forchhammer (2008) found forage emergence correlated with the degree of trophic mismatch between forage availability and calf production. A two-week advance in plant phenology, because of a 4.6°C March-May temperature rise, increased calf mortality seven-fold and caused a four-fold decline in calf production. As the season shifts earlier, calves are born later in the year, when there is lower forage abundance and a shorter period of higher food quality. This explains why higher calf mortality was associated with a greater trophic mismatch. Earlier and accelerating sea-ice melt has further increased vegetation productivity across the Arctic tundra. Over a 28-year period (1984-2012), positive trends in vegetation growth, biomass and abundance (often referred to as Arctic greening) occurred in tundra throughout Canada and Alaska (Ju & Masek, 2016). Plot-based evidence of vascular plant growth at 46 locations in pan-Arctic tundra from 1980-2010 also supports the trend in increased vegetation productivity associated with increasing temperatures (Elmendorf et al., 2012). Growing evidence suggests spatial heterogeneity in the patterns of vegetation responses across the Arctic (Elmendorf et al., 2012; Huang et al., 2017). Though some species may be benefiting, in terms of productivity, species in marine and freshwater environments are particularly sensitive to change. Sea-ice loss is causing population declines of polar bear (*Ursus maritimus*) (Regehr et al., 2007), walrus (*Odobenus rosmarus*), and ivory gulls (*Pagophila eburnean*) (Laidre et al., 2008a; Post et al., 2009). In addition, as sea ice provides a surface on which algae can grow, which forms the base of the marine food web, there will likely be major disruptions to communities across trophic levels.

Species' distributions are already changing across the Arctic. Elmhagen et al. (2015) found significant range contractions and declines in northern species across Arctic tundra across Sweden. Fischbach et al. (2007) evaluated the changes in distribution of polar bear denning between 1985 and 2005 in northern Alaska. The proportion of dens on ice packs declined from 62% (1985-1994) to 37% (1998-2004). They found a landward shift in denning and concluded it was a result of declining availability and suitability of sea ice. Furthermore, Arctic marine species may be highly sensitive to warming because of the velocity of climate change and shifts in seasonal timing of temperatures are greater in the ocean than on land (Burrows et al., 2011); something they struggle to keep pace with. Fossheim et al. (2015) surveyed demersal fish species in the Barents Sea between 2004 and 2012. They observed contractions of Arctic community ranges, composed predominantly of bigeye sculpin (*Triglops nybelini*), Greenland halibut (*Reinhardtius hippoglossoides*) and snailfish (*Liparis* spp.), and a 159km northward range shift of the entire community to the most northerly point of the surveyed area. Some species that were found on the northern shelf edge were found in deeper water than they formerly occupied, which implies depth-shifting responses. For those species capable of moving deeper in the water column to combat rising temperatures, seabed depth could limit responses to future climate change. As conditions such as light change with depth, this may also preclude species tracking favourable oceanic conditions to ever greater depths. Plant distributions are also changing in terrestrial Arctic ecosystems (Myers-Smith et al., 2011). Using satellite imagery, Arctic greening can be tracked and has shown an advancement of the shrub-line and increase in cover of woody plants (Myers-Smith et al., 2011). Arctic species are expected to undergo further changes in distributions under future climate change scenarios. Thus, reliable predictions of future range shifts are essential to develop appropriate conservation and management plans to mitigate climatic change impacts.

1.3.1 Biodiversity colonisation of the Arctic

In addition to distributional shifts of species within the Arctic, there are widespread expectations that species from temperate regions will move into the Arctic under climate change. Warming temperatures, sea-ice melt and changing ocean currents are driving a rapid process known as ‘borealisation’ of Arctic marine ecosystems (Mueter, 2022). The term ‘borealisation’ refers to the northward expansion of temperate ‘boreal’ fish species into Arctic waters. These shifts are likely to be much more prominent in marine systems due to faster range shifts in oceans than on land (Pinsky et al., 2013; Poloczanska et al., 2013). Cheung et al. (2009) found mean invasion intensity was nearly 5.5 and 2 times higher than the global average in the Arctic and Southern Ocean, respectively. Invasion intensity can be related to species’ characteristics. For example, intensity will generally be higher for pelagic marine species than demersal species due to greater dispersal capabilities (Cheung et al., 2009). Similarly, Cheung et al. (2015) predicted a higher rate of species invasion in the north Bering Sea and north Gulf of Alaska for pelagic species. Nye et al. (2009) found similar shifts for pelagic species only, although the range shifts they reported were larger than those recorded by Poloczanska et al. (2013). This difference could be explained by Nye et al. (2009) addition of demersal species. The northward expansion of suitable thermal habitat for boreal species in the Barents Sea has caused invasions of more southern fish such as Atlantic cod (*Gadus morhua*) into the Arctic (Fossheim et al., 2015). The consequences of these novel colonists in the Arctic remain relatively unknown.

Species invasions and colonisations due to range shifts could have cascading effects on Arctic systems. For example, the potential borealisation of the Arctic marine ecosystem could have profound implications on community structure and function (Fossheim et al., 2015; Grebmeier et al., 2006; Kortsch et al., 2015; Pecuchet et al., 2020). Arctic marine ecosystems are ice-dominated and consist of small-sized benthivores (Frainer et al., 2017). Incoming boreal species tend to be large generalists, such as cod and haddock (*Melanogrammus aeglefinus*), which will alter community composition by increasing food web connectivity between the benthos and pelagic community. This, in turn, may decrease modularity or compartmentalisation (modularity: where species within subgroups of the food web interact more with each other than with those outside of the subgroup) (Eskuche-Keith et al., 2023; Frainer et al., 2017; Kortsch et al., 2015; Pecuchet et al., 2020). The movement of boreal fish species such as cod into the Barents Sea implies increased predation pressure on small Arctic species and increased competition for the few larger Arctic predatory fish, such as Greenland halibut and Arctic skate (*Amblyraja hyperborean*) (Fossheim et al., 2015). Similarly, in the Bering Sea, the pelagic-dominant marine ecosystem of the subarctic is shifting northward and impacting benthic-feeding primary consumers (Grebmeier et al., 2006). In the Barents Sea, sea-ice loss has increased primary production due to increased light availability over a longer ice-free period, and caused a new, second phytoplankton bloom in autumn (Ardyna et al., 2014). Primary production has further increased where Atlantic and Arctic waters meet (Dalpadado et al., 2014), and coincides with observations of northward expansions of boreal fish (Fossheim et al., 2015). These changes are expected to continue given projected future change. Studies focusing on predicting future changes to community structures are relatively rare yet are going to be essential to understand the implications of climate change in the Arctic. Arctic ecosystems could be considered model study systems for investigating changing interactions and community composition, due to the relatively simple nature of some Arctic food webs.

It is thus critical for research to predict how such changes will impact terrestrial and marine ecology of the Arctic. In addition, human-mediated species invasions will increase due to increased human activity as sea ice melts and new areas become accessible (Chan et al., 2019). Conservation management of the natural spread of non-native species to the Arctic depends on an understanding of habitat suitability. We can then manage other human-mediated dispersal pathways to stop movements to suitable habitat that is beyond a species' natural dispersal pathway (Forrest et al 2009). Incoming species will consequently affect

Arctic communities that rely on functioning ecosystems to survive, making the Arctic a high-risk region (Chan et al., 2019). Producing more nuanced predictive models will help provide a more detailed outlook of how communities will respond to climate change.

1.4 Assessing the impacts of climate-driven range shifts

1.4.1 Measures of biodiversity

Assessing the impacts of climate-driven range shifts on biodiversity requires a multi-faceted approach that considers multiple measures of biodiversity (Alahuhta et al., 2018; Speed et al., 2019; Stewart et al., 2022). These measures include taxonomic, functional and phylogenetic diversity. Taxonomic diversity assesses the number and variety of species present in a given area and is by far the most popular method for assessing changing biodiversity under climate change (Antão et al., 2020; Hiddink & ter Hofstede, 2008; Kaschner et al., 2011; Parravicini et al., 2013). Going beyond taxonomic richness alone, researchers have advocated for studies that analyse patterns in two additional facets of diversity: functional and phylogenetic (Cadotte et al., 2011). Functional diversity reflects the ecological roles and traits of species within communities. As species' distributions shifts, so too do traits and trait combinations (Gallagher et al., 2013). As more information on species' traits becomes available, studies are emerging that assess future changes to functional diversity (Kuebbing et al., 2018; Mammola et al., 2021; Stewart et al., 2022). Changing distributions of species can also change the evolutionary heritage of the local community, or its phylogenetic diversity (Saladin et al., 2020). Phylogenetic diversity provides useful insights into the adaptive and evolutionary potential of a community facing environmental change (Faith & Hawksworth, 1997; Voskamp et al., 2022).

By employing multiple measures of biodiversity, researchers can gain a comprehensive understanding of the ecological consequences of shifts in species' distributions in the Arctic under climate change, facilitating informed conservation and management efforts in the region. While there has been an increased effort to measure alternative aspects of diversity, there remains a lack of studies, especially in the marine realm, that explore the potential impacts of future climate change on multiple facets of biodiversity and hence changing communities and ecosystems in the Arctic and beyond.

1.4.2 Changes to community structure and function

Range-shifting species could have cascading impacts at community and ecosystem levels in the Arctic. Losing fundamental ecological roles in the communities, such as those provided by keystone species, can cause a structural regime-shift in Arctic ecosystems (Griffith et al., 2019). Communities with high taxonomic diversity may be more resilient to the impacts of climate change, as these communities likely have high functional redundance, whereby multiple species play the same broad role within an ecosystem (Biggs et al., 2020). As such, these communities are considered buffered against species loss, as remaining species can continue to perform those core roles in the community. However, high biodiversity and subsequent functional redundancy may not actually translate to climate resilience. For instance, tropical reef fish communities display high over-redundancy, meaning the level of redundancy is not high for all roles in the community (Mouillot et al., 2014). Taxonomic and functional diversity are already increasing in the Arctic (Frainer et al., 2021) but broader-scale studies that assess the impacts of range-shifts on Arctic ecosystem structure and function are lacking. As the Arctic is expected to experience both gains and losses of species, it is uncertain as to whether incoming species can replace the important functions potentially lost with climate change.

1.4.3 Changes to trophic food webs

Arctic food webs could change drastically if a species not previously present in Arctic ecosystems form new interactions with current Arctic species, potentially disrupting previously stable biotic processes. This would cause changes to competition, predator-prey dynamics and parasite or pathogen transfer. Range-shifting species could trigger trophic cascades, whereby changes in trophic level affect the abundance or behaviour of species in non-adjacent trophic levels. Increasing abundances of the forage fish, such as capelin (*Mallotus villosus*), has already resulted in Arctic cod (*Arctogadus glacialis*) being replaced as the main diet of some seabirds (Hop & Gjøsæter, 2013). When Brünnich's guillemot (*Uria lomvia*) switched their diet to capelin due to their higher abundance, the growth rate of nestlings declined (Gaston et al., 2005). This may be due to the much lower lipid content in capelin than Arctic cod (Hop & Gjøsæter, 2013). Similarly, when harp seals switched their diet from Arctic prey to Atlantic species, their body condition declined due to the poorer nutritional quality (Øigård et al., 2013). Declining body condition of harp seals has also been attributed to increased competition with the boreal species, Atlantic cod (Bogstad et al., 2015).

Similar changes to trophic food webs have been observed in terrestrial systems with the addition of new herbivores. Alaskan moose (*Alces alces*) have extended their range from boreal forest into tundra as a result of increased warming, resulting in expanded shrub cover across Arctic tundra (Tape et al., 2016). The browsing effect of moose may change herbivory dynamics and regulate the expansion of fast-growing deciduous shrubs (Christie et al., 2015). Less palatable shrubs such as Siberian alder (*Alnus viridis*) and resinous dwarf birch (*Betula nana exilis*) could proliferate and expand faster than preferred forage (Christie et al., 2015). This could ultimately lead to declines in vegetation that support other herbivores or omnivores. The largest impacts will likely occur in communities composed of specialist species, small vulnerable populations, and those that have low genetic variability (Clavel et al. 2011). Studies of range shifts rarely document community impacts, which are vital for future conservation planning.

1.4.4 Changes to ecosystem services and the social-ecological system

A redistribution of Arctic species will not only impact natural systems but also fundamental aspects of human societies. Humans and nature are interdependent and connected in a socio-ecological system that is becoming ever more dynamic under environmental change (Solan et al., 2020). Not only will redistributions impact the people living in the Arctic, but also at global scales, as the Arctic is intimately connected to global ecological, geophysical and geopolitical processes (Arctic Council, 2016; Haldén, 2018). This will pose both economic and environmental challenges to the region's governance to maintain sustainable human-environment relationships (Young, 2010). Research needs to link projections of environmental change to their impacts on the services they provide human society.

The notion of ecosystem services (ES), referring to the benefits nature provides to human societies, provides a platform for investigating the impacts of Arctic change (Malinauskaite et al., 2019). Functioning ecological communities and ecosystems are fundamental to maintaining ES. This becomes important if temperate, southern colonists displace Arctic species of ecological and/or economic importance without bringing with them equivalent replacement service values. Changes to community dynamics and structure could affect the availability and provision of ES. Few assessments, however, link range shifts or novel colonists to ES. Even fewer apply the ecosystem service concept in an Arctic context (Malinauskaite et al., 2019). We need to consider both ecological and socio-economic impacts of range-shifting species under climate change to inform planning and management strategies. In the following sub-sections I briefly discuss key ES of the Arctic (provisioning, regulating, cultural and supporting) and identify potential impacts of redistributions of species.

1.4.4.1 Provisioning services

Provisioning services are those obtained directly from ecosystems such as wild animal and plant products, livestock, crops, fisheries, fresh water, hydropower, and fuel and timber (Millennium Ecosystem Assessment, 2005). Arctic fish stocks are expected to rise under global climate change as temperate species move into the Arctic and into parts of the Arctic Ocean previously under sea ice (Fossheim et al., 2015). Although large commercial companies will be able to exploit new distributions of fish stocks, local indigenous communities might not be able to adapt to the new resource and may be disproportionately impacted. Fishers from an Inuit community in Canada suspected that observed changes to the colouring of Arctic char (*Salvelinus alpinus*) meat and reduced overall fish stocks were caused by the expansion of capelin (Galappaththi et al., 2019).

The Saami are an Indigenous people inhabiting the northern regions of Norway, Sweden, Finland and the Kola Peninsula in Russia, whose traditional livelihoods include reindeer herding, fishing and hunting. In terms of fuel and timber, forests not only provide Saami with fuel and materials to build boats, tools and traps but are also vital as pastures for reindeer (Aiko & Müller-Wille, 2006). Forest pest species are expanding northward causing extensive forest damage such as defoliation and mortality. Range shifts of pests such as geometrid moths have been attributed to the expansion of mountain birch to higher latitudes and elevations (Jepsen et al., 2011). This will affect the services the forests provide to indigenous people.

1.4.4.2 Regulating services

Regulating services are those obtained from ecosystem processes such as climate regulation, water regulation, pest and disease regulation, water purification, natural hazard regulation, and air quality regulation (Millennium Ecosystem Assessment, 2005). Vegetation expansion may influence climate regulation because increased cover reduces albedo, increasing warming (Pearson et al., 2013). Boreal forest expansion into tundra may create an even larger climate feedback by replacing snow cover with a darker, absorptive surface that has an even lower albedo than tundra (Millennium Ecosystem Assessment, 2005). Models suggest forest expansion into tundra accounted for half of the observed warming during the Holocene at high latitudes (Foley et al., 1994). A model of hypothetical expansion of boreal forest in future showed that lower albedo from forest cover increased average local surface warming by 1-2°C at various locations (Liess et al., 2012).

1.4.4.3 Cultural services

Cultural services are the non-material benefits to human society including aesthetic values, recreation and tourism, knowledge and educational values, spiritual and religious values, and well-being (Millennium Ecosystem Assessment, 2005). Redistribution and replacement of polar species impacts cultural resources that are cherished by indigenous communities. Various species provide social and cultural services to Arctic people, including walrus, little auk (*Alle alle*) and reindeer (*Rangifer tarandus).* Reindeer especially are central to their cultural identities (Jansson et al 2015). In addition to direct shifting of species of cultural service value, range shifts of their important resources such as prey or forage will also impact these species. A change to only one component of a social-ecological system, such as the gain or loss of an individual species, can influence multiple ES. For example, Mosbech et al. (2018), describe the little auk as an ecological and social engineer which influences societies and cultures of local communities. In addition, changing climates and habitats may also influence how people use the Arctic region proper. For example, the expansion of woodlands into tundra, might increase summer tourism, perhaps with forest summerhouses to follow. Indeed, summer and winter tourism increased six-fold between 2006 and 2016 (Runge et al., 2020). By contrast, as the Arctic loses its unique species from many areas, tourism that is attracted to novel landscapes and species might decline (Grose et al., 2020). One of the most challenging aspects of ES assessment includes the benefits that comprise components of improving human well-being. These are by far the least considered ES as it is difficult to put an economic value on a ‘good life’ (Karlbolten et al 2017). Social identity and well-being in the Arctic are closely linked to landscapes and ecosystems, thus warranting closer attention.

1.4.4.4 Supporting services

Supporting services are indirect, on larger scales and underpin the services listed above. These include primary production, water cycling, nutrient cycling, soil formation, and food web maintenance (Millennium Ecosystem Assessment, 2005). Non-native species may change interactions and disrupt food webs by altering energy flows. The knock-on impact of larger, generalist fish species in Arctic seas could affect biomass production (Frainer et al., 2017) and shift trophic dynamics as large predators tend to interact with more diverse prey (Brose et al., 2012).

1.5 Methodological approaches to assessing the impacts of species' range shifts in the Arctic

1.5.1 Species distribution models

Species' distributions can be modelled as a function of the environment and/or climate in species distribution models (SDMs) (Elith et al., 2010; Latimer et al., 2006). SDMs relate the observed range of a species to contemporaneous climatic conditions to establish a species-climate relationship. The most common approach uses predictive SDMs know as bioclimatic envelope models or niche-based models (Pearson & Dawson, 2003; Thomas et al., 2004; Thuiller et al., 2005). SDMs have been applied to past climatic conditions to understand species' prehistoric distributions, but a considerable amount of literature focuses on extrapolating ecological models to provide tools for future policy and decision making (Guisan et al., 2013; Heikkinen et al., 2006; Pearson & Dawson, 2003; Thomas et al., 2004). Model-based extrapolation or forecasting to unsampled time and space applies the species-environment relationship to future climate scenarios (impacts of anthropogenic climate change) to identify areas that may be climatically suitable for a species in future (Elith et al., 2006; Pearson & Dawson, 2003). In this way, SDMs are useful techniques to assess the extent to which contemporary and future climate change will impact species and their distributions. SDMs have become one of the most widely utilised tools in the fields of ecology, biogeography and macroecology (Araújo et al., 2019).

SDMs have been widely applied but have important shortcomings that should be considered in their utility (Jarvie & Svenning, 2018). Correlative SDMs do not account for the underlying mechanisms that may determine species' distributions such as evolutionary processes, biotic interactions, physiological tolerances and life-history traits. In addition, the ability of species to disperse to new locations and the availability of suitable habitat could restrict species' range shifts, even though the areas might be projected to become climatically suitable. This is unlikely to present an issue for studies interested only in whether an area becomes climatically suitable in future. Additionally, SDMs have been considerably improved in recent years by incorporating dispersal abilities and habitat availability post-hoc, i.e. by clipping species' range projections by a dispersal distance and the availability of suitable habitat (Barbet-Massin et al., 2012; Stewart et al., 2022; Titley et al., 2021). As most SDMs are applied at relatively coarse spatial scales, it can be assumed that climate is more likely to be the most important factor in driving species redistribution. Despite some caveats, species distribution models remain an invaluable tool in forecasting range shifts to understand the impacts of anthropogenic climate change (Heikkinen et al., 2006; Sofaer et al., 2019), and have been shown to accurately predict species redistributions (Piirainen et al., 2023; Stephens et al., 2016). Understanding model limitations and uncertainties is essential in the application of these tools (Araujo et al., 2005; Pearson & Dawson, 2003; Yates et al., 2018).

1.5.1.1 Marine systems

SDMs have been applied considerably less in marine systems than terrestrial, though interest in marine-focused SDMs is rising (Robinson et al., 2017). Some of the largest changes of species' distributions are being observed in the marine domain, making them important systems in which to assess impacts of climate change on communities and ecosystems. There are particular challenges associated with marine SDMs that differ from terrestrial due to unique environmental characteristics (Robinson et al., 2011). One challenge includes the added dimension of the water column where species can shift from shallower to greater depths. Studies have observed species moving deeper to cooler waters to cope with higher sea temperatures (Fossheim et al., 2015). Though including the vertical position in the water column would improve model precision for some species (Duffy & Chown, 2017; Melo-Merino et al., 2020), other species will not be capable of moving deeper if they live in certain habitats, or already exploit a large extent of the water column. The highly mobile nature of marine species can further present problems in understanding the environmental variables that determine distributions. Species may move between habitat patches within a landscape such as between foraging grounds (Scales et al., 2016), meaning distributions are not static and are associated with variability in ocean environments. Marine environments are dynamic whereby conditions can change rapidly within relatively short time frames, causing changes to resource distribution and hence the occurrence of mobile species (Fernandez et al., 2017, 2018). For certain species, suitable environmental conditions change depending on life-history characteristics. For example, coral reef-associated fish and invertebrates use off-shore habitats such as mangroves and macroalgae as early juvenile nurseries, due to abiotic stressors or predation risk, before moving to reef habitats as adults (Dahlgren & Eggleston, 2000).

Practical issues with marine SDMs are similar to those for terrestrial. Data deficiencies play a large role in limiting marine SDMs as they rely heavily on presence-only information on where species occur. This means SDMs require a large number of background samples as pseudoabsences when information on true absences of species is lacking. Spatial bias also occurs due to clustered survey effort near coasts, shelves and developed countries (Vierod et al., 2014). Methods that split data into training and testing data like those in terrestrial applications can be used here. Research has further been hindered by appropriate environmental data relating to oceans, but recent development of global databases will help advance this field (Melo-Merino et al., 2020). Finally, similar issues of evaluating model performance and assessing uncertainties apply in marine SDM applications. Despite this, correlative models have the ability to improve our understanding of marine systems under climate change, and coupling them with mechanisms or processes would be an immediate step forward in marine ecosystem research (Twiname et al., 2020).

1.5.2 Marine ecosystem models

Marine ecosystem models offer a holistic approach to studying marine communities by integrating trophic interactions and energy flows among various species in an ecosystem. These models can account for interactions such as competition and predator-prey relationships to simulate the complex dynamics of food webs. Early types of ecosystem models typically only included a few ecosystem components. Over the last 45 years these models have been further developed to represent much of the ecological system and the associated abiotic environment (Fulton, 2010; Travers et al., 2007). Ecosystem or food-web models can be used as a method to examine the fundamental dynamics of ecosystems and assess their responses to environmental changes (Bryndum-Buchholz et al., 2019; Colléter et al., 2015).

Ecosystem models have been applied to hundreds of the Earth's ecosystems (Colléter et al., 2015), but only in recent decades have models been developed for Arctic regions (Hoover et al., 2013, 2022; Pedersen & Zeller, 2001; Pedro et al., 2023; Sora et al., 2022). Ecosystem models offer an exciting avenue for the exploration of the consequences of species' range shifts on trophic food webs in the Arctic. To date, however, few studies attempt to bridge the gap between the results of SDMs and food web models to explore the consequences of new species in Arctic food webs.

1.6 Thesis aims and outline

In this thesis, I aim to address some of the knowledge gaps outlined in the above review to further our understanding of the impacts of climate change on biodiversity changes in the Arctic. I aim to assess the potential for novel species to shift into the Arctic, and the potential for novel assemblages to form. I will explore the impacts of projected changes on Arctic terrestrial and marine ecosystems and will evaluate the impacts on human societies. The structure of this thesis follows a "Land, Sea, People" narrative as indicated by the overall thesis title, and is designed to capture the impacts of climate change on each of these systems and highlight the connectedness between the Land and Sea elements to people in the Arctic. The first section focuses on land-based changes in Arctic ecosystems, followed by an exploration of biodiversity changes in marine systems, before addressing the broader societal impacts. To understand the effects in the marine Arctic, the analyses of marine systems are global in scope. This is partly because of higher dispersal in marine environments and the need to account for the potential for incoming species from further afield, and partly because studies at this scale are limited in marine environments, so to understand the impacts of climate change in the Arctic it is necessary to compare them to species' responses in other marine ecosystems. Below, I provide five detailed aims of my thesis and describe the structure of the following chapters.

1. **To identify potential winners and losers to the terrestrial Arctic ecosystem under climate change**

   In Chapter 2, I use IUCN polygon data for terrestrial birds and mammals currently occurring in the Holarctic (Palearctic and Nearctic) to build SDMs for current and future time-periods under climate change scenarios. I analyse patterns of species' range shifts of Holarctic terrestrial birds and mammals, focusing on changes within each sub-region of the Arctic. I determine future changes in species richness, species range sizes and the emergence of novel communities.

2. **To determine how projected changes in the distributions of marine fish affect global functional diversity**

   To understand the future changes of marine fish biodiversity changes in the Arctic, it is important to ascertain how biodiversity is expected to change in the future at the global level. To this end, Chapter 3 explores potential global changes in taxonomic and functional diversity of marine fish globally. Using species' occurrence data from the Ocean Biodiversity Information System (OBIS) and the Global Biodiversity Information Facility (GBIF), I build presence-only SDMs for the world's marine fish species and project their distributions in 2100. Then, using information on species' traits, I analyse current patterns of functional diversity and how it is expected to change with climate change across 16 marine biogeographic realms. I assess whether changes in functional richness is driven by the gain or loss of functionally unique species and thus how ecosystem structure and function could change. I further identify which species' traits are becoming more or less common in future.

3. **To determine how projected changes in the distributions of marine mammals affect global functional and phylogenetic diversity**

   In Chapter 4, I perform a similar analysis to Chapter 3 but for marine mammals. As phylogenetic information exists for marine mammals, I also provide a detailed account of projected climate change impacts on global marine mammal phylogenetic diversity, as well as taxonomic and functional diversity. I identify hotspots of the world's oceans of communities most likely to be impacted by climate change. Given that marine mammals are a highly threatened group of vertebrates, I also identify threatened species (on the IUCN Red List) that are of particular importance to functional diversity.

4. **To explore the emergence of novel ecosystems in a high-Arctic marine ecosystem**

   In Chapter 5, I combine SDM projections and an ecosystem model to explore six potential scenarios of future change on the North Water (NOW) polynya, a highly productive and unique open-water ecosystem between the northmost parts of Greenland and Canada. The results of SDMs of three fish and one marine mammal species are used to inform the future ecosystem scenarios, which include the potential increases in boreal species and declines in Arctic species and the establishment of a novel predator to the food web. I further analyse how the food web is expected to change under each scenario and how energy flows may change between different trophic levels in the food web.

5. **To provide a detailed account of the impacts of range shifts on ecosystem service provision in the Arctic**

   Using results from my terrestrial and marine SDMs, in Chapter 6 I focus on species that are used and/or traded by humans across the Arctic to investigate how changes in species' distributions could affect provisioning services, and hence the impacts of range shifts on human society and Arctic communities. I analyse changes to species richness and gains and loss of species within each of the eight Arctic regions and identify which provisioning services may be at risk in future, and at what scale these changes may impact (local, national or international).

Chapter 2

Changes to Holarctic species' distributions with climate change: emerging winners and losers

2.1 Abstract

Climate change is threatening global biodiversity, with particularly severe impacts at Northern latitudes and within the Arctic. The Arctic is warming at over twice the rate of the global average, leading to profound impacts on ecological communities. Understanding is poor regarding the species most able to cope with the changing climate by, for example, range redistribution. Novel colonists shifting their ranges north into Arctic and boreal areas are likely to impact recipient communities and alter ecosystem functioning. Understanding factors that might limit or exacerbate range shifts will be key to facilitating ecosystem resilience and the persistence of biodiversity. Here, I use species distribution models to explore, for Holarctic birds and mammals, (1) the potential for the Arctic region to become newly climatically suitable for southern colonists, (2) the potential range shifts of current Arctic species, and (3) how species-specific dispersal capabilities and the availability of suitable habitat impact species' abilities to keep pace with shifting climate. By 2070, I identify, across all Arctic regions, 233 mammal and 283 bird species that are projected to have suitable climate in the Arctic for the first time in recent history. Range contractions are projected for 79% of birds and 100% of mammals that are currently resident in the Arctic proper (high and low Arctic), with overall range expansions more than two times their current ranges projected for novel colonisers. I demonstrate that, for most Arctic species, and especially for Holarctic mammals, suitable climate will persist in the future, but species' dispersal abilities and habitat limitations will preclude many species from tracking climatic niches. The high Arctic was projected to host the greatest number of novel communities in 2070 for both birds and mammals, with all grid cells in the high Arctic projected to be over 75% novel. The average level of novelty declined to ~50% for birds and 20% for mammals under scenarios accounting for dispersal and habitat, but the high and low Arctic remained the regions with the greatest number of novel communities. These results show that Holarctic mammals are most impacted by dispersal constraints and habitat availability, limiting their potential to keep pace with climate change. These results further highlight the emergence of novel communities under climate change, especially in the high and low Arctic, which will have knock-on impacts for the functioning of Arctic ecosystems.

2.2 Introduction

Climate change is threatening global biodiversity and driving a redistribution of the world's species (Loarie et al., 2009; Pecl et al., 2017). Estimates suggest thousands of species have already shifted their distribution in response to climate change (Chen et al., 2011; Poloczanska et al., 2016). In general, terrestrial species are moving to higher altitudes and latitudes, primarily in response to changing temperature and precipitation regimes on land (Chen et al., 2011; Lenoir & Svenning, 2015; Sunday et al., 2012). Similarly, latitudinal and water column shifts in the oceans are being driven by changes to water temperature and associated factors (e.g., salinity, CO_2, nutrients) (Lenoir et al., 2020; Lenoir & Svenning, 2015; Poloczanska et al., 2016). Reports of terrestrial species' responses to climate change are mixed, with some reporting lags behind temperature change (Devictor et al., 2008), others reporting that latitudinal shifts are keeping pace with warming conditions (Chen et al., 2011; Thomas, 2010), or that climate-driven changes are being masked by other factors (Howard et al. 2023).

Species' redistributions are likely to be greatest where climate change is greatest. The Arctic (above 66'33°N latitude) is now warming two to four times faster than the global average (Ballinger et al., 2020; Jacobs et al., 2021). The Arctic region is determined by distinct vegetation zones (Appendix Figure S2.1). The Arctic proper (most northerly region) consists of the high and low Arctic, distinguished by polar deserts and tundra, respectively (Peterson, 2014). The subarctic consists of a mix of tundra, barren land and northern boreal forest. The next southerly vegetation class is the northern and southern boreal forest or Taiga, dominated by conifer forest and is the world's largest land biome (Haila, 1994). Rapid climate change is already impacting Arctic regions and ecosystems, from a northward expansion of shrub habitats into tundra (Myers-Smith et al., 2011), to phenological mismatches between breeding predators and their prey (Senner et al., 2017). A northward shift in climatic conditions is expected to result in a corresponding poleward range shift of species native to the Arctic, causing a decline in suitable habitat, sometimes referred to as the 'arctic squeeze', whereby suitable conditions for terrestrial biota go beyond land area that is physically available at the North pole (Smith et al., 2020; Wauchope et al., 2017). In addition, novel colonists from temperate regions are expected to shift to higher latitudes with warming temperatures, disrupting Arctic systems (Fossheim et al., 2015; Myers-Smith et al., 2011; Poloczanska et al., 2013). There are signs this is already happening. For example, in response to 20th century climate-driven shifts in shrub habitats, Alaskan moose (*Alces alces gigas*) ranges expanded northwards from boreal forest into tundra (Tape et al., 2016). Yet, despite the magnitude of ongoing and likely future changes, compared to other regions of the world the Arctic remains relatively understudied in terms of its biodiversity and ecosystem responses to climate change.

Reliable projections of species' future ranges are essential to estimate the impact that climate change in the Arctic will have on species' distributions. Highlighting the possible consequences of novel colonists can inform policy decisions and conservation actions. It is important to understand the direction and magnitude of potential species range shifts and also changes in species richness and community composition (Hof et al., 2012). In addition, understanding how species-specific dispersal abilities and the availability of suitable habitat impacts distribution changes at higher latitudes will inform the likelihood of species keeping pace with climate change. Range-shifting species could alter the ecology and function of recipient environments, causing novel assemblages and communities to form (Grebmeier et al., 2006; Pecuchet et al., 2020). Such changes will affect human societies, especially those that most rely on the services provided by healthy functioning ecosystems (Malinauskaite et al., 2019). Yet, despite the number of both global and regional projections of range shifts in the terrestrial realm (Lenoir & Svenning, 2015; Pacifici et al., 2015), the Arctic region remains understudied. A major knowledge-gap is how vertebrate communities could change within the Arctic, subarctic and boreal regions, and how species' dispersal abilities and habitat availability could impact both novel colonisations and native species' redistributions at high latitudes.

Here, I investigate the impacts of climate change on terrestrial Holarctic birds and mammals, particularly in terms of their potential range redistributions across the various Arctic and subarctic regions. The Holarctic refers to the biogeographic region encompassing the Nearctic and the Palearctic, and within which the Arctic ecoregion makes up its northern margin. I use ensemble species distribution models (SDMs) to project changes, under four future climate change scenarios, for 953 mammal and 2,037 bird species. I explore changes in species richness and species-level range sizes across the Holarctic, focusing on the true Arctic (high- and low-Arctic) and subarctic (subarctic and boreal) regions. I then go on to use these projections to assess where novel assemblages could form in future, and whether novel communities are more likely to form within certain Arctic and subarctic regions.

2.3 Methods

2.3.1 Species distribution data

Species range data are available as polygons for 5,537 global terrestrial mammals, from the International Union for Conservation of Nature (IUCN) Red List (IUCN, 2021). Range data for 10,958 global bird species are similarly available from BirdLife International and *Handbook of the Birds of the World* (BirdLife International and Handbook of the Birds of the World, 2020), comprising almost all members of these taxa globally. The spatial scope of this Chapter is focused on the Holarctic region so, from these repositories, I compiled data for all species of birds (2,535 spp) and mammals (1,641 spp) associated with the Palearctic and Nearctic realms (Holarctic), based on the IUCN Red List information for the realms in which the species are associated. From these datasets, I excluded non-native and extinct species, and extracted breeding and resident range polygons for the remaining species. Areas of species' ranges that fell outside the Holarctic region were retained for modelling to better inform models of a species' full ecological niche including its limits. These polygons were rasterised to a Behrman equal-area projection and converted to a 0.5° resolution presence-absence grid. A species was classed as present within a grid cell if its range polygon intersected with at least 10% of the grid cell. Species were considered absent from all grid-cells falling outside the species' range polygon. Any species with fewer than 10 grid cells were excluded from further analysis due to potential problems of model fitting (and especially model validation) associated with so few data points. This left me with 953 Holarctic mammals and 2,037 Holarctic bird species for subsequent analyses.

2.3.2 Bioclimatic data

For both contemporary and future time periods, I downloaded five bioclimatic predictor variables (Table 2.1) at a spatial resolution of 5 arc-minutes from WorldClim v2.1 (Fick & Hijmans, 2017). The five variables were chosen to encompass the major climatic determinants of species' ranges, and have been shown previously, by a systematic analysis, to be the most parsimonious combination of such variables for simulating species ranges (Titley et al., 2021). Variables were downloaded for a baseline time period 1970-2000, to match the species' range data. I selected the period 2061–2080 as the future projection window, which balanced projecting sufficiently far ahead to highlight likely changes in the second half of the century whilst avoiding more temporally-distant projections with the increased uncertainty they bring. For brevity, I refer to this 20-year window as 2070 henceforth. Future climate variables were derived from CMIP6, the most recent projections to come from the Coupled Model Inter-comparison Project (CMIP). CMIP is a framework for climate model experiments that runs across institutions, allowing validation and comparisons across projects and models. Bioclimatic data were aggregated to a 0.5° resolution to match the gridded species distribution data.

Table 2.1. Final five bioclimatic variables available from WorldClim (Fick & Hijmans, 2017) that were chosen for fitting SDMs for Palearctic and Holarctic species.

Code	Variable
BIO1	Annual mean temperature
BIO4	Temperature seasonality
BIO13	Precipitation of the wettest period
BIO14	Precipitation of the driest period
BIO15	Precipitation seasonality

To account for variation among climate models, I used projections from three global circulation models (GCMs) BCC-CSM2-MR (China), CanESM5 (Canada) and MIROC6 (Japan). These GCMs were selected as they encompass a range of plausible future projections and are considered significantly improved relative to earlier simulations (Xiao-Ge et al., 2019). For each GCM, I considered four future emission scenarios, termed Shared Socioeconomic Pathways (SSPs), which covered the range of plausible future pathways for global gas emissions. These were 1-2.6 (SSP126), 2-4.5 (SSP245), 3-7.0 (SSP370), and 5-8.5 (SSP585). SSPs are the most recent update to the IUCN's representative climate pathways (RCPs) and are driven by socioeconomic factors, with their names representing the amount of radiative forcing expected by 2100; the four SSPs above indicate warming of, respectively, 1.4°C, 2.0°C, 4.1°C and 5.0°C.

2.3.3 Species distribution models

I modelled species-climate relationships using an ensemble of four commonly used modelling techniques, following an approach adapted by Titley et al. (2021) and others, which broadly follows the methods of Bagchi et al. (2013). The four modelling approaches were Generalized Linear Models (GLM), General Additive Models (GAM), Generalized Boosted Regression Models (BRT) and Random Forest Models (RF). These four models were chosen based on their prior performance and to provide contrast between regression-based and machine-learning techniques (Bagchi et al., 2013; Elith et al., 2006; Titley et al., 2021). These models relied on the generation of pseudoabsences sampled from areas outside the species' range polygon. I randomly sampled 1,000 pseudoabsences from the same realms the species currently occurs in (Titley et al., 2021).

2.3.3.1 Spatial autocorrelation and model validation

A common issue that requires consideration in species distribution modelling is the spatial dependence of the data. To minimise effects of spatial autocorrelation, I followed a "blocking" method, as per Bagchi et al. (2013), whereby the data were split into ten blocks (using 'blockTools' package in R (Moore & Schnakenberg, 2012)) each based on the terrestrial ecoregions of the world (Olson et al., 2001). Model performance could then be assessed using cross-validation across the ten blocks. Each model was trained on nine of the ten blocks and then model performance was tested on data from the semi-independent tenth block. This was repeated ten times, with overall model performance assessed using the area under the curve (AUC) of the receiver-operating characteristic (ROC) plot.

The ten models (from blocking) combined with the four modelling approaches resulted in 40 models for each species. These models were used to project climate suitability in the future for the three GCMs and for each of the four emissions scenarios, resulting in 120 projections per species (10 blocks x 4 SDMs x 3 GCMs), for each SSP. A brief summary of the four fitting methods is provided below.

2.3.3.2 GLMs

GLMs fit with third-order polynomials were run with species occurrence as the response variable and the five bioclimatic variables as predictors. Models were fitted to nine blocks whilst excluding one block at a time. Model performance was assessed on the omitted block using AUC. The combination of polynomial terms that maximized AUC across the 10 omitted blocks was used to fit a final set of 10 models.

2.3.3.3 GAMs

GAMs with thin-plate regression splines (within the 'mgcv' package in R (Wood, 2003)) were used to model species distributions from the presence-absence data. These regressions were run using a Bernoulli error distribution and logit link function. Again, models were fitted on nine blocks, omitting the tenth in turn to be used as the testing dataset for assessing model performance using AUC.

2.3.3.4 BRTs

BRTs, a machine learning method, were produced using the ‘gbm’ package in R (Greenwell et al., 2019). The models were parametrised using the following cross-validation approach. I excluded one block in turn and fitted a BRT with 5,000 trees using 0.001 as the learning rate and values of tree complexity varied between 1 and 4. The value of tree complexity that minimised the total error across the testing blocks was used to fit a final set of 10 models.

2.3.3.5 RFs

Random forests were generated using the ‘randomForest’ package in R (Liaw & Wiener, 2002). The models were cross-validated using a similar method to that described above. The number of predictors in each random subset used to build each tree varied between one and three. RTs were fitted initially with 1,000 trees, omitting one block at a time for cross-validation. I then increased the number of trees by 500 tree increments until AUC (model performance) was <1%.

2.3.4 Species dispersal

Terrestrial species may not fully track their climatic niche due to dispersal capabilities restricting the distance species can travel. I incorporated species-specific dispersal ability into future range shift projections by clipping areas of projected occupancy based on a species-specific dispersal buffer, following Voskamp et al. (2021). The dispersal buffer of species x was calculated using the following equation:

$$Dispersal\ buffer_x = \frac{\text{projection period}}{\text{age at first breeding}} \times natal\ dispersal\ distance$$

For birds, I modelled natal dispersal distances following the methodology of Stewart et al. (2021). Natal dispersal distance was calculated by modelling known natal dispersal distances (for 287 birds) as a function of range size, body mass, hand-wing index (HWI) and wing length. The best model was used to predict dispersal distances for all bird species. I collated trait data from various global trait datasets by Tobias et al. (2022), Pigot et al. (2020) and Stewart et al. (2021) for my study species. I collated Hand-Wing index (HWI) data from

Sheard et al. (2020) and information on generation length from Bird et al. (2020). The projection period used in my models was 70 years (2070-2000).

Estimates for natal dispersal for mammals were derived from Santini et al. (2013) who concluded that a simple power relationship with home range size is a good estimate of mammal dispersal for most applications:

$$Dispersal\ distance = 5.60 \times home\ range^{0.5}$$

I collated age at first breeding data from the PanTHERIA database (Jones et al., 2009). If either was unavailable for a species, I took the mean home range size from a congeneric species with a similar body mass (± 10%). If such data were not available, I used data from similarly-sized species in the same family or order. If there were no congeneric species within 10% body mass, I averaged home ranges across congeneric species regardless of body mass and did similar at family or order level for species without congeneric data.

2.3.5 Calculating Area of Suitable Habitat (AOH)

The ability for a species to colonise a new location depends not only on climate suitability but also on the availability of suitable habitat. To investigate whether area of habitat could restrict colonisers in the Arctic I clipped species' current and predicted distributions by the current occurrence of their preferred terrestrial habitat (based on IUCN Red List habitat preferences, these, in turn, coming from Jung et al. (2020)). These data are available for the year 2015 at ~100m and as fractional land coverage aggregated to 1km resolution (Jung et al., 2020). To minimise computational overheads whilst maintaining a fine resolution, the ~100m land cover data were aggregated, using a nearest neighbour approach, to a 1km resolution and then reprojected to an equal area grid. Land cover data were then aggregated to a 0.5° grid to match the species' distribution data, and the percentage of each habitat type per grid cell was calculated. A grid cell was classified as being suitable for a species if any suitable habitat occurred, in combination with the cell being predicted climatically suitable and within colonisation distance.

To investigate how dispersal capabilities and land cover affected new and current Arctic species' future distributions, I ran all the analyses detailed below under three different dispersal and habitat assumptions: unlimited dispersal, whereby species are assumed to be able to colonise all available suitable climate by 2070; species-specific dispersal capabilities whereby future projections are clipped by a dispersal buffer; and then finally, the impact of whether there is suitable habitat within that dispersal buffer.

2.3.6 Thresholding model values and calculating climate suitability

I took ensemble means, weighted by AUC, across the 120 SDM model projections (probabilities of occurrence, across GCMs) for each grid cell to derive final climate suitability projections for both the current period (2070-2000) and the future period (2070) for each SSP. I converted these ensemble means per species into binary presence and absence values (either suitable, 1, or unsuitable, 0) by applying thresholds. I used thresholds that maximised the sum of sensitivity and specificity (Liu et al., 2005).

2.3.7 Arctic regions overlap analysis

I obtained spatial data on the Arctic region from the Conservation of Arctic Flora and Fauna (CAFF) /Arctic Boundary Assessment GeoNetwork catalogue (CAFF, 2019), using the high-Arctic and low-Arctic boundaries as defined by the Circumpolar Arctic Vegetation Mapping Project - Bioclimatic subzones (CAVM Team, 2003) and the subarctic boundary, defined by the Arctic Biodiversity Assessment (ABA) (Figure S2.1). I used WWFs Terrestrial Ecoregions of the World (Olson et al., 2001) to define the boreal region, which was cropped to exclude the subarctic using ArcGIS Pro v2.8.6. True Arctic regions include the high- and low-Arctic, whilst subarctic regions refer to the subarctic and boreal regions, henceforth.

To investigate the potential for species to shift into the different Arctic and subarctic regions under climate scenarios, I calculated overlaps between the current and future projected occurrence for each species and the various regions. I did this by intersecting the species' range with the Arctic and subarctic region boundaries, using the 'sp' package in R (Pebesma & Bivand, 2005). For each species I calculated the proportion of a species' range that lie within the Arctic and subarctic regions in the present and future periods. Species were classed as occurring in a region at present if they occurred in at least 50% of the grid-cells within the corresponding region.

2.3.8 Summarising range changes and species richness

Using the ensemble model predictions, I generated species richness for current and future periods by summing the number of species projected to occur in individual grid cells. I calculated richness change as the percentage change in species from the present to future period. Species richness changes were summarised for birds and mammals, separately, across the Palearctic and Nearctic. I calculated range extent for each species as the total number of presences across grid cells (number of occupied cells), and range extent change as the future extent minus the present extent. I then also calculated the proportional change in range extent as the future range divided by the current range. I estimated range size changes in terms of species' global distributions. I estimated novelty, a measure of species turnover, at a cell level, as the proportion of new colonists relative to the present richness. Novelty and range size change metrics were summarised across the Holarctic and across each Arctic and subarctic region. To test for significant differences in the proportion of novel communities between Arctic and subarctic regions, generalised linear models with a gaussian family function were performed using the 'MASS' package (Venables & Ripley, 2002). These tests were run under each dispersal scenario (climate only, climate + dispersal, and climate + dispersal + habitat). For mammals, scenarios including dispersal and dispersal + habitat were zero-inflated. Thus, zero-inflated beta regression models were performed using the 'gamlss' package (Rigby et al., 2005). Multiple pairwise comparisons between all regions were performed using Tukey tests from the 'multcomp' package (Hothorn et al., 2008). Maps were all plotted in a Polar Stereographic projection. All analyses were performed using R v4.0.3 (R Core Team, 2020).

2.4 Results

2.4.1 Changes in species richness

SDMs for both mammals and birds had excellent model fit. The average AUC (± SD) for ensemble models of mammals was 0.951 (± 0.048) and 0.949 (± 0.049) for birds. For simplicity, I only present the results based on a high emissions scenario (SSP 5-8.5). There are minor differences between projections across scenarios whereby the patterns of change are qualitatively similar. Projected proportional shifts in species richness of birds and mammals across the Holarctic realm for the three other emissions scenarios are presented in the Supplementary Materials (Figures S2.3, S2.4 & S2.5). I project widespread changes in species richness within grid cells across the Holarctic realm under a high emissions scenario (Figures 2.1 & S2.2). The change in species richness between the current and future period (SSP 5-8.5 emission scenario) varies across regions for both mammals and birds (Figures 2.1 & S2.2). I project larger richness changes for birds (Figures 2.1a, c & e) than mammals (Figures 2.1b, d & e). Some of the largest projected gains in richness occur across northern latitudes, particularly areas of Northern Canada, Alaska and Northeast Russia.

Understandably, species richness declines are greater when projections are clipped by dispersal (Figures 2.1c & d), even more so when additionally limited by the availability of suitable habitat (Figures 2.1e & f). For birds, the average species richness change per grid cell is +35% in the Palearctic compared to +2% in the Nearctic, assuming species could colonise all suitable climate. After clipping future ranges by dispersal capabilities, richness per grid cell declines by 17% for birds in the Palearctic and 50% in the Nearctic. Future species' declines are greater for mammals in both the Palearctic and Nearctic, with declines of 60% and 71% respectively under a high emissions scenario. After additionally clipping by suitable habitat, regions such as Nunavut and Greenland that are previously projected to undergo gains in bird species richness, now lose species richness (Figure 2.1e). Similarly for mammals, when limited by habitat availability, species richness declines by 100% in northern Greenland (Figure 2.1f) which was previously only ~50% declines under scenarios constrained by dispersal only.

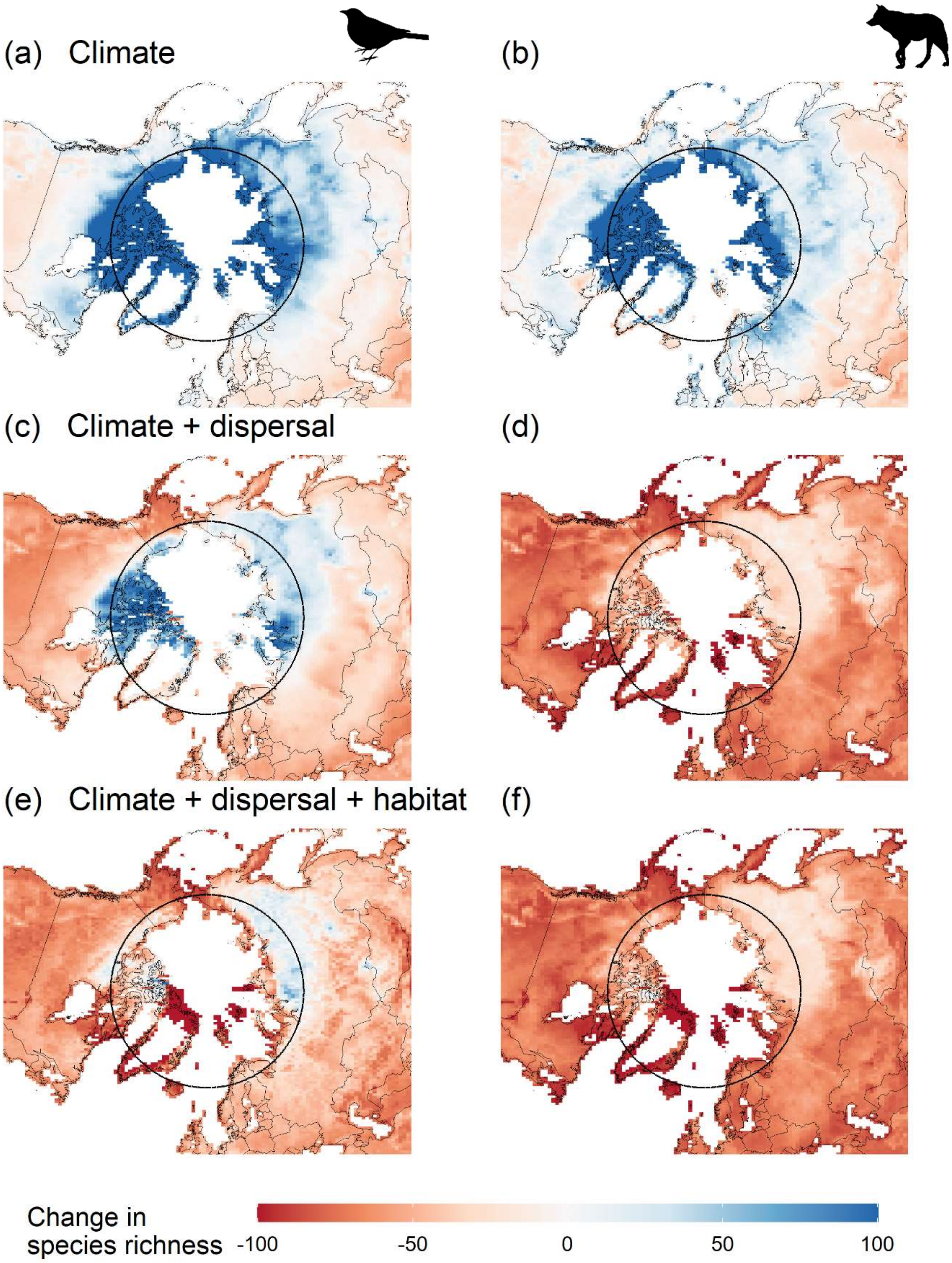

Figure 2.1. Projected change in proportional species richness by 2070 under SSP 5-8.5 for Palearctic and Nearctic terrestrial birds and mammals derived from summed individual species ensemble model projections. Richness for (a) birds and (b) mammals from models based solely on the extent of suitable climate. Richness for (c) birds and (d) mammals

accounting for both climate and dispersal capability. Richness projections accounting for climate, habitat and dispersal for (e) birds and (f) mammals. Proportional species richness change is capped at 100% increases. Black bold line shows the Arctic Circle. Species icons from phylopic (https://www.phylopic.org/).

2.4.2 Climate change impacts on Holarctic species

To explore the implications of climate change on Holarctic mammals and birds, I assessed how range sizes changed for 953 mammals and 2,037 birds (Figure 2.2). Assuming species can fully colonise areas with suitable climate, of the 2,037 birds, 64% would expand their range. 35% of birds experience range declines, where 28% of them will experience declines of over half their current predicted range. 23 bird species have no suitable climate in the future, and so, under these assumptions, could be at risk of extinction. Under the same criteria, range extent declines for 28% of mammal species, with 35% of those species with shrinking ranges losing over half of their current extent.

205 Holarctic birds and 75 mammals currently have at least one cell of suitable climate simulated within the low- or high-Arctic regions. For the mammals and bird species not currently projected to be present in the Arctic (n = 588 and n = 1152 respectively, with zero grid-cells present in the Arctic currently), I project gains in the extent of climatically suitable areas across all Arctic regions. Species present in most Arctic regions experience ranges declines (Figures 2.2a & b), with this number increasing considerably when ranges are clipped by dispersal ability and habitat availability (Figures 2.2c, d, e & f). Given unlimited dispersal and assuming no habitat specificity, boreal species typically expand their range under future climate change but when dispersal and habitat limitations are imposed, such range expansions are rarely realised.

Dispersal constraints lead to considerable differences in projections compared to unlimited dispersal scenarios (Figures 2.2c & d), especially when considering the likelihood of species colonising the Arctic region. Dispersal ability plays a much greater role in limiting species' range extent changes for mammals than birds (Figures 2.2c & d). Of the bird species that had the potential to expand their range by 2070, based on climate alone, 75% of these species cannot capitalise on such opportunities when dispersal ability and habitat availability are considered and instead are projected to experience range declines.

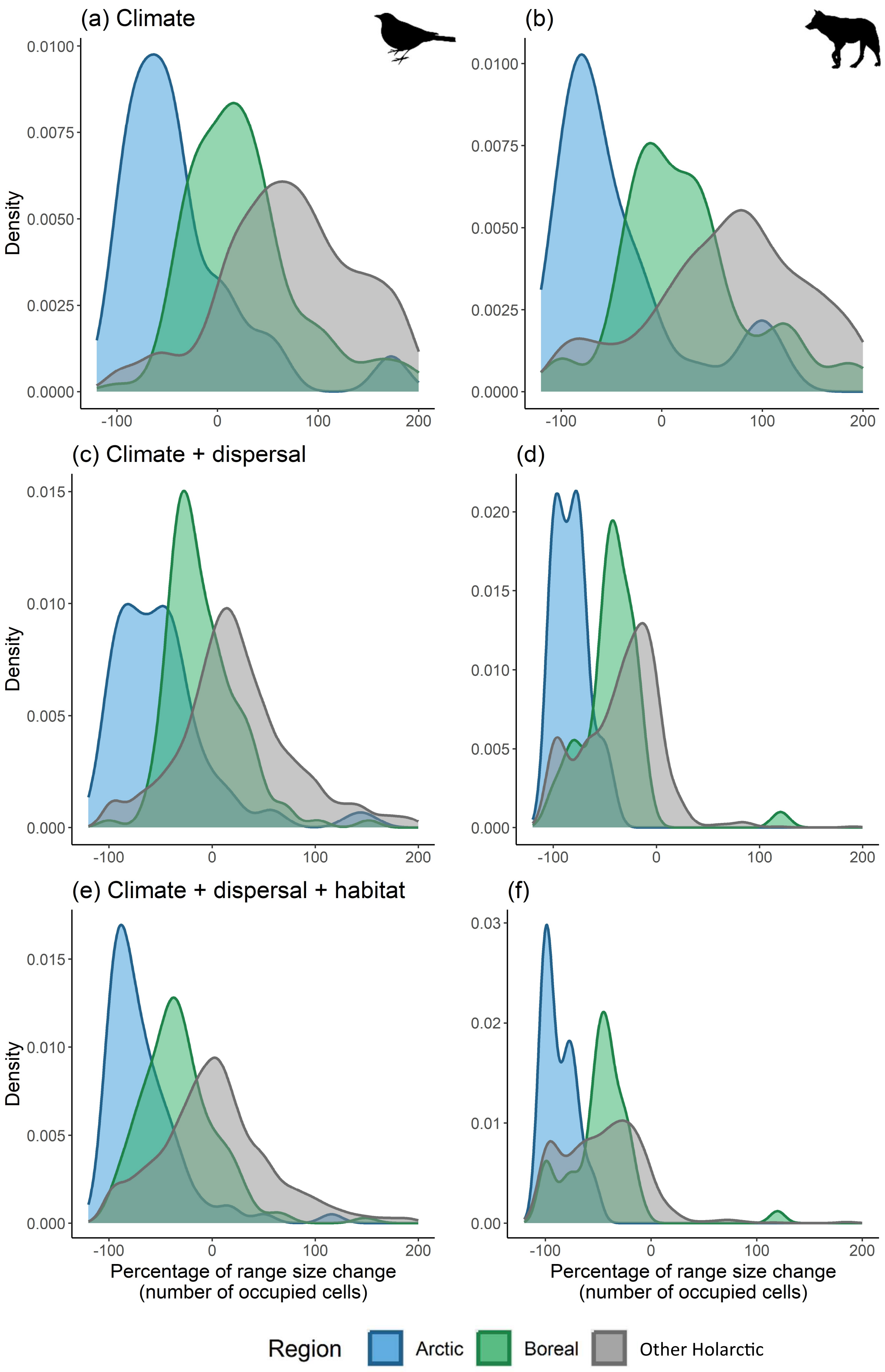
(a) Climate
(b)
(c) Climate + dispersal
(d)
(e) Climate + dispersal + habitat
(f)
Density
0.0100
0.0075
0.0050
0.0025
0.0000
0.015
0.010
0.005
0.000
0.020
0.03
0.02
0.01
0.00
-100
0
100
200
Percentage of range size change
(number of occupied cells)
Region
Arctic
Boreal
Other Holarctic

Figure 2.2. Density plots for projected changes in proportional range size for all Palearctic and Nearctic bird (n = 2037) and mammal species (n = 953) by 2070 under SSP 5-8.5. Colours indicate the region species are currently present in (with at least half of their range spanning any region). Arctic represents species currently present in high, low and/or sub-arctic, and boreal represents those in boreal and sub-arctic regions. Other Holarctic indicates all other Holarctic species not included in the previous categories. Range changes for (a) birds and (b) mammals from models based solely on the extent of suitable climate. (a) and (b) had hundreds of species expanding ranges by more than 200% and were removed from the plots to aid visualisation of Arctic and subarctic changes. Range for (c) birds and (d) mammals accounting for both climate and dispersal capability. Range change projections accounting for climate, habitat and dispersal for (e) birds and (f) mammals. Species' icons from phylopic (https://www.phylopic.org/).

2.4.3 Novel Arctic Colonists

By 2070, the high and low Arctic regions (true Arctic) are projected to become suitable for 283 novel bird colonists and 189 novel mammals. However, when these projections are constrained by species-specific dispersal, no mammals are projected capable of colonising the true Arctic, with only one, the raccoon (*Procyon lotor*), colonising the sub-Arctic. Similarly, when restricted by available habitat, no novel mammal colonists of the Arctic are projected. I found 60 birds are able to keep pace with climate change and colonise the Arctic given their dispersal capabilities. Only seven of them, however, expand their overall ranges and the rest undergo range contractions. The number of novel bird colonisers decline to 38 species further when the occurrence of suitable habitat is additionally considered.

2.4.4 Novel assemblages

Novel assemblages are predicted to form under future climate scenarios for both mammals and birds (Figure 2.3). Novel assemblages are projected to occur predominantly across northern latitudes, with the clearest trends showing especially in Northern America. Figures 2.3b, d, f, h, j & l indicate the pattern of the proportion of novelty in a grid cell for each Arctic and subarctic region. Novel communities significantly differ by region for both mammals (Climate only: GLM; F_3=755.5; P<0.001. Climate + dispersal: GAMLSS; X^2_3=3341.9; P<0.001. Climate + dispersal + habitat: GAMLSS; X^2_3= 3263.7; P <0.001) and birds (Climate only: GLM: F_3=9024.6; P<0.001. Climate + dispersal: GLM; F_3=5795; P<0.001. Climate + dispersal + habitat: GLM; F_3= 2229.6; P<0.001). The high and low Arctic are likely to experience the highest number of novel communities for birds and mammals, even after accounting for dispersal and habitat limitations. Indeed, for mammals, the most novel communities are projected for the high Arctic consistently (Figures 2.3d, h & l). Whereas for birds, after habitat is accounted for, the low Arctic is projected to have the highest number of novel assemblages (Figure 2.3j). However, the average percentage of novel species within a grid cell for mammals is much lower across all Arctic and subarctic regions when dispersal and habitat are included (Figures 2.3h & l).

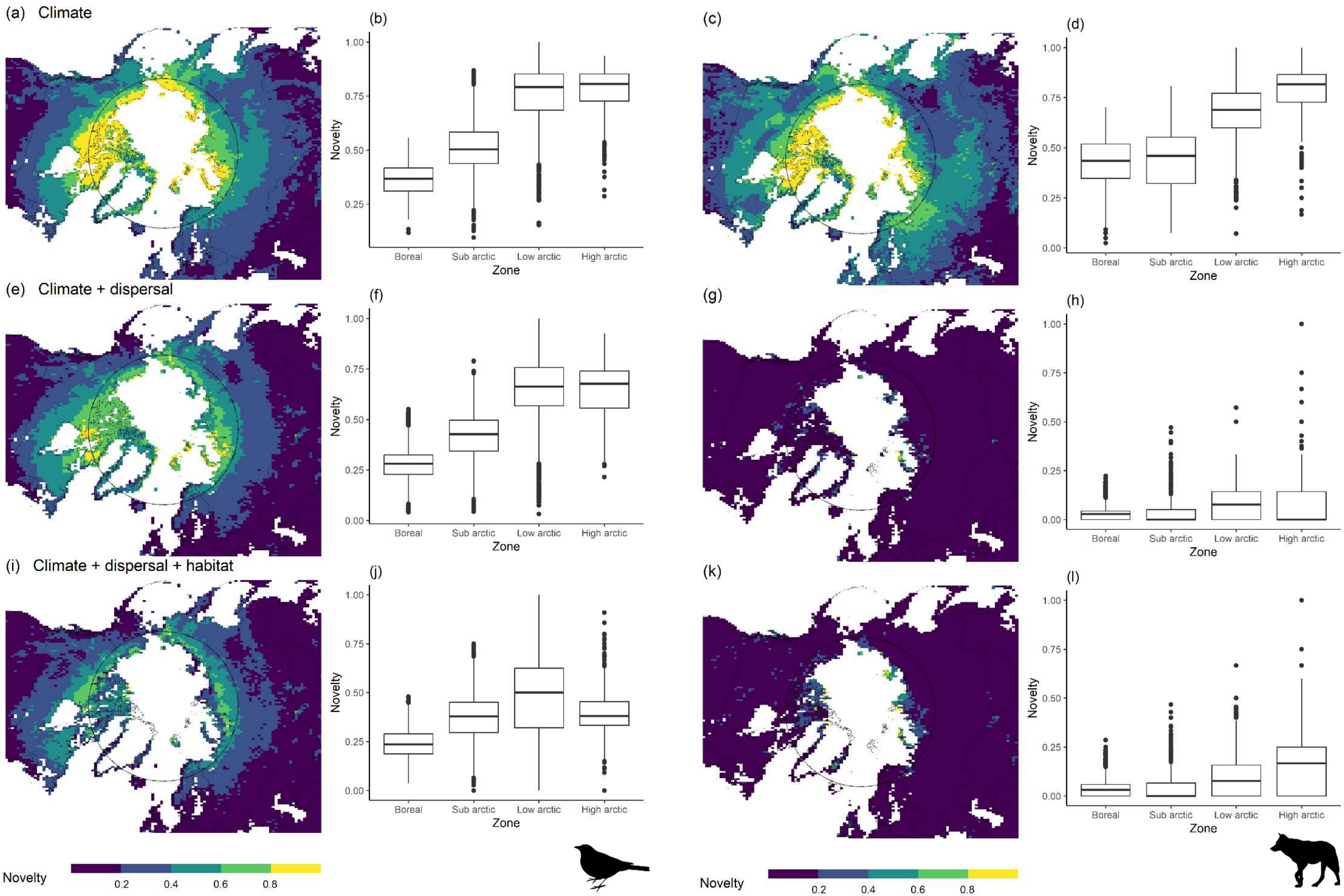
(a) Climate
(b)
(c)
(d)
(e) Climate + dispersal
(f)
(g)
(h)
(i) Climate + dispersal + habitat
(j)
(k)
(l)
Novelty
1.00
0.75
0.50
0.25
0.00
Boreal
Sub arctic
Low arctic
High arctic
Zone
Novelty
0.2
0.4
0.6
0.8

Figure 2.3. Projections of novel bird and mammal communities by 2070 under SSP 5-8.5 across the Holarctic and each Arctic and subarctic region (indicated by zone in boxplots), under different dispersal and habitat assumptions. Novelty is measured as the proportion of each grid cell that is projected to become a novel species community by 2070, where 1 indicates the species composition of the grid cell is 100% different to the current composition. (a), (e) and (i) for birds and (c), (g) and (l) for mammals show novelty assuming unlimited dispersal, accounting for both climate and dispersal capability and accounting for climate, habitat and dispersal, respectively. (b), (f) and (j) for birds and (d), (h) and (l) for mammals show the average and range of measures of novelty across each Arctic and subarctic region assuming unlimited dispersal, accounting for both climate and dispersal capability and accounting for climate, habitat and dispersal, respectively. Boxplots show median for each zone. *P* values for all pairwise comparisons between groups for each scenario and taxa are <0.001. Species icons from phylopic (https://www.phylopic.org/).

2.5 Discussion

In this chapter, I have expanded on previous research and provided new insights into the impacts of climate change on Holarctic, Arctic and subarctic terrestrial mammals and birds. I projected considerable changes in the distributions of Holarctic terrestrial birds and mammals under future climate change. I found large gains in suitable climate across all Arctic regions for birds and mammals. By including species-specific dispersal capabilities and land cover, I show that these changes become more pronounced for Holarctic species, with much large losses of mammal species. I found many Holarctic species could not keep pace with suitable climate, as dispersal abilities and the availability of suitable habitat restricted their distribution change. Even when taking dispersal and habitat into account, a number of bird species were still projected to shift into new regions in the Arctic, potentially disrupting Arctic communities. These results reveal which areas of the Holarctic, the Arctic and subarctic in particular, that become suitable for terrestrial mammal and birds species in future, and identifying for the first time the areas of the Arctic and subarctic in which novel communities are more likely to form.

2.5.1 Changes in species richness

The patterns of changes in species richness varied spatially across the Holarctic and this effect was projected for both birds and mammals. My results support existing evidence of species richness changes at high latitudes (Titley et al., 2021; Voskamp et al., 2022). However, I have also shown that the inclusion of both species-specific dispersal capabilities and land cover have an even larger impact on species richness changes for both Holarctic birds and mammals than previously thought. Indeed, when limited by dispersal and habitat, overall mammal richness declines across the Arctic indicating species losses are greater than species gains. This suggests mammals especially are unlikely to be able to track their climate niche as it shifts with future climate change. A previous study by Schloss et al. (2012) came to similar conclusions about mammals in the western hemisphere being limited by dispersal, and my results expand on these findings and show that similar patterns are projected at a larger geographic scale. My results further go beyond this study and suggest that habitat availability will also limit the ability of mammals to track climate change. The inability of species to track climate into the most northerly regions of the Arctic is understandable. This is probably explained by the inhospitable habitat across the high Arctic, such as considerable areas dominated by barren land and polar deserts (Peterson, 2014). Similarly, any boreal species which rely on forest habitat or Taiga to live will have no suitable habitat in the high and low Arctic if climate becomes suitable there in future. This may change in future, however, as shrubs expand into tundra habitat and the treeline shifts northward (Elmhagen et al., 2015; Liess et al., 2012; Myers-Smith et al., 2011). As such, future studies could build on my research here and also include projections for future land cover changes. These results suggest that dispersal and habitat counterbalance regional increases in species richness at high latitudes (Berteaux et al., 2018), and stress the importance of considering these factors when projecting species' distributions. Changing species richness could have profound implications on Arctic communities and ecosystem functions where species richness is generally low meaning each individual species likely plays an important role within a functional community. The decline or loss of these species altogether could have far-reaching impacts on the functioning of entire Arctic ecosystems.

2.5.2 Species-level range size changes in the Arctic

The range sizes of most species currently occurring within any of the Arctic and subarctic regions were projected to contract. As temperatures increase into the future, for species living in the high Arctic, there will not be suitable land to move to as species' ranges contract to the northern most boundaries of land available. In a smaller, regional study in the subarctic only, Hof et al. (2012) found similar results for sub-arctic mammal communities, whereby resident subarctic species contracted their ranges and also suggest constraints on species' dispersal ability is likely to be a greater threat. Another study on small mammal populations in Alaska, projected small mammal ranges to contract and shift northward in future, and the opposite was true for more southern species (Baltensperger & Huettmann, 2015). I predict a much greater number of range losses and potential extinctions, especially for those true Arctic species, and similarly for non-Arctic species, when constrained by dispersal ability and available habitat.

2.5.3 Novel communities in the Arctic

I found a large number of Arctic communities were projected to contain a high proportion of novel species across all Arctic regions. Novelty tended to increase with increasing latitude, with the high and low Arctic projected to contain a higher number of novel communities than the subarctic and boreal regions. Although almost all regions of the Arctic were projected to decrease in species richness, the high novelty here indicates a loss of many species currently occurring there and that they are being replaced by new ones. Species moving into these areas are likely to be coming from more southern, boreal communities as species' ranges are shifting further north (Berteaux et al., 2018; Burrows et al., 2011; Parmesan & Yohe, 2003; Virkkala et al., 2018). Novel colonists could be generalists with a broader diet, joining more specialised communities in the low and high Arctic (Lurgi et al., 2012). Generalists could out compete Arctic specialists and could have knock-on effects on Arctic food webs. If invasive herbivores moved into Arctic communities, these ecosystems could undergo large shifts in vegetation composition, especially if the southern colonisers introduce a novel disturbance to Arctic communities (Wardle et al., 2011).

2.5.4 Conclusion

In conclusion, this chapter significantly advances our understanding of the impacts of climate change on Holarctic terrestrial birds and mammals in the Arctic and subarctic regions. I provide new insights into the considerable shifts in the distributions of Arctic and subarctic communities and identify potential hotspots that are most vulnerable to change. Notably, while Arctic and subarctic regions show gains in suitable climate for birds and mammals, the inclusions of dispersal ability and available habitat reveals significant species losses, particularly among mammals unable to track their climate niche. These results highlight the critical role of habitat cover and dispersal limitations in shaping future species' distributions. Moreover, the projection of novel communities forming in the Arctic and subarctic regions, especially in the high and low Arctic, highlights the potential for profound ecological transformations, with implications for community dynamics and ecosystem functions. My findings stress the importance of understanding how ecosystems and vulnerable communities are likely to change in the future. I advocate for the results of such models to be incorporated into impact assessments and conservation management plans when working with the people impacted by such changes. Moving forward, integrating projections of future land cover and land-use changes will further enhance our understanding of the complex interplay between climate, habitat and species' distributions in the Arctic and subarctic regions.

Chapter 3

Future changes in functional diversity of global marine fish

3.1 Abstract

Recent climate change has been most extreme in polar ecosystems, impacting both terrestrial and marine systems. Marine fish communities play an important role in the world's oceans. Despite this, the impacts of climate change on global marine fish communities remains relatively understudied. As species undergo global redistributions, so too does the structure and function of marine communities, and hence functional diversity. However, there is a distinct lack of understanding of the likely impact of global environmental change on marine fish functional diversity. Here, I explore potential changes in the functional diversity of marine fish globally, under a plausible scenario of future greenhouse gas emissions. I combine biogeographic and community ecology approaches to investigate the potential effects of climate change on more than 9,000 marine fish species. The largest absolute increases in functional diversity are projected to occur in polar regions, with increases in functional diversity being larger than expected given the change in taxonomic richness. The Arctic, in particular, is likely to undergo a substantial reshuffling of trophic interactions as small, pelagic species with unique functional traits move into the region. Across all marine realms, the relative frequencies of fish with higher thermal tolerances, smaller body sizes and faster life histories are projected to increase. The most climate-vulnerable group of fish are the deep-sea species, particularly those that live on the seafloor, which decline across all the world's oceans. Overall, my simulations suggest the potential for marine fish assemblages to undergo considerable restructuring as a result of climate change. The substantial changes I project to both global taxonomic and functional diversity, highlight the potential vulnerability of the world's oceans, and consequently the future risk to human societies, most of whom are heavily dependent upon marine resources.

3.2 Introduction

Marine fish communities play a pivotal role in shaping the ecological balance of the world's oceans (Martin et al., 2023). The interplay between species, their functional roles, and their spatial distribution contributes to the resilience and adaptability of marine ecosystems (Åkesson et al., 2021; Grêt-Regamey et al., 2019; Thorogood et al., 2023). However, warming temperatures, shifting ocean currents, and altered environmental conditions (Gattuso et al., 2015a), are disrupting these delicate balances, which is leading to considerable challenges in the ocean's capacity to support life and to recover from disturbances. As global ocean environments change, species are redistributing to track their ecological niche (Lenoir et al., 2020; Lenoir & Svenning, 2015; Perry et al., 2005; Pinsky et al., 2013). As a result, entire ecological communities are reshuffling and reassembling, with further changes likely in future, triggering knock-on effects for ecosystem function (Pecl et al., 2017). This major restructuring of ecological communities into the future will have repercussions for human populations that rely on functioning ecosystems (Pecl et al., 2017). It is therefore vital to study these systems, to predict not only individual species' distribution shifts in the future but also to understand how communities may change, and the consequences for ecosystem structure and function.

Climate change studies, over both past and future periods, commonly explore changes in taxonomic richness, shedding light on changes to biodiversity patterns across different regions (Antão et al., 2020; Edgar et al., 2017). While these studies of biodiversity provide valuable insights, research that goes beyond taxonomic considerations is needed to understand the impacts on ecosystem structure and functions (McLean et al., 2019; Pinsky et al., 2020; Toussaint et al., 2018). Understanding the functional diversity and traits of marine fish assemblages and how they may change under future climate change scenarios is vital for predicting and mitigating the ecological impacts of environmental change (Pimiento et al., 2020).

Functional diversity, encompassing the variety of roles and traits exhibited by species within a community, is a key determinant of ecosystem stability and resilience (Petchey & Gaston, 2006; Villéger et al., 2008). Functional diversity is based on functional traits, which are an important tool in community ecology as they directly affect an organism's performance (McGill et al., 2006; Teixidó et al., 2018; Violle et al., 2007). Various functional traits, such as diet, trophic level, thermal preferences, and reproductive strategies, play a pivotal role in determining the ecological roles of species within their respective ecosystem (Gross et al., 2017). The intricate web of interactions between marine species and their functional roles influences ecosystem functioning, productivity, and the overall health of environments (Mouillot et al., 2013). As climate changes so too can a species' distribution, with a knock-on effect on taxonomic richness and trait composition of local communities. As such, any changes to the distribution of species within a community, and hence the composition of traits, under different climatic conditions can provide insights into potential changes to ecosystem function (Pimiento et al., 2020; Teixidó et al., 2018). The extent to which climate change will trigger (or is already triggering) changes to the number of functional traits present at regional and global scales of marine fish is, to date, uncertain. This largely results from the paucity of studies linking traits to biogeography in changing environments across other taxa (Pinsky et al., 2020). To date, there is a distinct lack of understanding of the likely impact of global environmental change on marine fish functional diversity.

The main aim of this chapter is to map current global functional diversity and structure of marine fish assemblages, along with projected changes to assemblages and their functional diversity by 2100. I do this by asking four main questions: (1) How does taxonomic richness and functional composition vary across global marine regions, and how does taxonomic and functional diversity change under future climate change projections?; (2) How does functional richness change with taxonomic richness and are changes in functional richness typically driven by losses or gains of functionally distinct species?; (3) Do the effects of climate change on functional trait space differ between communities in different realms?; and (4) Could some traits become commoner or rarer in the future with climate change, and are colonisations or extinctions (i.e. changes in functional space) linked to certain traits or trait combinations?

3.3 Methods

3.3.1 Species occurrence data

An initial global species list for marine fish was downloaded from the World Register of Marine Species (WoRMS) database (https://www.marinespecies.org/; Ahyong et al., 2023). The list was filtered to exclude any freshwater and/or part-terrestrial species. Occurrence data were then gathered for over 18,000 marine fish from the Global Biodiversity Information Facility (GBIF; http://data.gbif.org) and the Ocean Biodiversity Information System (OBIS; http://www.iobis.org). GBIF data were downloaded on 26th October 2022 using the 'rgbif' package (Chamberlain et al., 2023) using the download link https://www.gbif.org/occurrence/download/0121994-220831081235567 (GBIF.org, 2022). OBIS data were downloaded on the 31st October 2022 using the 'robis' package (Provoost & Bosch, 2017b). The occurrence data were cleaned and filtered to remove spurious records by: (1) removing records from land, (2) removing fossil specimens, (3) removing records missing coordinates, (4) removing duplicate records, and (5) removing occurrences recorded pre-dating 1945. Following this process, the GBIF and OBIS occurrences were combined and any duplicate records were removed. 404 species that had fewer than 10 occurrences after cleaning were also removed due to issues with modelling based on so few records. To account for the spatial clustering of occurrence records, species' occurrences were rarefied by gridding them to a 0.5 x 0.5 degree grid. Any species that had fewer than 10 occupied grid cells post-rarefication (6,337 spp.) were also dropped from the analysis. This resulted in a final species list of 9,713 marine fish species that we used for distribution modelling.

3.3.2 Environmental data

Environmental data were downloaded from the publicly available dataset, Bio-ORACLE v2.1 (https://www.bio-oracle.org/; Assis et al., 2018), using the R package 'sdmpredictors' (Bosch et al., 2016). The following seven environmental variables were chosen as predictor variables in the species distribution models: mean sea-surface salinity, mean sea-surface temperature, mean sea-bottom temperature, mean sea-surface chlorophyll concentration, mean sea-surface currents velocity, distance to shore and bathymetry. The first five variables are dynamic and liable to change over time, whilst the latter two remain static over our study period. All seven variables were downloaded for a current period (2000-2014), which is the only period of time available for current data from Bio-ORACLE (when downloaded in 2022). For the future time period (2090-2100, referred to as 2100 for the sake of brevity), the five dynamic variables were downloaded for a medium-high emissions scenario (RCP6.0), from the CMIP5 climate simulations models currently available on Bio-ORACLE. The environmental variables were chosen based on the methods described in Chapter 2 and represent those used in other species distribution models (SDMs) of marine species (Jones & Cheung, 2015). Environmental data were resampled to a 0.5 degree grid.

3.3.3 Presence-only species distribution models

Given the difference in the data modelled, being presence only rather than presence-absence, here I use different SDM methods than those described in Chapter 2 (Renner et al., 2015). Presence only SDMs require the generation of background data to be used as pseudoabsences (Valavi et al., 2021). Here, I use an ensemble of four SDM approaches: Maximum Entropy (MaxEnt), Generalised Additive Models (GAMs), Boosted Regression Trees (BRTs), and Random Forests (RFs). These model types were chosen due to their effectiveness in handling presence-only data (Valavi et al., 2021), and based on their prior performance in previous modelling studies. To fit SDMs to presence-only data, 10,000 background data (pseudo-absences) were randomly selected from the same realm(s) in which a target species currently occurs. This avoids selecting pseudo-absence points that are climatically suitable but are beyond the dispersal limits of a species.

Below, I outline the four modelling approaches along with the model-fitting process.

3.3.3.1 MaxEnt

MaxEnt models are a widely used SDM approach, specifically designed for handling presence-only species data (Phillips et al., 2006). Models were fitted using Maxent software version 3.4.3. I used the full available range of model regularization multipliers and features when running MaxEnt: 0.5, 1, 2, 3, 4 for beta-multipliers and LQHP, LQH, LQ, H, and L for feature types. Models were initially run using all combinations of multipliers and features and then fine-tuned by selecting the parameters for the best model, assessed using AUC. Models were run using the ‘maxent’ function in the ‘dismo’ package (Hijmans et al., 2022). Models were predicted using ‘cloglog’ response type.

3.3.3.2 GAMs, BRTs and RFs

Modelling methods for GAMs, BRTs and RFs were as described in Chapter 2.

3.3.3.3 Dealing with spatial autocorrelation

I dealt with the issue of spatial autocorrelation in a similar manner to that described in Chapter 2 but replaced the terrestrial ecoregions and realms with the Marine Ecoregions of the World (MEOW; (Spalding et al., 2007)) and Pelagic Provinces of the World (PPOW) (Spalding et al. 2012). The MEOW dataset contains 12 large biogeographical realms, covering shelf systems of the world’s oceans and the PPOW contains four broad pelagic biogeographic realms covering open ocean. I combined the latter two to get a final 16 biogeographic realms (Figure S3.1). For the ecoregions, I largely used the MEOW (containing 232 ecoregions), but they do not cover the entire world’s ocean. Therefore, I also used the PPOW to create an additional 37 ecoregions, so that there were no gaps of ocean that did not classify as a specific ecoregion. This resulted in a total 269 ecoregions covering the world’s oceans. Each block comprised a subset of the 269 ecoregions, such that each block samples parameter space adequately, whereby the total area and mean environmental data were approximately equal in each block and each block contained the full range of environmental data (Bagchi et al., 2013).

3.3.3.4 Model validation

Models were validated as described in Chapter 2, undergoing the same validation process for Maxent as the other models.

3.3.3.5 Fitting species distribution models

Models were fitted as in Chapter 2, trained on nine blocks, and leaving one block out in turn, resulting in 40 models (10 blocks x 4 SDMs) per species. These models were then used to project future suitable niche-space for species, across the same realms that they currently occupy, as well as in adjacent realms (using the MEOW and PPOW as described above). We assumed unlimited dispersal in ocean environments, whereby species can fully track their climatic niche in space and time. The resulting projected occurrence probabilities were converted to binary presence/absence values using a threshold that maximised the sum of sensitivity and specificity ('MaxSens+Spec'). The projection results were weight-averaged across the 40 models, with individual model weightings being based on the Area Under the Curve (AUC) of each model. AUC values provide a quantitative measure of a model's ability to correctly discriminate between presences and absences, with higher AUC scores indicating better model performance. In this sense, the best performing model in the ensemble would lend the greatest weight to the final projected species' distribution. After running SDMs, there was a total of 9,713 species with projected distributions.

3.3.4 Trait data

Trait data were collated from FishBase (www.fishbase.org/; Froese and Pauly, 2023). Ten traits were selected to represent the ecological functions that marine fish fulfil in the world's oceans. These included a selection of morphological (Albouy et al., 2011; Reecht et al., 2013), life-history, dietary and environmental traits (Gravel et al., 2016) for each species (Table 3.1).

Trait data were downloaded using the R package 'rfishbase' (Boettiger et al., 2012). For species missing trait information, traits were inferred using the machine-learning method *random forests*, from the 'missForest' package (Stekhoven & Bühlmann, 2012), which uses regression trees of observed trait data to infer missing values based on shared traits across related species (Penone et al., 2014). Of the 9,713 species with projected distributions, 19 species had no trait information in FishBase and so were discarded from further analyses. This resulted in 9,694 species being included in the final analysis.

Table 3.1 Description of marine fish functional traits used in functional diversity analysis. Abbreviations used in figures in results section are given for functional traits and their values is categorical. Includes main ecological interpretation to support the use of each variable.

Functional trait (abbreviation)	**Category**	**Type**	**Values (abbreviation)**	**Ecological interpretation**
Mean preferred temperature (MeanTempPref)	Environmental	Continuous		Indicates environments preferred by species.
Modal position in the water column	Environmental	Categorical	Bathydemersal (BAD), bathypelagic (BAP), benthopelagic (BEP), demersal (D), pelagic (P), pelagic-neritic (PN), pelagic-oceanic (PO), reef-associated (RA)	Indicates environment/ habitat type preferred by species. Demersal = seafloor 0-200m. Bathydemersal = seafloor below 200m. Bathypelagic= open water below 200m. Benthopelagic = both seafloor and open water 0-200m. Pelagic= open water 0-200m.
Maximum depth (DepthMax)	Environmental	Continuous		Reported for juveniles and/or adults (in m)
Trophic level (Troph)	Life-history	Continuous	Range from 1 (lower trophic levels) to 5 (higher trophic levels)	Indication of position in trophic food web, high trophic levels = predators.

Functional trait (abbreviation)	Category	Type	Values (abbreviation)	Ecological interpretation
Diet	Life-history	Categorical	Detritus (DE), nekton (NE), others (O), plants (PL), zoobenthos (ZB), zooplankton (ZP)	Main diet of species. Indication of feeding preferences
Lifespan (AgeMax)	Life-history	Continuous		
Growth coefficient (K)	Life-history	Continuous		Rate (1/year) at which the asymptotic length is reached. A faster growth rate indicates a faster life-history strategy.
Maximum length (MaxLengthTL)	Morphological	Continuous		Size traits indicate balance and energy flow. Maximum total adult length (in cm)
Adult swimming mode	Morphological	Categorical	Amiiform (AM), anguilliform (AN), balistiform (BAL), bathypteroiform (BAT), carangiform (CA), diodontiform (DI), ostraciiform (OS), labriform (LA), rajiform (RA), subcarangiform (SU), thunniform (TH)	Indication of hydrodynamics and swimming performance, a key determinant mediating fitness and survival.
Reproductive guild	Reproductive	Categorical	bearers (B), bearers external brooders (BEB), internal live bearers (BILB), guarders (G), brood hiders (GBH), clutch tenders (GCT), nesters (GN), guarders open water/substratum egg scatters (GOW), nonguarders (N),	Combined reproductive guilds I and II from FishBase. Guild I corresponds with first value and guild II the second value.

		nonguarders brood hiders (NBH), nonguarders external brooders (NEB), nonguarders open water/substratum egg scatterers (NOW)

3.3.5 Functional diversity of grid-cell assemblages

Of the ten functional traits gathered for each species, the five continuous traits were log-transformed and standardised using the z-score method. Firstly, a large dissimilarity matrix of the 9,694 fish species was computed, estimating Gower's distance – the functional distance between each pair of species according to their traits (Gower, 1971). I computed the matrix using the 'daisy' function from the package 'cluster' (Maechler et al., 2022). I projected these dissimilarities using a Principal Coordinates Analysis (PCoA) to create a varying number of functional trait spaces based on one to ten dimensions using the 'mFD' package (Magneville et al., 2022). The number of dimensions used in functional diversity analyses is a trade-off between the amount of information explained by the axes and the computational run-time (Maire et al., 2015). I used the 'quality.fspaces' function from the 'mFD' package to assess the quality of the resulting functional space. High quality functional spaces are defined by the species-pair distances in the functional space being similar to the initial functional distance computed based on species traits (Gower's distance) (Maire et al., 2015). This was done by comparing the root mean squared deviation (RMSD) for each dimension of trait space. The dimension with the lowest RMSD indicates lower deviations between trait-based and space-based distance between species, and hence the best quality space (Maire et al., 2015). The six-dimensional functional space had the lowest RMSD value, although the fourth and fifth dimensions had an RMSD only a fraction higher. Thus, only the first four principal axes of the PCoA were selected to build the multidimensional functional space as they explained over 75% of variance and the RMSD was only 0.002 higher than that for six dimensions. The contribution of each original trait to the PCoA axes (based on first four dimensions of the trait space) was extracted using the 'traits.faxes.cor' function.

For all current and projected future grid-cell assemblages, fish species' coordinates in the four-dimensional space defined by the four-dimensional PCoA were used to calculate three indices each representing a different element of functional diversity (Mason et al., 2005). These were functional richness (FRic), functional divergence (FDiv) and functional evenness (FEve). FRic is the proportion of functional space (convex hull volume) filled by all the species in each grid cell or community (depending on scale) (Villéger, Mason and Mouillot, 2008). Absolute values of FRic are arbitrary (ranging between 0 and any number) and cannot be compared between communities or sites. Hence, FRic values were standardised using the overall FRic value for the global fish community, thus bounding FRic between 0 and 1 so that different grid-cells and time-periods could be compared. FDiv is the deviation of species' biomass from the centre of the multidimensional functional space i.e. the extent to which species are spread out or clumped in trait space. FDiv will be low when most individuals have traits near the centre of functional space and will be greatest when individuals are positioned at the edges of the trait space (Mason et al., 2005). FEve is the regularity of spacing of species in the multidimensional trait space (Villéger, Mason and Mouillot, 2008). A high FEve indicates a more regular placement of species in trait space. FDiv and FEve are independent of taxonomic richness and so are useful indicators of functional diversity, whereas FRic can be easily affected by taxonomic richness (increasing species richness is more likely to mean increasing functional richness).

Functional diversity indices were calculated using the 'fundiversity' package in R. Functional diversity indices could not be calculated in cells with fewer species than the number of dimensions of multi-dimensional space. FRic values were standardised by the total volume of all species in the dataset so that FRic values could be compared between grid-cells (Villéger, Mason and Mouillot, 2008). To assess the impacts of climate change on functional diversity at the grid-cell level, I calculated differences between current FD indices and future FD indices by subtracting future values from present-day values per grid-cell assemblage.

3.3.6 Relationship between taxonomic richness and functional richness

To investigate whether changes in FRic per grid cell were primarily influenced by the loss or gain of functionally distinct species, I compared the observed ΔFRic to the predicted ΔFRic values expected from the ΔTRic. To do this, I followed the methods from Stewart et al. (2022). I modelled ΔFRic as a function of ΔTRic using robust regression, using the 'MASS' package (Venables & Ripley, 2002). The output of this model was used to predict the change in FRic from change in TRic. I calculated residual FRic as the difference between the observed ΔFRic and predicted ΔFRic. Each grid-cell assemblage was then categorised based on the percentage difference between observed and predicted change in FRic, calculated as the residual divided by the predicted. Separate categories were also made for grid-cells whereby FRic increased despite a loss of TRic (and vice versa) and where FRic changed despite no change in TRic.

3.3.7 Taxonomic richness and functional richness by realm

Changes in taxonomic richness (TRic) and functional richness (FRic) were also evaluated per biogeographic realm (as described in section 3.3.3.3) assemblage. FRic was calculated as described above, but rather than calculating FRic for each grid-cell assemblage, FRic was calculated for each of the 16 realms for both present-day communities and projected communities under the RCP 6.0 emissions scenario. Similarly, taxonomic richness was calculated as the sum of all species occurring across all grid-cells within each realm for present and future distributions.

3.3.7.1 Future changes in functional diversity

To compare the distribution of fish traits between current communities and those under the future emissions scenario in 2100, I plotted each species within the multi-dimensional functional space of each of the 16 biogeographic realms. Multidimensional trait spaces or functional spectra are useful to elucidate which traits might be vulnerable under climate change and how trait combinations might change with the addition or loss of certain species.

I first created a functional trait space for the present-day global marine fish community. I followed the methodology presented in Toussaint et al. (2021) who use the ‘TPD’ package to visualise trait space and calculate FRic using a density-based approach. Trait Probability Density (TPD) methods, using probabilistic hypervolumes, are an alternative way of calculating FRic. They are useful for visualising functional spaces in more detail compared to simpler convex hulls as they show the density of certain traits within the spectra and give information about functional redundancy (Mammola et al., 2021). I used the ‘TPD’ function to estimate probabilistic hypervolumes of marine fish species within the four-dimensional functional space (Carmona et al., 2019, 2021), by performing multivariate kernal density estimations. Each species’ kernel was a multivariate normal distribution, with the bandwidth unconstrained and selected using the ‘Hpi’ function from the ‘ks’ package (Carmona et al., 2021; Chacón & Duong, 2010). Following Toussaint et al. (2021), I split the functional space into a grid of equal-sized cells (200 per dimension) and calculated the TPD function value per cell. Splitting the functional space into grid-cells enables a clearer visualisation of the space. Each TPD function value per cell equals the density of species in that location in the functional spectra. Thus, a high value indicates many species with similar traits. I visualised the functional spectra as contours containing 50, 95 and 99% of total trait occurrence probability. Contours were calculated using the ‘emdbook’ function in the ‘HPDregionplot’ package. To identify which combination of traits that contributed most to each PCoA axis, I used the function ‘envfit’ from the ‘vegan’ package (Oksanen et al., 2022) to extract covariance values of each vector (continuous variables) and factor (categorical variables). I fitted trait-arrows to the trait space to indicate the contributions of continuous variables to the first two PCoA axes, whereby the length of the arrows was scaled by the R-squared values to indicate each variables contribution. Each categorical variable contribution was visualised by plotting the minimum convex hulls showing the distribution of trait categories within the trait space.

I then compared functional trait spaces between realms to observe each species in functional space and how this space is projected to change in future. Using the density-based (TPD) approaches described above for the global functional spectra, I assessed whether certain traits were projected to become more or less common with climate change and hence whether fish with certain traits are more vulnerable to environmental change. First, I estimated TPD functions of both present-day and projected future species’ distributions, using TPD methods in Toussaint et al. (2021), for each of the 16 biogeographic realms. Second, I calculated the differences in the TPDs between current assemblages and projected future assemblages, per realm. This made it possible to identify the potential effects of changes in species’ distributions in functional space with climate change. I calculated changes in FRic for each realm. To visualise changes in functional spectra, I expressed probabilities as quantiles and so could subtract quantile values of the TPD function of future spectra from the present day TPD function. Positive values indicate an increase in the relative frequency of those traits in that cell. I also plotted the relative frequencies of each trait category per realm (I converted continuous variables into discrete categories) and compared between current climate and future climate change.

3.3.8 Null models

As FRic is highly influenced by TRic, for each oceanic realm, I compared the observed current values of FRic with a null model where the same number of species were randomly selected from the world species’ pool. For each realm, I created 999 random assemblages and calculated each corresponding FRic and compared these FRic values to observed FRic values for current assemblages by calculating standardised effect sizes (SES) as the (current observed FRic – mean(null FRic))/SD(null FRic). I calculated the significance of the difference from null expectations using a two-tailed t-test. P-values lower than 0.025 indicate assemblages with FRic lower than expected (or functionally clustered) and p-values higher than 0.975 indicate assemblages with FRic larger than expected (or functionally overdispersed). P-values falling between these indicate FRic does not differ from expected, meaning similar amounts of functional space is filled in each realm regardless of the number of species present.

Finally, I also tested the deviation between the observed change in FRic (ΔFRic) and expectation given the number of species gained and lost per realm in 2100. I randomly removed and added species to current assemblages, maintaining the same number of gains and losses. I repeated randomisations 999 times. To measure the difference between predicted FRic change (loss or gain) values due to extinctions or colonisations and null expectation of FRic change, SES were calculated as the (observed ΔFRic– mean null ΔFRic)/SD(null ΔFRic). Again, I tested the significance of the difference from null expectations using a two-tailed t-test. I also tested whether the SES values for each realm were significantly different from each other using multiple pairwise comparisons. To obtain distributions of SES values for each realm, I calculated 99 SES values from a random sample of 99 ΔFRic values among the 999 simulations.

All statistical analyses were performed in R version 4.0.3 (R Core Team, 2020).

3.4 Results

3.4.1 Taxonomic richness and functional diversity worldwide

This study considered the impacts of climate change on 9,694 marine fish species across the world's oceans. SDMs performed well, with the average area under the curve (AUC) of ensemble models being 0.95 (± 0.05 SD). Overall, MaxEnt outperformed the other models (average AUC of MaxEnt: 0.96 ± 0.04), while GAMs performed the least well (average AUC of GAM: 0.94 ± 0.06) of the four models. RFs and BRTs performed almost as well as MaxEnt (average AUC for RFs and BRTs: 0.95 ± 0.05 and 0.95 ± 0.06, respectively). The resultant modelled taxonomic richness patterns from the SDMs (Figure 3.1a) were comparable with known current marine fish richness patterns (Tittensor et al., 2010) with highest richness in the tropics, and over 7,000 of the world's marine fish species projected to occur in the Indo-Pacific oceans.

Under a medium-high emissions scenario, at the global scale, only ten species are projected to have no suitable climate by 2100 and are projected by my models to go extinct. The effect of climate change, however, is not consistent across the world's oceans, with a highly variable pattern of projected changes to taxonomic richness in different regions (Figure 3.1b). There is a tendency for tropical regions to lose large proportions of taxonomic richness, indicated also by the large number of species loss (Figure 3.1c). Colder regions at high latitudes are projected to gain species (Figure 3.1d), with many areas projected to more than double their species richness by 2100 (Figure 3.1b). Indeed, some of these regions are also projected to become up to 100% novel in 2100 (Figure 3.1f). One major anomaly to this pattern in the northern hemisphere occurs in the Northern Atlantic region, where considerable losses in taxonomic richness, of up to 100% in places (and thus low novelty in Figure 3.1f), are projected. Patterns in the high latitude southern oceans are quite different, with apparent longitudinal banding, switching between species gains and losses at different latitudes.

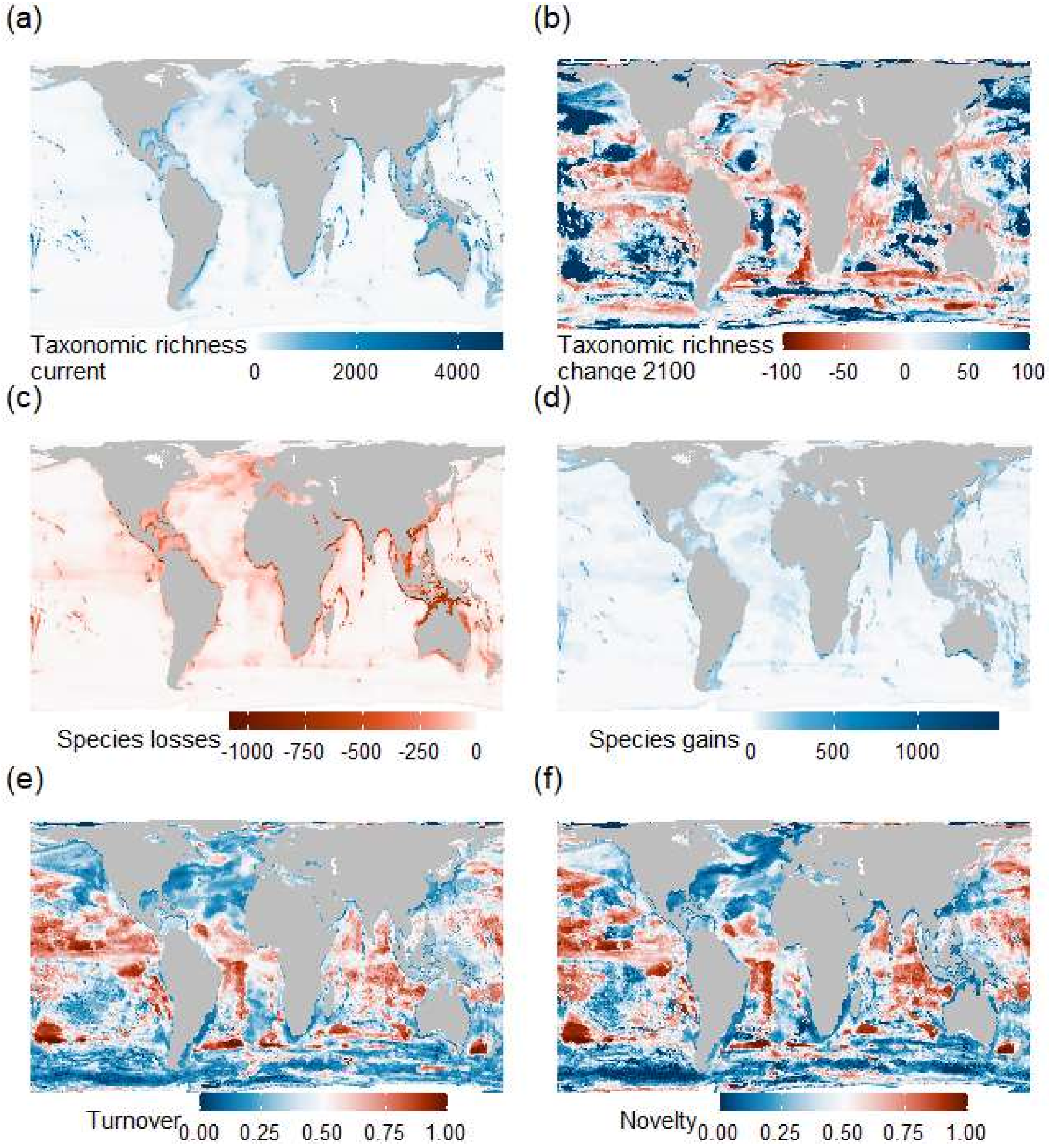

Figure 3.1. (a) Current taxonomic richness of world's marine fish (2000-2014), (b) proportional change, (c) losses and (d) gains in taxonomic richness in 2100 under a medium-high emissions scenario. Proportional gains in taxonomic richness are capped at 100% to aid visualisation of losses and gains. (e) Species turnover (Sorensen's dissimilarity) and (f) novel communities in 2100, with 0 indicating no turnover or novelty and 1 indicating 100% turnover or novelty.

Based on the projections of both current and projected future species' distributions, I calculated three indices to represent different aspects of functional diversity and compared these values for current and future fish assemblages at the grid-cell level. These predicted effects varied geographically for all three functional diversity indices. The regions that currently host the highest functional richness occur close to the coasts, or on shallow oceanic shelves, particularly in warmer waters (Figure 3.2a). Many of these tropical shelf areas are projected to lose functional richness by 2100 (Figure 3.2c). Positive changes in functional richness (FRic) are projected for open water regions and specific hotspots in the Northern Pacific, Bering Sea, Northern Atlantic, Labrador Sea and Baffin Bay, Hudson Bay, Barents Sea and the Southern Ocean (Figure 3.2c). However, increasing taxonomic richness does not manifest in increasing FRic in all areas. FRic is predicted to decline in the Tropical Eastern Pacific reefs, Northwestern Arabian Sea, Timor and Arafura Seas, East China Sea, and the Northern Atlantic West European Basin area. Only in some areas did this decrease in FRic reflect similar declines in FDiv and FEve (Figure 3.3). Most open water regions are expected to undergo changes in functional divergence (FDiv), but these changes vary spatially (Figure 3.3b). Fish assemblages in the South Pacific Ocean are expected to undergo the greatest declines in FDiv. Some of the largest gains in FDiv are estimated to occur in the mid Southern Indian Ocean, in the region between Australia and southern Africa. Changes in functional evenness (FEve) are similarly predicted in pelagic areas of the Pacific Ocean, though not necessarily in the same locations as the changes in FDiv (Figure 3.3d).

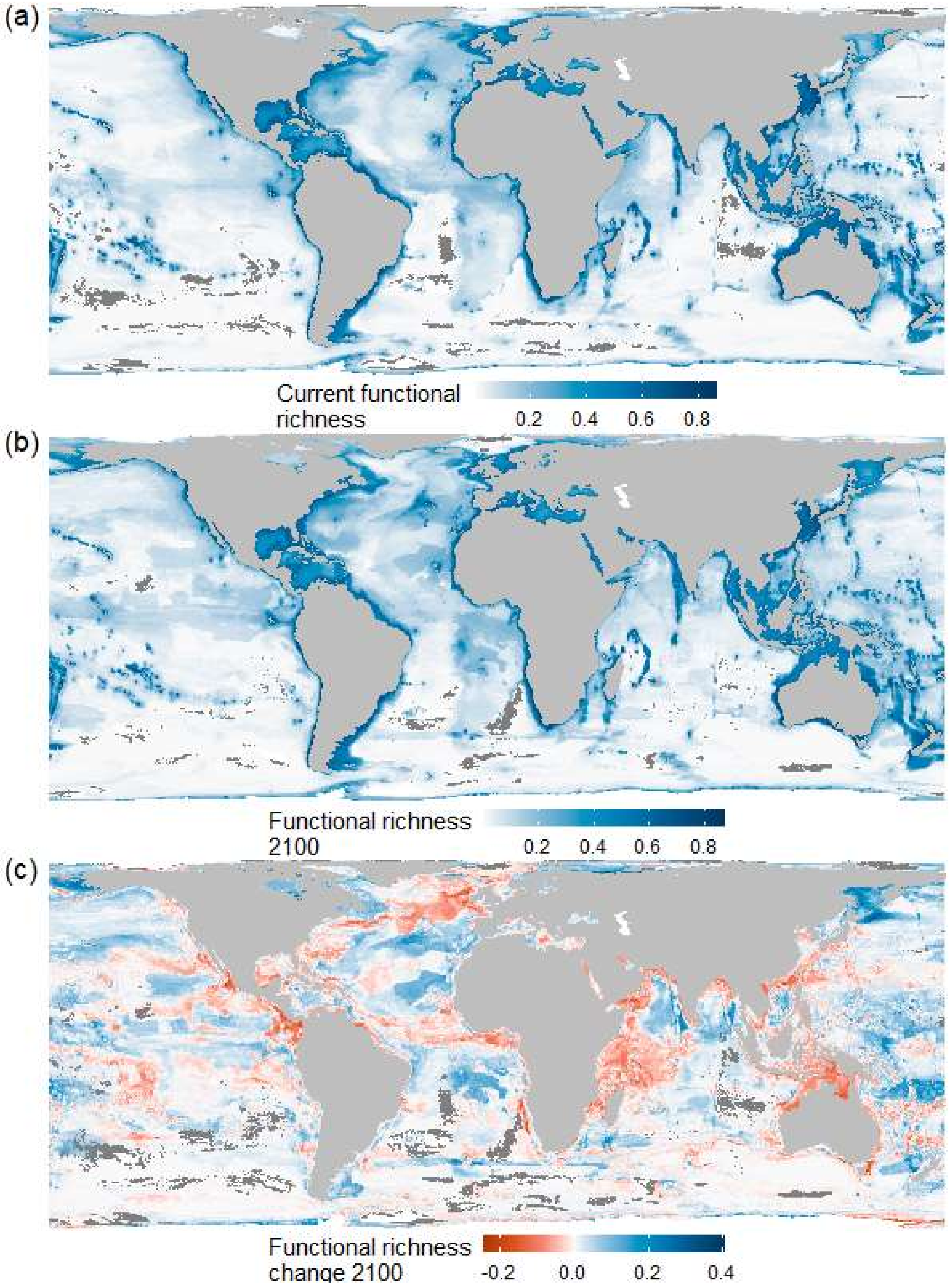

Figure 3.2. Functional richness (a) currently (2000-2014), (b) in 2100 and (c) change between current and 2100 under a medium-high emissions scenario. Functional richness values have been standardised by the global maximum FRic value (thus bounded between 0 and 1), so that comparisons between assemblages can be made.

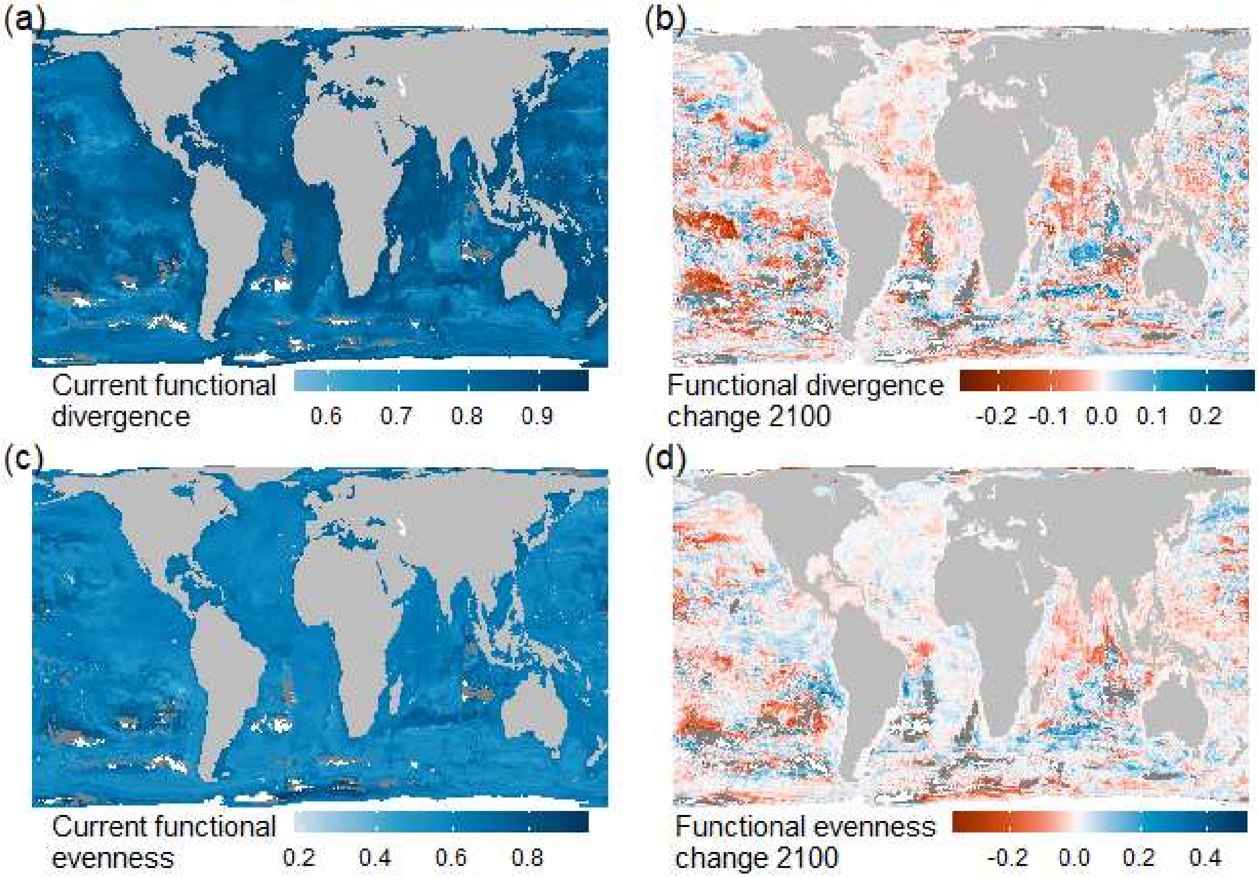

Figure 3.3. Functional divergence (a) currently (2000-2014) and (b) relative change between the current and 2100. Functional evenness (a) currently (2000-2014) and (b) relative change between the current and 2100. Dark grey and contiguous white indicate regions with fewer than four species so each index could not be calculated.

3.4.2 Relationship between functional richness and taxonomic richness

To understand the impacts of climate change on ecosystem structure and function, I analysed the changes in FRic in relation to taxonomic richness. For roughly 8,000 grid cells assemblages (of the total 189,556) (Figure 3.4c), functional diversity (FD) loss is more than 50% larger than expected from the change in taxonomic richness (TRic) (darker red shading in Figure 3.4). Most coastal areas in the tropics are predicted to have FRic loss 50% smaller than expected (yellow shading in Figures 3.4a & b). In principle, this indicates the loss of morphologically similar species which is less likely to have such immediate impacts because species remain to carry out vital functions. Most assemblages in the northern hemisphere and Arctic regions are dominated by the FD gain being more than 50% larger than expected from the change in TRic (purple shading in Figure 3.4a). Large areas of the Southern Ocean have a more than 50% lower-than-expected gain in FD compared to TRic (pale blue shading in

Figure 3.4a). Lastly, the large number of assemblages in red (more than 50,000 grid cells, Figure 3.4c) indicates high turnover, where there is a loss of FD despite a gain in TRic.

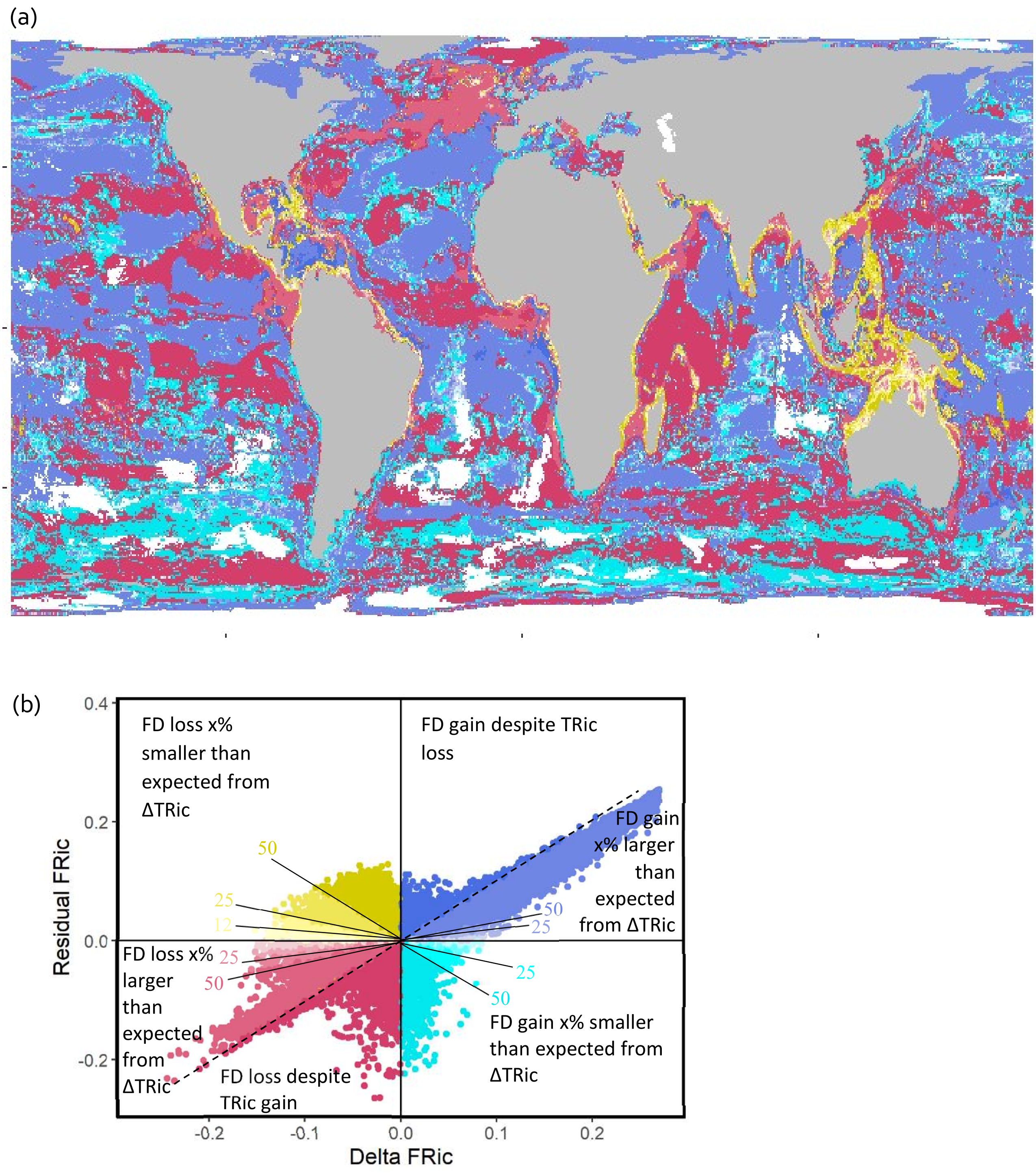

Figure 3.4. Relationship between the observed and predicted change in functional richness from taxonomic richness per grid cell (a). White areas in (a) are the grid-cells that had zero presences both currently and in 2100. (b) shows the relationship between the residual functional richness and change in functional richness, divided into four main categories representing functional richness gain or loss in relation to that expected from change in taxonomic richness. Grey indicates no change in composition.

3.4.3 Current biogeographic patterns of taxonomic and functional diversity

To understand how functional trait space changes with climate change, I first identified the contribution of each original trait to the first four PCoA axes of the global trait space for marine fish (Table 3.2). PCoA axes 1 and 2 explain 28.4% and 22.0% of global variation respectively. The first axis correlates with all functional traits, but most strongly with swim mode (Figure 3.5b), maximum depth (Figure 3.5a) and vertical position in the water column (habitat) (Figure 3.5d). Left areas of functional trait space tend towards species characterized by shallower maximum depths, higher temperature preferences, reef-associated habitats, and labriform and diodontiform swim modes seen in wrasses and porcupine fish (Figure 3.5). Reproductive Guild is represented well by both PCoA axes (Figure 3.5c), with species towards the bottom-right of the trait space being nonguarders, upper areas being open-water egg scatterers, and left most areas of PC1 tending towards guarding behaviours and more costly reproductive strategies such as clutch tenders, nesters and bearers. Species with higher values on PC2 (upper regions of trait space) tend towards nekton feeders (eating organisms that can swim freely in the water column) and those with lower values feed on zoobenthos.

Table 3.2. Contribution of each trait to each Principal Coordinates Analysis axis for the first four axes of the multi-dimensional trait space. Number given has p-value lower than 0.05 and bold indicates traits of greatest influence on each axis.

	PC1	**PC2**	**PC3**	**PC4**
Maximum length	**0.280**	**0.243**	0.141	0.029
Trophic level	**0.266**	0.024	0.049	0.004
K	**0.327**	0.079	0.083	0.070
Maximum depth	**0.675**	0.004	0.030	0.051
Maximum age	**0.263**	0.104	0.065	0.090
Temperature preference	**0.462**	0.041	0.033	0.057
Swim mode	**0.732**	**0.462**	**0.362**	**0.309**
Reproductive guild	**0.562**	**0.542**	**0.278**	0.085
Vertical position	**0.656**	**0.228**	**0.506**	**0.458**
Diet	**0.279**	**0.440**	**0.340**	0.209

Considering FRic and TRic are related to one another, I performed null models to investigate whether current FRic is larger or smaller than expected given the same number but a random assemblage of species in each realm. Nine of the sixteen realms exhibit FRic smaller than expected, indicating high functional redundancy or clustering within the functional space (Figure 3.6). For contemporary fish assemblages across oceanic realms, the Indo-Pacific Warm Water hosts most of the world's functional diversity (96.6%) and the highest taxonomic diversity (78.3%, Figure S3.1), though this was not significantly different from random (t-test; p=0.29). Similarly, six other realms did not differ from random, showing that there is similar FRic and functional space filled by species in these realms, regardless of differences in taxonomic richness. The species in the warmer water realms (redder colours in Figure 3.6) mostly exhibit higher temperature preferences and reef-associated traits (Figure 3.5), with a high number of areas in the trait space representing a high frequency of common traits or functional redundancy (Figure 3.5 & 3.6). Surprisingly, the Atlantic Warm Water, with just over half the number of species of the Indo-Pacific Warm Water, also hosts high functional diversity (89.2%), though FRic did not significantly differ from random (t-test; p-value=0.54). Similarly, the Temperate Northern Atlantic and Southern Cold Water both display relatively high functional diversity (86.9% and 89.4% respectively) but each hosting only 34.2% and 44.3% respectively of the world's taxonomic diversity (Figure S3.1). The current FRic of these two realms did not differ from chance (t-test: Temperate North Atlantic: SES=-0.10, p-value=0.45; Southern Cold Water: SES=-0.53, p-value=0.29), indicating the differing functional traits of these species can be explained by species richness alone. Colder realms (the lower, cooler-coloured bar charts in Figure S3.4) exhibit lower current FRic than expected by chance indicating cooccurring species within these realms are more similar in the functional traits than a random assemblage of species (Southern Ocean: t-test: SES=-3.99, p-value=<0.001; Arctic: t-test: SES=-1.40, marginally significant p=0.07). Arctic species are characterised mostly by demersal traits and higher maximum depth of occurrence (Figure 3.5), represented by the clustering towards the bottom right of the trait space (Figure 3.6).

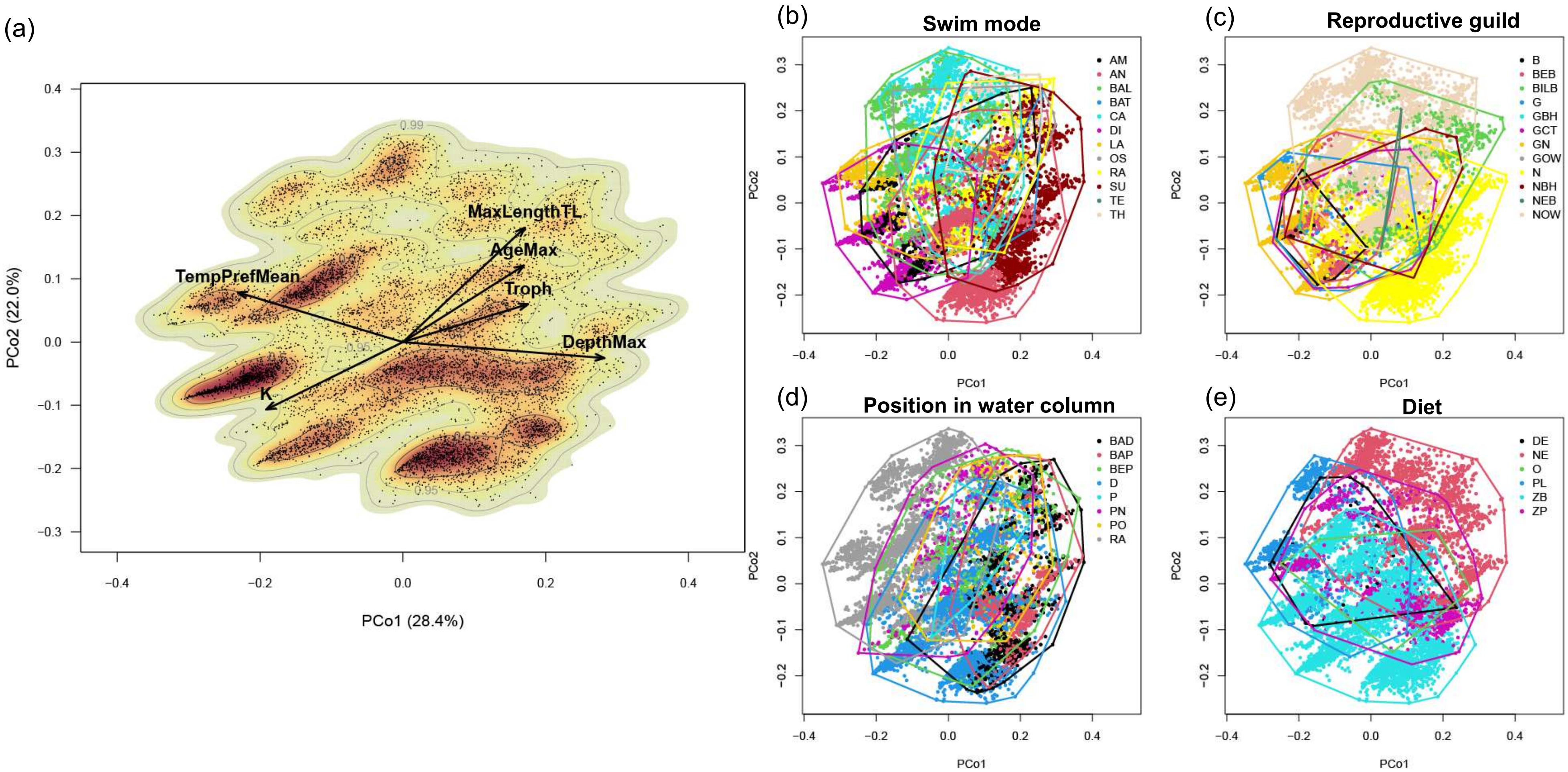

Figure 3.5. Global functional trait space of marine fish projected onto two major principal coordinates axes. Axes 1 and 2 explain 28.4% and 22.0% of global variation respectively. (a) Indicated by arrows, the continuous traits that contributed to the distribution of species along each axis. The colour gradient indicates 50, 95 and 99% contours of species density where darker red colours indicate hotspots of species density. (b-e) Convex hulls showing the distribution of trait categories within the trait space for the following categorical variables (refer back to methods for descriptions of these traits and their abbreviations) showing (b) swim modes, (c) reproductive guilds, (d) position in the water column, and (e) diet.

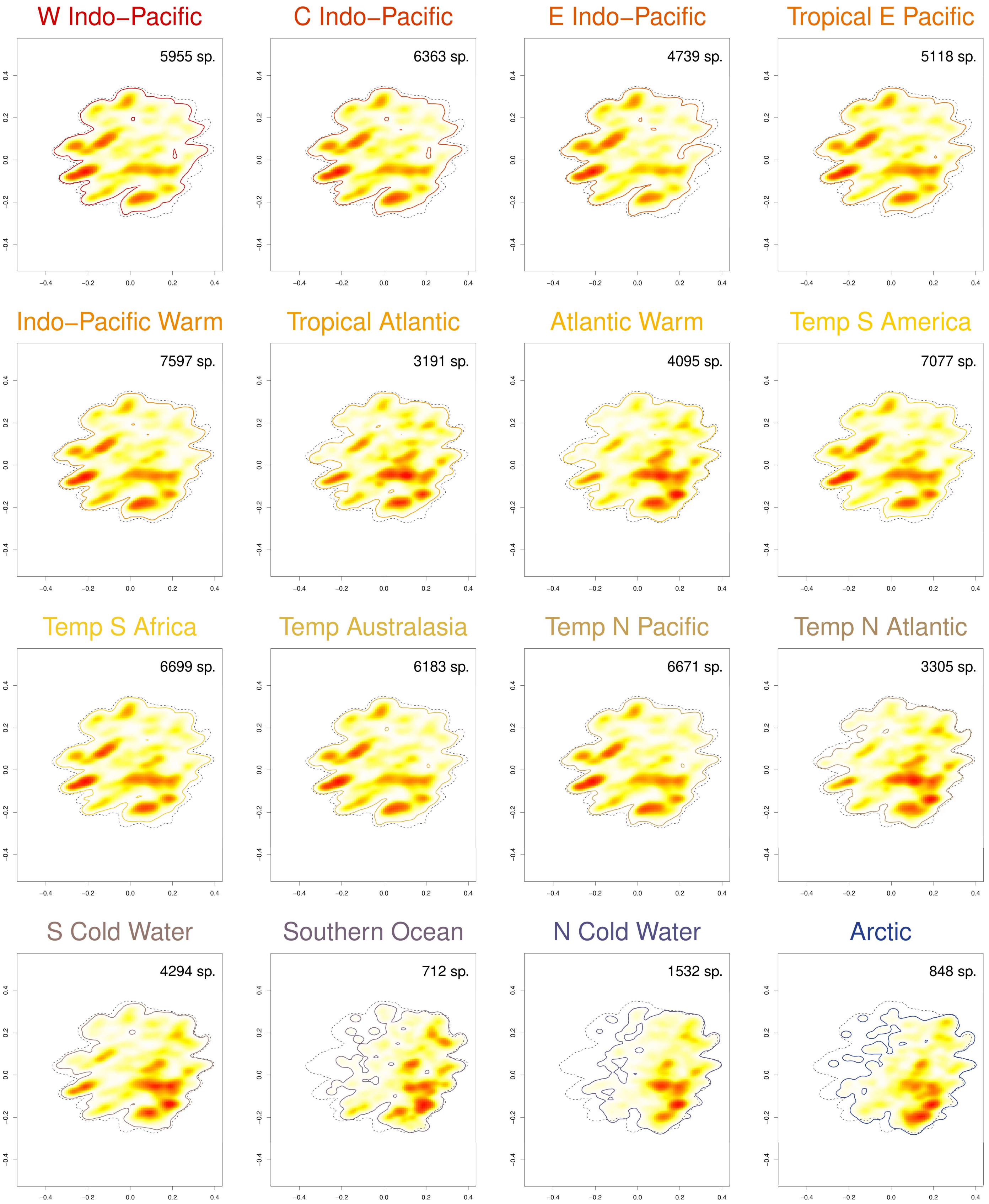
W Indo–Pacific
5955 sp.
C Indo–Pacific
6363 sp.
E Indo–Pacific
4739 sp.
Tropical E Pacific
5118 sp.
Indo–Pacific Warm
7597 sp.
Tropical Atlantic
3191 sp.
Atlantic Warm
4095 sp.
Temp S America
7077 sp.
Temp S Africa
6699 sp.
Temp Australasia
6183 sp.
Temp N Pacific
6671 sp.
Temp N Atlantic
3305 sp.
S Cold Water
4294 sp.
Southern Ocean
712 sp.
N Cold Water
1532 sp.
Arctic
848 sp.
−0.4
−0.2
0.0
0.2
0.4

Figure 3.6. Current functional spectra of marine fish in 16 biogeographic realms. The number of species within each realm is given. The contribution of each continuous and categorical trait to the first two PCoA axes of the four-dimensional trait space are shown in Figure 3.5. The grey dotted line indicates the global functional spectra (same as in Figure 3.5a). The colour gradient indicates 50, 95 and 99% contours of species density where darker red colours indicate hotspots of species density. Each functional spectra 99% contour is marked as a solid line in the associated realm colour (redder shades for warmer water realms and blue for colder water realms).

3.4.4 Impacts of climate change on biogeographic patterns of taxonomic and functional diversity

The trends in changes in taxonomic diversity and functional richness (FRic) were not uniform across biogeographic regions. By 2100, I project substantial increases in taxonomic diversity and FRic for cold water realms (Figures 3.7 and S3.1). 330 new species move into the Arctic region (Figures 3.7a and S3.1), increasing FRic by ~10% (Figure 3.7d). Similarly, the Northern Cold Water is expected to host 201 new species (Figure S3.1), resulting in a ~10% increase in FRic (Figure 3.7d). The most notable increases in taxonomic diversity are projected for the Southern Cold Water (Figure 3.7a), but this does not translate to a comparable increase in FRic (Figures 3.7b-d). Despite a similar gain in the number of species in Temperate South America (254 new species), FRic declined from 95.4% to 94.6% (represented as a proportion of the world's FRic; Figure S3.1). By 2100, the largest losses in taxonomic diversity are projected in warmer water regions, specifically the Western Indo-Pacific and Eastern Indo-Pacific (Figures 3.7b & d). Despite projected losses of 272 and 376 species, respectively, FRic decreases only marginally, by 2.2% and 2.1% respectively.

For each biogeographic realm, I then evaluated whether the observed change in FRic between current and future assemblages differed from expected given a random gain and loss of the same number of species. The significant largest increases in FRic occur in the Northern Cold Water and Arctic, compared to all other realms (Figures 3.7b, d & 3.8; Tukey post-hoc test; $p<0.05$). My analysis revealed that the observed increases in FRic in these two realms are, however, lower than expected (Figure 3.8). The Arctic mostly gains pelagic species (including benthopelagic), characterised by higher temperature preferences and faster life-histories (Figure 3.9), which decreases the relative frequency of demersal and deep-water species traits (Figures S3.3c & d). Similar patterns of lower-than-expected increases in FRic are shown for the Southern Ocean and Southern Cold Water, despite the large gain in species especially in the latter (Figures 3.7a & c). Interestingly, the lower-than-expected increase in FRic is more marked in the Southern Ocean than Southern Cold Water, meaning the species gained in the Southern Ocean share more similar traits, but are still relatively similar to species already present. The lower-than-expected gains in FRic in the Southern Ocean (Figure 3.8) may also be driven by a concurrent higher-than-expected loss in FRic. The Southern Ocean is projected to lose an area of trait space concentrated towards demersal and bathydemersal species, living at relatively shallow depths, that feed on zoobenthos and have more costly reproductive strategies (Figure 3.9).

My analysis revealed that there is a higher-than-expected decrease in FRic for all warm water realms, including all Indo-Pacific realms and tropical Atlantic (red and orange colours in Figures 3.7 and 3.8), with the most marked deviations between observed and expected in the Central and Western Indo-Pacific (Figure 3.8; t-test: SES < 0, $p < 0.05$). Functional losses are concentrated towards species with greater mean depth and lower temperature preferences, and species that are demersal or bathydemersal (Figure 3.9).

In temperate realms, overall changes in species composition resulted in higher-than-expected losses in FRic (Figure 3.7), especially in Temperate Australia (Figure 3.8). There is a high turnover of species within these realms. These realms lose species at higher trophic levels that are bathydemersal, with slower life-histories, deeper depth preferences and lower temperature preferences (Figure 3.9; Figure S3.3).

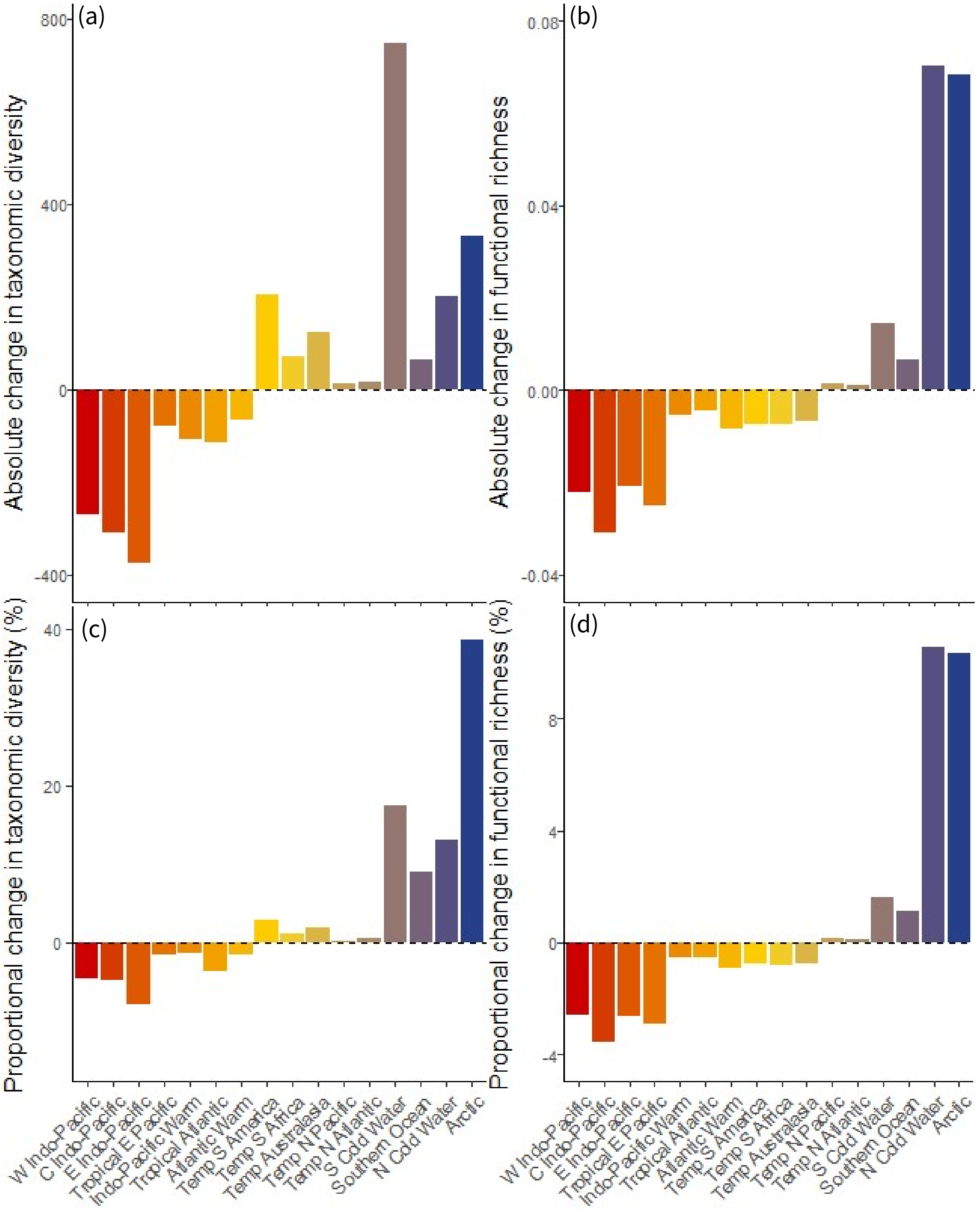

Figure 3.7. Absolute (a-b) and proportional changes (c-d) in taxonomic diversity (a) & (c) and functional richness (b) & (d) of marine fish by marine oceanic realm. Changes in taxonomic diversity are shown in (a) and (c), and changes in functional richness are shown in (b) and (d). Redder colours indicate warmer water realms (tropical regions), yellow indicate more temperate realms (mid-latitudes), and blue indicates cold water realms (polar regions).

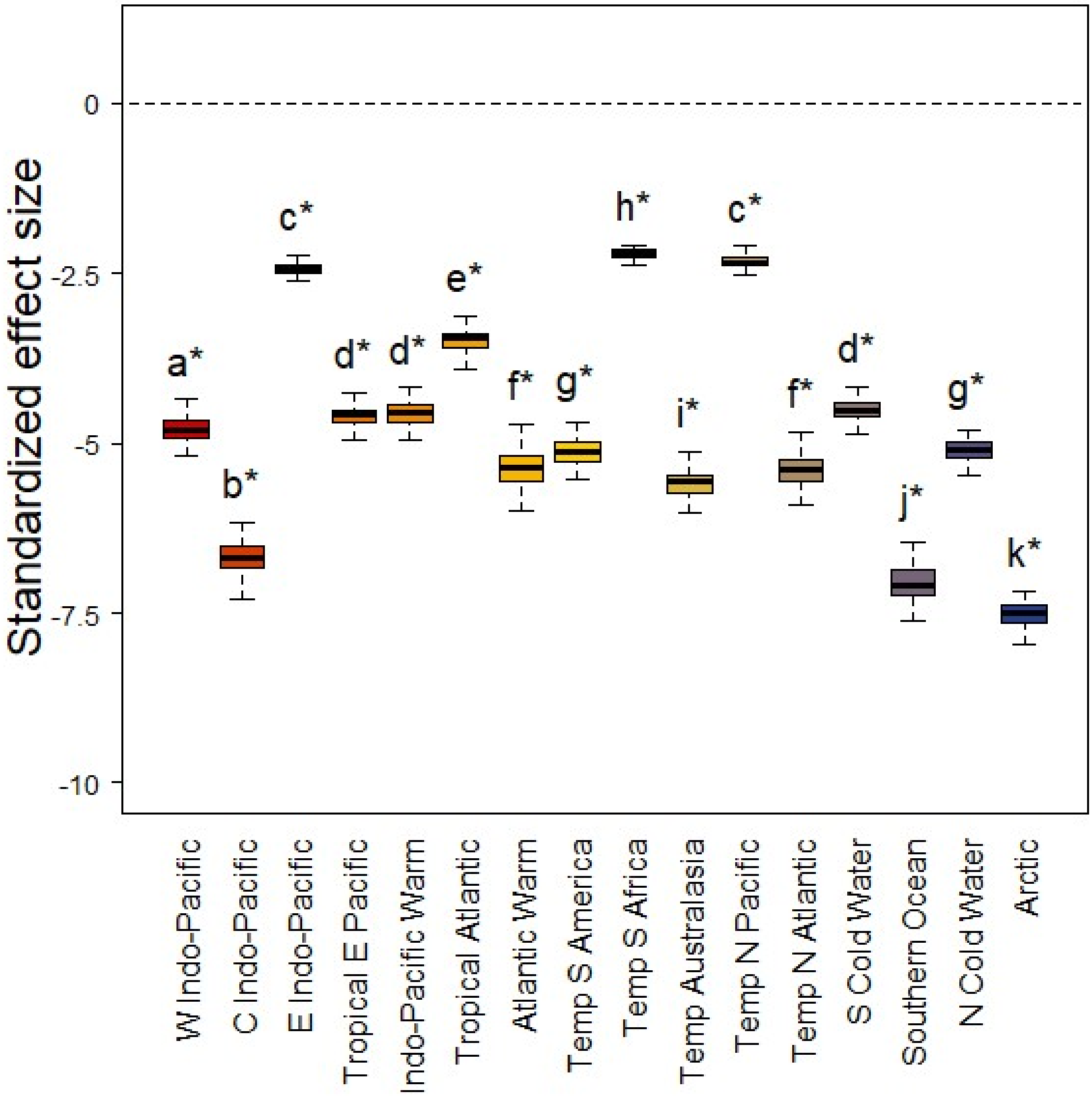

Figure 3.8. Standardised effect sizes showing deviations of observed change in functional richness change (between current and 2100) from null expectations for each oceanic realm. Negative SES represents a smaller observed FRic change than expected FRic change. Asterisks indicate SES values significantly different than expected from null models. Letter displays of all pairwise comparisons with p-values <0.05 between oceanic realms are shown. Colours indicate realm colours moving from warmer realms (redder colours) to colder water realms (more blue colours). Direction of the change in FRic (loss or gain) can be found in Figures 3.4b & d.

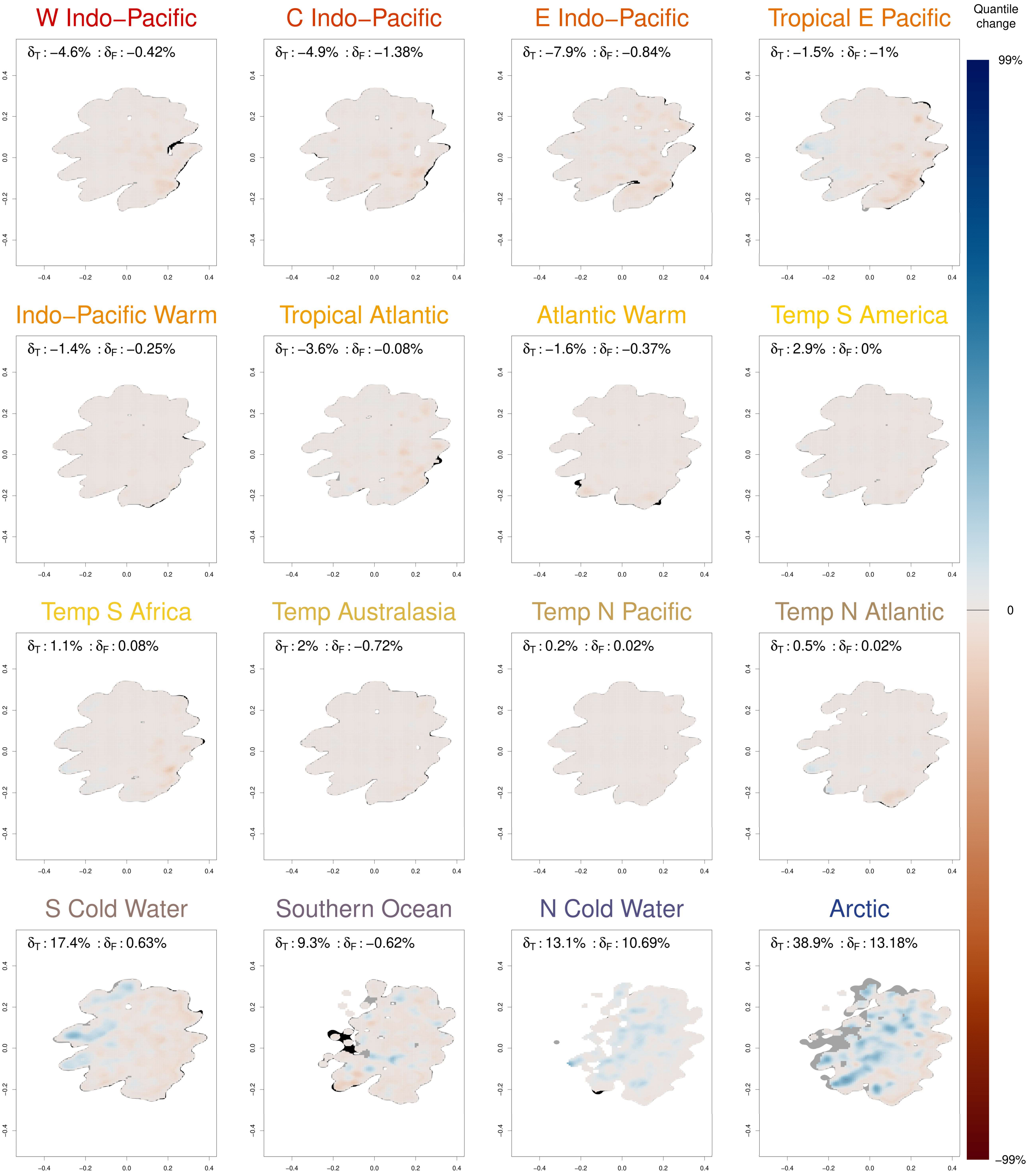

Figure 3.9. Changes in functional spectra by realm between current (2000-2014) and future (2100) assemblages under a medium-high emissions scenario. Dark grey shading indicates new regions of functional spectra which are not filled currently. Black shading indicates species loss and regions of functional space lost due to climate change. The blue-red shading indicates the quantile change in functional spectra between present-day assemblages and future assemblages, with blue indicating areas of trait space representing traits becoming more common with climate change and red indicating areas of trait space with traits becoming less common with climate change.

3.5 Discussion

In this Chapter, I present the results of a functional diversity approach to understanding the impacts of marine fish species' range shifts on ecosystem structure and function. To my knowledge, this is one of the first attempts to investigate the impacts of climate change on functional diversity of marine fish at a global scale. Here, I discuss these results in light of three key findings: (1) expected impacts of climate change on marine taxonomic and functional diversity globally; (2) expected relationship between functional richness and taxonomic richness; (3) expected differences in patterns among realms and expected variation in vulnerability of fish functional traits across realms.

3.5.1 Spatial variation of changes in taxonomic richness and functional diversity

By investigating changes in marine fish distributions at a global scale, and with the greatest number of species to date, I have revealed that changes in taxonomic richness varied geographically in response to climate change. Specifically, I found that across the tropics, taxonomic richness is projected to decline which aligns with existing literature and emphasises the vulnerability of tropical ecosystems to climate change (Lam et al., 2020; Parravicini et al., 2013). In large areas of polar oceans, taxonomic richness increases with climate change which corroborate existing literature on substantial range shifts at northern latitudes across various taxa (Antão et al., 2022; Root et al., 2003). This supports the idea that the greatest impacts of climate change will occur in areas most at risk, where temperature changes are the largest. Indeed, there is a growing body of literature providing consistent evidence of distributional shifts of marine biodiversity by the end of the century (Cheung et al., 2009). Lenoir et al.'s (2020) global synthesis of over 20 taxonomic classes revealed marine species (of which 80% of the data were ectotherms) have moved poleward by almost as much as six times faster than terrestrial species, a finding similarly found in a meta-analysis by Poloczanska et al. (2013).

The predicted effects of climate change on functional diversity varied geographically for all three functional diversity indices, which I have shown for the first time at a global scale. Different functional diversity components respond differently to climate change, even at the same location (Alahuhta et al., 2018; Scherer et al., 2023). Increases in FRic can occur alongside increasing, decreasing and stable FEve and FDiv (Trindade-Santos et al., 2020). My results suggest the greatest positive changes in FRic will occur in polar regions (hotspots in Bering Sea, Barents Sea and Southern Ocean). This is caused by an influx of species with more extreme trait values than those currently present and create a greater range of functional traits in the community. A high FEve and FDiv suggest functional complementarity, making the relationship with ecosystem functioning generally positive (Scherer et al. 2023). Increases in FEve indicate new species have moved into areas of the Southern Indian Ocean that have unique functional traits to the species already present in the recipient communities. The largest increases in FDiv were projected for the mid Southern Indian Ocean. Increases in FDiv could be caused by the addition of functional unique species to the grid-cell community. FDiv declined in many open areas of the world's oceans, with the largest declines projected in the South Pacific Ocean and Southern Ocean. Many such declines in FDiv are the result of additional species moving into communities, leading trait space to become more clumped in the niche. Declines in FDiv could suggest that incoming species are generalists that occupy the centre of functional space. This would not necessarily introduce new traits to the ecosystem, but likely increases habitat overlap and thus competition between resident and new species. Studies have suggested that climate change is likely to drive greater responses of generalist species as they exhibit traits that make them mobile and forage on a wide range of organisms (Bartley et al., 2019; Kortsch et al., 2015). Generalists thus have the potential to reshape food webs by changing both their topology and interaction strengths. The enhanced range shifts of generalist species could have significant implications for the functioning of marine ecosystems.

3.5.2 Variation in relationship between changes in taxonomic and functional richness

To look at the losses and gains of species in more detail, I visualised the relationships between changes in FRic and what we would expect from changes in taxonomic richness across grid-cell assemblages (Figure 3.4). By exploring these changes at a global scale, I was able to identify regions of the world's ocean that could potentially undergo shifts in community structure and function. The locations projected to undergo the greatest negative impacts of climate change occur in a large area of the Northern Atlantic, the Galapagos archipelago, Gulf of Mexico, Arabian Sea and Mozambique Channel. In these regions, the loss of functional diversity is more than 50% larger than expected from the change in TRic alone. This highlights a loss of distinctive species from assemblages which may create a shortfall in ecosystem functions. The presence of functionally distinct species in an assemblage is vital for maintaining a breadth of ecosystem functions and services. Fujiwara (2019) found declines in occupancy over the last 35 years of similarly distinctive fish in the Gulf of Mexico, including the bay anchovy (*Anchoa mitchilli*), crevalle jack (*Caranx hippos*), hardhead catfish (*Arius felis*) and two flounder species (*Paralichthys* spp.). Observed shifts in species' distributions in these coastal areas could be a result of altered salinity regimes from climate change by affecting river discharge (Fujiwara et al., 2019). In addition, recent results from the NOAA vulnerability analysis for fish and invertebrates in the Gulf of Mexico revealed that sharks, rays, groupers and snappers were the most vulnerable functional groups to climate change (Quinlan et al., 2023). This could explain the loss of functionally distinctive species in my results. These findings are also in line with Pimiento et al. (2020) who found FRic declines were 30% larger than expected for sharks compared to random species losses. The disproportionate loss of distinctive species from assemblages contributing to a decline in functional richness may create a shortfall in ecosystem functions, especially if they lose top predators.

Taxonomic richness declines in most shallow waters in the Tropics but the loss in FRic is less than expected. This result suggests that the species lost from tropical reefs have functionally less extreme trait values (Scherer et al. 2023). However, although this may suggest a high level of over-redundancy in these regions, indicating higher resilience to disturbances, Mouillot et al. (2014) demonstrate that even functionally over-redundant communities are vulnerable. They found fish were packed into only a few functional entities, leaving over a third of tropical reef fish functional entities vulnerable. This highlights how diversity may not provide the insurance we previously thought in ensuring resilience of ecosystems to disturbances.

My results indicate that many assemblages are projected to have a FD gain more the 50% larger than expected from the change in taxonomic richness. Both Arctic and Antarctic waters are dominated by these patterns, but there are also large areas across the world's oceans. A larger gain in FD than expected suggests an addition of functionally unique species to these assemblages. These functionally unique species could have a profound impact on the recipient community's ecosystem function (Oliver et al., 2015). Polar regions are characterized by a few, specialist species performing most of the specific roles within polar food webs (Ducklow et al., 2007; Hunt Jr et al., 2013; Hunt Jr & McKinnell, 2006). Species shifting into polar regions are likely to have contrasting traits to those in recipient communities as they have likely come from boreal regions and thus could cause substantial rearranging of trophic food-webs (Frainer et al., 2017, 2021). Species at the margins of trait space such as sharks and skates are likely to make up some of those functionally distinct species (Murgier et al., 2021). In addition, these FD changes could be driven by the movement of large, generalist predators such as Atlantic cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) into Arctic communities, which has already been reported due to warming in the Barents Sea (Fossheim et al., 2015; Frainer et al., 2021). These functionally distinct species can feed on different prey to Arctic residents (such as pelagic species as Arctic fish tend to rely on specialist benthic diets (Frainer et al., 2017)) or feed on the Arctic fish themselves. This demonstrates the importance of biotic interactions in determining if species successfully establish in these novel environments with future change.

These marked changes in functional richness in relation to taxonomic richness demonstrates important implications for global marine biodiversity. My findings highlight the importance of exercising caution when relying solely on taxonomic diversity as a measure of biodiversity change (Toussaint et al., 2018). This emphasises the necessity of incorporating functional diversity into research to gain a greater understanding of how climate change may impact species communities.

3.5.3 Idiosyncratic changes in functional trait space among biogeographic realms

By visualising current and projected changes to the functional trait space of species in the sixteen marine realms (and hence changes to the commonness of certain traits), my analysis provides crucial insights into the potential shifts in ecological roles and community composition due to climatic change. My results revealed the largest increases of species and trait space at northern most latitudes. For the first time, I found the projected increase in trait spaces in the polar regions is driven by an influx of species with higher thermal preferences, shorter-lived species that have faster life-histories. These results suggest that climate change will lead to a convergence towards traits more adapted for novel environments (McLean et al., 2019); traits that facilitate rapid adaptation and colonisation are likely to be favoured in these environments. As expected, my results support the idea that warming is driving species' redistributions, and as ocean waters warm, species with higher thermal tolerances shift northwards (Buisson et al., 2013); colder regions such as the Arctic thus become habitable for warmer water fish. Previous studies have seen and predicted similar increases in small body sizes and fast life histories (Álvarez-Noriega et al., 2023; McLean et al., 2019). Indeed, smaller fish, such as forage fish like capelin (*Mallotus villosus*) could shift into Arctic regions which could have considerable implications for resident Arctic species like Arctic cod. Capelin would directly compete with Arctic cod for food and resources, which could, in turn, cause dramatic changes in the Arctic food web. Fish with faster life-histories may be more responsive to warming (Free et al., 2019). Fish with faster reproductive strategies, such as pelagic species, allow small pelagic larvae to disperse further with ocean currents (McLean et al., 2018, 2019; Pecuchet et al., 2017). Interestingly, when looking at groups of fish from different habitats, the changes in TRic and FRic is largely being driven by an influx of reef-associated fish. These fish are filling areas of trait space previously unfilled in Arctic and Northern Cold-Water realms and could be caused by a northward shifts in boreal colder-water coral reef ecosystems (Chaudhary et al., 2023). For both realms, my results show the next largest increases in the number of pelagic and benthopelagic groups, but much less of an increase for bathypelagic fish. These results could be explained by the climate-driven advance of pelagic productivity (temperate phytoplankton (Oziel et al., 2020)) with the expansion of Atlantic waters and ocean stratification into Arctic realms (Frainer et al., 2021). This drives the arrival of new pelagic species, which will likely increase the biomass of incoming boreal species that take advantage of these resources. This could indicate future shifts in Arctic communities, which are usually indicative of a slower pace of life. Interestingly, the same pattern was not projected in the other polar region, where the gain of species to the Southern Cold Water had similar traits to those already present. Visualising changes in functional space did, however, reveal that FRic of bathypelagic fish increased more than the change in TRic. This could be driven by the expected increases in primary productivity in Antarctic waters due to nutrient trapping and remineralisation (Moore et al., 2018), providing support for the functioning of pelagic systems (Petrou et al., 2016).

The observed high degree of functional over-redundancy across all realms and habitats highlights the potential vulnerability of communities, otherwise left undetected without visualising functional spectra. The functional spectra revealed many hotspots of similar traits (over-redundancy) even, unexpectedly, in less speciose communities in polar regions. Clusters of redundancy may, however, leave other important traits at risk and even speciose communities of tropical reef fish can be highly vulnerable to change (Mouillot et al., 2014). The trait spaces for tropical realms reveal this pattern, whereby a few species are lost at the margins of trait space. Margins of trait space usually hold the most functionally distinct species within the community, and in the cases of the Indo-Pacific realms, these are larger bodied, faster-swimming fish that feed on nekton. This suggests that even losses of species within a community with high functional redundancy can have detrimental impacts on the ecosystem. For example, human-induced extinctions of bumphead parrotfish

(*Bolbometopon muricatum*) from Indo-Pacific reefs had detrimental impacts on key processes of reef bioerosion and sediment transport (Bellwood et al., 2011).

The disproportionately high impact of climate change on demersal, bathydemersal and bathypelagic fish across the world's ocean highlights, for the first time, the vulnerability of deep-dwelling species on such a large scale. Previous studies conversely found evidence for high functional redundancy of deep-sea fish communities (Farré et al., 2016), suggesting these communities may be resilient to climate change. In contrast, I found few hotspots of functional redundancy of deep-sea traits in the current functional spectra. This indicates there are few species that share similar traits (Farré et al., 2016), as such, if one species becomes locally extinct, there are no species to fill those functional roles. The losses of FRic in most of the warm-water realms suggests losses of ecosystem functions in deep sea communities. Species are expected to shift into cooler, deeper waters to escape the effects of climate change, but my findings suggest that even environments previously thought to provide refugia for species are at risk due to the combined effects of warming and oxygen loss (Gallo et al., 2020).

My results suggest that, across all realms, the species most vulnerable to climate change are those that are long-lived, have slower life-histories (lower K rate, internal live bearers), subcarangiform swimming modes, lower thermal preferences and are bathydemersal. A previous study by Cheung et al. (2013), who modelled the distribution and abundance of more than 600 marine fish under climate change by 2050, similarly identified that assemblage average body weight was expected to decline globally (and half being due to range changes). I have advanced their study by investigating trait changes for a much larger number of species and I have newly identified how the frequency of other traits might change with climate. The increases in relative frequency of shorter-lived species with faster life histories could be because fish with faster life histories are more responsive to warming (Free et al., 2019). Warmer waters have been found to result in faster growth but smaller body sizes. This concept is well-known in the responses of ectotherms to warming, including fish, and is known as the temperature size rule (D. Atkinson, 1994). Organisms that live in warmer environments often have smaller body sizes, and the case for fish in oceans is that growth is limited by lack of oxygen at warmer temperatures (Edeline et al., 2013). In addition, it comes as a surprise that I do not find notable changes in pelagic traits across all realms with ocean warming. Open-water pelagic species are highly mobile and motile compared to demersal species and are expected to undergo much more rapid range shifts (Cheung et al., 2009;

Pereira et al., 2010). I did, however, find increases in bathypelagic fish in the Arctic, Northern Cold Water and Southern Ocean. The projected changes in frequencies of traits such as the sizes of fish, changes in temperature preferences, and alterations in growth rates signify a broader restructuring of marine fish communities in response to climate change than previously thought.

Observed changes in the relative frequency of dietary traits signifies potential changes to trophic dynamics. Changes in prey availability and distribution can influence the composition of marine communities. Influxes of nekton feeders at higher latitudes might indicate a reorganisation of predator-prey interactions, with implications for the trophic dynamics of the entire ecosystem. Interestingly, I found increases in fish at lower trophic levels across all realms but also increases in the highest trophic levels in cold water realms. These findings thus support both suggestions of the increase in bottom-up control of food webs but also increases in generalist predators at the top of the food chain. The addition of species from higher trophic levels, such as cod and haddock in the Arctic, increases connectivity between pelagic and benthic habitats but decreases modularity as these generalists feed across modules and link them (Kortsch et al., 2015). This could have far-reaching implications for ecosystem functioning in polar regions, affecting the entire food-web network.

3.5.4 Future directions

Incorporating information on species' abundances is the next step to advancing these findings because population sizes could also change with climate change. It has increasingly been recognised that not only does information on functional diversity advance our understanding of the facets of biodiversity, but also the number of species present (Stuart-Smith et al., 2013). Further work should also consider species-specific dispersal constraints. Maximal dispersal may not be realistic for some species, although certainly in marine environments there are far fewer physical barriers restricting the dispersal of fish species. Lastly, work on investigating changes to marine biodiversity is hindered by the lack of long-term data on species' occurrences and known absences. Studies such as this analysis rely heavily on systematic data provided by teams in the field. Coverage of biodiversity data in the world's oceans is spatially and temporally patchy and incomplete, and further studies are required to improve our knowledge of biodiversity in marine environments. Long-term monitoring efforts will be instrumental in capturing the ongoing dynamics of marine fish communities and refining our understanding of the impacts of climate change on functional diversity.

3.5.5 Conclusions

To predict changes in biodiversity, it is essential to understand not only changes in taxonomic richness but also how shifts in species' ranges translate to changes in functional diversity. My results highlight this by underlining the importance of assessments of different metrics of biodiversity and across spatial scales for understanding the impacts of climate change in a holistic way (Törnroos et al., 2019). Future fish assemblages are likely to undergo substantial shifts in trait structure, with a magnitude of change greater than predicted from taxonomic richness alone. The direction of change varies according to geographical location. I found the potential for species to disperse into regions such as the Arctic from areas of trait space not occupied by the baseline assemblage. These functionally unique species could have a profound impact on the recipient community's ecosystem function. In addition, I found in specific realms, such as the Indo-Pacific, a loss of functionally distinct species from assemblages which may create a shortfall in ecosystem functions. Future studies will need to consider the socio-ecological impacts of changes to marine functional diversity and its implications worldwide. My findings demonstrate the need for region-specific conservation strategies, that consider both taxonomic and functional aspects of biodiversity to ensure the resilience of marine ecosystems in the face of ongoing climate change. Moreover, my results highlight the importance of ongoing monitoring efforts and adaptive management to address the dynamic nature of marine biodiversity and the impacts of climate change on ecosystem functioning.

Chapter 4

Climate change projections for global marine mammals

4.1 Abstract

Marine mammals play important roles in marine ecosystems and biodiversity. Yet anthropogenic pressures, such as climate change, are already threatening their communities. Successful conservation and management plans of marine mammal communities rely on knowledge of spatial patterns of biodiversity and how spatial patterns of biodiversity may change in the future. Despite the fact that marine mammals are a highly threatened group of species in the world today, there is a distinct lack of research exploring how climate change may impact global marine mammal distributions and diversity. In this chapter, I provide a detailed account of projected climate change impacts on global marine mammal taxonomic, functional and phylogenetic diversity, looking at a global grid-cell scale and at broader-scale patterns across marine realms. I used ensemble species distribution models to project species distributions under a medium-high emissions scenario. Considerable changes in all facets of biodiversity were projected by 2100. The largest declines in species richness and functional richness occurred in tropical regions. Losses in functional uniqueness and specialisation occurred in both the Arctic and Antarctic waters as well as the Indo-Pacific, indicating the loss of potential key functions and functional homogenization of these communities. The frequency of terrestrial traits declined across all realms, suggesting that pinnipeds, as a group, may be a highly vulnerable to climate change. The projected changes in multiple facets of marine mammal biodiversity suggests considerable reshuffling of marine mammal assemblages and highlights the potential for climate change to alter ecosystem structure and function.

4.2 Introduction

Human activities and stressors are impacting marine species and ecosystems at an increasingly alarming rate (Avila et al., 2018; Halpern et al., 2019). Marine mammals, comprising 121 species, are wide-ranging, occupy all the world's oceans and are particularly vulnerable to human activities and the deterioration of their environment (Davidson et al., 2012). Due to their typically wide distributions, many marine mammals are impacted by multiple anthropogenic stressors on regional and global scales (Avila et al., 2018). Such stressors include habitat loss, noise and chemical pollution (Erbe et al., 2019), transportation (Van Waerebeek et al., 2007; Walker et al., 2019), bycatch from fisheries (Lewison et al., 2004), and climate change (Kaschner et al., 2011; Laidre et al., 2008). Due to their large sizes, wide ranges and high historical abundances, marine mammals have a major influence on the structure and function of many marine ecosystems (Bowen, 1997; Roman et al., 2014). For example, cetaceans such as baleen whales play crucial roles in nutrient cycling in marine ecosystems. They release faecal blooms in surface waters, providing surface-dwelling species with otherwise unavailable deep-sea nutrients (Lavery et al., 2014). As such, human disturbances and any changes to oceanographic conditions due to climate change could affect ecosystem functioning, as marine mammal populations and ranges may shift in response to threats. Spatial patterns of marine biodiversity and its potential to change with climate change are critical for conservation science. Yet, to date, the impact of climate change on marine mammals remains poorly understood. While the full scope of impacts of climate change on marine mammals remains unclear, changes in abundances and distributions are expected (Kaschner et al., 2011).

Shifting distributions of marine mammals, in response to warming temperatures, have been observed across all oceans (Pinsky et al., 2013, 2020; van Weelden et al., 2021). For example, the Arctic endemic ringed seal (*Pusa hispida*) has shifted its foraging and movement patterns in Svalbard due to sea ice loss (Hamilton et al., 2015). Visual and acoustic data have also revealed that subarctic marine mammals, such as fin whales (*Balaenoptera physalus*), minke whales (*Balaenoptera acutorostrata*) and killer whales (*Orcinus orca*), have been observed more frequently in the southern Chukchi sea, a shallow Arctic shelf north of the Bering Strait, than historical records (Clarke et al., 2013). This may reflect emerging responses to ongoing climate change in the region. Shifts in marine mammal distributions have also been predicted using a range of modelling tools (Becker et al., 2019). Kaschner et al. (2011) found moderate effects of future climate on marine mammal distributions, predicting increases in cetacean species richness at high latitudes and decreasing richness of pinnipeds and cetaceans at lower latitudes. Yet, whilst early research focuses on the taxonomic (species) level, a multifaceted approach to understanding changes to biodiversity could reveal further consequences of such changes on the structure and functioning of marine communities.

Functional diversity (FD) refers to the variety of biological functions performed by different species or individuals within an ecosystem (Petchey & Gaston, 2006). It goes beyond taxonomic (species) diversity and focuses on the ecological and life-history traits that species possess. A diverse array of functional traits can enhance ecosystem resilience, stability and productivity (de Bello et al., 2021). Not all species, however, contribute equally to functional diversity (Pimiento et al., 2023); some exhibit traits which are highly dissimilar to others, thus displaying unique functional roles (functionally unique or original (FOri)), and/or some possess extreme trait values (functionally specialised (FSp)) (Mouillot et al., 2013).

There have been limited previous studies on the FD of marine mammals. Those that do exist have tended to focus on mammal sensitivity and vulnerability to climate change by investigating the impact of potential extinctions of species that are classified as vulnerable or endangered by the IUCN Red List (Albouy et al., 2020). They rarely consider the impacts of future climate change on species' redistributions, and how such movements could impact FD. Studies that have focussed on marine mammal biogeography rarely take into account variables besides sea surface temperature. Similarly, how changes in biogeographical patterns of marine mammals relate to changes in functional and phylogenetic diversity (PD) remains unknown.

The aim of this chapter is to project climate change impacts on global marine mammal taxonomic, functional and phylogenetic diversity. Firstly, I describe the structure and functional trait space of current marine mammal assemblages and marine mammal families globally**.** Secondly, I assess how multiple facets of marine mammal biodiversity vary at point (0.5 x 0.5° grid cell) and regional (summarised across grid cells) scales, and how they are projected to change in the future. Marine mammal diversity is assessed using seven indices, the first four are described in Chapter 3 and the last three have been discussed in this Introduction and later on in the Methods: taxonomic richness (TRic), functional richness (FRic), functional divergence (FDiv), functional evenness (FEve), phylogenetic diversity (PD), functional specialisation (FSp) and functional originality (FOri). Thirdly, I explore whether FRic changes with TRic and whether changes in FRic are typically driven by losses or gains of functionally distinct species. Lastly, I describe current functional trait spaces across each marine realm and assess whether some traits are becoming more or less common with future climate change in certain marine realms.

4.3 Methods

4.3.1 Species occurrence data

An initial global species list for 130 marine mammals was downloaded from the World Register of Marine Species (WoRMS) database (https://www.marinespecies.org/; Ahyong et al., 2023). The list was filtered in R to exclude Sirenia, sea otter (*Enhydra lutris*) and polar bear (*Ursus maritimus*), hence restricting analyses to pinnipeds and cetaceans following Kaschner et al. (2011) (n=122). Occurrence data were gathered and cleaned as described in Chapter 3. Four species (*Mesoplodon eueu*, *Mesoplodon traversii*, *Monachus tropicalis* and *Sagmatias cruciger*) had no available occurrence data. After removing these, and another ten species with fewer than 10 occurrences (n=108), the species occurrences were rarefied by gridding onto an equal area grid (as in Chapter 3). After gridding, three species (*Phocoena dioptrica, Phocoena sinus and Phocoena spinipinnis*) occurred in fewer than 10 grid cells and so were removed. This left 105 species that were considered in all subsequent modelling.

4.3.2 Environmental data

Environmental data were as described in Chapter 3.

4.3.3 Presence-only species distribution models

Presence-only species distribution modelling methods were as described in Chapter 3.

4.3.4 Trait data

Fourteen functional traits of marine mammals were gathered from the scientific literature, encyclopaedias, and the grey literature (Table 4.1). These traits were a mixture of quantitative and qualitative variables (adapted from traits used in Albouy et al. (2017, 2020)), and incorporated information relating to five major aspects of mammal ecology; these being feeding, reproduction, habitat choice, social behaviour and life history. Some of these traits act as proxies for harder-to-measure traits that more explicitly relate to a direct functional role (Albouy et al., 2017; Lavorel & Garnier, 2002). The following functional traits were used for each species in this analysis (plus abbreviations used): diet, foraging depth, foraging location, fasting strategy (fasting), breeding location, degree of 'terrestriality' (terrestriality), age at sexual maturity (maturity), gestation length (gestation), interbirth interval length (interbirth), weaning age (weaning), social behaviour, social group size (grpsize), maximum body mass (mass) and sexual dimorphism (Table 4.1). All continuous variables were log-transformed.

Table 4.1. Description of functional traits used in the marine mammal functional diversity analyses. The final column highlights the ecological rationale to support the use of each variable.

Functional trait	Category	Type	Values	Ecological interpretation
Diet	Feeding	Categorical	Zooplankton, benthic invertebrates (excluding squid), squid, fish and higher vertebrates	Main diet of species. Indication of feeding preferences and trophic level Pauly et al 1998.
Foraging depth (position in the water column)	Feeding	Categorical	Epipelagic, mesopelagic, benthic, all depths	Resource use in the ocean
Foraging location	Feeding	Categorical	Continental shelf, slope, cont. shelf + slope, offshore, all	Habitat use when foraging
Fasting strategy	Feeding	Binomial	1/0	Any period of fasting either during reproduction/maintaining territories in pinnipeds or during migrations
Breeding location	Habitat	Categorical	Ice/land, coastal, oceanic	Exploitation of terrestrial realm
Terrestriality	Habitat	Binomial	1/0	Exploitation of terrestrial realm
Age at sexual maturity	Reproduction	Continuous		Average age (in days) when female becomes sexually mature
Gestation length	Reproduction	Continuous		Reproductive strategy
Interbirth interval	Reproduction	Continuous		Reproductive strategy

Functional trait	Category	Type	Values	Ecological interpretation
Weaning age	Reproduction	Continuous		Average age (in days) when young is weaned
Social behaviour	Social behaviour	Categorical	Mostly social, social and solitary, mostly solitary	Facilitative behaviour.
Social group size	Social behaviour	Continuous		Facilitative behaviour. Average number of individuals in a pod or average number of females in a harem (pinnipeds).
Body mass	Life history	Continuous		Mass balance and energy flow. Maximum adult body mass (kg).
Sexual dimorphism	Life history	Categorical	None/low, moderate, strong	

4.3.5 Taxonomic, functional and phylogenetic diversity

TRic was estimated as the number of marine mammals per grid-cell. PD was calculated using a subset of a recent phylogenetic supertree of mammals (Upham et al., 2019). The phylogeny subset tool (available at https://vertlife.org/) was used to produce 100 randomly selected distributions of trees with my marine mammal species list. Faith’s phylogenetic diversity was calculated for each of the 100 trees using the ‘pd’ function in the ‘picante’ package (Kembel et al., 2010). This index represents the sum of the total phylogenetic branch length for a given set of species on the tree (Faith, 1992). The mean PD across all 100 trees was used as the final value for each assemblage. Functional trait space calculations were as described in Chapter 3. To estimate how complex a trait space (in terms of how many dimensions) to include, I explored root mean squared deviation (RMSD) values and selected a dimension level that combined low deviance with high explanatory power, whilst being mindful that FRic cannot be calculated for assemblages with fewer species than the number of PCoA dimensions. Hence, I selected a combination that satisfied the above criteria whilst permitting the inclusion of the majority of cells (assemblages). When assessing the quality of functional space, the seven-dimensional space had the lowest RMSD value, with five- and six-dimension spaces were only slightly higher. As such, I retained the four-dimensional trait space for analysis to include the highest number of grid-cells as possible. The 4D trait space explained 70% of variance and the RMSD was only 0.02 higher than the 5D space.

FD was calculated as described in Chapter 3, though two additional FD indices were calculated per grid-cell assemblage: functional specialisation (FSp) and functional originality (FOri). FSp is the mean distance to the mean position of species from the assemblage pool, or centre of trait space (i.e. niche breadth). Thus, species further from clumped centres of trait space are likely to be functionally specialised, and those in the centre are generalists. FOri (which is also interchangeable with the term functional uniqueness (FUn)) is the mean distance to the nearest species from the assemblage pool (i.e. the distance to that of the most functionally similar species). The FUSE index (Functionally Unique, Specialized, and Endangered) was also computed for each species, which combines individual species' metrics of FSp, functional uniqueness (FUn) (same as FOri but the term used in the FUSE index) and their IUCN threat status (Pimiento et al., 2020). This gives an indication of threatened species that are of particular importance to FD. To explore current patterns in marine mammal trait space and species-level FUn and FSp, global trait spaces were visualised for each marine mammal family (n=7) and order (Carnivora and Cetartiodactyla). Trait spaces were only plotted for families with more than three species (n=7) because convex hulls require a minimum of three data points. Changes in diversity indices (between present and 2100) were calculated per grid-cell assemblage and these changes were summarised across biogeographic realms (Figure S4.1). Assemblages with fewer species than the number of dimensions of the PCoA were removed for calculating FRic, FEve and FDiv. When calculating FSp and FOri, assemblages with more than two occurrences were retained to maximise the data for these two indices. FRic, FEve and FDiv were calculated using the 'fundiversity' package in R whilst FSp and FOri were calculated using the 'mFD' package. To investigate whether changes in FRic were primarily driven by the loss or gain of functionally distinct species, I compared the observed ΔFRic to the predicted ΔFRic values expected from the ΔTRic using the same methods as in Chapter 3. Finally, I investigated whether traits were projected to become more or less common with climate change by plotting current functional spectra per realm and future changes in functional spectra by realm as in Chapter 3.

4.3.6 Null models

Null modelling methods were as described in Chapter 3.

All analyses were performed in R version 4.0.3 (R Core Team, 2020).

4.4 Results

This study considered the impacts of climate change on 105 marine mammal species across the world's oceans. SDMs performed extremely well, with the mean area under the curve (AUC) of ensemble models being 0.94 (± 0.07 SD). All model types performed equally well (average AUC of MaxEnt: 0.94 ± 0.07, GAM: 0.94 ± 0.07, RFs: 0.93 ± 0.08, and BRTs: 0.94 ± 0.07).

By 2100, 72% of marine mammal species are projected to contract their ranges and 28% projected to expand their range. Six marine mammals are projected to lose more than 50% of their current range, with the Spinner dolphin (*Stenella longirostris*) and melon-headed whale (*Peponocephala electra*) projected to lose the greatest area. The largest range expansions (>50% gain) are projected for the Irrawaddy dolphin (*Orcaella brevirostris*) and the Indo-Pacific finless porpoise (*Neophocaena phocaenoides*).

After plotting and assessing the quality of the functional trait space, the first Principal Coordinates Analysis (PCoA) axis is strongly driven by 'terrestriality' (with terrestrial species occupying lower values), breeding location (with species breeding on ice or land occupying lower values) and interbirth interval (with species with larger inter-birth intervals occupying higher values) and age at sexual maturity (with species reaching sexual maturity at greater ages occupying higher values) (Table 4.2; Figure 4.1). The second axis is largely driven by trophic level (with species at higher trophic levels occupying lower values), foraging location (with species foraging in all locations and offshore occupying lower values and those foraging on the continental shelf occupying higher values), diet (plankton feeders occupying higher values and squid feeders occupying lower values) and foraging depth (with epipelagic feeders occupying higher values and mesopelagic feeders occupying lower values) (Table 4.2; Figure 4.1).

Table 4.2. Contribution of each trait to each Principal Coordinates Analysis (PCoA) axis for the first four axes of the multi-dimensional trait space. Number given has p-value lower than 0.05 and bold indicates traits of greatest influence on each axis.

	PCoA1	**PCoA2**	**PCoA3**	**PCoA4**
Mass	0.193	0.156	0.261	0.090
Gestation	**0.384**			
Interbirth interval	**0.556**			
Age sexual maturity	**0.551**			
Social group size	0.040	0.135	0.081	
Terrestriality	**0.846**			
Weaning age	**0.298**		0.254	0.048
Diet	0.281	**0.424**	**0.543**	0.127
Trophic level	0.050	**0.542**		0.089
Foraging depth	0.065	**0.410**	**0.304**	0.060
Foraging location	0.273	**0.470**	**0.308**	0.163
Fasting strategy	0.170			0.065
Breeding location	**0.626**	0.299		**0.311**
Social behaviour	0.222	0.176	**0.405**	0.109
Sexual dimorphism	0.165	0.150	0.069	0.472

Amongst the marine mammals, earless seals (*Phocidae*) and oceanic dolphins (*Delphinidae*) span the largest extent of global trait space (Figure 4.2b). Porpoises (*Phocoenidae*) and baleen whales (*Balaenidae*) span the smallest area of trait space, likely a consequence of these latter families containing only a few species. Five of the 12 top FUSE species are currently on the IUCN Red List (Figure 4.2c). The top five FUSE species are Southern Elephant seal (*Mirounga leonina*), Bearded seal (*Erignathus barbatus*), Galapagos fur seal (*Arctocephalus galapagoensis*), Northern fur seal (*Callorhinus ursinus*) and North Atlantic right whale (*Eubalaena glacialis*). The *Phocidae* family consists of some of the most functionally unique and specialised species (Figure 4.2d).

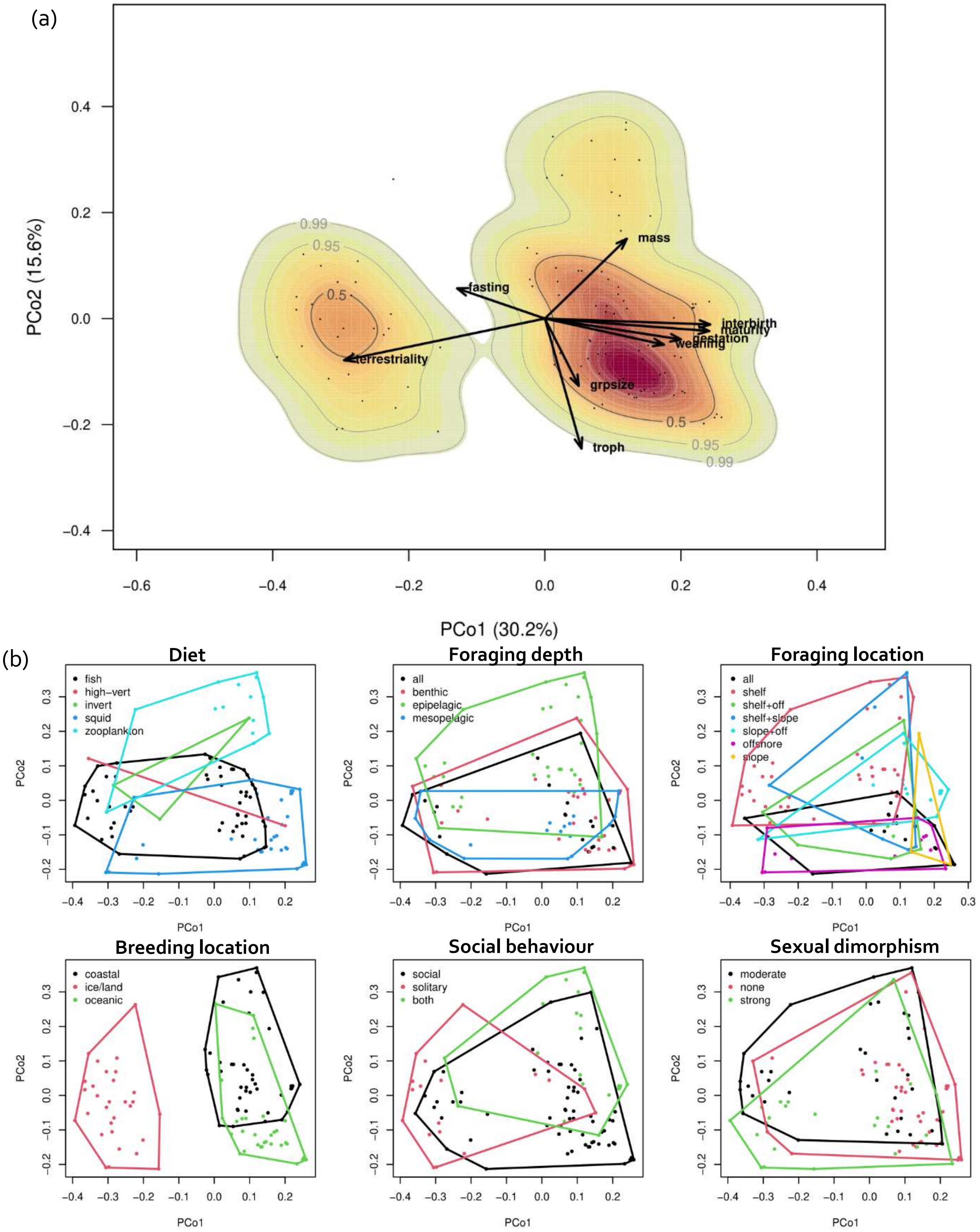

Figure 4.1. (a) Global functional trait space of marine mammals projected onto PCoA 1 and 2. Arrows indicate the continuous traits that contributed to the distribution of species along each axis. The colour gradient indicates 50, 95 and 99% contours of species density where darker red colours indicate hotspots of species density. (b) Convex hulls showing the distribution of trait categories within the trait space for: diet, foraging depth, foraging location, breeding location, social behaviour and sexual dimorphism.

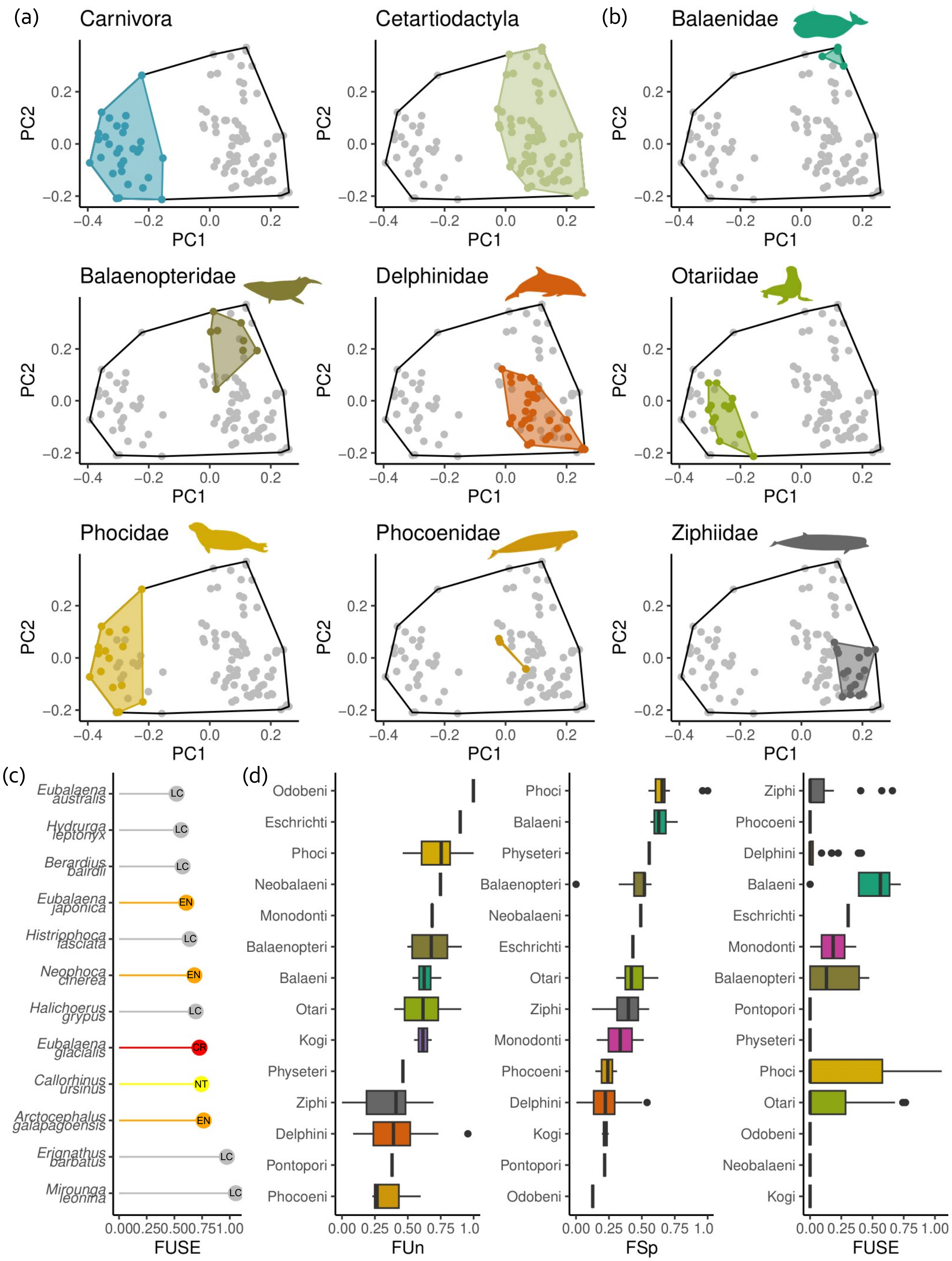

Figure 4.2. Functional diversity of marine mammals. (a) Functional trait space (first two axes) occupied by the two orders of marine mammals, Carnivora and Cetartiodactyla. (b) Functional trait spaces occupied by seven of the most speciose marine mammal families. (c) Top 12 species with highest FUSE scores. (d) FUn, FSp and FUSE per species within each family (names abbreviated by removing 'dae' suffix), plotted in descending order based on the median of each family. The animal icons were downloaded from www.phylopic.org.

4.4.1 Projected changes in biogeographical patterns of marine mammal diversity

Based on the four-dimensional global functional space for marine mammals, changes in TRic and five functional diversity indices under future climate change were quantified: FRic, FDiv, FEve, FOri and FSp. TRic is projected to undergo considerable losses across low latitudes and coastlines of the tropics, especially in the Eastern Pacific (Figures 4.3a & b). There are also up to 100% projected losses in taxonomic richness in areas surrounding New Zealand, Ireland, Spain and northwestern Africa. Gains in TRic are projected for large regions of the Southern and Antarctic oceans, North Pacific and very northern regions of the Arctic. The main hotspot of FRic loss occurs in the Northern Atlantic and Arctic Ocean between Greenland and Norway (Figure 4.3d). FDiv and FEve remain largely unchanged under future climate change (Figures 4.3f & h), aside from projected declines in FDiv in the Arctic Ocean above Iceland and off the NW coast of North America (Figure 4.3f). The Southern Ocean, Antarctic and northern latitudes support high FOri and FSp (Figures 4.4a & c) but are also the regions that are projected to lose the most functionally novel and specialised species in future (Figures 4.4b & d). This is especially so in the Southern Ocean, where FSp declines markedly (Figure 4.4d). Losses to PD largely mirror TRic, with 100% losses of PD throughout many tropical and temperate regions (Figures 4.4e & f). However, cells supporting the highest levels of PD do not change. Additionally, the top 25% FUSE species are all projected to decline in TRic across low latitudes (Figure 4.4h). There are gains in top FUSE species in the Antarctic and areas of the North Pacific and Arctic.

4.4.2 Grid-cell changes in functional richness in relation to taxonomic richness

Most coastal regions in the tropics have FD losses 50% smaller than expected from change in TRic (darker yellow shading in Figure 4.5a, b). The most commonly projected impact of future climate change is of FD declining by >=50% more than expected from ΔTRic (O in Figure 4.5c). Most of these assemblages occur in the Labrador strait, North Sea, Mediterranean and Arctic Ocean, between Greenland and the top of Sweden (second darkest red in Figure 4.5a). FD losses occur despite gains in TRic, in areas such as the North Pacific (off NW North America) and NE Russia (darkest red shading in Figure 4.5a). The second most commonly projected future impact is for FD gain to be >=50% more than expected from ΔTRic (G in Figure 4.5c). Assemblages impacted in this way occur in areas of the high Arctic, above Russia, and in the NW Pacific (second darkest blue shading in Figure 4.5a).

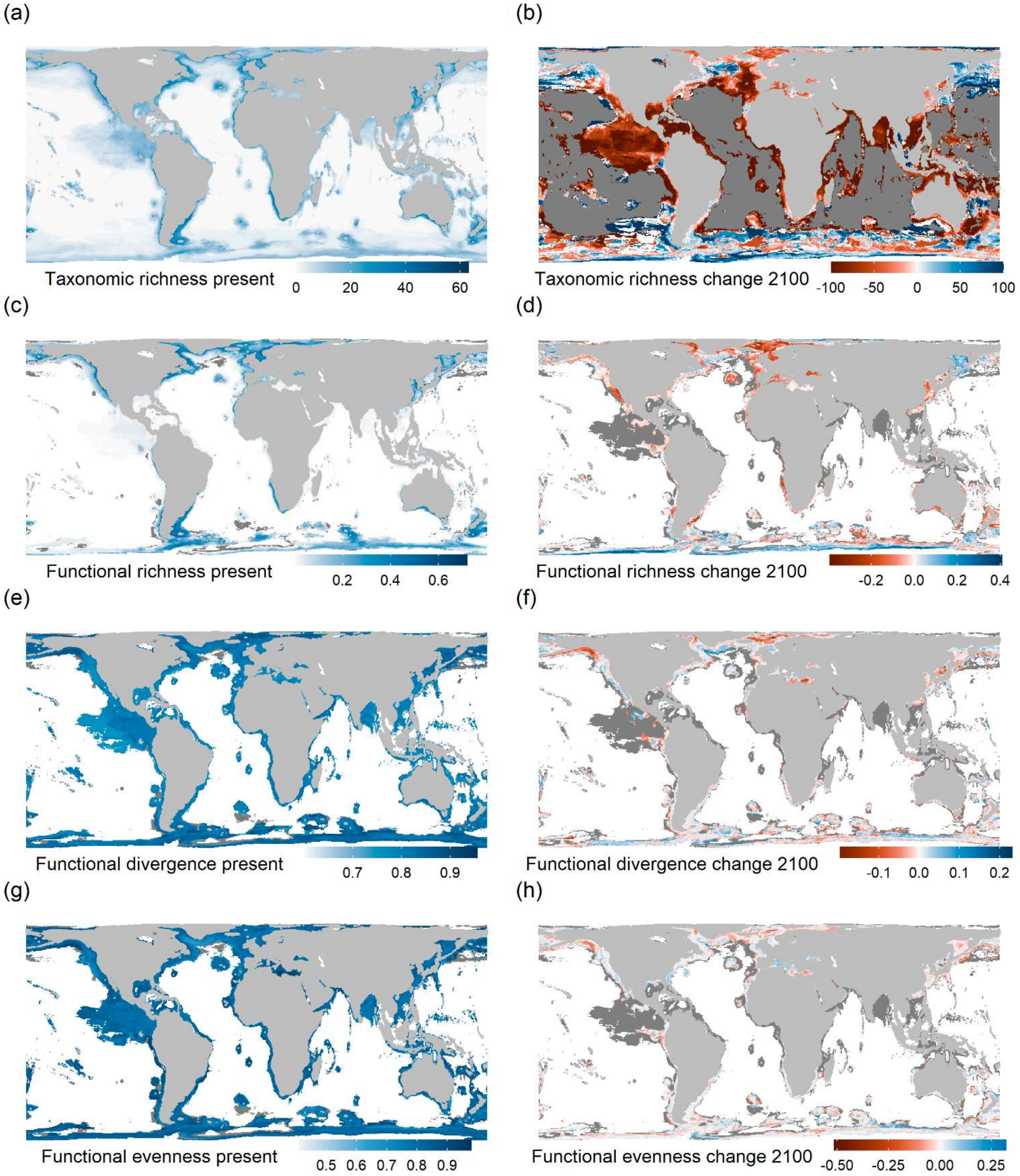

Figure 4.3. Biogeographic patterns of taxonomic and functional diversity (TRic and FD) of marine mammals. (a,c,e,g) present TRic, functional richness, functional divergence and functional evenness. (b,d,f,h) indicate change in TRic and FD indices between present and 2100 under RCP6.0 emissions scenario. Dark grey indicates grid cells with fewer than four species present (and so in some instances change cannot be calculated).

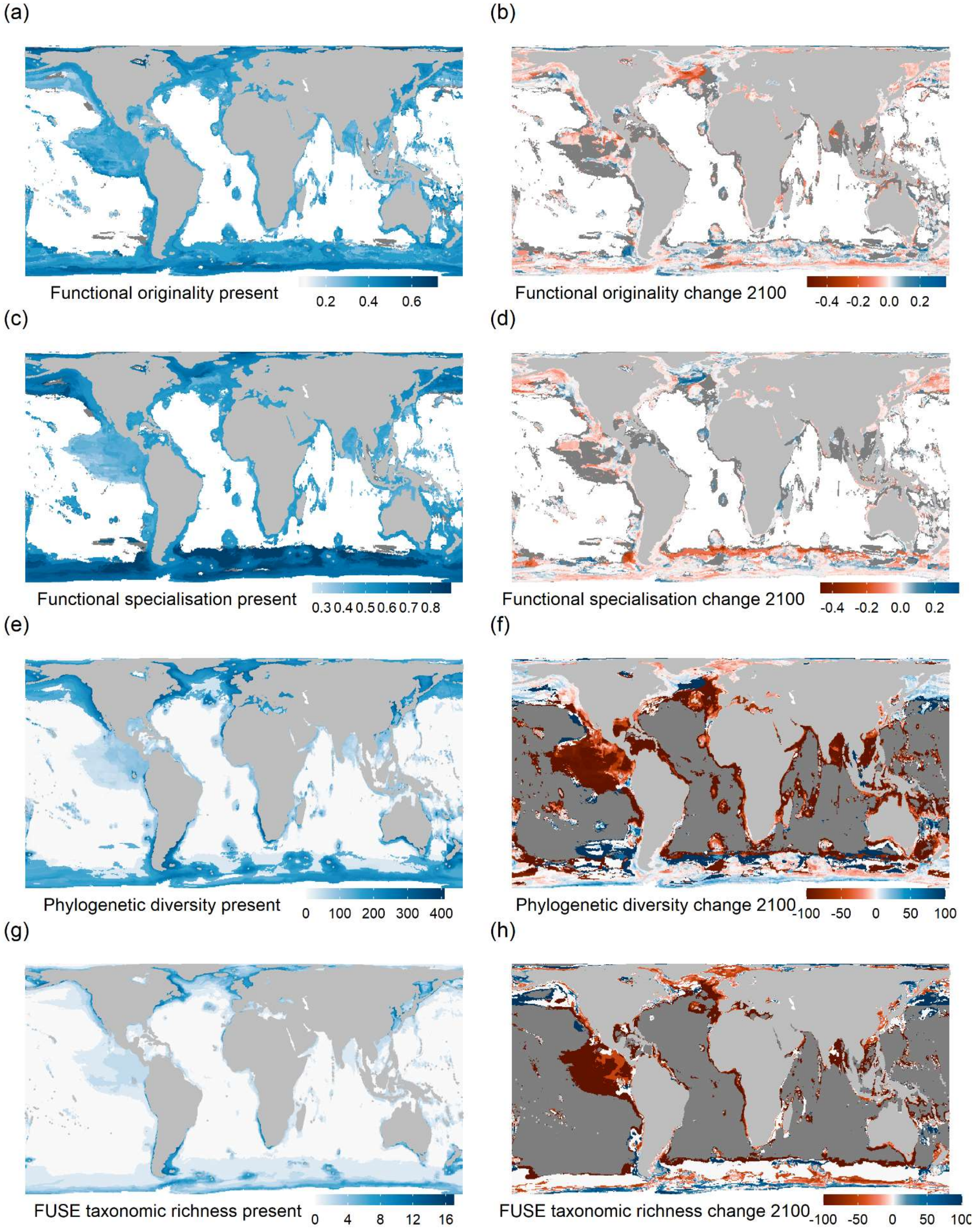

Figure 4.4. Biogeographic patterns of functional diversity (FD) phylogenetic diversity (PD) of marine mammals. (a,c,e,g) present functional originality (FOri), functional specialisation (FSp), PD and TRic of top 25% FUSE species (n=26). (b,d,f,h) indicate change in FD indices, PD and TRic of top 25% FUSE species between present and 2100 under RCP6.0 emissions scenario. Dark grey indicates not enough species to calculate the corresponding indices.

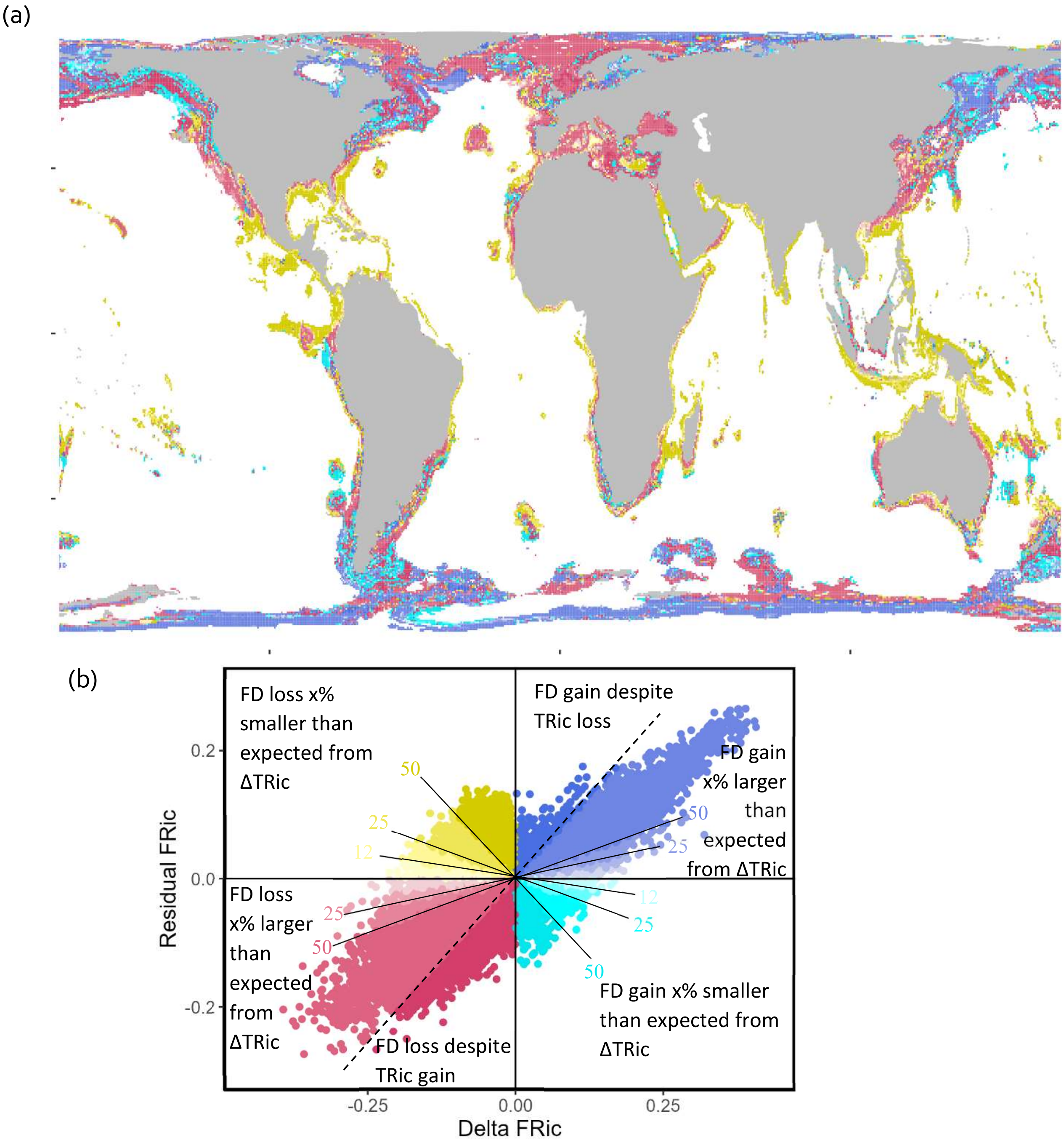

Figure 4.5. Relationship between the observed and predicted change in functional richness from taxonomic richness per grid cell (a). White areas in (a) are the grid-cells that had zero presences currently and by 2100. (b) shows the relationship between the residual functional richness and change in functional richness, divided into four main categories representing functional richness gain or loss in relation to that expected from change in taxonomic richness. Grey indicates no change in composition.

4.4.3 Marine mammal diversity by realm

I performed null models to assess whether current FRic is higher or lower than expected given the number of species in each biogeographic realm. Most realms, including all Indo-Pacifics and Temperate Australasia and Africa, have a current FRic lower than expected by chance (SES<0). This indicates species are more clustered in trait space, indicating environmental filtering or trait convergence (Figure S4.2). Temperate N Atlantic and N Pacific did not differ from random (t-test: $p = 0.37$ and 0.22, respectively). The N Cold Water, Arctic and Southern Ocean have a current FRic higher than expected, though this was only slightly insignificant (t-test: SES>0; p>0.8). This indicates trait divergence, whereby species in these realms are more distinct traits than expected by chance.

4.4.4 Marine mammal diversity changes by realm

TRic and FRic are projected to increase under future climate change at higher latitudes and decrease in warmer water realms (Indo-Pacific, Tropical Pacific and Atlantic) (Figures 4.6a & b). This is expected given that warm water realms are projected to become less suitable for some current inhabitants whilst colder waters at high latitudes are warming rapidly, making them suitable for many novel colonists. FDiv and FEve generally stay the same across all realms but increase in the Eastern Indo-Pacific (Figures 4.6c & d). Median FSp declines across all Indo-Pacific realms (Figure 4.6e). Interestingly, the median change in FOri is negative in the Northern Cold Water and Arctic (Figure 4.6f). This indicates that species moving into these assemblages are more similar, and/or unique species have been lost.

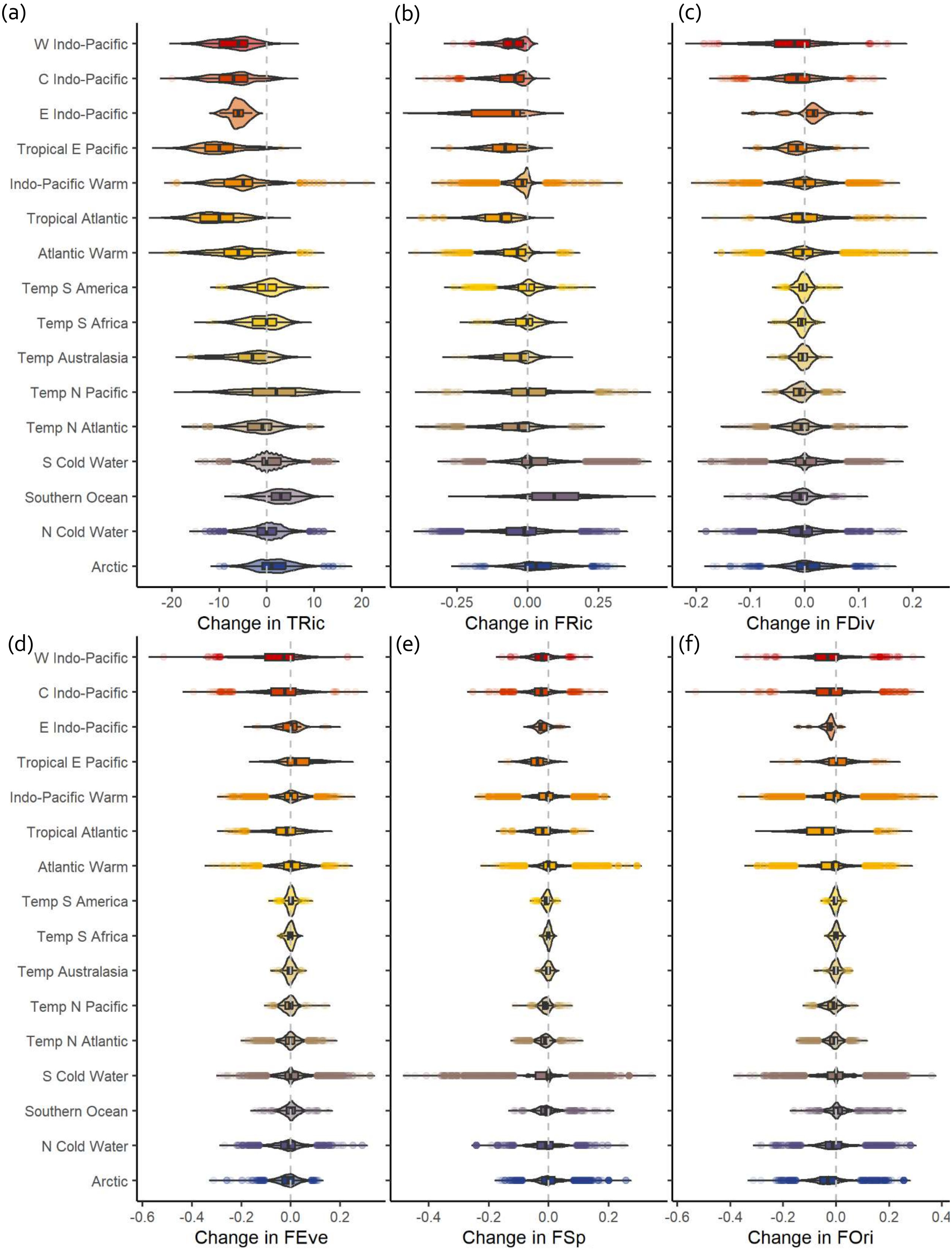

Figure 4.6. Changes in taxonomic and functional diversity (TRic and FD) indices between the present and 2100 (latter under RCP 6.0 emissions scenario) for each marine realm. Results are presented as the mean change across grid-cells within each realm for: (a) TRic , (b) FRic, (c) FDiv, (d) FEve, (e) FSp and (f) FOri. TRic is based on medians across all grid cells, whilst FRicm, FDiv and FEve are based only on grid-cells with >4 species, and FSp and FOri based on only grid-cells with >2 species in. Plots show median, 25th and 75th percentiles, violin of data range and density (width of violin). Map of realms shown in Figure S4.1.

4.4.5 Changes in marine mammal functional spectra by realm

The largest losses of trait space are projected for the Eastern Indo-Pacific (Figure 4.7). Given that this realm is projected to lose the highest number of species, it is understandable that it has the largest losses in FRic. Null models indeed reveal a two times higher-than-expected loss of FRic in the E Indo-Pacific (t-test: SES<0, p<0.05; Figures 4.7 & 4.8). These losses are clearly driven by losses in terrestrial marine mammals such as seals and sealions that rely on land or ice to breed and reproduce (Figures 4.7 & 4.1). The Eastern Indo-Pacific is projected to lose both eared and earless seals. Indeed, losses of *Phocidae* and *Otariidae* are projected across most realms, resulting in traits such as carnivory, piscivory and fasting strategies to decline (Figures 4.7 & 4.1). In addition, I project decreases in the commonness of species of larger body masses, those that are epipelagic feeders on zooplankton, and that occupy lower trophic levels. This pattern is seen predominantly in the Western and Eastern Indo-Pacific, the temperate Northern Atlantic, Atlantic warm, and the Arctic (Figure 4.7). In the temperate N Atlantic and Atlantic warm water, the loss of FRic is almost three times higher than expected given the random loss of the same number of species (t-test: SES<0; p<0.05; Figure 4.8). These changes are likely to be a consequence of the projected declines in species belonging to the *Balaenidae* and *Balaenopteridae* families. Interestingly, across all realms, faster life-histories become less common, regardless of latitude. Species associated with lower trophic levels also become less common, an effect which is likely to be driven by declines in filter feeders such as baleen whales that are dependent on zooplankton and krill. Aside from the Southern Ocean, the overall gains in trait space and FRic in cold water realms (bluer shades in Figure 4.7) are lower than expected by chance. In the Southern Ocean, however, there is a higher-than-expected gain in FRic (SES>0). This indicates the incoming species have traits that are more distinct from those already occurring in the realm. The functional gains are driven by both an increase in squid eaters at higher trophic levels, and also an increase in fish eaters that exhibit some degree of terrestriality such as seals and sealions (Figures 4.7 & 4.1).

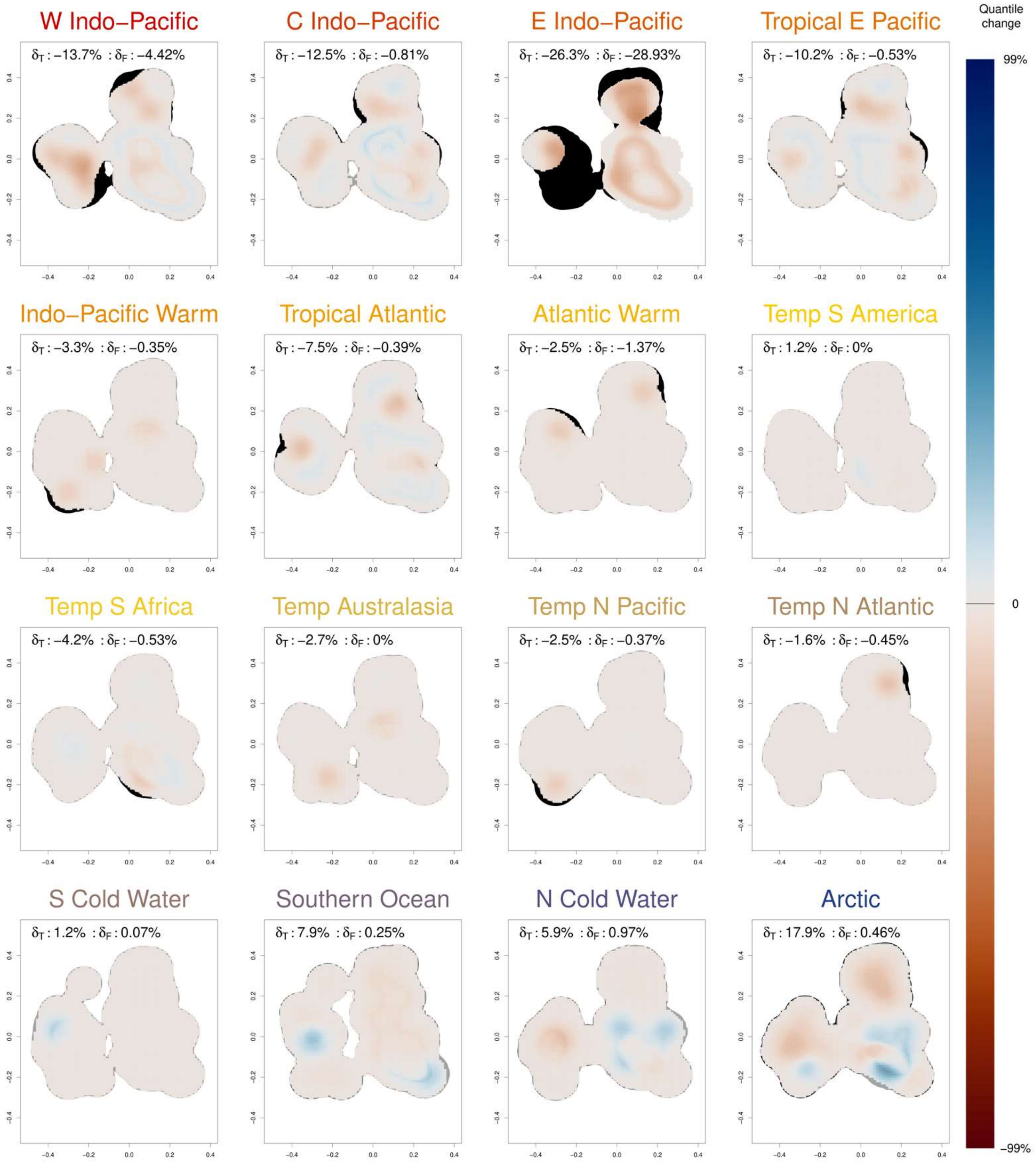

Figure 4.7. Changes in functional spectra by realm between current and future assemblages under a medium-high emissions scenario. The contribution of each continuous and categorical trait to the first two PCoA axes of the four-dimensional trait space can be found in Figure 4.1. Grey shading indicates new regions of functional spectra which are not filled currently. Black shading indicates species loss and regions of functional space lost due to climate change. The blue-red shading indicates the quantile change in functional spectra between present-day assemblages and future assemblages, with blue indicating areas of trait space representing traits becoming relatively more common with climate change and red indicating areas of trait space with traits becoming relatively less common with climate change. For each panel, the proportional change in taxonomic richness (δT) and functional richness (δF), expressed as a percentage of the current TRic and FRic respectively, is shown. Current functional space for each realm can be found in Figure S4.2.

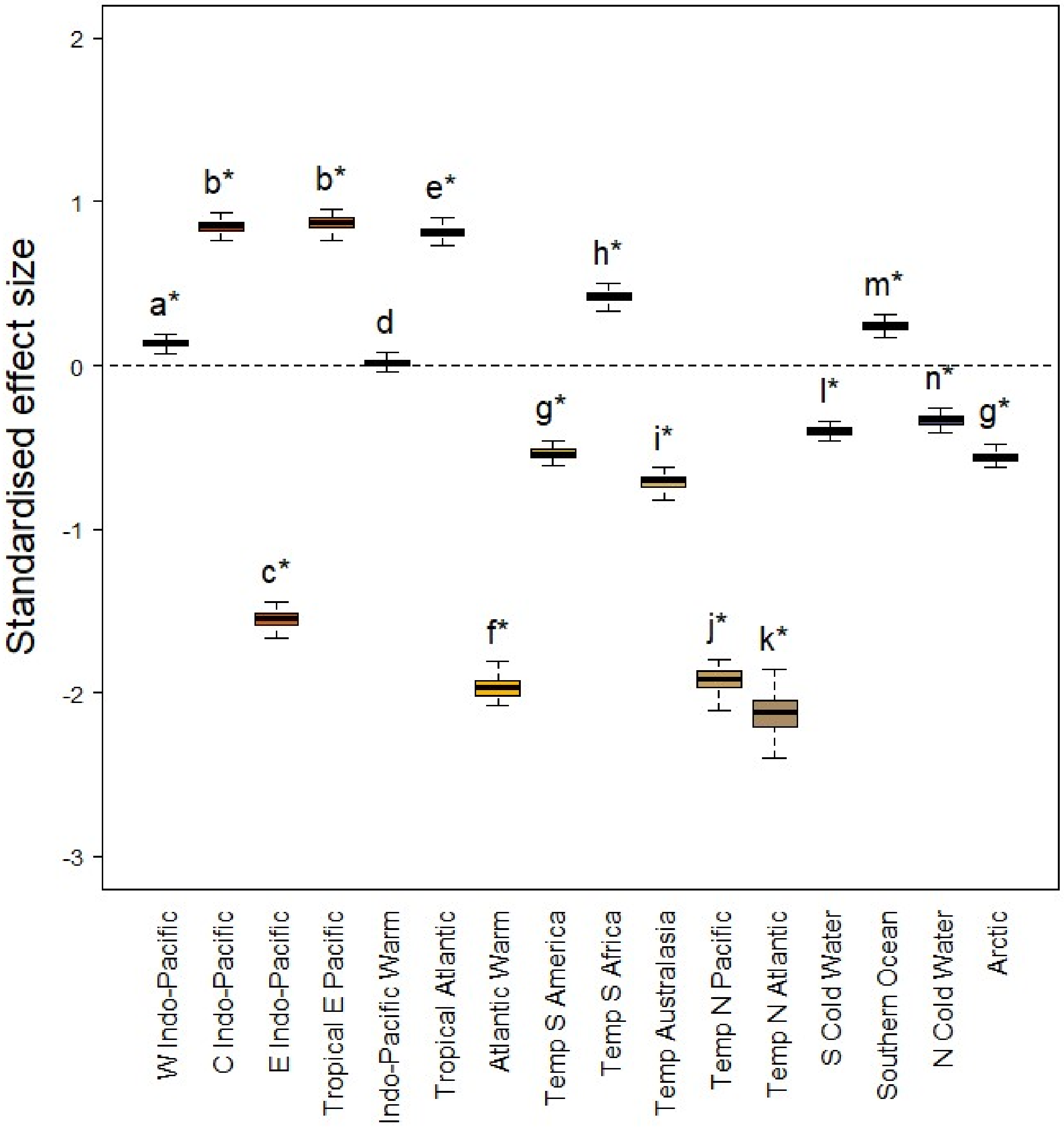

Figure 4.8. Standardised effect sizes showing deviations of observed change in functional richness change (between current and 2100) from null expectations for each oceanic realm. Negative SES represents a smaller observed FRic change than expected FRic change. Asterisks indicate SES values significantly different than expected from null models. Letter displays of all pairwise comparisons with p-values <0.05 between oceanic realms are shown. Colours indicate realm colours moving from warmer realms (redder colours) to colder water realms (more blue colours). Direction of the change in FRic (loss or gain) can be found in Figure 4.7.

4.5 Discussion

In this chapter, I combined species distribution models and functional trait-based approaches to quantify present-day and future diversity and distribution of marine mammals. Forward projections suggested considerable changes in most facets of biodiversity, with the direction and magnitude of these changes depending on geographic location. I found large declines in taxonomic and functional richness at lower latitudes and increases at higher latitudes. Exploration of additional functional diversity indices revealed, for the first time, hotspots of losses of functionally unique and specialised species in both tropical and cold-water realms.

4.5.1 Changes in taxonomic, functional and phylogenetic diversity

The results presented here match relatively well with projections made by Kaschner et al. (2011), who used a relative environmental suitability model to project marine mammal distributions under two emissions scenarios by 2050. Both approaches projected gains of species in the central Bering Sea, high Arctic waters and Antarctic waters (the Weddell Sea, in particular), and species losses along coastlines, and in the Barents Sea, Galapagos, Coral Triangle and around the 30° south latitudinal line. Although Kaschner et al. (2011) do not show total species richness change, my results suggest much greater effects of climate change, with more losses of species in the East and North Pacific, tropical coastal regions, and temperate regions of the North Atlantic. This discrepancy is unsurprising as I consider a greater number of bioclimatic variables in my models, including bathymetry, chlorophyll-a, and salinity, which are expected to influence marine mammal foraging and/or breeding habitats (Cox et al., 2018; Druon et al., 2019; Tittensor et al., 2010). I also project distributions to 2100 compared to 2050, demonstrating that impacts might worsen with ongoing climate change. Furthermore, my approach provides a more extensive investigation of the impacts of climate change on biodiversity as I did not restrict my analysis to change in taxonomic richness alone. These results should still be treated with caution given the caveats of SDMs and will need to be corroborated and scrutinised alongside empirical evidence as it becomes available in order to be used in management plans and conservation.

Changes in marine mammal diversity differed among marine realms, but functional and phylogenetic diversity indices declined across most warm water regions by 2100. The projected negative change in median TRic and FRic was highest in all realms of the Pacific, Tropical Atlantic and Atlantic Warm. Albouy et al. (2020) undertook a similar analysis, though they used a trait-based approach and did not project species' distributions with SDMs.

Nonetheless, their results are somewhat comparable with mine. They predicted the most vulnerable and sensitive species to future climate change were the North Pacific Right Whale, Gray whale, Northern Elephant seal and walrus. These species are also within the top marine mammal families I found with the highest functional originality. Shifts in the ranges of these species could be driving the projected declines in FOri at high latitudes and in Northern Pacific regions of the Arctic in the Bering Sea. Indeed, recent detections of the critically endangered North Pacific Right whale in the north Bering Sea suggests this species is moving north in response to zooplankton moving northward with retreating ice (Filatova et al., 2019; Wright et al., 2023). Losses of FOri species in the Greenland Sea, Baffin Bay and Bering Sea may further explain the FRic loss larger than expected from ΔTRic alone, as FUn species contribute disproportionately to FD (Kuebbing et al., 2018). Losses of unique species could have implications for ecosystem stability, as the range of functional traits in an ecosystem strongly influence the transfer of matter and energy (Díaz & Cabido, 2001; O'Gorman et al., 2010).

The decline in functional specialisation in the Arctic is likely explained by losses of *Balaenidae* species at Northern latitudes and losses in species from *Phocidae* families as I found these were some of the most specialised species of marine mammals. Gray whale (*Eschrichtius robustus*) populations in the Bering Sea have undergone major mortality events with increased warming (Stewart et al., 2023). This supports the loss of original trait combinations at high latitudes as Gray whales have one of the longest migrations from breeding grounds in Mexico to feeding grounds in the Bering and Chukchi seas. If feeding grounds are shifting for whales, such as this example in the Arctic, and at high latitudes, communities could become functionally homogenised. Simmonds and Eliott (2009), who studied the effects of climate change on cetaceans, also found losses of polar specialist species and found a general shift of temperate species towards the poles. This could cause increased competition for resources (Moore & Huntington, 2008).

Using the FUSE index, I identified hotspots of functional unique, specialised and threatened species that might lose or gain suitable climate under climate change. Alarmingly, for the first time I found that almost all of the top 25 FUSE species were lost from the Eastern Pacific, Northern Atlantic and from the region of the 30° south latitudinal band. My results identify these regions as hotspots of species with unique combinations of functional traits and are highly specialised in their ecological role. The species using these regions may also become much more endangered in the future. These hotspots additionally occur in regions of high fishing intensity and vessel traffic which, combined with warming, could impact these populations further.

4.5.2 Changes in functional trait space by realm

By examining changes to functional trait space, I found modest changes in traits specific to certain marine mammal families. Losses of pinniped-based traits in future is somewhat understandable as they rely on land or ice for hauling out and breeding. Sea ice is already melting at an alarming rate due to climate warming, leading to breeding habitat loss, particularly for seals in the Arctic. Using a relative environmental suitability model, Kaschner et al. (2011) created future projections of marine mammals and found similar losses of pinnipeds across low latitudes. Declines in the commonness of pinniped-specific traits in tropical regions could result from impacts of climate change on El Nino events. These events cause harmful algal blooms that reduce pinniped productivity and survival as a result of decreased prey availability. Pup-drowning from storms is also becoming more frequent. This could be driving declining ranges of Galapagos fur seal, in line with Kaschner et al.'s (2011) findings. My results also suggest climate change could cause increases of *Ziphidae* and *Delphinidae* families in the Arctic and Southern Ocean. This is supported by the increase in reported sightings of common dolphin in the North Sea between England and mainland Europe (MacLeod et al., 2009).

The consistent vulnerability of Mysticeti (baleen whales) – and with that, the loss of specific traits such as zooplanktonic and epipelagic feeding, across most marine realms may have important implications for nutrient cycling, which in turn will affect other ecosystem processes. Baleen whales, such as gray, bowhead and right, are particularly important for benthic-pelagic coupling and drive the availability of benthic nutrients to other pelagic feeders at the top of the water column (Roman et al., 2014). The shifts I project in this study match predicted distribution shifts of baleen whales made by others on smaller scales, in particular range shifts in the Pacific towards cooler waters (Kaschner et al., 2011; Whitehead et al., 2008). The higher vulnerability of baleen whales, particularly across the Indo-Pacific, Atlantic Warm and Temperate Northern Atlantic, may be because species feeding at lower trophic levels are more tightly coupled to the physical environment, so they are more likely to shift their distributions in response to food availability (Pendleton et al., 2022). Climate change is driving declines in the abundance of zooplankton and shifting seasonal temperatures and ocean circulation patterns have driven right whales to feed in different places and increase their use of marginal habitats (Ross et al., 2021). Krill populations have declined by as much as 80% in Northern Antarctic Peninsula, resulting in a corresponding decline in baleen whales (Atkinson et al., 2004). Additionally, Visser et al. (2011) found fin and humpback whales have altered their timing of migration to track secondary primary production (chlorophyll-a) generated by northern Atlantic spring bloom. Ultimately, changing distributions of baleen whales could have implications on food webs and ecosystem stability. Changing distributions of baleen whales could further overlap with vessel traffic in habitats not accounted for by existing regulations, and mortality from vessel strikes and gear entanglements could increase (Gavrilchuk et al., 2021; Meyer-Gutbrod et al., 2021). Future work would benefit from exploring the effects of climate change on breeding and feeding grounds separately, and how shifting distributions could interact with other anthropogenic pressures.

4.5.3 Conclusion

By integrating SDMs, to model future marine mammal diversity distributions, and a trait-based approach to explore associated changes in trait space, this chapter provides new insights that reveal that marine mammal taxonomic, functional and phylogenetic diversity are projected to undergo considerable shifts under climate change. The projected declines in warm water realms in particular highlight the urgency of addressing climate impacts on marine assemblages. In addition, I show how climate change impacts vary geographically, with highly original and specialised species projected to be lost from tropical and high latitude regions. This, in turn, suggests that communities may undergo substantial restructuring in future, with knock-on effects for ecosystem resilience and stability. Overall, this chapter contributes substantially to our awareness of the relationship between climate change, marine mammal diversity, and ecosystem dynamics, and urges for a concerted effort to mitigate and adapt to impending challenges.

Chapter 5

Exploring novel North Water Polynya ecosystems under climate change

The chapter has now been published. It is reproduced here in full, with some minor formatting changes. There is therefore some repetition in the modelling methods already described in Chapters 2 and 3.

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5.1 Abstract

Climate change is rapidly reshaping species distributions in the Arctic, which could profoundly impact ecosystem structure and function. While considerable effort has focused on projecting future species distributions, assessing the impacts of range-shifting species on recipient communities and subsequent disruptions to food webs remains largely unstudied. Here, we address this gap by combining species distribution models and ecosystem models to explore the emergence of novel ecosystems in the North Water Polynya. The North Water Polynya is an open-water area between Greenland and Canada, surrounded by sea ice and one of the world's most productive ocean ecosystems. Using existing literature and projections from species distribution models of four marine species, we develop six plausible future ecosystem scenarios for the North Water Polynya. These scenarios include changing biomass of primary producers, changing biomass and size structure of copepods, shifting abundances of forage fish species, and the establishment of killer whales. We find that the biomass of higher trophic levels show pronounced decreases in response to the decrease in pelagic primary producers, with polar bear biomass halving compared to present conditions. Changes in the copepod size structure has the largest impact on the entire ecosystem compared to the other novel ecosystem scenarios, suggesting a strong reliance of higher trophic levels on large, lipid-rich copepods. We further show that increasing capelin with a simultaneous decrease in Arctic cod biomass causes large decreases in the biomass of marine mammals such as polar bear, beluga and ringed seal. Finally, we show the establishment of killer whales as a key novel predator could have cascading top-down effects on the North Water Polynya ecosystem. The framework presented here provides an approach for exploring the emergence of novel ecosystems and highlights how climate change could disrupt a high Arctic ecosystem.

5.2 Introduction

Climate change is rapidly altering Arctic marine ecosystems (Fossheim et al., 2015; Wassmann et al., 2011). Sea ice is melting at an increasing rate (Kim et al., 2023), waters are warming, and species are shifting their distributions to keep pace with changing climate (Pinsky et al., 2013). As species shift their ranges, that biotic interactions and ecological communities change (Pecl et al., 2017), as local extinctions and invasions affect the respective food web structure and functioning (Kortsch et al., 2015; Pecuchet et al., 2020). For example, the potential borealisation of the Arctic marine ecosystem could have profound implications on community structure and function (Fossheim et al., 2015; Grebmeier & Barry, 2007; Kortsch et al., 2015; Pecuchet et al., 2020). In the Barents Sea, reduced sea ice and increasing water temperatures have led to colonization by boreal species, such as cod (*Gadus morhua*) and haddock (*Melanogrammus aeglefinus*) (Frainer et al., 2017; Kortsch et al., 2015). These species are large, generalists that increase food-web connectivity between the benthic and pelagic communities (Frainer et al., 2017; Kortsch et al., 2015; Pecuchet et al., 2020). The movement of cod into northern regions of the Barents Sea also implies increased predation pressure on native Arctic cod (*Boreogadus saida*) (Fossheim et al., 2015; Pedro et al., 2023; Renaud et al., 2012). Such climate-driven range changes are likely to lead to formation of novel ecosystems, though the consequences of these new species interactions remain largely unknown (Gilman et al., 2010; Wallingford et al., 2020). Thus, a major challenge facing both biogeography and community ecology today is to understand how food webs may change with climate-induced range shifts, and the implications of these changes for ecosystem structure and function (Albouy et al., 2014; Bartley et al., 2019).

Climate change is presently impacting much of the Arctic, including the North Water (NOW) Polynya (Pikialasorsuaq Commission, 2017; Ribeiro et al., 2021). The NOW (Kalaallisut: *Pikialasorsuaq*; Inuktitut: *Sarvarjuaq*), a region in northern Baffin Bay, is the largest and most biologically productive polynya north of the Arctic circle, sustaining, for millennia, the world's northernmost Inuit communities and several keystone Arctic species, including Arctic cod, beluga whales (*Delphinapterus leucas*), narwhals (*Monodon monoceros*), Atlantic walrus *(Odobenus rosmarus*), and polar bears (*Ursus maritmus*) (Buchart et al., 2022; Ribeiro et al., 2021). Due to climate change, the NOW Polynya formation has become less stable (Pikialasorsuaq Commission, 2017; Vincent, 2019), threatening ecosystem structure and function, as well as Inuit communities on both sides of the polynya (Pikialasorsuaq Commission, 2017).

With climate-related changes in water temperatures and reduction in sea ice, the northward expansion of southern species into the NOW is expected (Hornby et al., 2021). For example, capelin (*Mallotus villosus*) has an unknown role in the current NOW ecosystem (Coad & Reist, 2017; Hornby et al., 2021) but it may increase in the region in future, competing with Arctic cod and zooplanktivorous birds for *calanoid* copepods (Kyhn & Mosbech, 2019). Furthermore, increasing catches of Greenland halibut (*Reinhardtius hippoglossoides*) on the eastern side of the NOW Polynya suggest an abundance increase in the region, likely due to climate change (Heide-Jørgensen, 2019). However, the impacts of future climate-driven range shifts on the NOW Polynya ecosystem remains unknown.

Species distribution models (SDMs) are a popular method to understand and predict shifts in species' ranges in response to changing environmental factors (Elith & Leathwick, 2009; Pinsky et al., 2013). These models use statistical relationships (correlations) between species occurrence data and environmental variables to infer the ecological niche of a species (Elith et al., 2010). One limitation of SDMs is that they do not explicitly account for, or quantify, food-web interactions (Araújo & Luoto, 2007), hence the consequences of species distribution shifts cannot be quantified. The limitations of SDMs have been widely discussed in the literature but, notwithstanding these limitations, they have the ability to improve our understanding of marine systems under climate change. Coupling SDMs with mechanisms or processes could result in a step-change in our understanding of the likely impact of climate change on marine systems (Twiname et al., 2020).

In contrast to SDMs, marine ecosystem models offer a holistic approach to studying community ecology by integrating trophic interactions and energy flows among various species in an ecosystem (Steenbeek et al., 2021). These models can account for interactions such as competition and predator-prey relationships to simulate the complex dynamics of ecosystems (Heymans et al., 2014). Ecopath with Ecosim (EwE, http://www.ecopath.org) is one such modeling approach that has been widely applied to aquatic ecosystems since its development in the 1980s (Polovina, 1984). Ecopath represents static mass-balanced models of marine ecosystems, and Ecosim is an extension that simulates temporal dynamics (Christensen & Walters, 2004; Walters et al., 1997). EwE models can be used to examine the fundamental dynamics of ecosystems and assess their responses to environmental changes and fishing exploitation (Bryndum-Buchholz et al., 2019; Colléter et al., 2015). Marine ecosystem models have been developed for several Arctic coastal and shelf ecosystems (Hoover et al., 2013, 2021; Pedersen & Zeller, 2001; Pedro et al., 2023; Sora et al., 2022), including the NOW (Bryndum-Buchholz et al., 2024). EwE models have been used to investigate the implications of different harvesting policies, identify data gaps, describe ecological dynamics for marine conservation purposes, and develop ecological indicators to evaluate the ecosystem-wide impacts of climate change (Coll et al., 2015; Hyder et al., 2015; Mackinson et al., 2009). In this context, EwE can be used to explore novel ecosystems, as species abundances increase or new species emerge and establish themselves in an ecosystem (e.g., Arranz (2023)).

To understand the impacts of shifting species distributions on the structure and function of the NOW Polynya ecosystem, information on the potential distribution shifts, of both key novel and native species, can be integrated into EwE models. Unlike SDMs, EwE models were not developed to predict novel colonists. As a result, the integration of SDMs into ecosystem models is a very active field (Murphy & Smith, 2021). Understanding the dynamics of species responses can aid in anticipating and mitigating the ecological consequences of climate change and facilitating informed conservation strategies.

Here, we combine SDMs with the EwE moedling framework to explore novel NOW Polynya ecosystems under two future climate change scenarios. Using the combined model approach, we address the following question: What are the ecosystem implications for the NOW Polynya due to climate change driven shifts in species distributions?

5.3 Materials and Methods

5.3.1 The North Water Polynya ecosystem

The North Water (NOW) polynya, situated in northern Baffin Bay between Ellesmere Island (Canada) and northwest Greenland, is linked to Lancaster Sound, Jones Sound, Kane Basin, Lincoln Sea, and central Baffin Bay (Figure 5.1). It has an average depth of 300 m, (range 170-600 m; Bâcle (2000); Tremblay & Smith (2007)) and experiences strong seasonal variation, through changing light availability, ice breakup, open water periods, and the timing of the spring phytoplankton bloom (Hornby et al., 2021; Klein et al., 2002; Ringuette et al., 2002; Tremblay et al., 2002).

The NOW is one of the most productive Arctic ecosystems (Klein et al., 2002), attributed in part to early open water conditions that prolong the exposure of primary producers to light, resulting in an unusaully early spring bloom (Lewis et al., 1996; Tremblay et al., 2006). The energy generated during the spring bloom predominantly accumulates in surface waters, and is subject to intense grazing by herbivorous zooplankton, such as *Calanus hyperboreus*. Tremblay et al. (2006) estimated that only 27% of particulate primary production during a spring bloom exits the upper 50 m, with 1-7% reaching the benthos, contingent on water depth. Lower trophic level prey, including Arctic cod and meso-zooplankton, assume a crucial role in transferring energy to higher trophic level seabirds and marine mammals (Hobson et al., 2002).

Delineating the precise boundaries of the NOW proves challenging due to sea ice dynamics. Sea-ice melting commences in the spring in the southeast with the return of daylight, progressing northwest under the influence of the warmer West Greenland Current. Extensive open water becomes prominent by May, reaching its maximum extent by late June or early July (Barber et al., 2001; Barber & Massom, 2007; Dunbar, 1969; Pikialasorsuaq Commission, 2017). The polynya continues to expand until it merges with open water moving northward from Davis Strait, leading to the dissolution of the NOW Polynya as it joins the and the ocean by August (Barber et al., 2001; Preußer et al., 2015). The Ecopath model used in this study represents the period of polynya formation, full open water extent, and dissolution (from April to October). The model area boundaries are 76-78.5°N and 80.5-65°W (Bryndum-Buchholz et al., 2024). This region represents the NOW Polynya, with an approximate size of 85,000 km^2, reflecting the observed peak extension in 2000 (Moshøj, 2015).

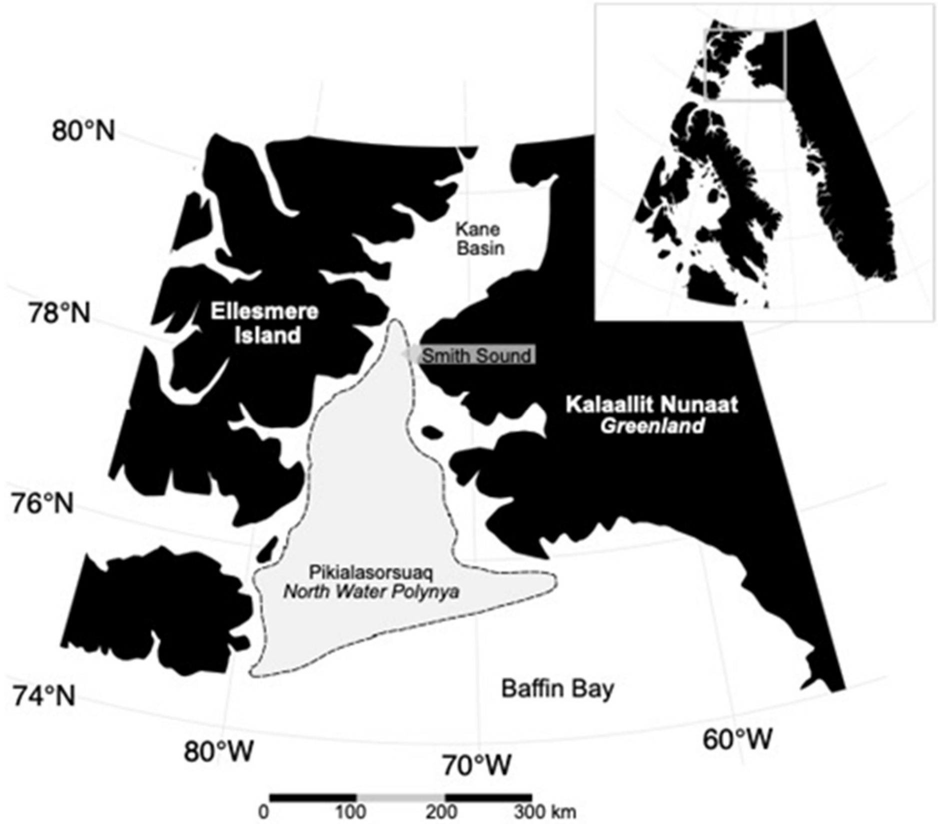


Figure 5.1. Overview of the study area, representing the maximum, open water extent of the North Water Polynya. From Bryndum-Buchholz et al. (2024).

5.3.2 Species distribution modelling

5.3.2.1 Selected species and occurrence data

Three fish and one marine mammal were selected for species distribution modeling, comprising: one important fish species already present in the NOW Polynya, Arctic cod (*Boreogadus saida*); one small pelagic fish expected to increasingly move into the polynya with warming, capelin (*Mallotus villosus*); one commercially important demersal fish species, Greenland halibut (*Reinhardtius hippoglossoides*); and one top marine predator, killer whale (*Orcinus orca*). We chose to include capelin and Greenland halibut because previous studies suggest their distributions and abundances are already increasing in other Arctic regions (Carscadden et al., 2013; Heide-Jørgensen, 2019; Howell & Filin, 2014). Current information on killer whales in the NOW Polynya is limited (Jourdain et al., 2019) but they are considered occasional visitors to the western part of the polynya (Higdon et al., 2013; Lefort et al., 2020). Sightings and reports suggest they are mainly observed south and southwest of the NOW (Higdon et al., 2013; Matthews et al. 2021). Thus, we chose to model the potential habitat in the NOW Polynya of killer whales under climate change scenarios.

Occurrence data were gathered for the selected species from the Global Biodiversity Information Facility (GBIF; http://data.gbif.org) and the Ocean Biodiversity Information System (OBIS; http://www.iobis.org). GBIF data were downloaded on 26th October 2022 using the 'rgbif' package (Chamberlain, et al., 2023) using the download link https://www.gbif.org/occurrence/download/0121994-220831081235567 (GBIF.org, 2022). OBIS data were downloaded on the 31st October 2022 using the 'robis' package (Provoost & Bosch, 2017). The occurrence data were cleaned and filtered to remove spurious records by (1) removing records from land, (2) removing fossil specimens, (3) removing records missing coordinates, (4) removing duplicate records, and (5) removing occurrences predating 2000 to match the temporal range of the environmental data to be used for elucidating species-environment relationships. Following this process, the GBIF and OBIS occurrences were combined and any duplicate records were removed. To account for the spatial clustering of occurrence records, species occurrences were rarefied by gridding them to a 0.5 x 0.5 degree grid. During the gridding process only one occurrence record per grid cell was retained. This is analogous to thinning occurrence records with a distance equal to that of the pixel size of the grid. As the grid was a relatively coarse size, the gridding process was adequate in thinning presence records whilst retaining as much data as possible.

5.3.2.2 Environmental data

Environmental data were downloaded from the publicly available dataset, Bio-ORACLE v2.1 (https://www.bio-oracle.org/; Assis et al. 2018), using the R package 'sdmpredictors' (Bosch et al., 2016). The following seven environmental variables were chosen as predictor variables in the SDMs: mean sea-surface salinity, mean sea-surface temperature, mean sea-bottom temperature, mean sea-surface chlorophyll concentration, mean sea-surface currents velocity, distance to shore and bathymetry. The first five variables are dynamic and liable to change over time, whilst the latter two remain static over our study period. All seven variables were downloaded for a current period (2000-2014). For the future time periods (2040-2050 and 2090-2100), the first five environmental variables were downloaded for all emissions scenarios, available on Bio-ORACLE v2.1 as averaged data from three atmosphere–ocean general circulation models (CCSM4, HadGEM2-ES and MIROC5) provided by the Coupled Model Intercomparison Project Phase 5 (CMIP5) (Assis et al., 2018). The emissions scenarios, known as Representative Concentration Pathways (RCPs), comprised RCP 2.6 (a stringent mitigation scenario aiming to limit warming to below 2°C above pre-industrial levels), RCP 4.5 (a stabilization scenario where emissions peak around 2040 and then decline), RCP 6.0 (a stabilization scenario where emissions peak around 2080 and then decline), and RCP 8.5 (a high emissions scenario with increasing emissions over the century) (van Vuuren et al. 2011). For brevity, future time periods 2040-2050 and 2090-2100 are referred to as 2050 and 2100, respectively. The environmental variables were chosen based on the methods described in Titley et al. (2021) and represent those used in most SDMs of marine species (Jones et al., 2015). Stratification was not considered in our models as Bio-ORACLE does not provide environmental variables at multiple layers of the ocean. We do, however, include sea-bottom temperature as a variable in our models which was not collinear with sea-surface temperature and was found to be an important predictor in the SDMs. The environmental data were resampled to a coarser resolution to match the gridded occurrence data (0.5 x 0.5 degree grid).

5.3.2.3 Presence-only species distribution models

We modelled species-climate relationships following an approach adapted by Titley et al. (2021) and others, which broadly follows the methods of Bagchi et al. (2013), and further adapted for presence-only SDMs. We used occurrence data from species presence databases, locations where species are absent are unknown (Renner et al., 2015). Presence-only SDMs are an appropriate and commonly used approach, requiring the generation of background data to be used as pseudo-absences (Valavi et al., 2021). Here, we used an ensemble of four model types to predict species distributions: Maximum Entropy (MaxEnt), Generalized Additive Models, Boosted Regression Trees, and Random Forests. These model types were chosen due to their effectiveness in handling presence-only data (Valavi et al., 2021), and based on their prior performance in previous modelling studies (Li & Wang, 2013; Chollet et al., 2023). To fit SDMs to presence-only data, 10,000 background pseudo-absences were randomly selected from the same realm(s) in which the target species currently occur. This minimized the selection of pseudo-absence points that are climatically suitable but unreachable. A brief summary of the four fitting methods is provided in the supporting information (S1 Text, Supplementary methods).

5.3.2.4 Model validation

A common issue that requires consideration in SDM techniques is the spatially dependent nature of the data. To reduce the effects of spatial autocorrelation, we followed a “blocking” method as per Bagchi et al. (2013), whereby the gridded occurrence data were split into ten blocks (using ‘blockTools’ package in R (Moore & Schnakenberg, 2012b)), based on marine realms and ecoregions using the Marine Ecoregions of the World (Spalding et al., 2007) and

Pelagic Provinces of the World (Spalding et al., 2012). We combined the latter two to get 16 oceanic realms. For the ecoregions, we largely used the Marine Ecoregions of the World but as they do not cover the entire world's ocean, we used the Pelagic Provinces of the World to create an additional 37 ecoregions, so that there were no gaps of ocean that did not classify as a specific ecoregion. This resulted in a total 269 ecoregions covering the world's oceans. Each block comprises a subset of the 269 ecoregions, such that each block samples parameter space adequately. The blocking approach minimizes spatial autocorrelation of the data points used in the model fitting and testing.

Model performance was assessed using 10-fold cross-validation using the ten blocks. Each model was trained on nine of the ten blocks and then model performance was tested on the remaining tenth block. This was repeated ten times for each of the modelling approaches (resulting in 40 models per species for both 2050 and 2100). Model performance was assessed using the Area Under the Curve (AUC) of the receiver-operating characteristic plot. AUC values provide a quantitative measure of a model's ability to correctly discriminate between presences and absences, with higher AUC scores indicating better model performance (Fielding & Bell, 1997). These models were then used to project future suitable niche-space for species in 2050 and 2100 (40 models per species for each emissions scenario), across the same realms that they currently occupy, as well as in adjacent realms. Projection results were weight-averaged across the 40 models (per emissions scenario), with individual model weightings based on the AUC scores of each model. In this sense, the best performing model in the ensemble lent the greatest weight to the final projected species distribution.

The current and future habitat suitabilities (probability of occurrence) were binarized based on species-specific thresholds that maximized sensitivity and specificity (Thresholds: *B. saida* = 0.07; *M. villosus* = 0.12; *R. hippoglossoides* = 0.23; and *O. orca* = 0.27) to summarize potential changes to species occupancy in the NOW Polynya. We also presented the results of the raw habitat suitabilities for each species when mapping changing habitat suitability under emissions scenarios, as thresholded suitabilities can overestimate occurrences.

5.3.3 Ecosystem model

We expanded a published Ecopath model for the NOW Polynya (Bryndum-Buchholz et al., 2024) by adding the following functional groups: Bowhead whale (*Balaena mysticetus*), Greenland halibut, and capelin (overview of all functional groups in Table 2). All of these species have been observed in the NOW Polynya (Hornby et al., 2021). Killer whale was added as a functional group as part of a novel ecosystem scenario in Ecosim to represent a novel establishment of this apex predator in the NOW Polynya (see below section 2.4 for more details on the justification of adding killer whales as a novel scenario). With these additions, the Ecopath model included 24 separately defined functional groups (see Table S5.1) to characterize the NOW Polynya ecosystem. Parameter estimates were based on qualitative and quantitative studies from the NOW Polynya or other Arctic regions if local data were not available (Table S5.1). Details on the Ecopath modelling framework are described in the Supporting Information (S1 Text, Supplementary methods).

5.3.3.1 Functional groups

For each functional group, biomass (B; tonnes per km2) was estimated from abundance data found in survey reports and peer-reviewed research specific to the NOW Polynya (S1 Table). Production to biomass (P/B) was estimated by either computing values using total mortality rates (natural mortality rate (M) + fisheries mortality rate (F)) or from FishBase (www.fishbase.org). FishBase integrates mortality rates, parameters of the Bertalanffy growth function, and mean temperature to calculate M [86]. Estimates of M to calculate P/B were sourced from published literature for the NOW or other Arctic ecosystems. In cases where explicit information on F was unavailable in the literature, we computed F as total fish catch over the estimated biomass, based on reported subsistence catches from Canada and Greenland (NAMMCO, 2016). Consumption to biomass (Q/B) was primarily acquired for taxa in the NOW when available (S1 Table). In instances where information from the NOW was lacking, we used values from the literature or from other Ecopath models deemed most suitable for the NOW ecosystem or similar Arctic regions (S6 and S7 Tables). A diet matrix (S2 Table) was formulated using published diet studies for NOW taxa, when accessible. In the absence of diet studies specific to the NOW Polynya, we used diet composition estimates from the literature deemed most appropriate for the NOW region or from similar Arctic species (S5.1 Table). We categorized each data source using the Ecopath pedigree index that describes the origin of input data and assigns confidence intervals based on source to quantify uncertainty associated (Christensen et al., 2008; Pauly et al., 2000; S6 and S7 Tables). Please refer to Bryndum-Buchholz et al. (2024) for a detailed description of the initial functional groups and the "North Water Polynya" model in the Ecopath repository Ecobase (https://ecobase.ecopath.org/) to access the base model.

Parameterizations for the additional functional groups of the expanded Ecopath model are given below. Data used for the parameterization were based on qualitative and quantitative studies from the North Water Polynya or other Arctic regions if local data were not available, as well as other Arctic Ecopath models. An overview for all data sources for each functional group and parameter can be found in Table S5.1.

Marine mammals – bowhead whales and killer whales - Data for the relevant populations or sub-populations were obtained from empirical studies and other Arctic Ecopath models, assuming that all marine mammals inhabited the NOW Polynya throughout the defined model timeframe. To estimate *B*, the number of individuals was multiplied by the average weight per individual (in tonnes), and then divided by the total model area (km^2). *B* estimates for bowhead whale were based on aerial observations in 2009 (Boertmann et al., 2015), 2010 (Heide-Jørgensen et al., 2013), and tagging studies from 2014 (Heide-Jørgensen et al., 2016), because direct observations for the NOW were not available for the base model timeframe. *P/B* and *Q/B* for bowhead whale considered *M* from the Western Baffin Bay Ecopath model (Pedro et al., 2023) and *F* based on North Atlantic Marine Mammal Commission (NAMMCO) catch statistics (NAMMCO, 2016). Due to a lack of data for killer whales in the NOW, low initial values for *B* were defined for Scenario 4 (See next section), and *P/B* and *Q/B* values from the Western Baffin Bay Ecopath model were used.

Fish – Greenland halibut and capelin - *B* estimates for Greenland halibut were based on September trawl surveys for 2004, 2010, and 2012 for the Area A0 of the Northwest Atlantic Fisheries Organization (Treble 2005; Treble 2013), because direct observations for the NOW were not available for the set model timeframe. *P/B* was calculated accounting for *M* only (no commercial fisheries for Greenland halibut in the NOW polynya), which was derived from the FishBase Life-history tool. *Q/B* was also derived from the FishBase Life-history tool. Due to a lack of data for capelin in the NOW, Ecopath estimated *B,* based on *P/B*, and Q/B estimates from the FishBase Life-history tool.

5.3.4.1 Ecological indicators, network analysis, and SURF index

To evaluate the ecological roles of the defined functional groups in the NOW Polynya, we analyzed benthic-pelagic coupling. To evaluate the role of individual functional groups in benthic-pelagic coupling in the NOW Polynya ecosystem, we assigned domains based on feeding behavior - pelagic, bentho-pelagic, demersal, and benthic - to each functional group and let Ecopath calculate the consumption rate (t km^2 t^{-1}). The domains were used to determine the strength of direct interactions (i.e., amount of consumption) among functional groups across domains. Further, we conducted a Lindeman spine analysis of trophic flows, following Lindeman (1942) and a Mixed Trophic Impact (MTI) analysis to gauge the direct and indirect impacts of changes in the biomass of one group on the biomass of other groups within the ecosystem (Christensen et al., 2005). Ecopath estimated omnivory and connectance indices, which quantify the width of the trophic spectrum for each functional group and provide a measure of food-web complexity and interconnection, respectively (Christensen et al., 2005, 2008).

We derived ecosystem indicators for the NOW Polynya from the summary statistics and network analyses provided by Ecopath, including (i) Finn's Cycling Index, which indicates the fraction of total system biomass flow recycled in the system before leaving; (ii) Finn's Mean Path Length, which represents the average length of each cycle flowing through the food chain), and (iii) mean trophic transfer efficiency, representing the proportion of mean energy passed between trophic levels in ecosystems (refer to Christensen et al. (2008), for detailed explanations of individual Ecopath statistics and network indices). To identify important prey species, we computed the SUpportive Role to Fishery ecosystems index (SURF; Essington & Plagányi (2014)) for consumers (excluding polar bears). This index accounts for the level of reliance on prey by predators and adjusts for the overall number of connections in the food web. Species with values closer to zero are deemed non-key forage species, while larger values indicate key forage species. If the SURF index exceeds 0.001, the species is categorized as a central prey species within the ecosystem.

5.3.5 Novel ecosystem scenarios

SDMs were not coupled to the ecosystem models per se, as SDM results only provide information on the distribution of species rather than their local abundance. Instead, SDM results were used to infer plausible changes in species present to inform six novel ecosystem scenarios for the NOW Polynya (Table 5.1). The rationale, hypotheses, and key literature for each scenario are briefly described below and presented in Table S5.3; the modified biomass values for each scenario are in Table 5.1. The values of the scenario-specific biomass changes in Table 1 were, when available, defined based on maximum future projected changes for the respective functional groups as found in published literature (Table S5.3). When projections were unavailable, biomass values were defined to reflect the underlying assumptions of the respective scenario (Table S5.3). The SDM model projections were used to inform the direction of biomass changes in the respective scenarios (Tables 5.1 & S5.3).

Scenario 1.1 and 1.2: Changes in biomass of primary producers - Climate change is likely to impact future primary production in the NOW Polynya (Hornby et al., 2021). Whether primary production will decrease or increase in the polynya is not yet determined. For the Arctic Ocean more generally, primary producer biomass is expected to increase due to a longer growing season caused by increases in both the extent and duration of the open water season and increasing storminess, enhancing average annual light availability for photosynthesis (Arrigo & van Dijken, 2011). Congruently, projections by Earth System Models of primary production and phytoplankton biomass show increases for the NOW polynya (Meredith et al., 2019; Tittensor et al., 2021). In contrast, if the Nares Strait ice-bridge disappears completely; primary producer biomass in the NOW polynya is expected to decrease due to nutrient limitation caused by reduced mixing and/or upwelling, increased stratification, and reduced light penetration due to increased drifting of ice through the polynya (Buchart et al., 2022; Noh et al., 2023). Consequently, to consider these two possible future scenarios in our modelling, we devised two scenarios representing an increase (Scenario 1.1) and a decrease in the biomass of primary producers by the end of the 21st century (Scenario 1.2) (Table 5.1).

Scenario 2.1. and 2.2: Changes in biomass and size structure of copepods - Due to climate-change driven environmental alterations, such as increasing sea temperature, shifts in zooplankton distribution are expected to impact zooplankton biomass and species composition (Hornby et al., 2021). Shifts in the size composition within the NOW *Calanus* community are expected in the future due to increasing biomass of smaller, less fatty calanoid copepod species, such as *Calanus finmarchicus* (Heneghan et al., 2023; Møller & Nielsen, 2020). This shift is suggested to decrease energy transfer in the NOW Polynya ecosystem, since larger copepods are richer in lipids, and so provide a higher energy intake per calorie spent searching and handling prey by consumers (McGinty et al., 2021). Overall, copepod biomass is expected to decrease in the NOW region, caused by an earlier onset of the phytoplankton spring bloom (Bélanger et al., 2013). The earlier spring phytoplankton bloom escapes the copepod grazing, due to a mismatch between onset of the spring bloom and the end of the copepod diapause (Møller & Nielsen, 2020), leading to reduced food availability for the copepod community in the spring (Bélanger et al., 2013). Based on these two possible future changes in the copepod community, we devised two scenarios representing a change in the biomass ratio of large and medium copepods (Scenario 2.1) and a second representing a decrease in overall copepod biomass by the end of the 21st century (Scenario 2.2) (Table 1).

Scenario 3: Shift in forage fish species abundances - With the projected northward shift of capelin into the NOW Polynya, the Arctic cod population may be negatively impacted through direct competition for zooplankton prey (Hornby et al., 2021; Pedro et al., 2020). Corroborated by our SDM projections for capelin and Arctic cod, and the existing literature (e.g. Rose (2005), Chambellant et al. (2013); Gaston & Elliott (2014); (Geoffroy et al., 2023)), in Scenario 3 we assume that Arctic cod will decrease in their biomass, and capelin biomass increase in the ecosystem.

*Scenario 4: Establishment of killer whales - A*s the sea ice free season lengthens with a warmer climate, better access results in abundance increases of marine top predators (Hornby et al., 2021). Killer whales were added as a functional group because SDMs projected suitable habitat for them currently (2000-2014) in the NOW. Currently, killer whales are only considered as ‘occasional visitors’ to the western part of the NOW (Higdon et al., 2012, 2013; Lefort et al., 2020), which corroborates our SDM projections. The NOW is at a considerably higher latitude than where sub-populations of killer whales currently inhabit in the Arctic - the largest population being in the Northwest Pacific. Populations in Nunavut and the NOW could largely be restricted by sea ice extent, and killer whales were never found in the past in Western Hudson Bay and in the High Arctic Islands. Their sightings have been steadily increasing in the high Arctic region since the 1950s (Barber et al., 2001; Meredith et al., 2019). Only recently have sightings suggested that killer whales have expanded their ranges into areas like Hudson Bay and northwest of Baffin Island (Higdon et al., 2009, 2013), and has been linked to declining sea ice (Higdon et al., 2009). Additionally, more prey such as capelin could become available in the NOW with increasing climate change so the killer whale population may become more established and an ecosystem component. The increased frequency and possible establishment of a novel apex predator indicates a greater predation pressure on other large Arctic mammals, such as narwhals, belugas, and seals.

Table 5.1. Overview of novel ecosystem Ecopath with Ecosim (EwE) scenarios for the North Water Polynya and associated biomass (*B* in t km^2) changes. Lg = Large. Med = Medium. Sm = Small. Lg copepods include *Calanus hyperboreus*, *Calanus glacialis, and Metridia longa*; Med copedods include *Pseudocalanus spp, and Calanus finmarchicus*). The

percent values for the respective biomass changes are based on published literature, presented in Table S5.4.

Scenario		Baseline *B*	Total biomass change	EwE *B*
1.1	Increase in pelagic primary producers	Lg pelagic Producers (>=5 µm): 25.00 Sm pelagic producers (0.7-5 µm): 13.00	+20%	Lg pelagic producers (>=5 µm): 27.50 Sm pelagic producers (0.7-5 µm): 14.30
1.2	Decrease in pelagic primary producers		-30%	Lg pelagic producers (>=5 µm): 21.5 Sm pelagic producers (0.7-5 µm): 11.05
2.1	Change in copepod community size-structure	Lg copepods: 23.42 Med copepods: 9.49 (ratio ~ 70 (lg copepods): 30(med copepods)	Change in ratio to 10 (lg copepods): 90 (med copepods).	Lg copepods: 3.35 Med copepods: 29.65
2.2	Decrease in copepod biomass	Lg copepods: 23.42 Med copepods: 9.49	-30%	Lg copepods: 21.08 Med copepods: 8.541
3	Shift in forage fish species abundances	Capelin: 0.026 Arctic cod (Age 1+): 5.50	+40% capelin -15% Arctic cod (Age 1+)	Capelin: 0.0364 Arctic cod (Age 1+): 4.675
4	Establishment of killer whales	—--------	+ killer whale +40% capelin -15% Arctic cod (Age 1+)	Killer whale: 0.00014 Capelin: 0.0364 Arctic cod (Age 1+): 4.675

5.3.5.1 Ecopath with Ecosim simulations

To simulate the ecosystem response to B changes in the above described functional groups (Table 5.1), we used B values as the representation of future ecosystem scenarios. In other words, B values for the manipulated functional groups in each scenario were used as biomass forcing to simulated ecosystem wide responses due to these changes. We ran each simulation for 100 years for each novel ecosystem scenario and reported the mean B values for the last decade, for each functional group, after each simulation reached equilibrium. To avoid sudden ecosystem responses or collapse, the forcing commenced after 50 years, after a tune-up phase of steady biomass increase based on the estimated baseline model B from 2005-2007. Details on the Ecosim framework are described in the Supporting Information (S5.1 Text, Supplementary methods). Finally, for each scenario, we identified which functional groups differed by <20%, 20-40% and >40% in biomass compared to the baseline biomass estimates and calculated the proportion of functional groups impacted at each level (leaving out the impacting group).

5.3.5.2 Sensitivity analysis

We performed a sensitivity analysis for each novel ecosystem scenario. We ran two simulations to represent a range of parameter values (Table S5.4). For *B*, where possible, the parameter range was based on the lowest, mid, and highest projected values found in the literature (Table S5.4). When projections were unavailable, initial *B* estimates were increased and decreased by increments of 5% to determine the effect on the ecosystem. For each analysis, we identified which functional groups differed by <20%, 20-40% and >40% and calculated the proportion of functional groups impacted at each level (leaving out the impacting group).

5.4 Results

5.4.1 Projections from species distribution models

SDMs performed well, with the average Area Under the Curve (AUC) of ensemble models being 0.97 (± 0.03 SD), with values ranging from 0.88 and 1.0 (see S5.5 Table for all AUC results). Overall, the AUCs for Random Forests were slightly higher than the other models (average Random Forests AUC = 0.98 ± 0.02, c.f. averages of 0.97 ± 0.03, 0.97 ± 0.03 and 0.96 ± 0.03, for Boosted Regression Trees, MaxEnt and Generalized Additive Models respectively). Full model outputs from each SDM type are available on Figshare (Gillie et al., https://doi.org/10.6084/m9.figshare.c.7420774).

The NOW Polynya is projected to become climatically suitable for most of the modeled species. Suitable climate for capelin increased by 2050 and 2100 under both emissions scenarios, especially in northern and western areas of the polynya (Figs 5.2A(b), 2C(c) and S5.5B(b), S5.5C(c) Figs). Median habitat suitability for capelin increased in the polynya by 13% by 2050 under RCP 4.5. In 2100, capelin range is projected to extend to occupy 80% of the polynya. Suitable habitat for Arctic cod in 2050 declined in the southwestern region of the polynya but increased slightly in central areas (Fig 5.2E(e)), resulting in an average habitat suitability decrease of 5%. Suitable climate in 2100 generally shifts northward under a medium emissions scenario (Fig 5.2).

Under the high emissions scenario (RCP 8.5), by 2100, Arctic cod is projected to experience large declines in habitat suitability across the polynya (S5.5F(f) Fig). Arctic cod is projected to occur in all grid cells at present (2000-2014) but to decline in range by 10% by 2050 and 2100 under RCP 8.5. Suitable climate for Greenland halibut was identified in the south-western region of the polynya (S5.6A(a) Fig) and was projected to shift towards the northeast of the polynya and northwest below Ellesmere Island by 2100 (under RCP 4.5 and RCP 8.5). The SDM results suggest that at present (2000-2014), there may be suitable climate for killer whales in the polynya. Habitat suitability for killer whales generally declined by 2050 under RCP 4.5 across the polynya (Fig 5.2H(h)) by as much as 70% by 2100 (Fig 5.2I(i)).

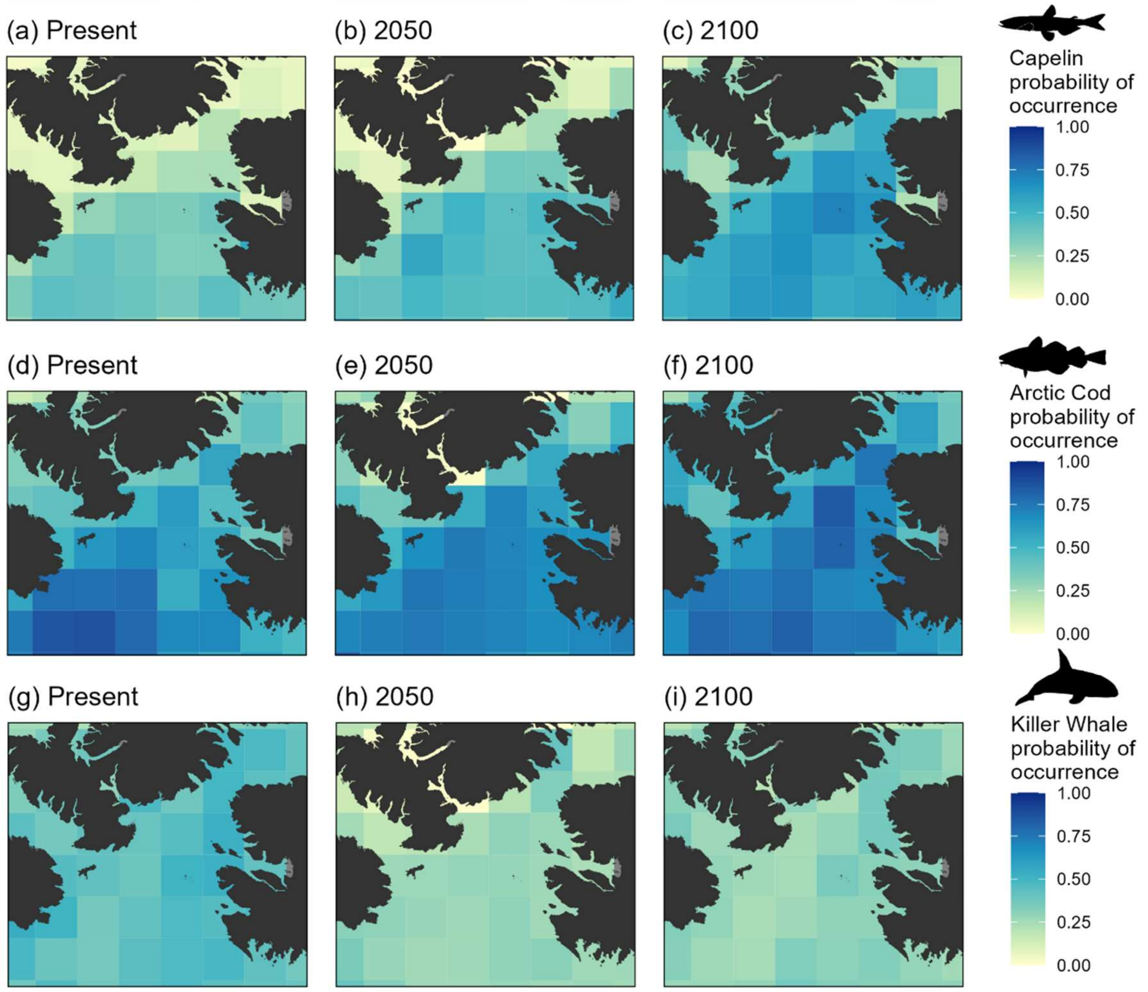


Figure 5.2. Ensemble projections of capelin (*Mallotus villosus*) (a-c), Arctic cod (*Boreogadus saida*) (d-f) and killer whales (*Orcinus orca*) (g-i) distribution in the North Water Polynya from present-day (2000-2014) to 2050 and 2100 under RCP4.5 emissions scenario. Projection results for the individual model types for each species are provided in the Supporting Information (S5.1, S5.2, S5.3 and S5.4 Figs). Killer whale icon created by authors, other icons are public domain silhouette images by Milton Tan (*Gadus morhua*) and xgirouxb (*Thaleichthys pacificus*), via PhyloPic (www.phylopic.org).

5.4.2 Ecopath base model

5.4.2.1 Model parameters

The pedigree index for biomass parameters was dominated by values between 4 and 6, meaning that the data relied heavily on local samples and indirect approximations (Tables S5.5 & S5.6). For production and consumption to biomass ratios (*P/Q* and *Q/B*, respectively), the pedigree index was dominated by values between 3 and 4, indicating the input relied heavily on Ecopath models from other Arctic regions and empirical relationships (Tables S5.5 & S5.6). Values for diet parameters were dominated by the index of 2, indicating the input relied heavily on Ecopath models from other Arctic regions (Tables S5.5 & S5.6). The average pedigree score for the entire base model was 3.61.

5.4.2.2 Model balancing

This study used a balanced model (Bryndum-Buchholz et al., 2024). To achieve mass-balance after adding new functional groups, parameter adjustments were made to the biomasses and *P/Q* of bowhead whale, Greenland halibut, and Arctic cod (Age 1+) (Table S5.7). We considered the model balanced when Ecotrophic Efficiency (EE) < 1 for all functional groups (Table 5.2).

5.4.2.3 Trophic levels and flows

In the base model, trophic levels (TLs) ranged from 1 to 4.73 (Table 5.2; Fig 5.3), with polar bear occupying the highest trophic position in the food web, followed by narwhal (TL 4.35), and beluga (TL 4.02). The groups of walrus, ringed seal, little auk, Greenland halibut, capelin, Arctic cod (Age 1+), and ‘other fish’ had estimated TLs between 3 (other fish) and 3.77 (Greenland halibut). Arthropods, bivalves, echinoderms, worms, the zooplankton groups, and Arctic cod (Age 0) had TLs between 2.06 (Arctic cod (Age 0)) and 2.50 (echinoderms). Primary producers and detritus were at the bottom of the food web with TL 1. In general, these estimated TLs agreed with the range of values reported in the literature for the NOW Polynya and other Arctic ecosystems (S5.9 Table). Trophic flows estimated by the model indicated that pelagic and benthic communities were primarily connected by Arctic cod (Age 1+), bowhead whale, walrus, and ringed seal (Fig 5.3). The Lindeman spine analysis indicated that most energy flows occurred in the first two TLs, representing 53.3% of the total system throughput (TST; S5.8 Fig; TL1=23.56%, TL2=29.74%). TL2 largely contained large copepods (23.42 t km2), other meso-zooplankton (12.2 t km2), bivalves (10.95 t km2), echinoderms (12.10 t km2), and worms (13.78 t km2) (Fig 5.3; Table 5.2), representing 44.64% of the total biomass excluding detritus. Average transfer efficiency (TE) for the NOW Polynya ecosystem was 9.17% (S5.10 Table), with the highest TE for TL2 (11.18%; S5.10 Table).

5.4.2.4 Ecological indicators, network analysis, and SURF index

The NOW Polynya ecosystem is characterized by many benthic-pelagic couplers, defined by the feeding domains of the specific functional group (i.e., pelagic, bentho-pelagic, demersal, and benthic). Consumption rates across feeding domains ranged from 9.11 × 10-7 t km2 t-1 for killer whales to 59.95 t km2 t-1 for Arctic cod (Age 0) in terms of total rates (S5.7 Fig). Notably, the pelagic and benthic-pelagic functional groups, such as walrus, narwhal, ringed seal, capelin, and Arctic cod (Age 1+) couple the pelagic and benthic domains by feeding on the entire range of domains. Arthropods, echinoderms, and worms, all of which are benthic invertebrates, couple the pelagic and benthic domain by scavenging on deposits of functional groups originating from the pelagic domain.

The MTI analysis (S5.9 Fig) revealed that, generally, most functional groups had a negative impact on themselves, reflecting intraspecific competition for resources, and a negative impact on their respective prey due to predation pressure. Bowhead whale, walrus, capelin, other fish, worms, and Arctic cod (Age 0) had very low to no impact on other groups, likely due to their relatively low B or Q/B ratios. Bivalves showed the largest positive impact on walrus, reflecting the diet of walrus in the NOW Polynya. Small pelagic producers had the largest positive impact on Arctic cod (Age 0), through their large role as prey for that age group. Arctic cod (Age 1+) largely consumes zooplankton and benthic invertebrates (as shown in the diet matrix in S5.2 Table) and has a negative impact on these functional groups. The largest negative impact was observed for little auk affecting Arctic cod (Age 0), as well as for beluga on capelin, through predation and, in the case for little auk, interspecific competition for resources, such as zooplankton. Interestingly, based on the MTI analysis, Arctic cod (Age 1+) had a relatively strong negative impact on capelin; however, capelin showed no impact on Arctic cod (Age 1+).

Key ecosystem properties (total system throughput, sum of consumption, exports, production, and total biomass) of the current iteration of the NOW model were largely comparable to values for the base model for the NOW Polynya (S5.11 Table). The system omnivory index for the NOW Polynya was low, indicating a relatively high diet specialization among the individual functional groups (S5.11 Table). Finn's Cycling Index was similar between the two models, signifying a relatively short cycling of biomass flow through the ecosystem (Finn, 1976). Finn's mean path length was similar between the two models. Mean transfer efficiency increased from 8.18% in the first iteration of this model to 9.17% in this model (S5.11 Table), highlighting that the ecosystem with additional functional groups is more productive but with less energy being transferred to higher trophic levels. The SURF index identified large copepods, Arctic cod (Age 1+), other meso-zooplankton, medium copepods, bivalves, arthropods, ringed seal, worms, echinoderms, and Greenland halibut as key forage species (S5.10 Fig). Large copepods and Arctic cod (Age 1+) showed values at least an order of magnitude higher SURF index than the other functional groups (S5.10 Fig).

5.4.3 Novel ecosystem scenarios and sensitivity analysis

Scenarios 1.1 and 1.2: Changes in biomass of primary producers - with increasing biomass of pelagic primary producers (Scenario 1.1), higher trophic level functional groups showed a moderate increase in biomass, with the exception of "other fish", which showed a biomass decrease (Table 5.3; S5.11 Fig). Biomass across all functional groups responded to a decrease in pelagic primary producers (Scenario 1.2), with pronounced biomass decreases in higher trophic levels, especially for polar bear, Greenland halibut, beluga, walrus and ringed seal (Table 5.3; S5.12 Fig). Notably, for TLs > 4, biomass was halved compared to the base model (S5.12 Fig). For both scenarios, the sensitivity analysis showed less pronounced biomass responses in the ecosystem with lower changes in the biomass of pelagic primary producers (S5.12 Table).

Scenario 2.1. and 2.2: Changes in biomass and size structure of copepods - Changes in the copepod size structure (Scenario 2.1) had the largest impact on the entire ecosystem compared to the other novel ecosystem scenarios. For this reason, we chose to highlight this scenario in Fig 3 and have included diagrams of the other scenarios in the Supporting Information (S5.12, S5.13, S5.14 and S5.15 Figs). Under this scenario, the relative biomass of the highest TLs (> 4) decreased substantially, to almost a third of the biomass of the baseline model (Fig 5.4A). Biomass of key prey species, such as ringed seal, and Arctic cod

(Age 1+) declined while capelin biomass increased by > 40% (Table 5.3; Fig 5.3). Biomass of ringed seal – one of the main predators of Arctic cod (Age 1+) – declined drastically (>40%). Bowhead whale and little auk biomasses increased by > 40% (Table 5.3; Fig 5.3). In comparison, an overall decline in copepod biomass (Scenario 2.2) did not have as large an effect on the NOW Polynya ecosystem (Table 5.3; Fig 5.4; S5.13 Fig). A copepod biomass decline of 20-30% produced the largest impacts on polar bear, bowhead whale, beluga, and little auk (Table 5.3; S5.13 Fig; S5.12 Table).

Scenario 3: Shift in forage fish species abundances - An increase in capelin with a simultaneous decrease in Arctic cod (Age 1+) biomass had the largest effect on marine mammals in the ecosystem (Table 5.3; Fig 5.4; S5.14 Fig). Here, the largest declines were for polar bear, beluga, and ringed seal, in the scenario itself and the sensitivity analysis (Table 5.3; S5.12 Table).

Establishment of killer whales - In response to increasing killer whale biomass, polar bear biomass decreased, as the biomass of their main prey, such as beluga, narwhal, and ringed seal decreased (Table 5.3; Fig 5.4A; S5.15 Fig). This pattern was also observed in the sensitivity analysis (S5.12 Table).

Table 2. Parameters from the balanced Ecopath model for the North Water Polynya in 2005-2007. Values estimated by Ecopath are in italics; values adjusted during model balancing are in bold. TL = Trophic level; *B* = Biomass (t km^2); *P/B* = Production/biomass ratio (yr^{-1}); *Q/B* = Consumption/biomass ratio (yr^{-1}); *EE* = Ecotrophic efficiency (the fraction of total production of one functional group that is consumed by other groups; unitless); *P/Q* = Production/consumption (yr^{-1}). Lg = Large; Sm = Small; Med = Medium. PEL = Pelagic; BP = Bentho-pelagic; DEM = Demersal; BENT = Benthic. Gray shading: functional group added to the base model for Scenario 4. Original parameter values were obtained from (Hoover et al., 2013).

Functional group		**TL**	**Domain**	***B***	***P/B***	***Q/B***	***EE***	***P/Q***
1	Killer whale	4.77	PEL	0.00014	0.03	9.11	*0.00*	*0.00*
2	Polar bear	4.73	PEL	0.001	0.40	6.00	*0.02*	*0.07*
3	Bowhead whale	3.16	PEL	**0.002**	0.07	9.50	*0.00*	*0.01*
4	Beluga	3.95	PEL	0.01	0.29	17.00	*0.33*	*0.02*
5	Narwhal	4.35	PEL	0.10	*0.001*	19.80	0.76	*0.00*
6	Walrus	3.18	PEL	0.01	1.23	30.4	*00.01*	*0.04*
7	Ringed seal	3.68	PEL	0.08	0.18	16.5	*0.31*	*0.01*
8	Little auk	3.14	PEL	0.13	0.15	64.61	*0.00*	*0.00*
9	Greenland halibut	3.77	DEM	**1.73**	0.51	1.30	*0.86*	*0.39*
10	Capelin	3.17	PEL	*0.026*	0.66	4.40	0.64	*0.15*
11	Arctic cod (Age 1+)	3.20	BP	**5.50**	**0.50**	2.63	*0.85*	*0.19*
12	Other fish	3.00	BP	*1.53*	0.51	2.40	0.95	*0.21*
13	Arthropods	2.48	DEM	9.00	0.75	6.00	*0.96*	*0.13*
14	Bivalves	2.16	BENT	10.95	0.62	6.33	*0.92*	*0.10*
15	Echinoderms	2.50	BENT	12.10	0.55	2.20	*0.97*	*0.25*
16	Worms	2.21	BENT	13.78	0.95	4.00	*0.86*	*0.24*
17	Lg copepods	2.17	PEL	23.42	5.50	20.00	*0.13*	*0.28*
18	Med copepods	2.12	PEL	9.49	18.00	45.00	*0.99*	*0.40*
19	Arctic cod (Age 0)	2.06	PEL	0.46	31.60	105.00	*0.11*	*0.30*
20	Other meso-zooplankton	2.22	PEL	12.20	22	80.00	*0.60*	*0.28*
21	Lg pel. producers	1.00	PEL	25.00	34.50	-	*0.71*	*0.00*
22	Sm pel. producers	1.00	PEL	13.00	64.87	-	*0.60*	*0.07*
23	Pelagic detritus	1.00	PEL	0.50	-	-	*0.29*	-
24	Benthic detritus	1.00	BENT	0.05	-	-	*0.88*	-

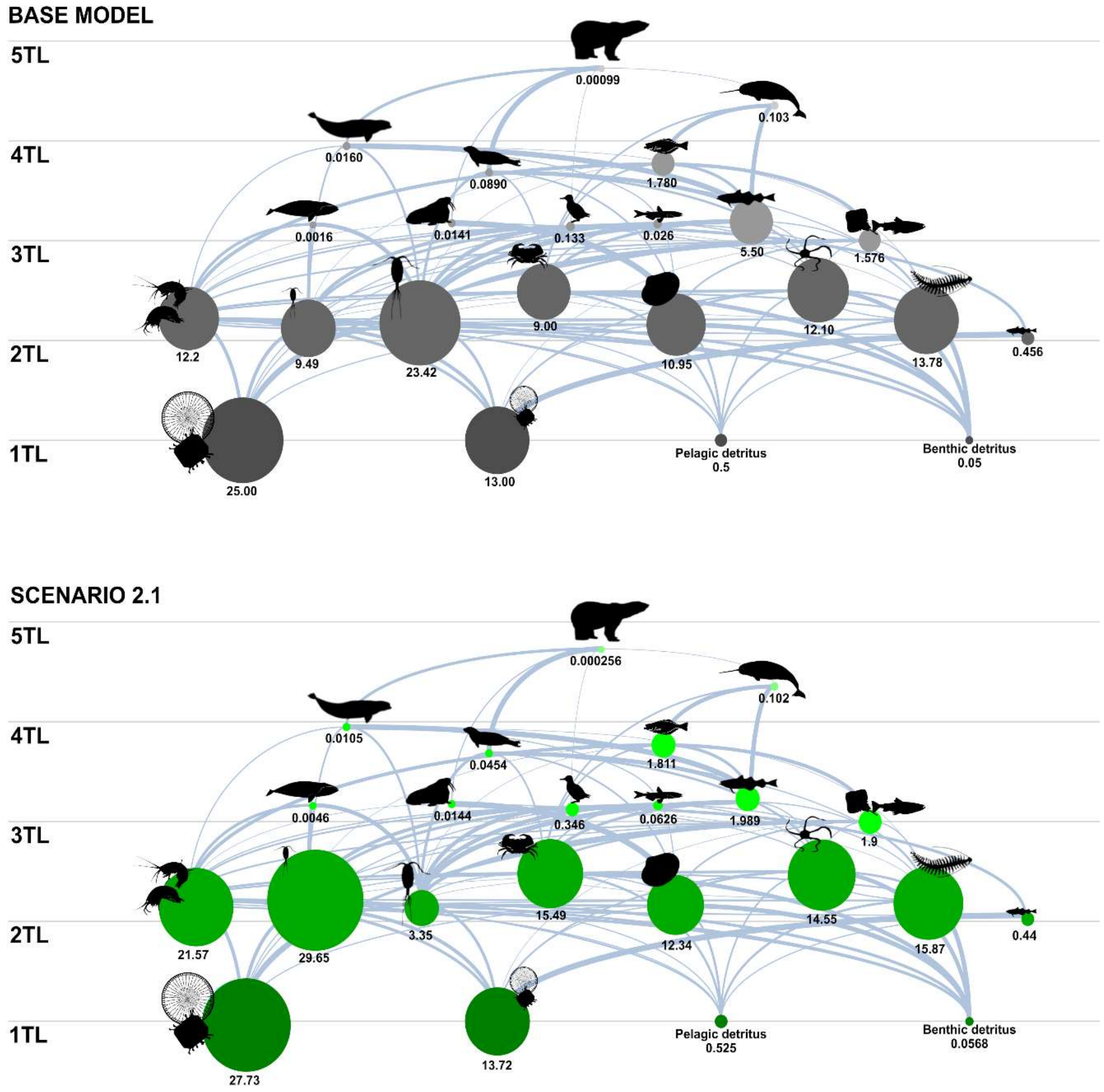


Figure 5.3. Ecopath base model flow diagram (upper panel), Ecosim flow diagram Scenario 2.1 (lower panel). The size of circles is proportional to the amount of biomass. Numbers below circles represent the biomass of the functional group in t km^2. TL = trophic level. Direction of energy flow is represented by position of line with relation to circle: flows positioned on the top of a trophic group indicate biomass outgoing, while flows positioned on the side indicate entering biomass. The weight of the line indicates the amount of energy flowing between nodes. Narwhal (*Monodon monoceros*) icon created by authors, all other icons are public domain silhouette images by Tracy Heath (*Ursus maritimus*), Margot Michaud (*Odobenus rosmarus*) and others, via PhyloPic (www.phylopic.org).

Table 5.3. Direction of biomass change by functional groups for each North Water Polynya Ecosim scenario. Blue shading indicates biomass increases; red shading biomass decreases. Grey shading are functional groups that were modified as input for a given scenario. One arrow: < 20% change; two arrows: 20-40% change; three arrows: > 40% change; / = functional group is not part of the scenario. TL = Trophic level. Lg = Large; Sm = Small; Med = Medium.

Functional group		**TL**	**Direction of biomass change by scenario**					
			1.1	***1.2***	***2.1***	***2.2***	***3***	***4***
1	Killer whale	4.77	/	/	/	/	/	↑↑↑
2	Polar bear	4.73	↑↑	↓↓↓	↓↓↓	↓↓	↓↓	↓↓
3	Bowhead whale	3.16	↑	↓↓	↑↑↑	↓↓	↑	↑↑↑
4	Beluga	3.95	↑↑	↓↓	↓↓	↓↓	↓↓	↓↓
5	Narwhal	4.35	↑	↓	↓	↓	↓	↓↓
6	Walrus	3.18	↑	↓↓	↑	↑	↓	↓
7	Ringed seal	3.68	↑↑	↓↓	↓↓↓	↓	↓	↓↓
8	Little auk	3.14	↑	↓↓	↑↑↑	↓↓	↑	↑
9	Greenland halibut	3.77	↑↑	↓↓	↑	↓	↓	↓
10	Capelin	3.17	↑	↓	↑↑↑	↓	↑↑	↑↑
11	Arctic cod (Age 1+)	3.20	↑	↓↓	↓↓↓	↓	↓	↓
12	Other fish	3.00	↓	↓	↑↑	↑	↑↑	↑
13	Arthropods	2.48	↑	↓	↑↑↑	↑	↑	↑
14	Bivalves	2.16	↑	↓	↑	↑	↓	↓
15	Echinoderms	2.50	↑	↓	↑↑	↑	↓	↓
16	Worms	2.21	↑	↓	↑	↑	↓	↓
17	Lg copepods	2.17	↑	↓	↓↓↓	↓	↑	↑
18	Med copepods	2.12	↑	↓	↑↑↑	↓	↓	↓
19	Arctic cod (Age 0)	2.06	↑	↓	↓	↑	↑	↑
20	Other meso-zooplankton	2.22	↑	↓	↑↑↑	↑	↓	↓
21	Lg pel. producers	1.00	↑	↓	↑	↑	↓	↓
22	Sm pel. producers	1.00	↑	↓	↑	↑	↑	↑
23	Pelagic detritus	1.00	↑	↓	↓	↑	↓	↓
24	Benthic detritus	1.00	↑	↓	↓	↑	↑	↑

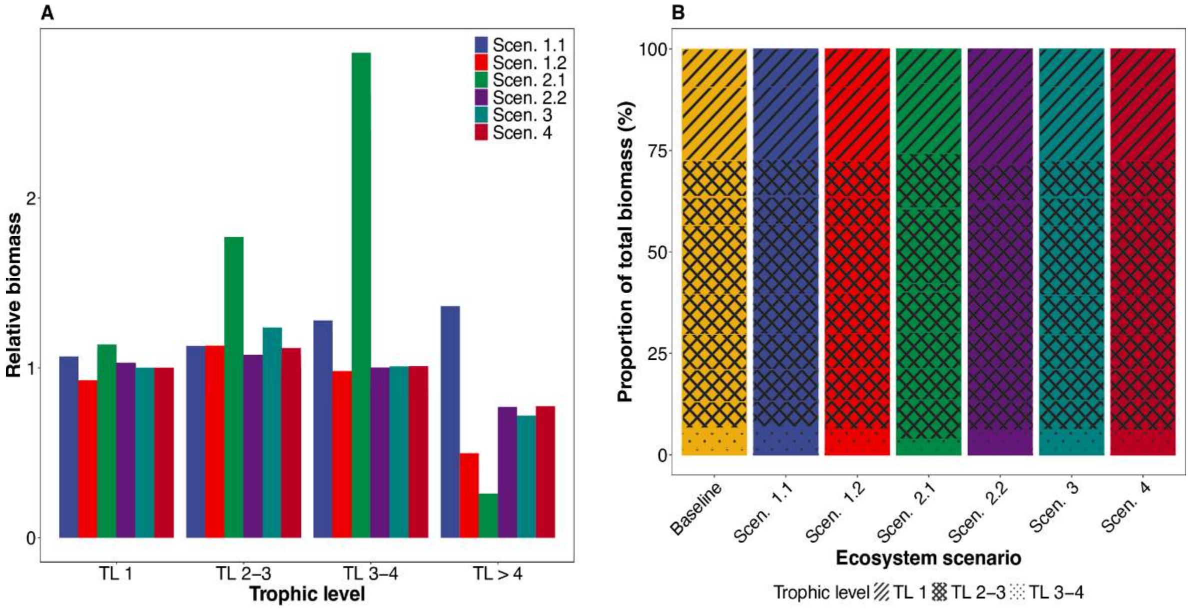


Figure 5.4. Biomass of trophic groups in the base ecosystem model and Ecosim scenarios by trophic level in the North Water Polynya ecosystem. (A) Biomass changes relative to the base ecosystem scenario. (B) Biomass proportion relative to the total biomass in the ecosystem. The different colors match the colors in (A); the shading represents the different trophic groups. Proportion of TL > 4 is < 0.005 in the base ecosystem and across Ecosim scenarios; hence not visible in panel (B). See biomass proportion relative to the total biomass for TL > 4 in S5.16 Fig.

5.5 Discussion

Climate change is rapidly altering species distributions, which could have profound implications for the structure and function of ecosystems. Whilst the potential for future changes in species distributions has been extensively explored, largely using correlative models (Cheung et al., 2010; Cheung et al., 2009), we currently lack a framework to assess the impact of range shifting species on recipient communities and the subsequent disruptions to the ecosystem. Here, by combining two modeling frameworks, SDMs and ecosystem modeling, we explored the emergence of novel ecosystems in the NOW Polynya considering both climatic and ecosystem impacts.

5.5.1 Trophic flows

The NOW Polynya supports a high benthic biomass due to strong benthic-pelagic coupling (Grebmeier & Barry, 2007). One of the main underlying processes for this pattern is the high primary productivity despite the lower average transfer efficiency of 9.17% in the NOW polynya compared to other ecosystems in the region, such as Western Baffin and Western Greenland (Bryndum-Buchholz et al., 2024; Klein et al., 2002). The spring bloom allows sufficient new production to reach the seabed and support the benthic community (Grebmeier

& Barry, 2007). This pattern is also supported by our analysis, where the benthic invertebrate groups have relatively high consumption rate on prey from the pelagic domain.

Climate change is expected to increasingly affect benthic-pelagic coupling, for example, via (i) phenological shifts leading to trophic mismatches due to reduced sea ice as a result of increasing water temperatures, (ii) poleward shifts of pelagic and demersal species, (iii) and changing stratification patterns due to increasing storminess, vertical mixing, and changes in freshwater influx (Baustian et al., 2014; Farmer et al., 2021; Grebmeier et al., 2006, 2010; Hordoir et al., 2022). These mechanisms can manifest in changes in trophic interactions within an ecosystem. Scenario 2.2 explored the potential of such a trophic mismatch, whereby the phytoplankton blooms avoid substantial copepod grazing, reducing copepod biomass. The reduced grazing pressure by the copepod community benefits the benthic invertebrate community, as the phytoplankton carbon supply to the benthic zone from the surface increases.

The opposite can occur if the phytoplankton biomass decreases, as explored in Scenario 1.2, due to increasing stratification caused by increasing water temperatures and freshening (Buchart et al., 2022; Noh et al., 2023), reducing biomass across functional groups in the ecosystem. These responses have already been observed in other Arctic regions, such as the Chukchi Sea (Jay et al., 2012; Moore et al., 2003). Moore et al. (2003) showed that a decline in benthic prey, due to a reduction in phytoplankton carbon supply from surface waters, caused apex predators dependent on benthic prey (such as gray whales, *Eschrichtius robustus*) to shift their foraging ranges northward (Moore et al., 2003). Years with reduced sea ice in the Chukchi Sea caused Pacific walrus (*Odobenus rosmarus*) to arrive earlier, stay longer and concentrate their foraging efforts in nearshore areas rather than offshore waters (Jay et al., 2012). While our framework did not resolve movements due to changes in food supply specifically, we illustrated biomass change within a specific system, which could also reflect distribution shifts away from the study region.

5.5.2 Effects of changing copepod size-structure

The larger ecosystem impact of changing size-structure (Scenario 2.1) compared to changing overall biomass of copepods suggests a strong reliance of higher trophic levels on larger, lipid-rich copepods. Indeed, large, diapausing copepods are a crucial food source for fish and some Arctic whales (Cronin et al., 2017), especially for bowhead whales (Laidre et al., 2007). They are larger targets for visual foragers and richer in lipids, and so provide a higher energy intake per calorie spent searching and handling prey by consumers (McGinty et al., 2021). Large copepods in the Arctic depend on sea-ice or deep sea habitats to survive, which reflects their dependence on local food availability, temperature refugia, and refugia from visual predators (Fortier et al., 2001). With climate change driving sea-ice melt and retreat, larger zooplankton species are already declining in some regions of the Arctic (Møller & Nielsen, 2020). Our results support previous evidence that large copepods are an important trophic link in Arctic marine ecosystems (Langbehn et al., 2023; Record et al., 2018), and implies climate change could strongly disrupt Arctic ecosystems by reducing trophic transfer efficiency, if smaller, less fat copepods replace their larger congenerics. For example, in the Labrador Sea, capelin body size and condition have declined over 40 years (Renkawitz et al., 2015) in response to a decline in large zooplankton (Mills et al., 2013), as capelin grow faster when feeding on larger *Calanus* species (Hedeholm et al., 2010). Similar effects have also been predicted for little auk (Stempniewicz et al., 2007). Moreover, because of the variation in life histories and cycles (e.g., diapause timing, generation time, and breeding type) of large compared to smaller copepods, climate-driven shifts in the size-structure can also affect the timing of energy transfer to higher trophic levels (Møller & Nielsen, 2020). In Disko Bay, Greenland, longer open water periods resulted in *Calanus glacialis* changing from a biennial to an annual life cycle as a result of a change in available lipids. Sea-ice cover is expected to decline further with climate change in the NOW polynya (Buchart et al., 2022). As a result, reduced reproductive success and condition of predators is likely due to changes in their copepod prey, with potential ecological consequences.

5.5.3 Effects of changing forage fish biomass

The projected increases in habitat suitability for capelin and the subsequent declines for Arctic cod replicate empirical data indicating a shifting prey base in the Arctic (Marsh & Mueter, 2020; Ulrich & Tallman, 2021). However, the effect of changes in forage fish biomass (as a prey base) on higher trophic levels was not as strong as expected. The sensitivity analysis emphasized the role of Arctic cod (Age 1+) as a key prey species for predators such as ringed seals, beluga and narwhal. The decrease in beluga biomass could reflect reduced energy transfer and nutrition as a result of fewer Arctic cod (Age 1+) in their diet (Geoffroy et al., 2023). This suggests the increasing abundance of a boreal species such as capelin may not substitute losses of Arctic cod in high-Arctic ecosystems. Indeed, the maximum lipid content of capelin is almost three times lower than Arctic cod (Hop & Gjøsæter, 2013). Seabirds can shift their diet depending on local abundance of fish, but when, for example, Brunnich's guillemot switched to capelin, the growth rate of nestlings declined (Gaston et al., 2005).

Generally, Arctic cod and capelin are significant consumers of zooplankton in marine ecosystems (Hop et al., 2013; Maes et al. 2022) (S5.2 Table), indicating a potential increase of resource competition between these two species in the future. However, the diet of Arctic cod differs with their size (Majewski et al., 2016), hence prey competition may differ as well (Geoffroy et al., 2023). As seen in the diet matrix (S5.2 Table), immature and adult Arctic cod show a broader prey spectrum compared to more juvenile stages (Geoffroy et al., 2023; Hope et al., 2013; Maes et al., 2022); amphipods and copepods represent the largest fraction in their diet across age and sizes (Geoffroy et al. 2023; Majewski et al. 2016). Notably, krill is preyed upon by both Arctic cod and capelin; however, the contribution to the prey field is larger for capelin compared to Arctic cod (Hop et al., 2013), suggesting that competition between capelin and Arctic cod may be limited. This species-specific differentiation across the prey field for capelin and Arctic cod was not captured in our model.

5.5.4 Cumulative impacts of changes in prey base and increasing biomass of apex predator

Our SDMs did not project any substantial increases in habitat suitability for killer whales in the NOW polynya by 2050 or 2100. Killer whale movements in the Arctic are likely more dependent on the open-water season and so may not be distributed in the Arctic year-round (Matthews et al., 2021). As the SDMs did not distinguish summer vs. winter distributions of species, they may not have captured the full extent of killer whale occurrences and movements with climate change. Also, it is important to note that high or low climate suitability does not necessarily mean high or low abundance, especially for populations that change rapidly. SDM simulations suggested that all regions of the NOW are currently suitable for killer whale populations, which supported Scenario 4 of our analysis to explore the impacts of the addition of an apex predator to the NOW Polynya ecosystem.

The frequency of killer whale sightings in the NOW has increased since the 1950s (Higdon et al., 2012, 2013), and the increasing ice-free, open waters in the Arctic have provided killer whales with better, more prolonged access to the high Arctic (Higdon & Ferguson, 2009). As such, we would expect the direct consumption of Arctic marine mammals to rise (Breed, 2021; Lefort et al., 2020). Our simulations supported this, showing biomass decreases in the main prey species of killer whales: narwhals, beluga and ringed seals, and also in its main competitor, the polar bear. Killer whales will not only directly affect prey abundances but could also disrupt prey behaviour and ultimately their distributions (Breed, 2021; Garroway et al., 2023). These results suggest the addition of a key apex predator such as killer whales to the NOW Polynya ecosystem could have cascading ecosystem effects.

Further, in Scenario 4, bowhead whales responded with a large biomass increase, possibly due to a release of resource competition, as ringed seals and beluga decrease, which outweighed any increased predation by killer whales on bowhead whales. Killer whale predation was considered to be low in the model, reflecting the uncertainty of their predation effects on bowhead population sizes, distributions or habitat selection (Breed, 2021). Predation of bowhead whales might increase due to longer ice-free periods which provide killer whales better access (Breed, 2021). Despite this, other studies found killer whales did not have specialized diet preferences for bowhead whales (instead feeding mainly on narwhals and beluga) (Remili et al., 2023), and their feeding habits on bowhead whales can vary seasonally and regionally depending on population (Ferguson et al., 2012). The specific feeding preferences of killer whale populations in the NOW Polynya remain unknown, and any potential changes to killer whale predation on bowhead whales are not reflected in the model, but could be integrated by manipulating consumption rates of killer whales in separate scenarios, which goes beyond the present study.

5.5.5 Using SDMs to inform ecosystem scenarios

In this study, we present a new method using both SDMs and food-web models to explore potential future changes to an Arctic ecosystem with climate change. Since ecosystem models act as a ‘snapshot’ in time and space, we were able to use the results of SDMs to inform novel ecosystem scenarios for the NOW Polynya. Most attempts to date have used food-web models to improve outputs of SDMs which do not account for species interactions (Albouy et al., 2014; Pellissier et al., 2013). Previous studies have not used the output of SDMs to alter food webs created by Ecopath (but see Albouy et al. (2014)). Our modeling approach allows us to determine the implications of introducing or increasing southern species to Arctic ecosystems by analyzing the changing feeding links, biomass and energy transfer between species in an ecosystem. Further studies can build on this novel approach and answer questions about the consequences of climate-driven changes to species distributions for food-web structure and function. Our approach may also allow the testing of impacts of local species extinctions on ecosystems. A next step could be to integrate other human stressors such as fisheries which may spread and develop in the high Arctic as previously unreachable seas become available for human extraction.

The framework we developed is not limited to the NOW Polynya and could be applied across other ecosystems in both marine and terrestrial realms. Our approach applied climate change scenarios to a time static model with a defined change in biomass values. Another approach could use time dynamic projections with different climate change scenarios to run scenarios. These are not yet available, however time-series for functional groups are currently increasing due to increasing sampling efforts and collaborations with Indigenous Knowledge holders (Jennings et al., 2023). In addition, regional climate forcings for the NOW region have not yet been developed. Downscaling of global climate forcings is possible, but there are large uncertainties, especially in sea-ice systems (Lafferty & Sriver, 2023; Mason et al., in review). One avenue for future work to overcome the lack of data for ecosystem models would be directly modeling species abundances in addition to species distributions. Then, information on projected species abundances could be used to infer biomass values for future scenarios of the NOW Polynya ecosystem.

The approach we developed here is not without its limitations. Marine SDMs are particularly hindered by a lack of full coverage of survey data, and still much is unknown with respect to the distributions of marine species. However, continuing survey efforts and increasing empirical data are expected to improve species distribution data over time. In addition, indirect effects of temperature changes, such as changes in biotic interactions and population dynamics, cannot be captured using SDMs (Heikkinen et al., 2006). Our approach also does not account for the timing of species distribution shifts and the model results are only a snapshot in time. As such, SDM results should always be treated with caution. Despite this, we argue they can be viewed as a complementary tool to explore the potential impacts of climate-driven range shifts on an Arctic marine ecosystem. Modelled species ranges can be refined and validated as more empirical data becomes available.

5.5.6 Conclusion

We present a novel framework for exploring the impacts of climate-driven range shifts on the NOW polynya food web, and which could be applied across other ecosystems in both marine and terrestrial realms. We further demonstrate the applicability of integrating SDM and ecosystem modelling methods in new and unexplored ways. We highlight key benthic-pelagic couplers in the food web, with Arctic cod (Age 1+) and walrus standing out. Moreover, across all novel ecosystem scenarios, we demonstrate that changes in the copepod size structure had the largest impact on the entire food web, suggesting a strong reliance of higher trophic levels on larger, lipid-rich copepods. Further, shifts in forage fish abundance had the largest effect on marine mammals in the food web. Finally, the addition of a key apex predator such as killer whales to the NOW polynya food web could have cascading effects on an Arctic ecosystem. We hope our method can be adopted and built on to explore the potential emergence of novel ecosystems with future climate change in the Arctic and beyond.

Chapter 6

Impacts of climate-driven range shifts on provisioning services in the Arctic

6.1 Abstract

Climate change is driving a redistribution of Arctic species and will change ecosystems in unprecedented ways. The reshuffling of terrestrial and marine Arctic communities will impact the people reliant upon the functioning of these ecosystems for income and fundamental services. Yet, to date, studies that explore the impacts of climate-driven range shifts on provisioning ecosystem services, and hence the direct impact on human society, are rare. In this chapter, I use species distribution models (SDMs) to provide a detailed account of how species richness (SR) of terrestrial and marine species that are used and/or traded by humans will change in the Arctic with climate change. The two focal terrestrial taxa (birds and mammals) show strong future declines of traded species for much of Arctic Europe, Canada and Alaska, though with increases in traded species projected across much of Russia. Used/traded terrestrial SR is already low in Greenland but, by 2080, nearly all used/traded mammals and birds are projected to disappear. Both the largest gains and losses in used/traded fish SR are projected for continental shelf areas off Norway, the Faroe Islands and the Denmark Strait, indicating high species turnover. Many novel colonisations of internationally traded species are projected for all Arctic countries, which could cause conflicts over the governance of resources between Arctic nations. The movement of such species, especially fish, could impede national adaptations to climate change. SR changes of used/traded marine mammals were far smaller, though even small changes could have profound implications for Arctic communities. By 2100, losses are projected for key used/traded marine mammals that provide traditional food and clothing to Arctic communities. Ultimately, the losses and gains of traded species in the Arctic will affect food security, with implications for the Arctic economy, livelihoods and societies. New policy solutions will be necessary to allow for adaptation to the consequences of range-shifting species.

6.2 Introduction

The redistribution of Arctic species under climate warming will change ecosystems in unprecedented and uncertain ways (Bonebrake et al., 2018; Pecl et al., 2017; Poloczanska et al., 2016). Such changes are expected to have profound consequences on fundamental aspects of the socio-ecological system, which is becoming ever more dynamic (Solan et al. 2020). These changes will impact Arctic inhabitants, but also human populations globally, as the Arctic is intimately connected to global ecological, geophysical and geopolitical processes (Arctic Council 2016; Haldén 2018). This will pose both economic and environmental challenges to the region’s governance, if sustainable human-environment relationships are to be maintained (Young 2010). Thus, it is important for research to link environmental change to the impacts of this change on ecosystem services.

The notion of ecosystem services, referring to the benefits that nature provides to human societies (Millennium Ecosystem Assessment, 2005), provides a platform for investigating the impacts of ecological change in the Arctic (Malinauskaite et al. 2019). For example, a novel threat might be that temperate, southern colonists displace Arctic species of ecological and/or economic importance. Terrestrial and marine ecosystems will face likely changes in the abundance and distribution of species that are currently used or traded by people. This, combined with novel colonists could, on balance, alter aggregate economic income from such traded species (Ojea et al., 2020; Pinsky et al., 2018). Shifts in target species could directly affect catches or harvest of marine and terrestrial species (Pinsky et al., 2020). This could be particularly important for local subsistence harvesting and small-scale fisheries (Cinner et al., 2018), which are often dependent on local populations and resource availability (Ojea et al., 2020). On the other hand, incoming species may provide new opportunities. For example, climate-driven range shifts in the commercially important fish *Scomber scombrus* (mackerel), resulted in the establishment of a new fishery in the Iceland exclusive economic zone (EEZ). At the same time, these shifts in mackerel created conflicts between neighbouring nations (Spijkers & Boonstra, 2017), highlighting the additional governance issues and management challenges that can arise when commercial species shift across political boundaries and international borders (Pinsky et al., 2018; Spijkers & Boonstra, 2017; Titley et al., 2021).

Given the above, assessments of changing species’ distributions that can shed light on altered ecosystem service provisioning will be especially valuable. To date, few studies have assessed the community and ecosystem impacts of species' range changes at high latitudes. Even fewer have evaluated ecosystem services changes in an Arctic context (Malinauskaite et al. 2019). There are now recommendations for new research to assess the costs and benefits to community structure and ecosystem services of both areas of species loss and gain (Balvanera et al., 2014). Those assessments can then be used to develop policy and conservation strategies.

The aim of this chapter is to provide a comprehensive evaluation of projected climate change impacts on provisioning services in the Arctic, looking at both local and regional taxonomic richness changes of terrestrial birds and mammals, and marine fish and mammals. I use species' 'use and trade' information provided by the IUCN Red List to identify terrestrial and marine species that are important for providing provisioning services to people in the Arctic. Firstly, I assess, at a circa 50km resolution, patterns of current species richness (SR) of important trade species in the Arctic and how this is projected to change by 2100. Secondly, I assess the consequences of the gains and losses of traded marine and terrestrial species for provisioning services in the eight regions forming the Arctic, and identify the associated scale (subsistence or local, national, international) at which each species is used or traded.

6.3 Methods

6.3.1 Species occurrence data

Species occurrence data were as described in Chapters 2, 3 and 4 for terrestrial birds and mammals, marine fish, and marine mammals respectively.

6.3.2 Environmental data

Environmental data for terrestrial and marine analyses were as described in Chapter 2 and Chapter 3 respectively. Unlike the terrestrial analyses in Chapter 2, in this chapter I used future climate data for only one future scenario, a medium-high emissions scenario, SSP3.70. This scenario was used as the scenario from CMIP6 that most closely corresponded to temperature changes for RCP6.0 from CMIP5 used in the marine models. It is also important to note at the outset that the future projection window for terrestrial data was 2060-2080 (referred to as 2080 hereafter) but the future year for marine data was 2090-2100 (referred to as 2100 hereafter). This difference arose from the need to use different online data sources at the time (in 2022) for the marine versus terrestrial realms.

6.3.3 Species distribution models

Species distribution modelling (SDM) methods for terrestrial species were as described in Chapter 2. Presence-only SDM methods for marine species were as described in Chapter 3.

6.3.4 Use and trade

Information on the end use of global terrestrial birds and mammals and marine fish and mammals harvested from the wild was compiled using the IUCN Red List (IUCN, 2024). Species lists from Chapter 2, 3 and 4 were used to query the IUCN Red List and download information on the 'end use' of harvested species (Table 4.1). This included information on the use and trade (Table 4.1) and also the associated scale for each end use (Table 4.2). The global use and trade dataset across the entire globe consisted of a total of 7,307 traded species, consisting of 1,705 birds, 277 mammals, 5,256 fish and 69 marine mammals. Only a subset of these species, those currently occurring and/or projected to occur in future in the Arctic (in this chapter I consider all areas above 60° North), were used in the analyses in this chapter. This subset totalled: 808 birds, 137 mammals, 1020 fish, and 45 marine mammals. Species' use and trade data were not distinguished to the location at which a species is traded – hence here I assume a species has the potential to be traded in a location if it occurs within that region.

Table 6.1. Use and Trade classifications and their description. Adapted from the General Use and Trade Classification Scheme (IUCN, 2020).

End use	Abbreviation	Description	Examples
Food - human	Food	Species used as food or drinks for human consumption	Shark fins for human food; deer (or venison) for human food
Food - animal	Feed	Species used as food/feed for animals	Herring or anchovies used in fishmeal to feed farmed fish
Medicine - human & veterinary	Med	Species used as materials to treat or prevent illness or injury	Bear bile used to treat liver disease; tiger bone used to treat chronic pain
Wearing apparel, accessories	Wear	Species used to make clothes, bags, shoes, belts etc.	Buffalo used for leather; pigskin used for wallets; mink and fox furs used for coats and hats

Handicrafts, jewellery, etc.	Craft	Species used to make goods with a primary decorative/ornamental function.	Reindeer antlers, whale bones, bird feathers
Pets/display animals, horticulture	Pet	Species used for pets and/or display animals (e.g. in zoos)	Finches, songbirds
Sport hunting/specimen collection	Sport	Includes collections and preservation of dead specimens for personal pleasure	

Table 6.2. Scales of use and trade and their description. Adapted from the General Use and Trade Classification Scheme (IUCN, 2020).

Scale	Description
Subsistence	Harvesters make use of the species or product themselves locally. Reliance on species for local livelihoods. Also includes the commercial use of a product at the local level and generates income for local livelihoods.
National	Species are used or sold commercially at the national level – within the same country but away from where the species was harvested.
International	Species are used or sold commercially at the international level – outside the country it was harvested in.

6.3.5 Richness changes of traded species

Thresholding was used to convert simulated suitability output from SDMs into modelled species occurrences, which, in turn, were used to calculate current SR, changes in SR between the current and future periods, proportional changes in SR over that period, and SR losses and gains. These variables were calculated per 0.5 x 0.5° grid cell, for all cells above 60° North, and per Arctic region. Arctic regions were defined as the eight Arctic countries, Canada, Alaska (United States), Greenland (Denmark), Iceland, Norway, Sweden, Finland and Russia. For marine species, richness changes were calculated for each marine exclusive economic zone (EEZ) corresponding to each Arctic country (https://marineregions.org/downloads.php; Flanders Marine Institute, 2020). The Faroe Islands EEZ were classed as Greenland (for Denmark) and the Svalbard EEZ and Jan Mayen EEZ were classed as Norway. The non-Arctic components of countries and EEZs that fall below 60° North (non-Arctic Denmark and rest of United States) were excluded from each region. As such, SR variables were only calculated for those portions of the countries that are above 60° North. Each component of SR change was calculated using only the occurrences that overlapped with each Arctic region. The specific trade/use and scale of use of species gains and losses per Arctic region were then summarised, by splitting species gain and losses into their use and trade (see Table 6.1) and its associated scale (see Table 6.2).

6.4 Results

Species level changes in range size of traded species varied across the four taxa. 45% of all birds (n = 794 spp) that currently (2000-2014) occur in at least one grid-cell above 60° North are projected to have no suitable habitat or climate in 2080. Most of the birds with no suitable climate in 2080 occur close to the 60° North line. 18% of birds (144 of 808) were projected to expand their ranges (by at least one grid cell), and of these, 14 species do not currently occur in the Arctic. 15 traded birds are novel to the entire Arctic region in 2080. Strikingly, 70% of the mammals currently occurring above 60° North (n = 137) are projected to have no suitable co-occurring habitat and climate in 2070.The European hare (*Lepus europaeus*) is the only mammal species projected to expand its range by 2080. In 2080, there are no new traded mammal species in the Arctic region. 77% (n = 1,020 spp) of marine fish are projected to expand their ranges by at least 1% by 2100. Only 5% of fish species have no suitable climate in 2100. 217 fish not currently present above 60° North are projected to newly colonise the Arctic region. Most marine mammals are projected to expand their ranges by 2100, with only 13 species (of 45) projected to contract their range. The species with the largest projected future range contractions are the hooded seal (*Cystophora cristata*; 60% range decline), found in central and western North Atlantic, and the harp seal (*Pagophilus groenlandicus*; 45% decline), native to much of the Northern Atlantic and Arctic oceans. Only one traded marine mammal (*Monachus monachus*) is new to the region above 60° North.

6.4.1 Spatial changes in traded species richness

Spatial patterns in the net changes in traded species richness varied across the two terrestrial and two marine taxa (Figure 6.1). The largest net losses in SR, of both traded birds and mammals, occur across Alaska and Europe (Figures 6.1a & b), and is largely coincident with current areas of high species richness. The net losses are more notable for birds than mammals, with larger areas of Alaska and Canada losing over 50% of species. Much of Greenland is projected to lose all of its traded/used terrestrial birds and mammals. Elsewhere, net gains of traded bird species (up to 49 species) are projected in a band across the middle latitudes of Russia (Figure 6.1a). By contrast, far fewer areas are projected net gains in traded mammal species; such gains only occur in parts of Russia and in Nunavut, Canada (Figure 6.1b). The highest SR of traded fish currently occurs around the continental shelf off Norway and the Gulf of Alaska (left panel in Figure 6.1c). The most notable net gains in traded SR are projected for the continental shelf off Norway, the Barents Sea and the Bering Sea (right panel in Figure 6.1c). Net losses in SR of traded fish are projected in and south of the Denmark strait between Greenland and Norway, and in the Beaufort Sea. Hotspots of traded marine mammal SR currently occur in the Barents Sea, Bering Sea, Baffin Bay and Denmark Strait (left panel in Figure 6.1d). The largest net losses in absolute SR of marine mammals are projected in the Greenland Sea, around Jan Mayen and the Norwegian Sea, while smaller net losses are projected in the waters above Russia, Alaska and Canada (right panel in Figure 6.1d). Net gains in marine mammal SR are projected throughout Nunavut waters, the Arctic Ocean and the Bering Sea. Relative change of marine mammal species richness is projected to be negative across much of the study region, with only some areas of the Arctic Ocean and Nunavut showing positive changes (Figure S6.1).

6.4.2 Spatial changes in the gains and losses of traded species

The richness of traded species in the two terrestrial taxa is projected to substantially decline for much of Europe, Russia and Alaska, while the greatest increases in traded terrestrial species are projected for most of Russia (Figures 6.2a & b). In addition, there are also large increases in traded birds for much of Europe (Figure 6.2a). Interestingly, both the largest gains and losses in fish SR are projected across the continental shelf area off Norway, the Faroe Islands and the Denmark Strait, indicating areas of high species turnover (Figure 6.2c). The areas of species losses and gains differ for marine mammals compared to fish, whereby the largest losses of marine mammals are projected for the continental shelf north of Norway and Finland (south Barents Sea) and areas of Baffin Bay and the southwestern Greenland coast (right panel in Figure 6.2d). The largest gains of marine mammals are projected around Svalbard, Franz Josef Land in the north of the Barents Sea, Bering Sea and much of Nunavut (right panel in Figure 6.2d).

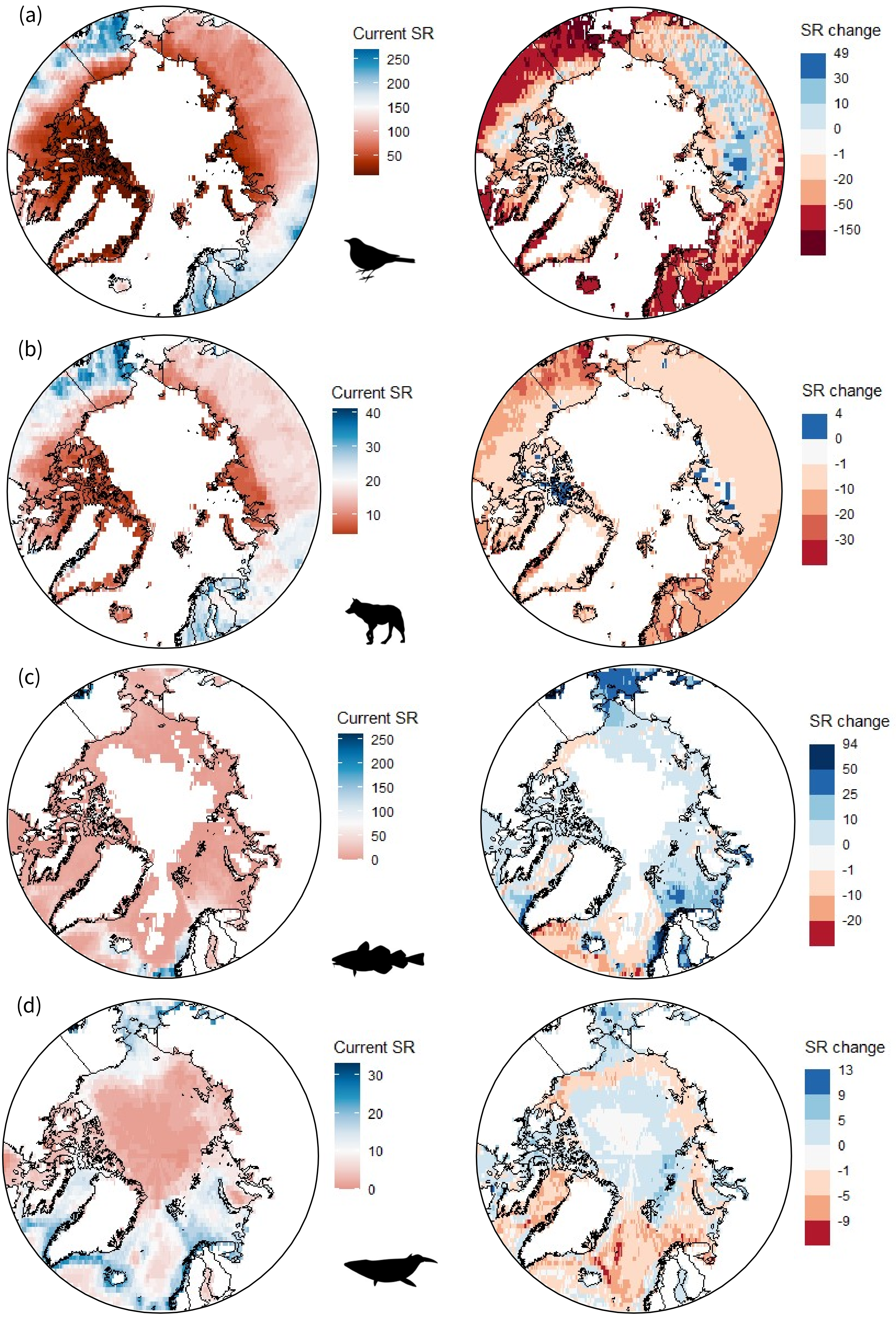

(a)
Current SR
250
200
150
100
50
SR change
49
30
10
0
-1
-20
-50
-150
(b)
Current SR
40
30
20
10
SR change
4
0
-1
-10
-20
-30
(c)
Current SR
250
200
150
100
50
0
SR change
94
50
25
10
0
-1
-10
-20
(d)
Current SR
30
20
10
0
SR change
13
9
5
0
-1
-5
-9

Figure 6.1. Simulated current richness (left) and absolute changes in richness (right) for important trade species of two terrestrial (birds and mammals) and two marine (fish and mammals) taxa (a-d) in the Arctic. Future changes are projected to 2080 under SSP3.70 for terrestrial taxa and 2100 under RCP6.0 for marine taxa.

6.4.3 Changes in trade type and scale by Arctic region

Most notably, none of the birds that are lost or gained in the future are used internationally, regardless of end use (Figure 6.3a). The majority of bird species projected to be lost from the Arctic are currently used as food for humans or for sport, particularly in Alaska, Canada and Greenland. Bird species lost include from the *Phasianidae* family (pheasants and partridges), garganey (*Spatula querquedula*), duck species (*Mareca strepera*) and waders (Whimbrel (*Numenius phaeopus*), Pin-tailed Snipe (*Gallinago stenura*), sandpipers (*Tringa* spp.)). Bird species gains do not outweigh the provisioning services lost in 2080.

There are large projected future losses of mammals used for food at a subsistence and/or national level in Alaska, Canada and Greenland. Important food species lost include caribou or reindeer (*Rangifer tarandus*), moose (*Alces alces*) and bison (*Bison bison*). Regardless of the trade or use, the richness of species gained does not compensate for those projected to be lost by 2080 (Figure 6.3b). The largest impact on terrestrial mammal trade is expected in Iceland, which is projected to lose traded species but to gain no new tradeable species. The mammals projected to be lost from Norway are currently used for handicrafts (such as hare species, bison and reindeer), food (such as reindeer, squirrels and wild boar) and medicine (brown bear (*Ursus arctos*), edible dormouse (*Glis glis*)) at international and national levels. Some regions, such as Alaska, Canada and Russia, generally gain mammals that are eaten by humans, both for subsistence and for national/international trade. Across all regions, for all traded products besides food for humans, SR losses are larger than SR gains across most scales of trade. This is particularly true for species of national and/or subsistence use value (Figure 6.3b).

A prominent pattern in the changing SR of fish in the Arctic is the substantial gains in potential fish important for human consumption. This is particularly the case in the waters of Norway, Iceland and Greenland (Figure 6.4a), for example gaining fish from the *Acipenseridae* family (Sturgeons), *Sciaenidae* family (croakers such as White seabass (*Atractoscion nobilis*)), red mullet (*Mullus barbatus*) and *Sparidae* family (seabreams). All regions also lose valuable fish harvested for human consumption, which are utilised at local, national and international levels. All Arctic regions lose all species used as feed from all areas, particularly those traded internationally and globally (Figure 6.4a). Colonisation by sports fish is projected in all regions, particularly Norway and Iceland, and most of these colonising species are important for small-scale fishing. Novel sports fish projected to colonise some Arctic regions include shark species (such as Smooth-hound (*Mustelus mustelus*)), croakers, seabreams, fish from the *Carangidae* family (mackerel scads), seabasses (Kelp bass (*Paralabrax clathratus*)), and white trevally (*Pseudocaranx dentex*). Furthermore, a similar number of fished species are also lost from Norway and Iceland, and fished locally, nationally and internationally. All regions are projected to gain species important in the pet trade, especially Norway, Greenland, Iceland and Russia, and a large proportion are internationally valuable (Figure 6.4a).

Marine mammal losses are heavily dominated by species used at a subsistence and/or national scales across all trade/use and regions (Figure 6.4b). Some of the marine mammals lost that are currently subsistence hunted include walrus (*Odobenus rosmarus*), harp seal (*Pagophilus groenlandicus*) and ringed seal (*Pusa hispida*). Finland has the most notable losses and gains of potential species used for food both locally and nationally, indicating high turnover. All regions lose species used for clothing and apparel (seal species), and only in Alaska is there one new species that could potentially be used for apparel (Figure 6.4b).

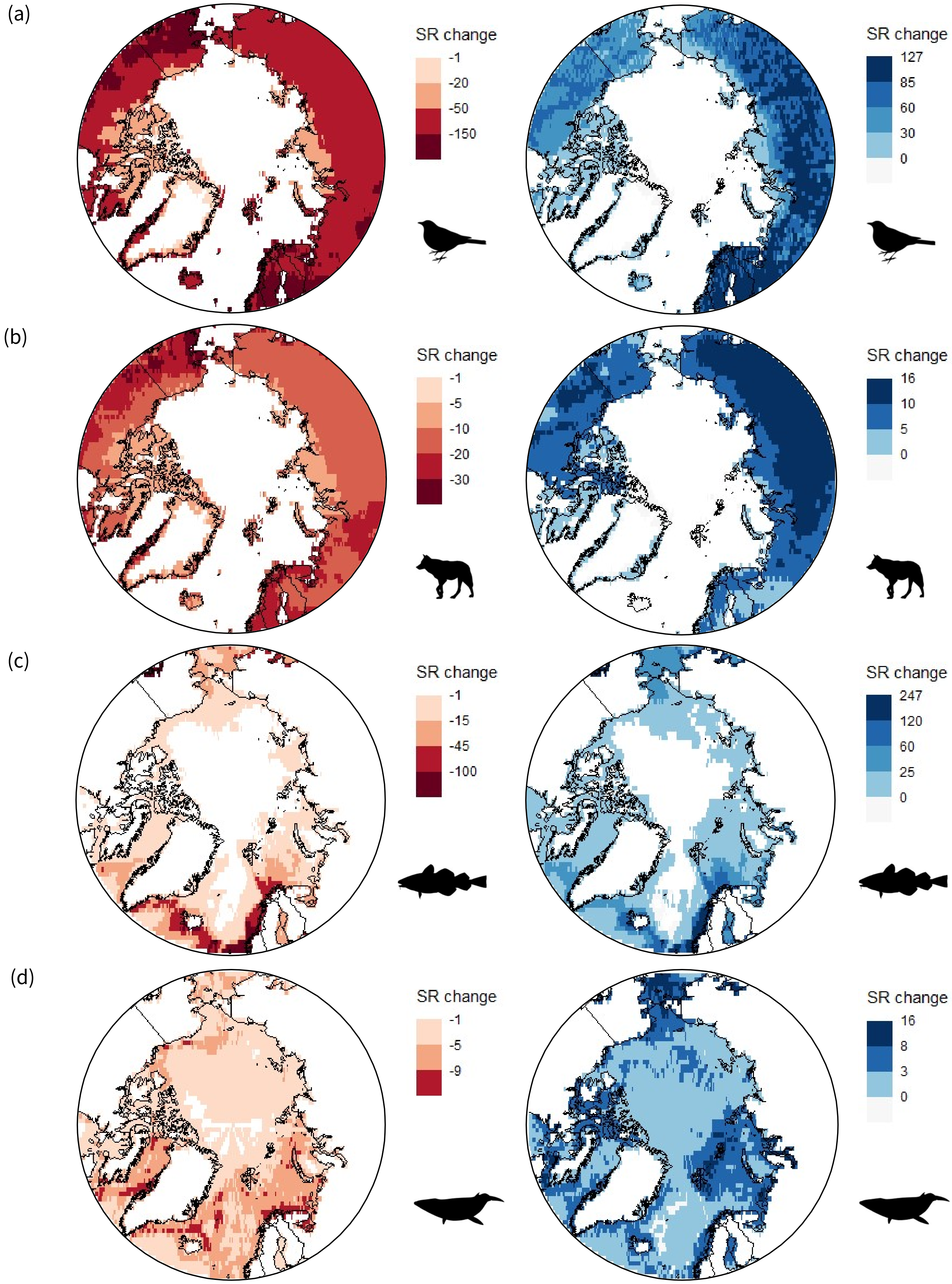

(a)
SR change
-1
-20
-50
-150
SR change
127
85
60
30
0
(b)
SR change
-1
-5
-10
-20
-30
SR change
16
10
5
0
(c)
SR change
-1
-15
-45
-100
SR change
247
120
60
25
0
(d)
SR change
-1
-5
-9
SR change
16
8
3
0

Figure 6.2. Future species richness (SR) change separated into gain (right) and loss (left) components per two terrestrial (birds and mammals) and two marine (fish and mammals) taxa (a-d) of important trade species in the Arctic. Future changes are projected to 2080 under SSP3.70 for terrestrial taxa and 2100 under RCP6.0 for marine taxa.

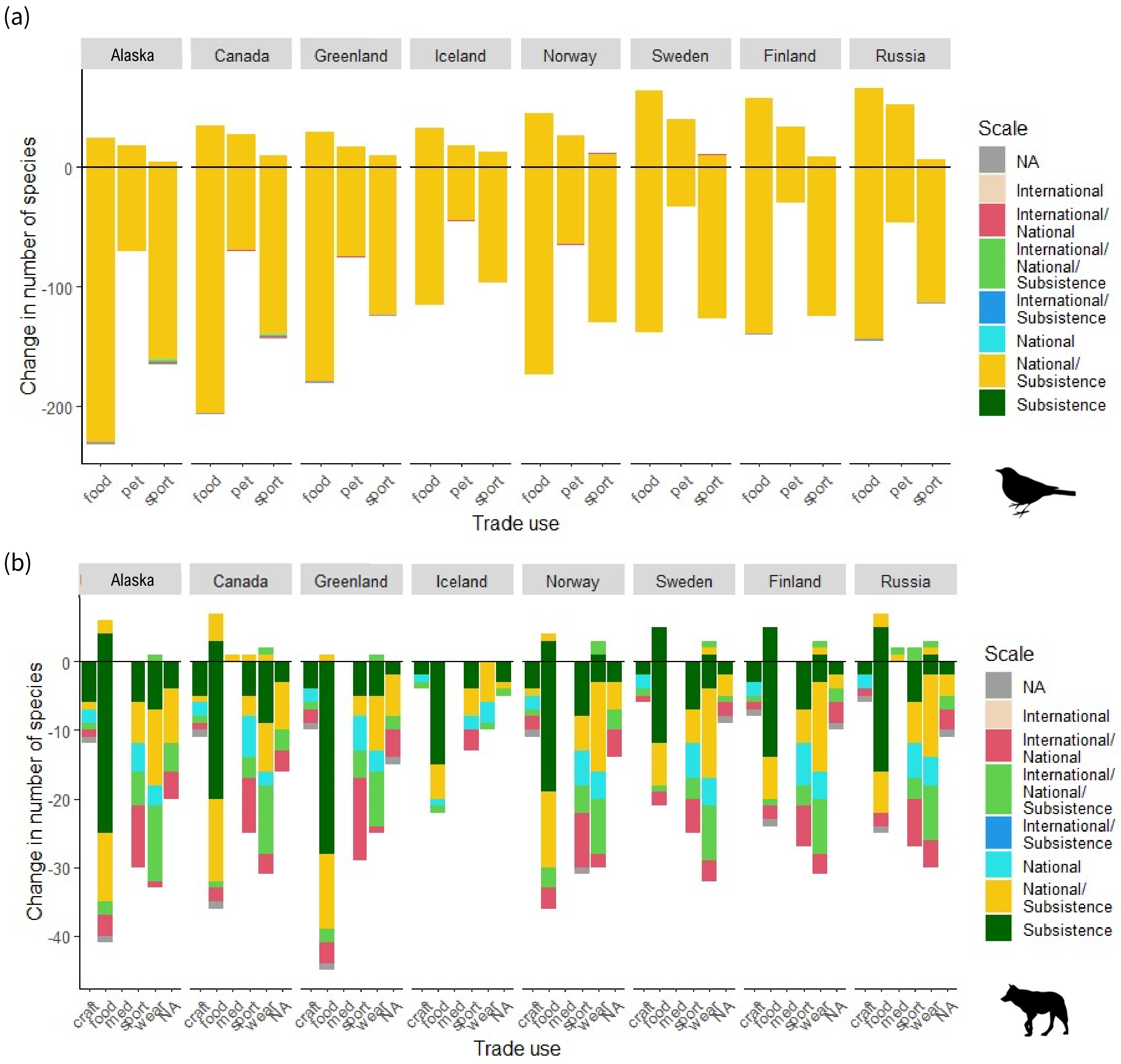


Figure 6.3. Losses and gains of terrestrial birds (a) and mammal (b) species for eight Arctic regions split by use and trade and their associated scale. Use and trade of birds are food – human (food); pets/display animals, horticulture (pet); and sport hunting/specimen collecting (sport). Use and trade for mammals are handicrafts/jewellery (craft); food – human (food); medicine – human and veterinary (med); sport hunting/specimen collecting (sport); and wearing apparel, accessories (wear). Some species have multiple uses. NA represents species with no scale of use/trade information. See Table 6.2 for descriptions of scale.

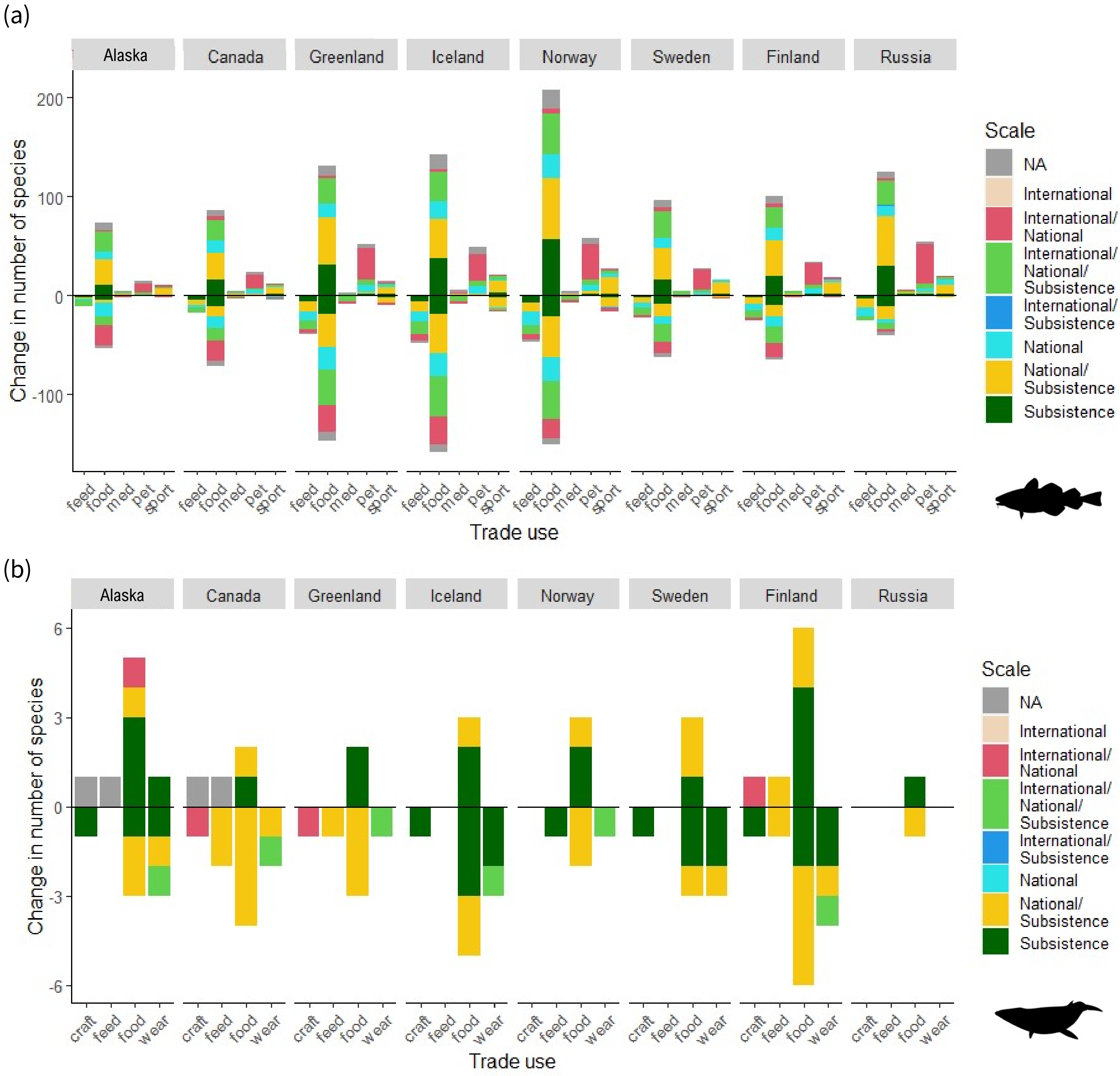


Figure 6.4. Losses and gains of marine fish (a) and marine mammal (b) species for eight Arctic regions split by use and trade and their associated scale. Use and trade of fish are food – animal (feed); food – human (food); medicine – human and veterinary (med); pets/display animals, horticulture (pet); and sport hunting/specimen collecting (sport). Use and trade for marine mammals are handicrafts/jewellery (craft); food – animal (feed); food – human (food); and wearing apparel, accessories (wear). Some species have multiple uses. NA represents species with no scale of use/trade information. See Table 6.2 for descriptions of scale.

6.5 Discussion

In this chapter I show that climate change is likely to drive substantial shifts in distribution of traded species that are important for provisioning services in the Arctic. To the best of my knowledge, this is the first attempt to investigate the impacts of climate-driven range shifts on specific provisioning services provided by wild species across the entire Arctic. Here, I discuss my results in light of previous findings and provide suggestions for future research.

Projected changes in SR of terrestrial birds by 2080 are heavily dominated by losses of economically valuable food and game species across all Arctic regions. Previous research has suggested that important game species such as Ptarmigan will be negatively impacted by climate change in some areas (Jansson et al., 2015), which could have societal consequences. Disturbances such as loss of suitable vegetation communities and declines in simulated climate suitability will result in fewer hunting opportunities as there are fewer species to hunt. Many wetland and coastal bird species inhabit Arctic areas for the breeding season but migrate southwards using major flyways including those along the west coast of the Pacific Ocean and numerous Asian countries, and the North American flyway. Migratory waterfowl such as Red knot (*Calidris canutus*), Curlew (*Numenius Arquata*), Bar-tailed godwit (*Limosa lapponica*) and Whimbrel are legally hunted across both breeding and stop-off areas (Klokov et al., 2023). This, in turn, provides important ecosystem services of economic value to people in the Arctic and sub-arctic (Goldstein et al., 2014; Semmens et al., 2011). The types of change I am projecting are consistent with what others are already starting to observe from monitoring studies of Arctic-breeding birds investigating the impacts of anthropogenic climate change (Doyle et al., 2020). Anderson et al. (2023) show temperature changes are causing the movement of warmer-breeding species, those that typically utilise warmer areas to breed, into the Canadian Arctic while colder-breeding species are shifting northward. One caveat of my study, however, is how the IUCN use and trade data is derived; some of my results may reflect losses and gains of species that may be used or traded in one country but not traded in another. For example, if a species is hunted only in Japan, then it will show as a tradable resource everywhere, even in areas where it might never be utilised. Some species, especially birds may be traded outside of Arctic regions, or more so in the southern part of the Arctic countries, especially southern Russia and Europe. Some wild bird harvest could be unsustainable or unregulated illegal hunting in countries beyond the Arctic but are species that breed or migrate further north (above 60° North). Thus, this factor should be considered when drawing conclusions from these results, and I emphasise they are what could happen with climate change. This work remains essential as a first step to identifying the possible impact of range-shifting species on providing services in the Arctic.

I found all regions of the Arctic are projected to lose terrestrial mammal species that, at present, are predominantly traded principally at local and national levels. This suggests that local people reliant on mammals such as reindeer, sable, foxes, and squirrels, as subsistence for livelihoods could be the worst impacted by climate change. Alaska, Canada and Greenland are some of the most affected in terms of the losses of traded mammal species, and the southwestern areas of these countries had the greatest SR losses. My results show large losses of mammal species from most Arctic countries used for handicrafts and clothing, and the wild fur industry. Sales of native handicrafts are often an important source of money in the economy of the northern Arctic (Fast & Berkes, 1998). Both climate change and habitat fragmentation in Canada and Alaska may explain the projected future losses of species used for subsistence hunting and sport in these areas. Large carnivores such as the Brown bear and Eastern wolf (*Canis Lycaon*) are usually hunted for sport to control livestock predation (Darimont et al., 2021). In addition, large herbivores such as reindeer, moose and bison comprise some species, used for food or sport, lost with climate change. This is consistent with other studies that have projected habitat suitability declines currently for multiple megaherbivores, such as muskox and moose, in Europe and North America (Jarvie & Svenning, 2018; Rosvold et al., 2013; Weiskopf et al., 2019). The consistent future projected losses of mammals used for sport and hunting, especially at national and international scales, could have societal and economic consequences. Such changes could result in hunting in novel, unregulated areas or, by contrast, losses of current hunting opportunities and their associated revenue (Jansson et al., 2015). The guided hunting industry in Alaska alone amounted to $91.8 million economic output in 2019, with the industry providing local employment, revenue for wildlife conservation, and game meat that is shared with local communities (McDowell Group, 2020). In 2019, hunters shared an estimated 2.3 million dollars' worth of traditional game meat from moose, deer, sheep, mountain goats and caribou with Native communities, needy families, elders and traditional food programmes (McDowell Group, 2020). Losses of moose from Alaska and Canada could have profound implications for indigenous communities as moose have a strong cultural significance in indigenous peoples' traditions (Rosa et al., 2020). Moose hunts are an integral part of indigenous cultures, not just for subsistence, but also for sacred rituals, reinforcing the connection between nature and humans (Rosa et al., 2020). Another important mammal for human consumption in the Arctic is reindeer. Communities may be less vulnerable to climate-driven range shifts of reindeer because most reindeer are farmed by local people in the Arctic, and so movements will be governed, to some extent, by herders rather than climate change (Tyler et al., 2021). However, as climate change is driving a decline in reindeer livestock, the quality of reindeer pastures, and altering their accessibility to food, current movement possibilities may have to change irrespective of traditional herding practices. Such changes to habitat quality are being driven by warmer temperatures and increasing rain-on-snow and thaw-freeze events (Tyler et al., 2021). Reindeer meat is hugely important for Arctic peoples and losing this traditional diet component could increase the prevalence of obesity, chronic bronchitis and other diseases (Andronov et al., 2021), as more modern, carbohydrate-rich foods are consumed instead.

The most notable gains in traded fish are projected for the Bering, Barents and Norwegian Seas. If the warming trends increase, the mean sea-surface temperatures in these regions are expected to increase by 1-3°C over the next 50 years, with the greatest changes in the northernmost parts of these regions (Stenevik & Sundby, 2007). Consequently, the expectation is that the distribution of all species will move poleward and that the abundance of fish stocks of these Arctic and sub-Arctic regions will increase (Stenevik & Sundby, 2007). My findings are also in line with other research which projected that, by 2100, 45% of transboundary fish stocks could shift in distribution, with 80% of the world's EEZs seeing at least one stock shift (Palacios-Abrantes et al., 2022). Even these figures could be conservative, however, as the above study focused only on shared stocks between EEZs and not the arrival of new stocks to EEZs. My projections for considerable gains and losses of traded species in the Norwegian Sea are also consistent with previous research, which both projected and observed high levels of turnover of fish stocks with climate change in the North Atlantic and Arctic (Gordó-Vilaseca et al., 2023; Lam et al., 2016). These changes are likely driven in many areas by the loss of colder-water species and gains of boreal fish (Fossheim et al., 2015). The North Atlantic Oscillation (NAO), differences in sea-level atmospheric pressure between the low-pressure zone south of Iceland and the high-pressure zone over the Azores, has shown an upward trend since the 1960s due to climate change (Parsons & Lear, 2001). Higher NAO increases the transport of Atlantic water into the Norwegian and Barents Sea (Tsubouchi et al., 2021), increasing water temperatures in these regions (Stenevik & Sundby, 2007). These warmer waters are likely to have driven the movement of more boreal species, such as capelin and herring, into more northern regions (Sundby, 2000).

The considerable projected gains across the Arctic of fish used for human consumption may produce new trade opportunities across Arctic regions. Indeed, incoming new commercial fish stocks in Norway could provide new fishing opportunities in more northern waters (Stenevik & Sundby, 2007). New fisheries have already become established such as the mackerel fishery in Iceland, a species which was sparsely distributed and in low abundance prior to ocean warming in the region in 2007 (Astthorsson et al., 2012). This resulted in a 'mackerel war' as the mackerel fishery was previously governed by the EU, Norway EEZ and Faroe Island EEZ before shifting into the Iceland EEZ (Spijkers & Boonstra, 2017). This highlights the potential repercussions that range shifts of internationally targeted fish stocks could have in new EEZs, with conflicts arising between nations. In the case of the mackerel fishery, this ultimately led to the overexploitation of the mackerel fishery in Iceland (Spijkers & Boonstra, 2017). In addition to fish stocks becoming extinct or newly arriving in national EEZs, many target species that are currently shared across EEZs are also changing their dynamics substantially (Palacios-Abrantes et al., 2022). The establishment of newly exploitable fish species in a region may not, however, be a direct substitute for target species that are lost with climate change. My results suggest the species lost, particularly in Europe and Russia, may be those of particular importance to those local communities that rely on fish for livelihoods and to feed families. Climate-driven movements of fish, resulting in reduced catches of important fish stocks in the Yakutia region of Russia have been recorded recently (Backhaus et al., 2017), particularly for species that migrate between marine and freshwater environments. In addition, as local fishing communities are often accustomed to fishing for specific species, they may be incapable (due to, for example, a lack of resource, equipment or training) of targeting new species. They might also be reluctant to adapt to fishing for new species in new ways.

My results highlight the substantial changes that climate is likely to have on local and national trade of marine mammals across all regions, which are used mainly for food and apparel. The indigenous hunting of marine mammals includes, for example, bowhead whale (*Balaena mysticetus*) hunting by Inuit in Alaska and minke whales (*Balaenoptera acutorostrata*) in Greenland, to provide food and clothing. Such activities form a large part of Inuit culture and ideology in Alaska, Canada and Greenland (Jensen et al., 2018). As such, if climate change makes these waters uninhabitable for certain whale and seal species, such cultural and subsistence practices may no longer survive. Accessibility to subsistence resources, such as those provided by marine mammals, has reportedly already decreased with climate change due to sea ice loss in Alaska (Brinkman et al., 2016). This could have major consequences for indigenous communities, who have relied heavily upon whale and seal subsistence hunting for millennia to feed their families and communities. Access to wild foods is also important in helping to mitigate issues of indigenous food insecurity (Panikkar & Lemmond, 2020). For example, in 2013, changing weather patterns and lack of sea ice in the Bering Sea meant two Inuit communities were unable to hunt bowhead whales and walrus that year (Panikkar & Lemmond, 2020). Consequently, the following year, the communities required emergency food assistance from the state.

The results presented in this chapter provide promising avenues for future research. Further studies can build on this work by attempting to value the direct costs and benefits of the losses and gains of traded species in the Arctic. Although species' distribution projections need to be treated with caution, estimating the direct increases or decreases in trade output (such as the direct economic value of a species for a certain country) could provide a more detailed analysis of the consequences of range shifts on Arctic economy. To do this, future studies could directly model species' abundances, as in Howard et al. (2014), and calculate projected economic losses or gains due to both richness and abundance changes. To develop a fuller picture of the impacts of range shifts on ecosystem services, additional studies will be needed that value not only provisioning services, but also cultural services. Such data are rare for the entire Arctic region, and only a few attempts have previously been made to value ecosystem services in the Arctic (Malinauskaite et al., 2019). Additional research is needed to better understand the potential impacts of climate-driven range shifts on the human communities and societies that rely on species and ecosystems to live.

Here, for the first time, I have projected potential changes in distributions of important traded species belonging to two terrestrial and two marine taxa across the Arctic and subarctic, highlighting major changes in species richness and community compositions. The movement of economically important species across international borders could be extremely disruptive, adding to existing conflicts of transboundary terrestrial species' harvest and marine fisheries (Ojea et al., 2020; Pinsky et al., 2018). My findings are consistent with previous research in other regions showing substantial shifts in both terrestrial and marine traded species (Gattuso et al., 2015; Post et al., 2019), but here I provide the first Arctic focused results. Shifting trade species are expected to cause considerable national and international conflict over terrestrial and marine resources, impeding effective and sustainable adaptation to climate change. Importantly, I have also shown the potential impacts of species richness declines for local subsistence of Arctic human communities, especially in terms of the impacts of changes to the terrestrial and marine species used for human consumption. These results highlight the growing importance of understanding the impacts of climate-driven range shifts on provisioning ecosystem services, which would aid the development of management strategies to help Arctic peoples and nations adapt and mitigate the effects of future climate change.

Chapter 7

General Discussion

7.1 Summary

In this thesis, I have advanced our understanding of the impacts of climate change on terrestrial and marine biodiversity in the Arctic under climate change, and the consequences for human societies. The main aims of this thesis were: (1) to determine the potential for novel species to shift into the Arctic and (2) the potential for novel assemblages to form, (3) to assess the impacts of projected changes on Arctic terrestrial and marine ecosystems and (4) to evaluate the impacts on human societies. Firstly, using species distribution models (SDMs) to investigate species richness and range changes in the terrestrial Arctic under climate change, I found there is a high likelihood that novel assemblages will form in future, especially in the high and low Arctic. However, I also found that species-specific dispersal abilities and the availability of suitable habitat limited terrestrial species' abilities to track suitable climate. Secondly, to understand future changes of marine fish and mammal biodiversity in the Arctic, it is important to ascertain how biodiversity is expected to change in the future at the global level. To further investigate how species' range shifts in the Arctic could impact ecosystem functioning I used an additional measure of biodiversity, functional diversity. Hence, for the first time at such a large scale, I found large changes in the functioning of marine systems globally, with high functional redundancy in tropical regions and gains in functional diversity in the Arctic. Incoming species to the Arctic had distinct traits relative to recipient Arctic communities, with the frequency of faster life-history traits increasing with climate change. At the same time, I found important implications of losses of species, especially marine mammals that are functionally highly specialised and unique in Arctic communities. Then, using a high-arctic marine polynya, the North Water Polynya, as a case study, and combining species distribution models with food-web models, I found incoming boreal species may not adequately replace Arctic specialists in terms of energy transfer within the food web. I also show for the first time how changes to copepod size-structure at the base of the food web can cause drastic changes to higher trophic levels, especially marine mammals. Finally, by investigating changing distributions of traded species in the Arctic with climate change, I demonstrated that although new species may provide new trading opportunities for people, incoming species are unlikely to replace the provisioning services of species lost. Importantly, climate change disproportionately impacted people at subsistence/local scales.

In the remainder of this chapter, I will summarise and synthesise my findings in more detail. I will also expand upon their potential to contribute more widely to our understanding of the impacts of biodiversity colonisation of the Arctic under climate change. I will discuss these findings in terms of three main themes that emerged whilst addressing the principal motivation of the thesis. Lastly, I will identify future avenues for further research and discuss the broader implications for conservation planning.

7.2 Synthesis

7.2.1 Spatial variation in the impacts of climate change in the Arctic on terrestrial and marine species

As a result of this thesis, we now know that there is a high potential for novel species to move into the Arctic under climate change, in both terrestrial (Chapter 2) and marine environments (Chapters 3 and 4). For the first time, I found variation in the spatial pattens of species richness changes and the emergence of novel communities between terrestrial (Chapter 2) and marine (Chapter 3 and 4) ecosystems. In Chapter 2, I showed that all regions of the Arctic become climatically suitable for new terrestrial birds and mammals with clear increases in species richness as latitude increases. However, when dispersal and habitat were considered, many species were unable to track their climate niche. Fewer novel mammal communities than novel bird communities were projected by 2070, and there were more novel communities projected for the high and low Arctic. However, in Chapters 3 and 4 I found a much more varied response to future climate change of marine species than terrestrial. I showed gains in very high Arctic waters of the Arctic Ocean, but also that some regions of the Arctic are projected to lose over 50% of their marine mammal (Chapter 4) and fish (Chapter 3) species by 2100 – especially in the Norwegian Sea, Barents Sea and northern Atlantic. These findings suggest similar responses of marine fish and marine mammals to climate change but diverging size and location of responses to terrestrial birds and mammals. These discrepancies may partly be explained by the different environmental variables used in terrestrial versus marine SDMs to project species' distributions in future. Previous studies have found the signature of warming to be larger in marine assemblages than terrestrial (Antão et al., 2020), but most previous studies have disregarded the impacts of other environmental variables, such as chlorophyll and salinity, in driving species range shifts. Results in Chapters 2, 3 and 4 suggest there are likely to be greater proportional gains in species richness in the marine Arctic than the terrestrial Arctic, particularly when terrestrial species' dispersal abilities and available habitat are incorporated into models. Though other variables besides temperature will affect marine range shifts, the more pronounced change in marine systems is somewhat unexpected considering that temperature changes in the ocean are typically smaller than those on land (Antão et al., 2020). This may highlight greater response lags among terrestrial species than marine species (Burrows et al., 2011; Devictor et al., 2008; Pinsky et al., 2019). Greater colonisation and dispersal abilities of marine species (Poloczanska et al., 2013) may also help such species persist under future climate change. Despite this, many marine species are still projected to become lost from assemblages in the Arctic by 2100 (Chapters 3 and 4). Hence, contrary to previous studies, I highlight that the nuances of marine species' responses to climate change and species gains are not uniformly distributed across the Arctic.

7.2.2 Formation of novel assemblages and changing community function

The implications of changes in species' distributions and communities on ecosystem functioning are relatively understudied, especially in marine environments. In this thesis I have provided new insights into the impacts of novel assemblages in the Arctic on community structure and function. In both Chapters 3 and 4, I projected increasing functional diversity in the Arctic as a result of species gains. These findings are in accord with the predictions of others that functional diversity will increase at high latitudes under climate change (Frainer et al., 2021; Pimiento et al., 2020; Scherer et al., 2023; Stewart et al., 2022). My findings further project that the functional diversity increases in many regions of the Arctic are greater than expected by chance, suggesting incoming boreal species have distinct traits from recipient Arctic communities (Chapters 3 and 4), which could alter community structure and function. In Chapter 3, I demonstrated for the first time at a global scale that climate change is projected to drive an increase in the commonness of faster-life history traits and smaller-sized species in marine fish communities in the Arctic. I also found increases in the commonness of smaller marine mammal species in the Arctic (Chapter 4). These future projections oppose recent observations from smaller-scale studies that looked at recent changes to functional biogeography in the Arctic. The latter found that, commonly, those species moving into the Arctic for the first time are larger, and longer-lived species relative to current Arctic species (Frainer et al., 2017). Smaller, shorter-lived species with high fecundity are more likely to tolerate changing climate (Perry et al., 2005). Species with faster life-histories are likely to reproduce faster and hence the likelihood of rapidly establishing a population in the Arctic is greater (García et al., 2007; Wiedmann et al., 2014). Sea-ice loss is driving rapid habitat changes in the Arctic, increasing primary production and enhancing the carrying capacity of the pelagic component of the water column (Ingvaldsen et al., 2021).

This increase in food availability and primary productivity will likely promote the establishment of smaller, currently more southerly-distributed species, as projected for the future in Chapter 3 (fish) and Chapter 5 (boreal fish and small copepods). Projected changes to trait frequencies in the Arctic by 2100 (Chapters 3 and 4) imply that biodiversity colonisation could impact Arctic communities by causing a change in their functional structure and characterisation. These incoming new functional traits, and the associated losses of Arctic specialist traits such as benthic, lower growth rate and longer life history traits, will likely lead to changes in the functional organisation and structure of Arctic communities (Frainer et al., 2017, 2021). The increase in functional diversity in the Arctic (Chapters 3 and 4) could increase the adaptive capacity of the Arctic to further changes to environmental conditions and stressors, but perhaps at the cost of Arctic specialists (Aune et al., 2018; Frainer et al., 2021; Ingvaldsen et al., 2021). These findings expand on other work and emphasise the importance of considering alternative measures of biodiversity to investigate the impacts of climate change on community composition.

7.2.3 Can novel colonists fully replace species lost from communities?

Despite the considerable gains of novel species (both to individual Arctic regions and to the entire Arctic) across terrestrial (Chapter 2) and marine Arctic ecosystems (Chapters 3 and 4), throughout the thesis I have found significant implications of concurrent losses of species from the Arctic. It is important to realise that both losses and gains have implications for Arctic ecosystems, as some functions may increase and other functions decrease. Although overall functional richness increases in the Arctic (Chapters 3 and 4), losses of functionally unique and specialised species could have impacts on ecosystem functioning in these communities (Chapter 4). For the first time, I have projected that filter-feeding specialists such as baleen whales will be lost at high latitudes (Chapter 4). Baleen whales are important nutrient cyclers and benthic-pelagic couplers (Roman et al., 2014). If baleen whales are lost from high Arctic systems, this could affect the nutrients available to pelagic species that otherwise would not access these resources (Roman et al., 2014). My findings highlight that, in terms of ecosystem services, equal attention must be paid to species lost and gained in communities. I show that even few local extirpations from Arctic communities can have disproportionate (Chapter 4) negative impacts on such relatively simple ecosystems.

In Chapter 3, I show that, regardless of region, demersal traits decline in commonness, suggesting demersal species are more vulnerable to climate change. Incoming, more pelagic species will not replace the major roles carried out by benthic species in the overall energy flow on Arctic ecosystems. The increase in pelagic fish and concurrent decreases in demersal species suggests a shift in primary energy flows in the Arctic from benthic to pelagic. Benthic Arctic communities rely heavily on ice algae and phytoplankton (McMahon et al., 2006), but the amounts of each reaching the seafloor will change with climate change and ongoing sea-ice loss (Lannuzel et al., 2020). Indeed, in Chapter 5, I found that scenarios that included the colonisation of an Arctic polynya by more southerly distributed less-fatty copepods, which are increasing in the Arctic with climate change, decreased energy transfer to higher trophic levels. Additionally, increases in pelagic consumers may 'intercept' food that originally drifted in the water-column down to the seafloor, causing higher energy retention in the pelagic system (Zhulay et al., 2023). As benthic species are important food sources for higher trophic levels in Arctic food webs, changes to benthic-pelagic coupling may have resounding effects throughout the Arctic ecosystem (Cochrane et al., 2009; Grebmeier et al., 2006).

The introduction of novel species into Arctic ecosystems can disrupt existing food webs by altering trophic interactions and resource availability. In Chapter 5, I simulated that increases in biomass of boreal species like capelin, driven by climate change, would not fully compensate for the role of Arctic cod as a key forage fish in a high Arctic food web. Increasing numbers of boreal colonists and declines in Arctic cod numbers were projected to reduce energy transfer to higher trophic levels, especially for belugas. Similarly, I have shown that changing copepod size structure had a detrimental effect on a high Arctic food web (Chapter 5). My findings imply that climate change could disrupt Arctic marine ecosystems substantially, by reducing trophic transfer efficiency, if smaller less-fatty copepods replace their larger congenerics.

Provisioning ecosystem services provided by Arctic species are crucial for local communities, livelihoods and cultural practices. Traditional subsistence harvests of marine mammals and fish play a central role in indigenous cultures and economies. My findings in Chapter 6 indicate that while novel species may offer new trade opportunities and contribute to Arctic economy, the loss of native Arctic species, especially birds and mammals, may outweigh these gains. However, for most Arctic regions, I conversely found that gains in traded fish species outweighed losses (Chapter 6), in terms of species richness, meaning novel colonists could have the potential to replace species lost. New incoming species that are used as food for humans could have both positive and negative impacts on people. Large gains in food fish species (Chapter 6) would require human communities to adapt to the arrival of new resources and transition away from reliance on formerly native species that are lost from Arctic regions (Lawlor et al., 2024). The climate-driven arrival of new species has enabled some places to establish new commercial and/or recreational fisheries (Pecl et al., 2019), but have reduced county-level wages and employment and increased travel and fishing pressures to harvest target native species that have shifted to new regions (Lawlor et al., 2024; Young et al., 2019). Beyond provisioning services, indigenous communities in the Arctic have deep cultural connections to specific species, which extend beyond their economic value. These species hold spiritual, social and cultural significance, and novel species are less likely to replace the potential loss of indigenous identities and traditional knowledge systems (Pearson et al., 2021).

7.3 Limitations and future directions

One limitation of the methods used in this thesis is the use of species range polygon data as input for SDMs (Chapter 2). Range polygons, while often the best available source of data for many taxa, are inherently coarse and generalised representations of a species' distribution. These polygons do not account for the heterogeneity within a species range, such as areas where the species is absent despite suitable environmental conditions. Therefore, the area over which climatic suitabilities were calculated may not accurately reflect the areas used by a species and could be overestimating the range shifts expected as a result of climate change. If anything, this would tend to underestimate some of my more alarming results. In particular, I project large losses in species' range sizes, especially in the Arctic, and if that is an overestimate then more species could be at risk than suggested by Chapter 2. In Chapters 3, 4 and 5, I used species' occurrence data from online, open-access sources as presence-only data for marine SDMs. These also have problems when estimating species ranges as they have inherent biases (discussed in Chapters 1 and 3). To account for these issues, I used vigorous cleaning protocols and blocking methods to account for these issues. The availability of empirical data of species' occurrences and ranges, especially in the Arctic, remains one of the greatest challenges facing Arctic research and performing SDMs. Establishing long-term monitoring programmes for Arctic ecosystems can provide more data to feed into SDMs and further help track shifts in species' distributions and community compositions over time. This could provide empirical data to validate model projections and identify any unforeseen changes or trends. Modern technology has significantly advanced our ability to acquire data on species and communities (Davidson et al., 2020). Remote sensing (Jetz et al., 2022; Zong et al., 2022), drones (Hodgson et al., 2018) and biologging

(Clermont et al., 2021; Harrison et al., 2022) offer new ways to monitor Arctic environments and species across large scales (Davidson et al., 2020), providing fine-scale information about abiotic and biotic conditions and spatial ecology.

The spatial and temporal resolution at which global or continental scale SDMs are typically run can introduce some limitations. Coarse spatial resolutions, while computationally efficient and often necessary for large-scale studies, may fail to capture the fine-scale environmental heterogeneity on which species may rely (Edgar et al., 2017). This could lead to inaccurate predictions, particularly for species with narrow ecological niches or those sensitive to microhabitat conditions. For example, critical habitat features such as small water bodies, vegetation patches, or localised thermal refugia may be undetected at coarse spatial scales, leading to underestimation of suitable habitat. Similarly, coarse temporal scales can mask important seasonal or interannual variations in species distributions and environmental conditions. Many species exhibit dynamic distributions in responses to short-term climatic events, life-cycle stages, or migratory behaviour (van Weelden et al., 2021). When SDMs are built using averaged environmental variables over long time periods, they may overlook these temporal dynamics, leading to overgeneralised predictions that may not accurately reflect real-world variability. Projecting species distributions to many time periods was beyond the scope of this thesis, especially as future climatic data available for marine environments was limited, but future work could compare these findings to projections to decadal time steps as new data become available. Future improvements could further address these challenges by integrating multi-scale approaches that combine fine-resolution environmental data with broader-scale analyses. Advances in remote sensing and computational power now enable the collection and processing of high-resolution spatial and temporal data (Jetz et al., 2022), making it increasingly feasible to run SDMs at scales more appropriate for individual species' ecologies. Despite this, SDMs run at coarse scale are still useful in capturing important broad-scale divers of species distributions.

Expanding the scope of marine SDMs to account for species shifting to greater ocean depths, and the associated behavioural and physiological limits that might prevent such water column range shifts, represents a critical avenue for future research in understanding the impacts of climate change on marine Arctic ecosystems. While I included depth and sea-bottom temperature as key environmental predictors, the inability to predict range shifts to deeper in the water column poses challenges in assessing the full extent of species' responses to changing environmental conditions (Duffy & Chown, 2017; Melo-Merino et al., 2020). It is important to recognise that not all species are able to shift their zone of occurrence to greater depths (Liu et al., 2024). Future research could explore the mechanisms driving depth-dependent responses of marine species to climate change (Twiname et al., 2020). This could involve small-scale studies investigating how changes in temperature, oxygen levels and food availability influence species' vertical movements in the water column. Or studies could investigate the range of depths at which species occur in the natural world across their range, and what drives these elevation (depth) limits in different areas. Advanced modelling techniques, such as SDMs that incorporate three-dimensional habitat data or machine learning algorithms (Duffy & Chown, 2017; Valle et al., 2024), could predict species' redistributions across depth gradients. These models, however, are complicated and difficult to implement at broad, global scales (Duffy & Chown, 2017; Valle et al., 2024).

Predicting the outcomes of new biological interactions that arise in novel communities is a major scientific challenge. As species communities reassemble, there could be changing biotic interactions, increased competition and phenological mismatches (Kordas et al., 2011). Arctic species may experience increased competition and predation pressure from novel species' range shifts. Hence, the outcome of novel interactions between species that may never have interacted before remains uncertain and difficult to predict. The magnitude of the impacts of new biotic interactions will depend on species-specific adaptability, phenotypic plasticity and eco-evolutionary experience (Saul & Jeschke, 2015). Methods for predicting interactions between species exist but are difficult to apply at large scales and generally are only based on one mechanism, such as phylogenetic distance, functional trait matching or trophic level (Strydom et al., 2021). However, the combination of machine learning methods and mechanistic models present an opportunity to predict ecological dynamics more robustly under climate change (Desjardins-Proulx et al., 2019; Strydom et al., 2021).

The next step to understanding the impacts of species' range shifts in the Arctic on human communities is to summarise the economic gains and/or losses associated with range shifts of traded species. The landings of harvested species for each Arctic nation can be used as an indicative measure of income and changing income. One method of doing this is to assign typical landing values across species-specific projected occupied habitat, then multiply these values by price per unit. This could then be extended to future projections, hence modelling changing national income. This would enable an assessment (albeit rather crude) of how changing species' distributions might translate to an increase or decrease in the economy of each Arctic nation. In addition, future work could also usefully build on the impacts of range-shifting species on human societies by evaluating potential changes to supporting and cultural services.

7.4 Conservation implications

My findings throughout this thesis are informative, not only for providing insights into the impacts of biodiversity colonisation in terrestrial and marine Arctic ecosystems, but also for the implementation of conservation management plans. With the knowledge of hotspots of species' vulnerability and of areas that may become important climate refuges for range-shifting species, conservation organisations, governments and policymakers can better focus conservation efforts to best conserve and restore species communities. Protected areas are essential for conserving species, and new protected areas will need to be established as range-shifting species are likely to shift beyond current protection (Berteaux et al., 2018; Gallardo et al., 2017; Mouillot et al., 2016; Schmidt et al., 2022; Voskamp et al., 2021). Movement corridors between protected areas will benefit from increased restoration to increase the connectivity between protected areas (Berteaux et al., 2018).

Range shifts of commercially important species (Chapter 6) highlight the need for transboundary management strategies as species' distributions move across borders (Lawlor et al., 2024; Palacios-Abrantes et al., 2023). Transboundary conflicts over harvested species have already been identified as a priority in the management of international resources (Pinsky et al., 2018). The need for transboundary management and governance will only increase with ongoing climate change (Lawlor et al., 2024), given the high number of important species projected to shift into new Arctic regions (Chapter 6; Palacios-Abrantes et al., 2023). Arctic nations will likely be disproportionately impacted as indigenous communities and local people rely heavily on certain species as a food base and may have a lower capacity to adapt (Lawlor et al., 2024; Melbourne-Thomas et al., 2022).

Incoming non-native species may negatively impact the ecosystem structure and function of Arctic communities (Chapter 5). At the same time however, the establishment of novel species may become key in some regions to replace functions and services lost by local extirpations of native species (Chapters 3 and 4) (Berteaux et al., 2018). Thus, deciding which regions and species to prioritise for conservation efforts will become an important challenge for practitioners.

Finally, the considerable projected changes in species richness, ranges and functional diversity at high latitudes emphasises the problem of conservation plans that only preserve a snapshot of today's biodiversity (Berteaux et al., 2018). Current conservation action plans may fail to protect species under future climate change (Lawler et al., 2015). This is why future projections of biodiversity change, such as those in this thesis, are essential in informing conservation for the future. Conservation action needs to become 'future-oriented' (van Kerkhoff et al., 2019) to better accommodate climate-affected futures. Management bodies need to investigate the governance mechanisms and policy frameworks needed to address the complex challenges posed by biodiversity changes in the Arctic. This includes assessing the effectiveness of existing conservation policies, identifying gaps in governance structures, and developing adaptive management strategies that consider both ecological and socioecological factors. Conservationists will need to agree on how best to value novel or altered ecosystems and whether or how to act in facilitating change. Interdisciplinary collaboration between scientists, policymakers and conservation practitioners will be key to achieving future-oriented conservation and adapting in the face of climate change.

7.5 Conclusions

In summary, this thesis has significantly advanced our understanding of the impacts of biodiversity colonisation in the Arctic under climate change. I found the potential for novel assemblages to form in both terrestrial and marine ecosystems in the Arctic. By integrating SDMs with assessments of ecosystem functioning, I have discovered profound shifts in species compositions and community dynamics, especially in marine ecosystems, highlighting the nuanced responses of Arctic ecosystems to climate-driven species redistributions. Importantly, my research demonstrates the disproportionate impacts of climate change on local peoples, who rely heavily on native Arctic species for sustenance and cultural identity. Moving forward, future research endeavours should prioritise assessing the economic implications of species' range shifts for Arctic economies. Proactive conservation strategies are imperative to safeguard Arctic biodiversity in the face of ongoing environmental change. Engaging stakeholders, including local communities, scientists, policymakers and industry representatives, in collaborative research and decision-making processes, and adopting future-oriented conservation approaches, will be crucial to ensuring resilient and adaptive conservation frameworks that effectively address the complex challenges posed by biodiversity colonisation in the Arctic under climate change.

Appendix A: Supporting material for Chapter 2

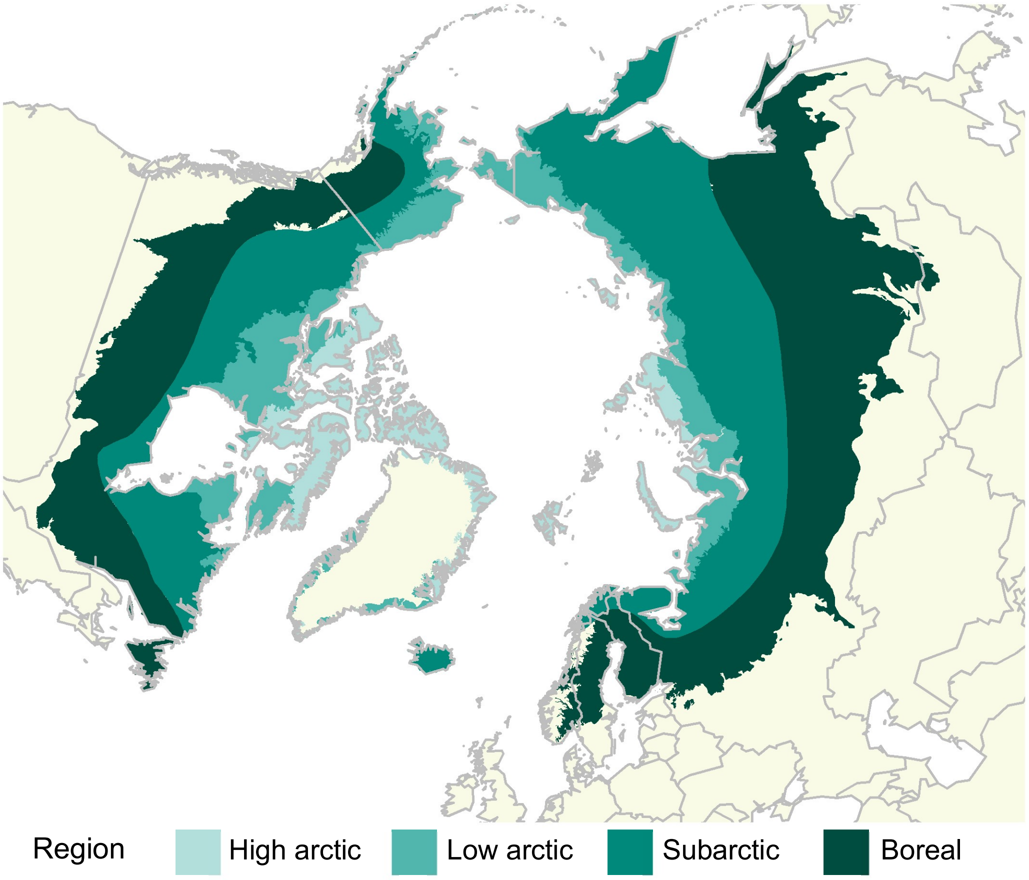


Figure S2.1. Arctic and subarctic regions. Polygons for High, Low and subarctic were from the Conservation of Arctic Flora and Fauna (CAFF) /Arctic Boundary Assessment GeoNetwork catalogue (CAFF 2019), as defined by the Circumpolar Arctic Vegetation Mapping Project - Bioclimatic subzones (CAVM Team 2003) and the Arctic Biodiversity Assessment (ABA). Boreal region from WWFs Terrestrial Ecoregions of the World (Olson et al. 2001), and was cropped to exclude the subarctic using ArcGIS Pro v2.8.6.

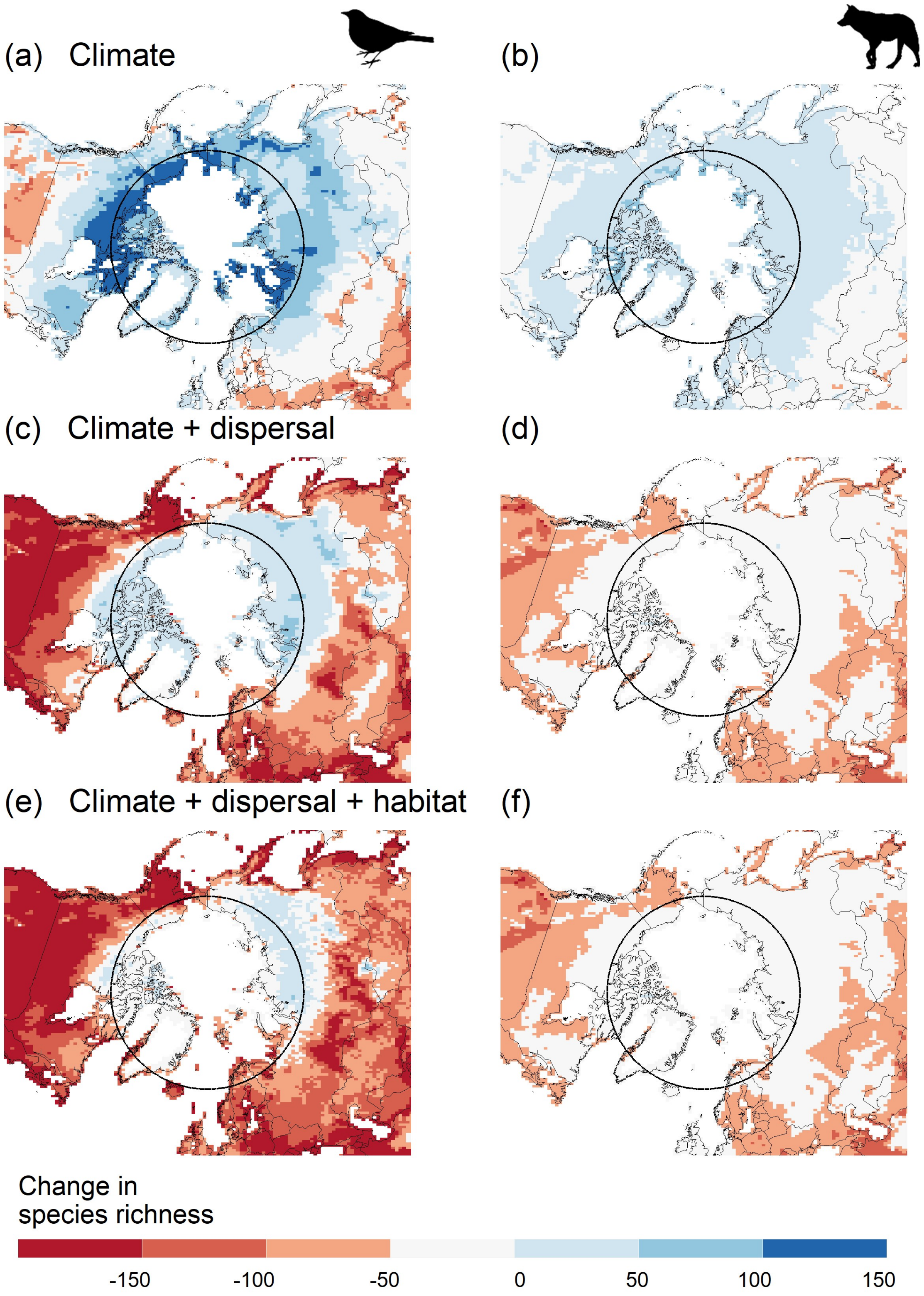


Figure S2.2. Projected change in species richness by 2070 under SSP 5-8.5 for Palearctic and Nearctic terrestrial birds and mammals derived from summed individual species ensemble model projections. Richness for (a) birds and (b) mammals from models based solely on the extent of suitable climate. Richness for (c) birds and (d) mammals accounting for both climate and dispersal capability. Richness projections accounting for climate, habitat and dispersal for (e) birds and (f) mammals. Maps plotted in Polar Stereographic projection. Black bold line shows the Arctic Circle. Species icons from phylopic (https://www.phylopic.org/).

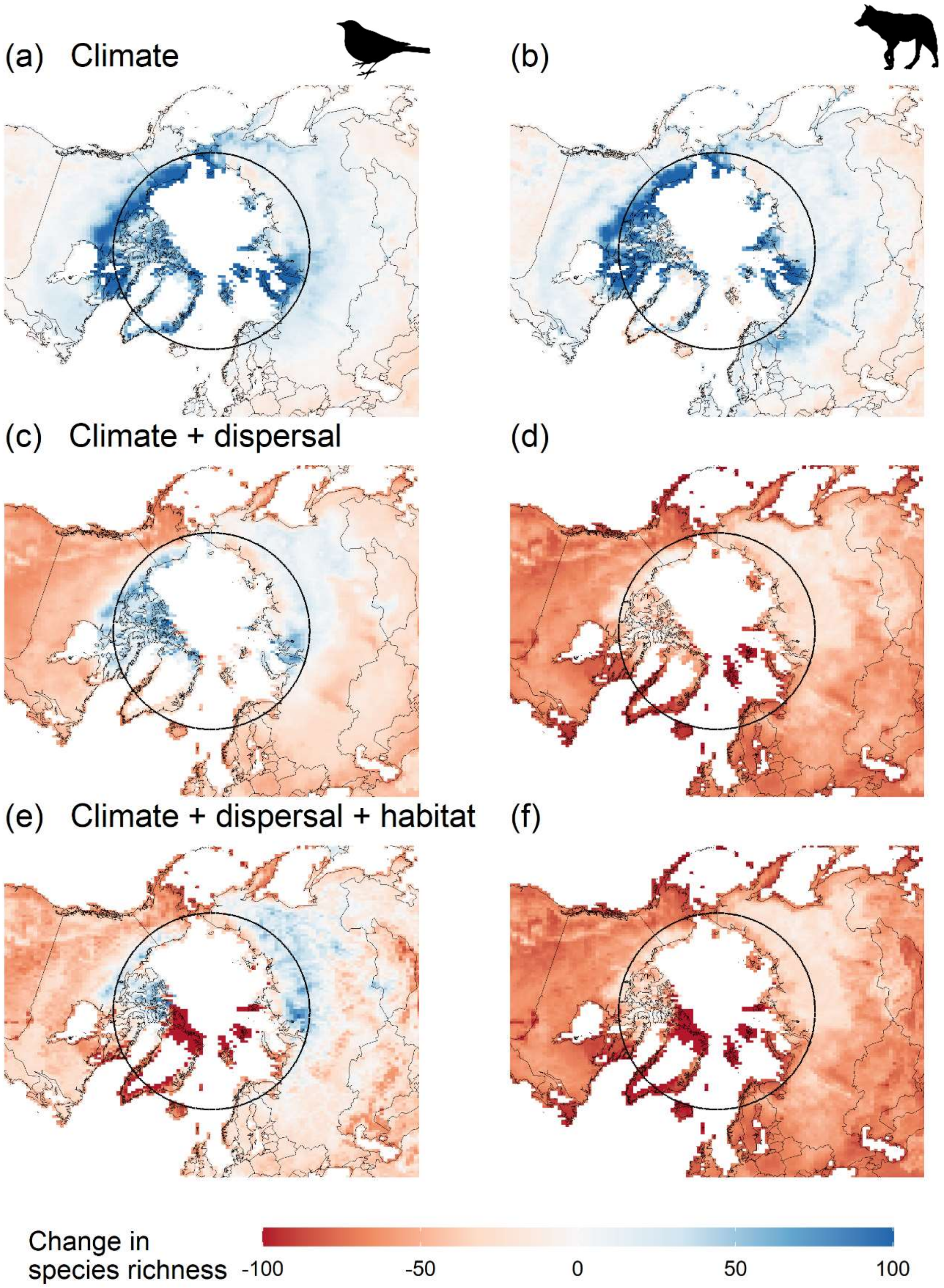
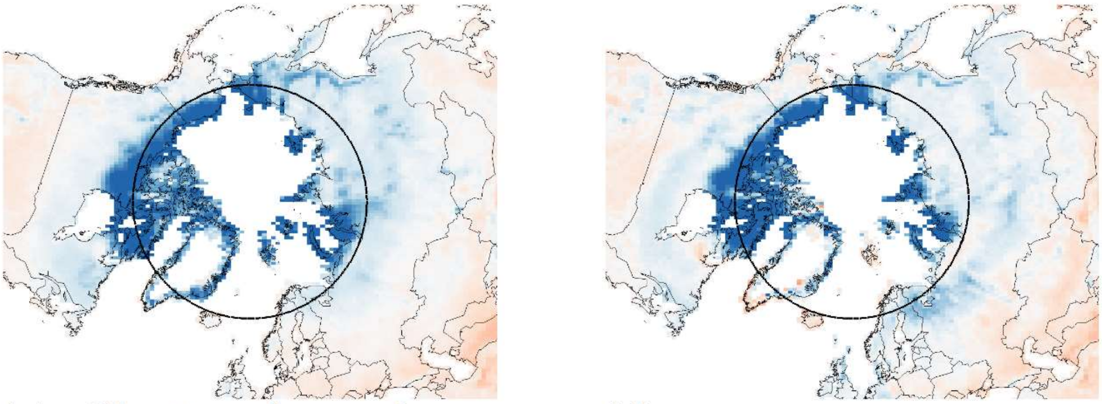
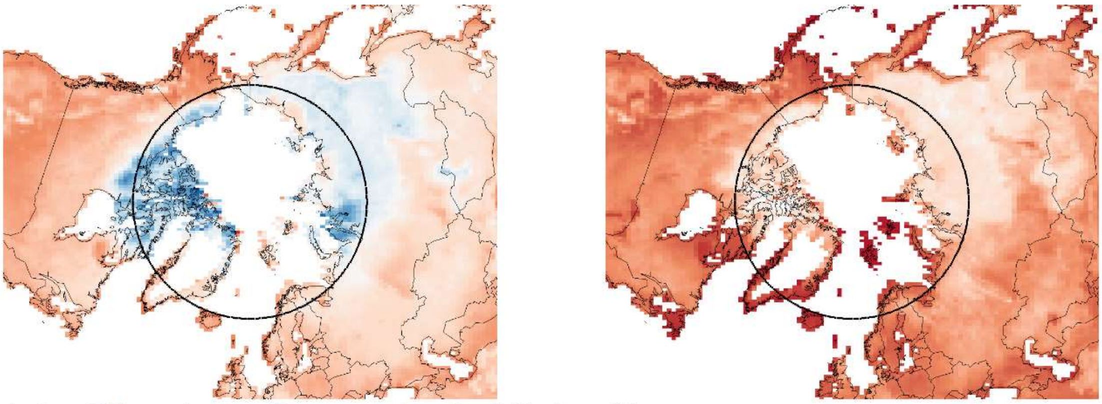


Figure S2.3. Projected change in proportional species richness by 2070 under SSP 1-2.6 for Palearctic and Nearctic terrestrial birds and mammals derived from summed individual species ensemble model projections. Richness for (a) birds and (b) mammals from models based solely on the extent of suitable climate. Richness for (c) birds and (d) mammals accounting for both climate and dispersal capability. Richness projections accounting for climate, habitat and dispersal for (e) birds and (f) mammals. Maps plotted in Polar Stereographic projection. Black bold line shows the Arctic Circle. Species icons from phylopic (https://www.phylopic.org/).

(a) Climate (b)



(c) Climate + dispersal (d)



(e) Climate + dispersal + habitat (f)

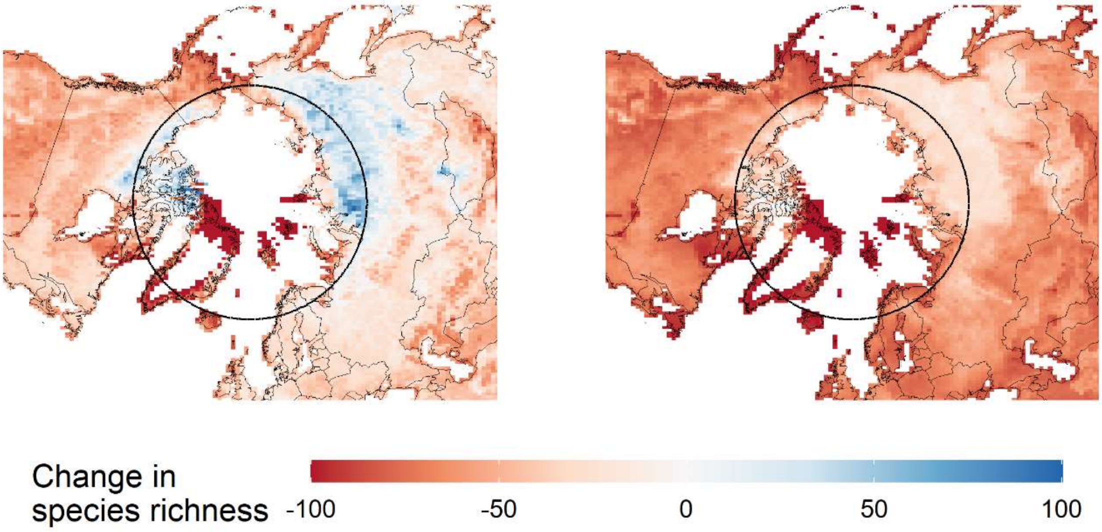
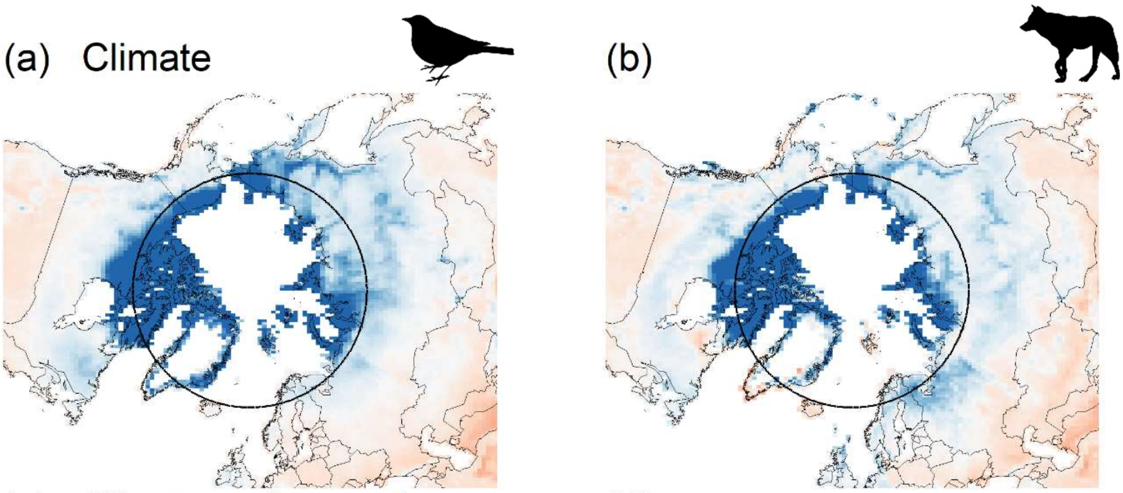
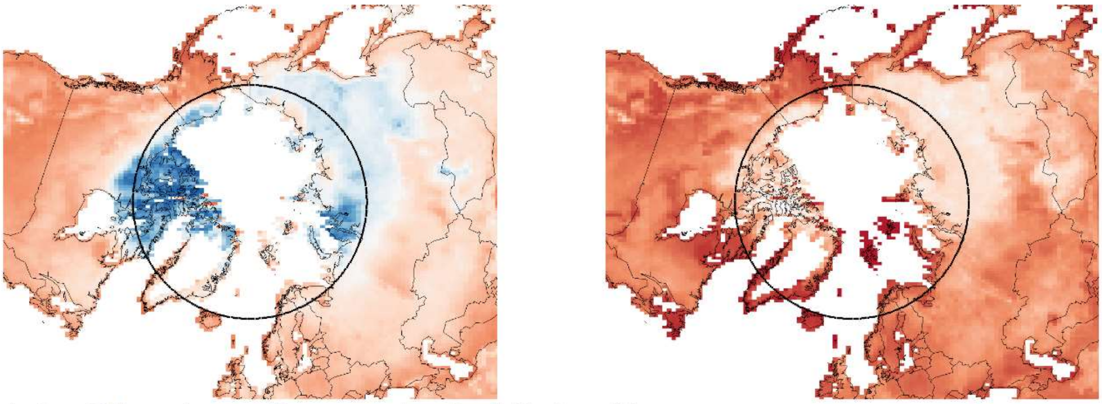


Figure S2.4. Projected change in proportional species richness by 2070 under SSP 2-4.5 for Palearctic and Nearctic terrestrial birds and mammals derived from summed individual species ensemble model projections. Richness for (a) birds and (b) mammals from models based solely on the extent of suitable climate. Richness for (c) birds and (d) mammals accounting for both climate and dispersal capability. Richness projections accounting for climate, habitat and dispersal for (e) birds and (f) mammals. Maps plotted in Polar Stereographic projection. Black bold line shows the Arctic Circle. Species icons from phylopic (https://www.phylopic.org/).

(a) Climate (b)



(c) Climate + dispersal (d)



(e) Climate + dispersal + habitat (f)

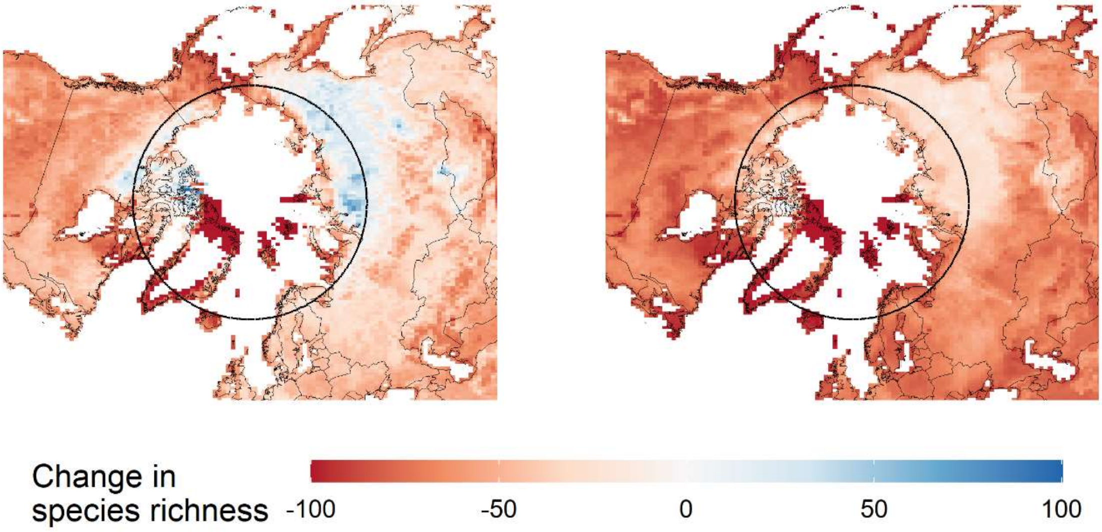


Figure S2.5. Projected change in proportional species richness by 2070 under SSP 2-4.5 for Palearctic and Nearctic terrestrial birds and mammals derived from summed individual species ensemble model projections. Richness for (a) birds and (b) mammals from models based solely on the extent of suitable climate. Richness for (c) birds and (d) mammals accounting for both climate and dispersal capability. Richness projections accounting for climate, habitat and dispersal for (e) birds and (f) mammals. Maps plotted in Polar Stereographic projection. Black bold line shows the Arctic Circle. Species icons from phylopic (https://www.phylopic.org/).

Appendix B: Supporting material for Chapter 3

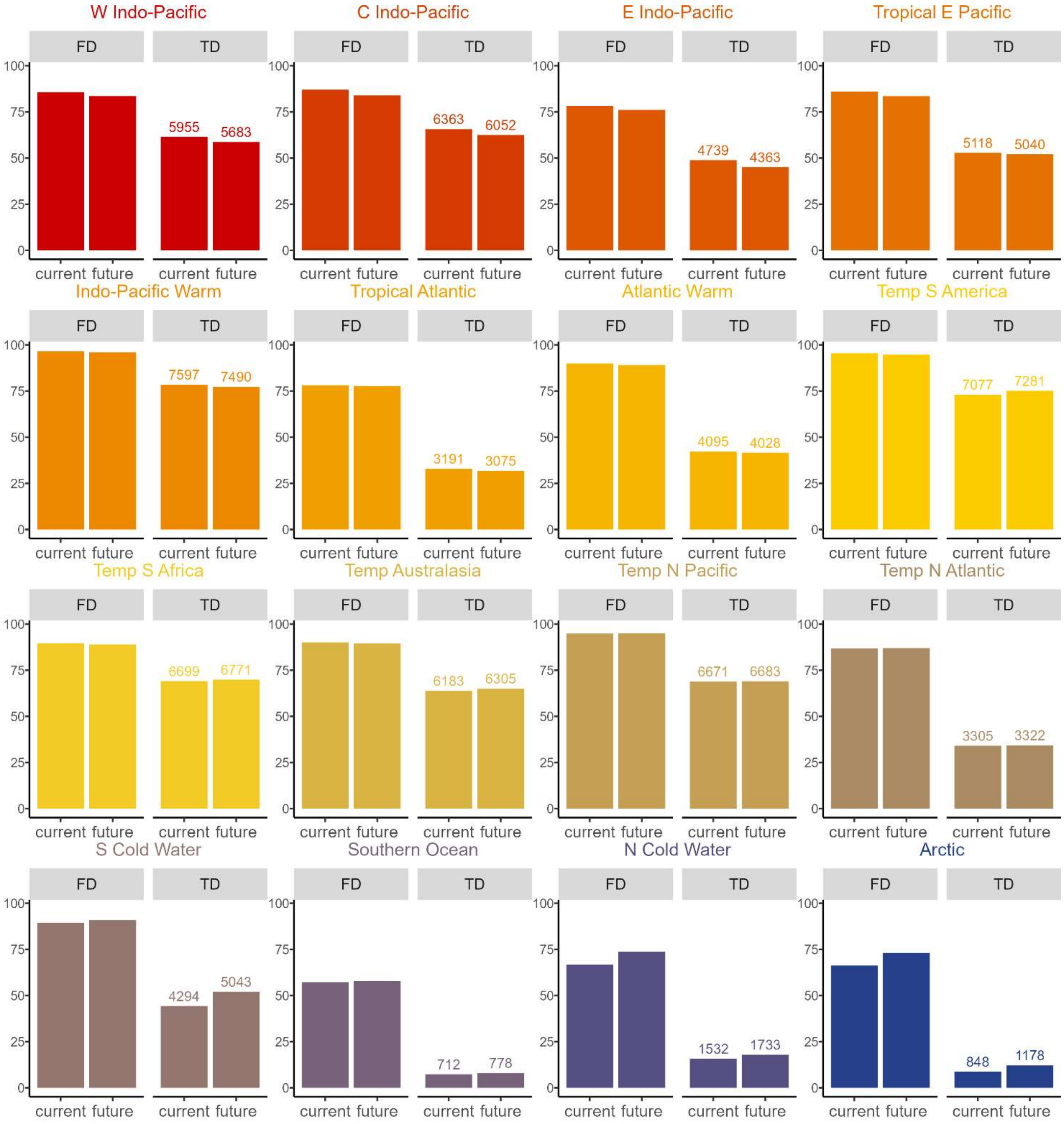


Figure S3.1. Functional diversity (FD) and taxonomic diversity (TD), represented as a proportion of the global diversity, for current fish assemblages and under RCP 6.0 climate change scenario (2100) for the 16 biogeographic realms (shown on the map in Figure S3.2). Total number of species projected to occur in each realm and each time-period is shown above the TD bars.

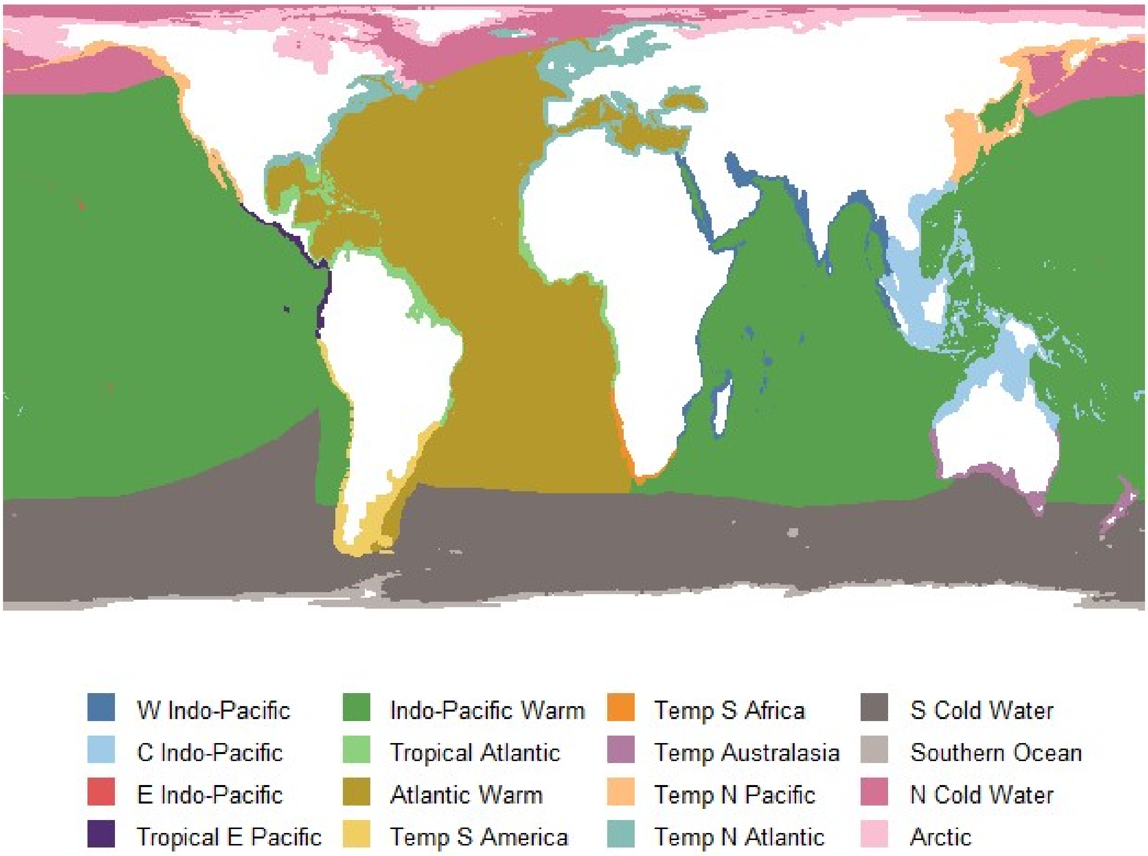
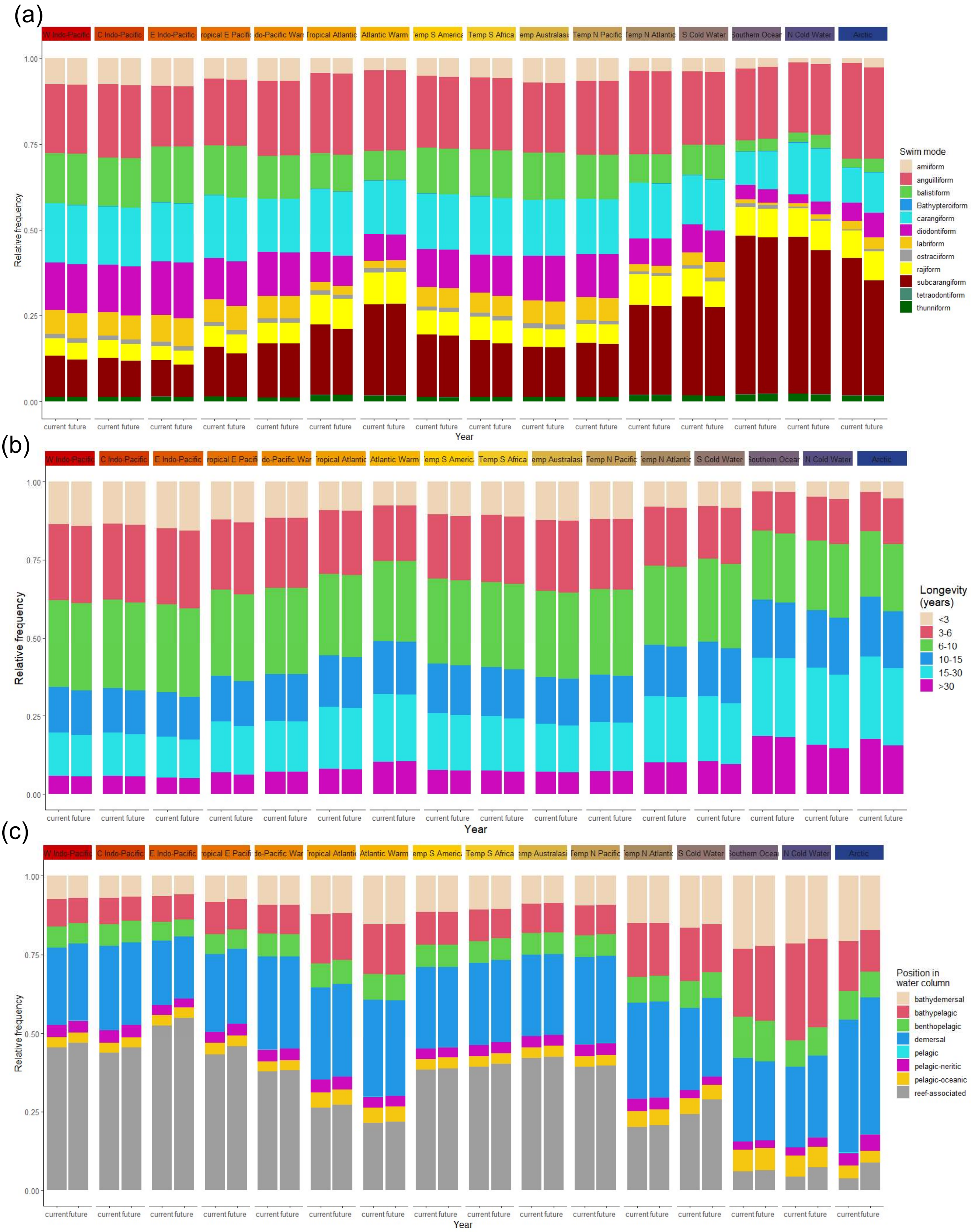
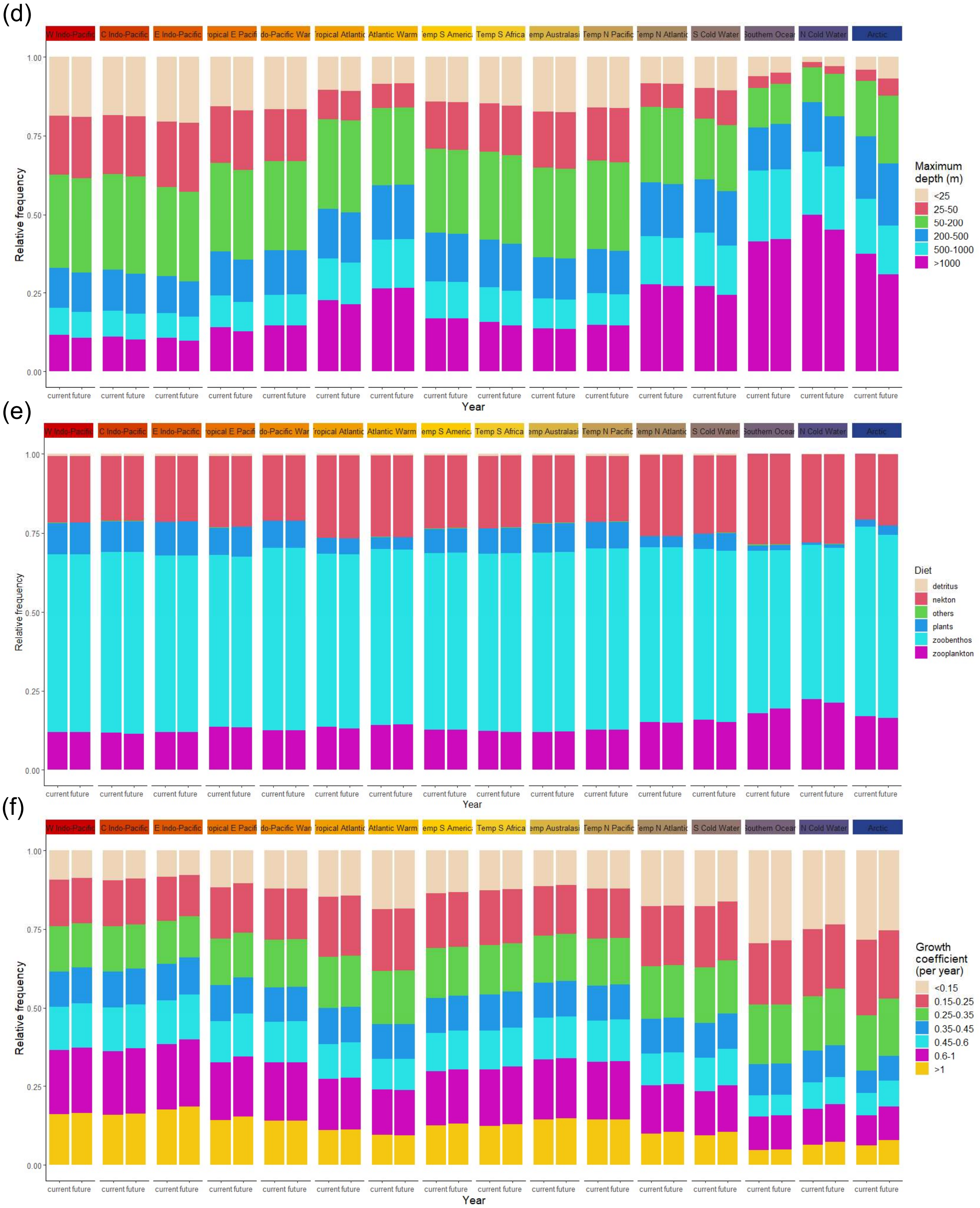
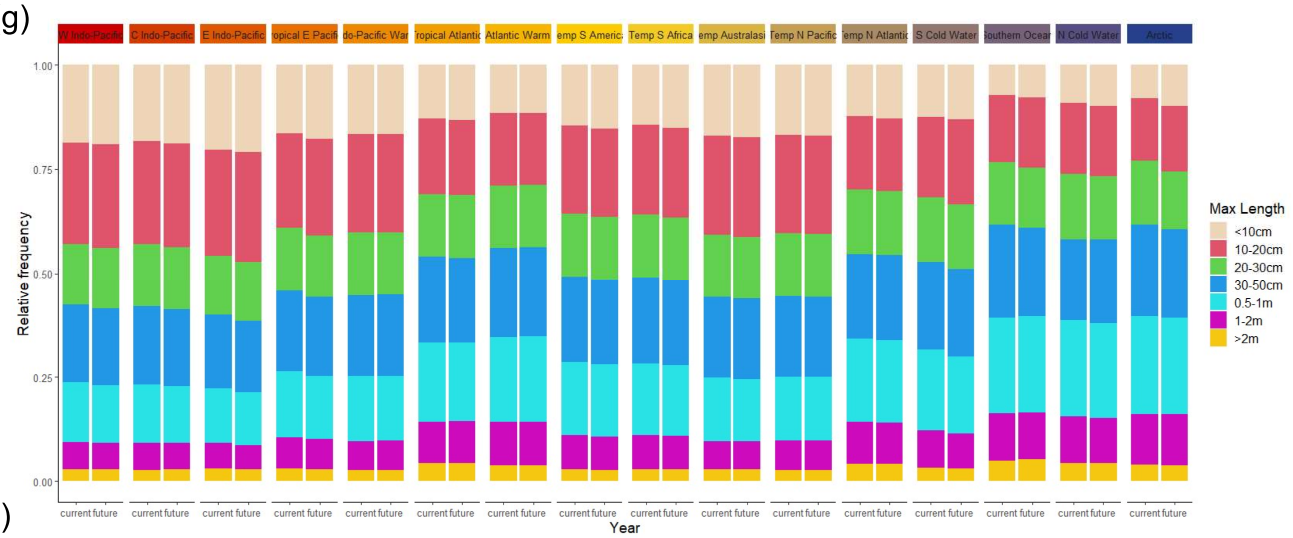


Figure S3.2. Map of marine biogeographic realms created using the Marine Ecoregions of the World (MEOW; (Spalding et al., 2007) and Pelagic Provinces of the World (PPOW; Spalding et al. 2012).


(a)
W Indo-Pacific
C Indo-Pacific
E Indo-Pacific
ropical E Pacific
do-Pacific War
Tropical Atlantic
Atlantic Warm
Temp S America
Temp S Africa
emp Australasi
Temp N Pacific
Temp N Atlantic
S Cold Water
Southern Ocean
N Cold Water
Arctic
Relative frequency
1.00
0.75
0.50
0.25
0.00
current future
Year
Swim mode
amiiform
anguilliform
balistiform
Bathypteroiform
carangiform
diodontiform
labriform
ostraciiform
rajiform
subcarangiform
tetraodontiform
thunniform
(b)
Relative frequency
Year
Longevity (years)
<3
3-6
6-10
10-15
15-30
>30
(c)
Relative frequency
Year
Position in water column
bathydemersal
bathypelagic
benthopelagic
demersal
pelagic
pelagic-neritic
pelagic-oceanic
reef-associated


(d)
W Indo-Pacific
C Indo-Pacific
E Indo-Pacific
ropical E Pacifi
do-Pacific War
ropical Atlantic
Atlantic Warm
emp S Americ
Temp S Africa
emp Australasi
Temp N Pacific
emp N Atlantic
S Cold Water
Southern Ocear
N Cold Water
Arctic
Relative frequency
1.00
0.75
0.50
0.25
0.00
current future
Year
Maximum depth (m)
<25
25-50
50-200
200-500
500-1000
>1000
(e)
Diet
detritus
nekton
others
plants
zoobenthos
zooplankton
(f)
Growth coefficient (per year)
<0.15
0.15-0.25
0.25-0.35
0.35-0.45
0.45-0.6
0.6-1
>1

(g)


W Indo-Pacific
C Indo-Pacific
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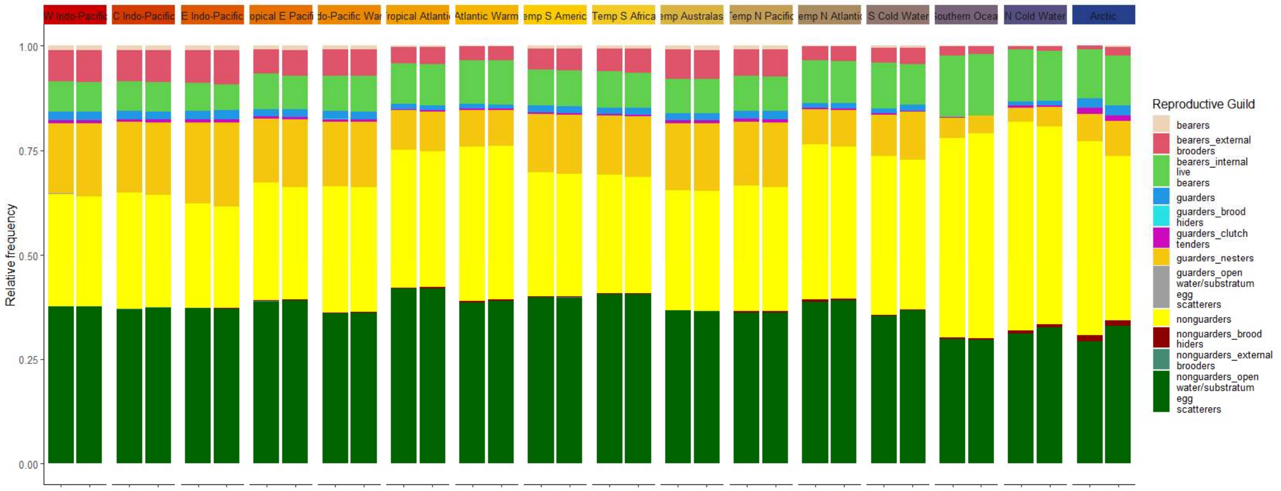
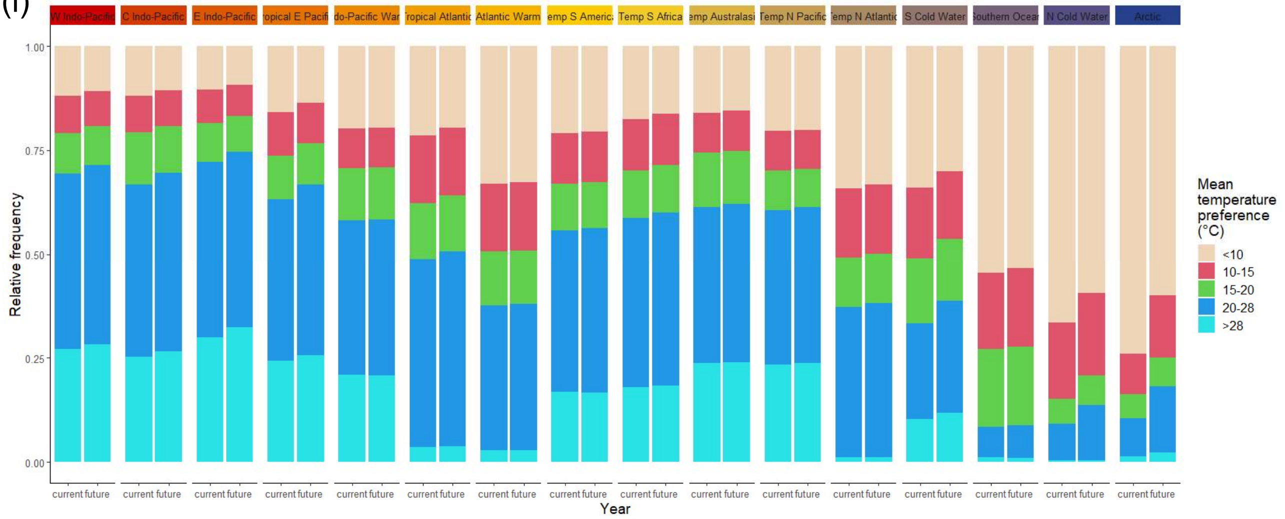
do-Pacific War
ropical Atlantic
Atlantic Warm
emp S Americ
Temp S Africa
emp Australas
Temp N Pacific
emp N Atlantic
S Cold Water
outhern Ocea
N Cold Water
Arctic
1.00
0.75
0.50
0.25
0.00
Relative frequency
current future
Year
Max Length
<10cm
10-20cm
20-30cm
30-50cm
0.5-1m
1-2m
>2m

(h)


W Indo-Pacific
C Indo-Pacific
E Indo-Pacific
opical E Pacifi
do-Pacific War
ropical Atlantic
Atlantic Warm
emp S Americ
Temp S Africa
emp Australas
Temp N Pacific
emp N Atlantic
S Cold Water
outhern Ocea
N Cold Water
Arctic
1.00
0.75
0.50
0.25
0.00
Relative frequency
current future
Year
Reproductive Guild
bearers
bearers_external brooders
bearers_internal live bearers
guarders
guarders_brood hiders
guarders_clutch tenders
guarders_nesters
guarders_open water/substratum egg scatterers
nonguarders
nonguarders_brood hiders
nonguarders_external brooders
nonguarders_open water/substratum egg scatterers

(i)


W Indo-Pacific
C Indo-Pacific
E Indo-Pacific
opical E Pacifi
do-Pacific War
ropical Atlantic
Atlantic Warm
emp S Americ
Temp S Africa
emp Australas
Temp N Pacific
emp N Atlantic
S Cold Water
outhern Ocea
N Cold Water
Arctic
1.00
0.75
0.50
0.25
0.00
Relative frequency
current future
Year
Mean temperature preference (°C)
<10
10-15
15-20
20-28
>28

(j)

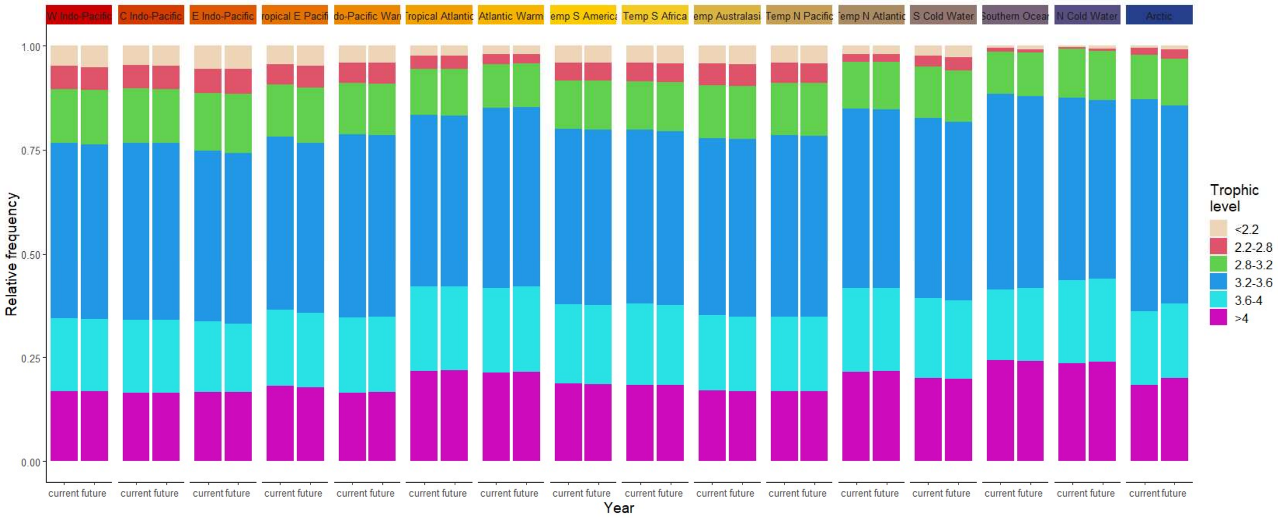


Figure S3.3. Comparison between the relative frequencies of trait categories (a-j) for each realm for current climate and future climate change under RCP 6.0. Descriptions of traits can be found in Chapter 3 Table 3.1. Continuous traits were binned into relevant categories.

Appendix C: Supporting material for Chapter 4

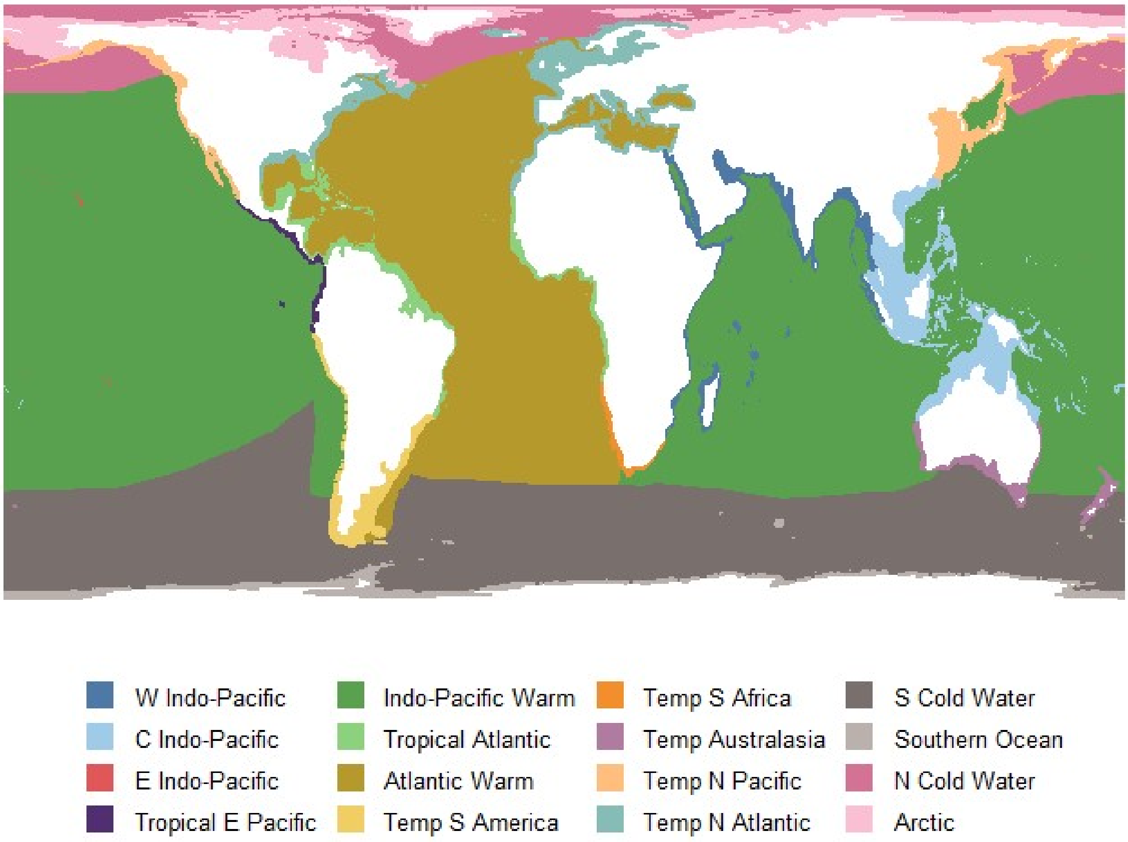


Figure S4.1. Map of marine biogeographic realms created using the Marine Ecoregions of the World (MEOW; Spalding et al., 2007) and Pelagic Provinces of the World (PPOW; Spalding et al. 2012).

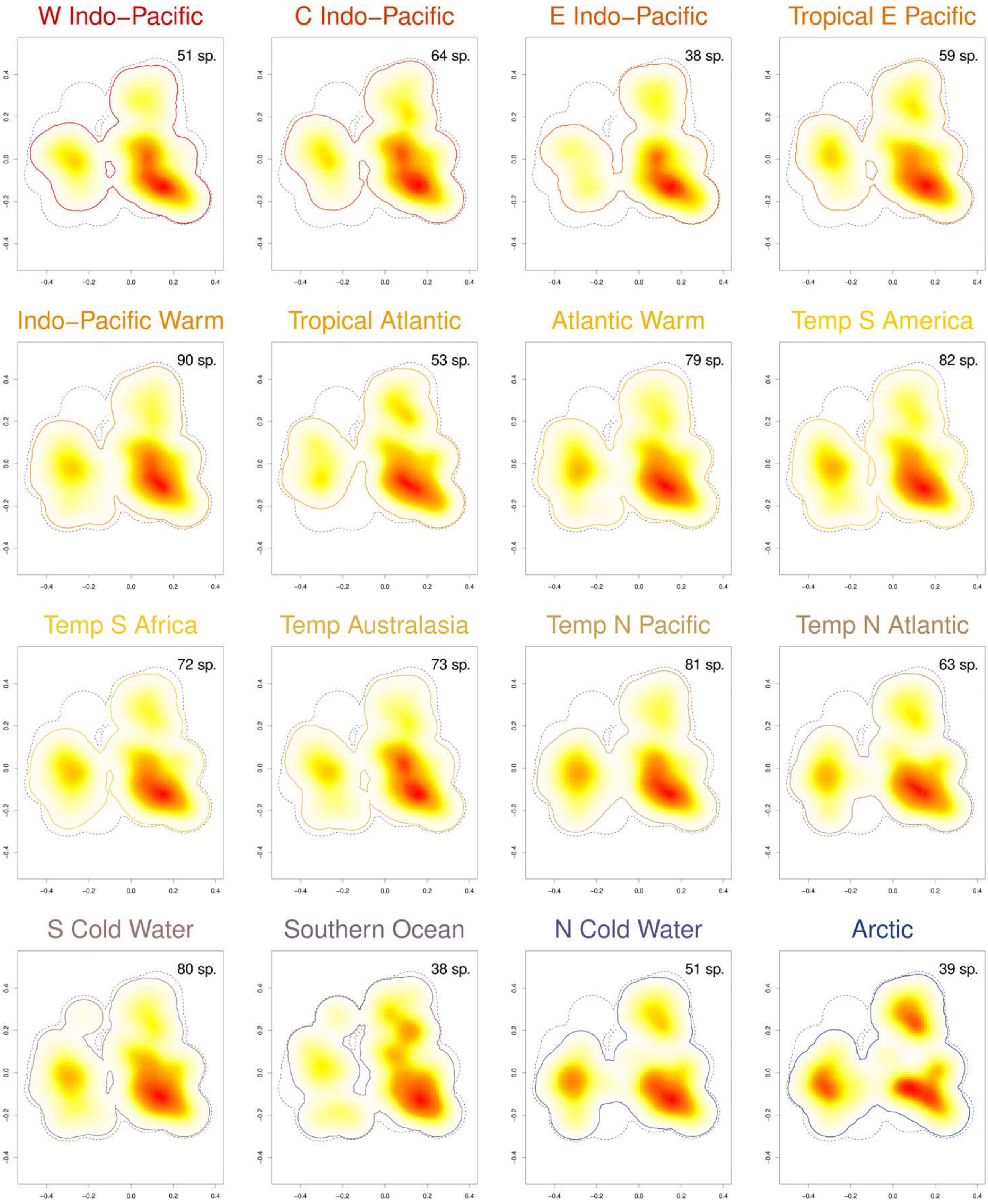


Figure S4.2. Functional spectra of marine mammals by marine realm. Contribution of each continuous and categorical trait to the first two PCoA axes of the four-dimensional trait space can be found in Fig. 1. The number of species within each realm is shown. The grey dotted line indicates the global functional spectra. The colour gradient indicates 50, 95 and 99% contours of species density where darker red colours indicate hotspots of species density. Each functional spectra 99% contour is marked as a solid line in the associated realm colour.

Appendix D: Supporting material for Chapter 5

Supplementary methods

Species distribution models (SDMs)

MaxEnt

MaxEnt models are a particularly popular method for SDMs and were specifically designed for handling presence-only species data (Phillips et al., 2009). Models were performed using Maxent software version 3.4.3. We used the full available range of model regularization multipliers and features when running MaxEnt: 0.5, 1, 2, 3, 4 for beta-multipliers and LQHP, LQH, LQ, H, and L for feature types. Models were initially run using all combinations of multipliers and features and then fine-tuned by selecting the parameters for the best model. Models were run using the 'maxent' function in the 'dismo' package (Hijmans et al., 2022). Models were predicted using 'cloglog' response type.

Generalised Additive Models (GAMs)

GLMs fit with third-order polynomials were run with species occurrence as the response variable and the five bioclimatic variables as predictors. Models were fitted to nine blocks whilst excluding one block at a time. Model performance was assessed using the omitted block using AUC. The combination of polynomial terms that maximized AUC across the 10 omitted blocks was used to fit a final set of 10 models.

Boosted Regression Trees (BRTs)

BRTs, a machine learning method, were produced using the 'gbm' package in R (Greenwell et al., 2019). The models were parametrized using the following cross-validation approach. We excluded one block in turn and fitted a BRT with 5,000 trees using 0.001 as the learning rate and values of tree complexity varied between 1 and 4. The value of tree complexity that minimized the total error across the testing blocks was used to fit a final set of 10 models.

Random Forests (RFs)

RFs were generated using the 'randomForest' package in R (Liaw & Wiener, 2002). The models were cross-validated using a similar method to that described above. The number of predictors in each random subset used to build each tree varied between one and three. RTs were fit initially with 1,000 trees, omitting one block at a time for cross-validation. We then increased the number of trees by 500 tree increments until AUC (model performance) was <1%.

Ecopath with Ecosim (EwE) models

Ecopath food web model (baseline model)

Ecopath with Ecosim (EwE) version 6.6.8 modelling software was used for ecosystem model development (Christensen & Walters, 2004; Walters et al., 1997). Ecopath models are a time-static, mass-balanced 'snapshot' of biomass in an ecosystem, represented by trophically linked functional groups for a specific time-period. To ensure that the total energy flow between functional groups is balanced, energy production of lower trophic levels must be able to support the energy demands of higher trophic levels (Eddy et al., 2021). Functional groups of the food web are characterized by production and consumption rates and are connected through feeding interactions (Equation. 1).

$$B_i \cdot \left(\frac{P}{B}\right)_i = \sum_j B_j \cdot \left(\frac{Q}{B}\right)_j \cdot DC_{ij} + Y_i + E_i + B_i \cdot \left(\frac{P}{B}\right)_i \cdot (1 - EE_i) \qquad (1)$$

Where B_i = biomass of functional group i; P/B = production per unit of biomass of the functional group i; $(Q/B)_j$= consumption per unit of biomass of the predator j of biomass B_j; DC_{ij} = proportion of prey i in the diet of predator j; Y_i = exports from the system as fishery catches; E_i = net migration; EE_i = ecotrophic efficiency (the fraction of total production of one functional group that is consumed by other groups) of the functional group i. Losses of energy intake or consumption for each functional group are represented by Equation 2

$$B_i \cdot \left(\frac{Q}{B}\right)_i = B_j \cdot \left(\frac{P}{B}\right)_j + B_j \cdot \left(\frac{R}{B}\right)_j + \left(\frac{U}{Q}\right)_j \qquad (2)$$

Where $(R/B)_j$ = respiration rate per unit of biomass; $(U/Q)_j$ = fraction of food consumption that is not assimilated. Consumer functional groups are balanced energetically such that consumption for each trophic group is the sum of production, respiration, and unassimilated food (Christensen & Walters, 2004; Walters et al., 1997). At least three of the four basic parameters (*P/B*, *Q/B*, *B*, and *EE*) in the two equations, as well as diet compositions and fisheries catch (and migration if known) must be input directly, while ideally, *EE* is estimated, as no procedure exists for its field estimation. The model is considered balanced when the *EE* for each group is between 0 and 1 indicating that there is enough production from prey to support predator consumption. In cases where *B*, *P/B* or *Q/B* are unknown, *EE* can be input, forcing the model to estimate the other key parameters (Christensen et al., 2008; Heymans et al., 2014). The model is considered balanced when EE < 1 for all functional groups.

Ecosim model (Novel ecosystem scenarios)

The Ecosim framework, simulates the dynamics of marine ecosystems, with the key initial parameters provided by the baseline Ecopath model. Ecosim focuses on modeling the interactions between different species within an ecosystem. This includes predator-prey relationships, competition for resources, and other ecological processes that influence the population dynamics of species. Ecosim models the changes in the ecosystem over time. It takes into account factors like reproduction rates, mortality rates, and environmental changes to simulate how the populations of different species evolve and interact with each other over days, months, or years. Once the model is set up, Ecosim runs simulations to see how the ecosystem responds to different scenarios; in our case, responses to defined biomass changes of specific functional groups or the introduction of new species to understand how these factors impact the overall food web (Christensen et al., 2008).

Supplementary tables

Table S5.1. References for parameter estimates for the North Water Polynya Ecopath model. *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio. Modified from Bryndum-Buchholz et al. (Bryndum-Buchholz et al., 2024).

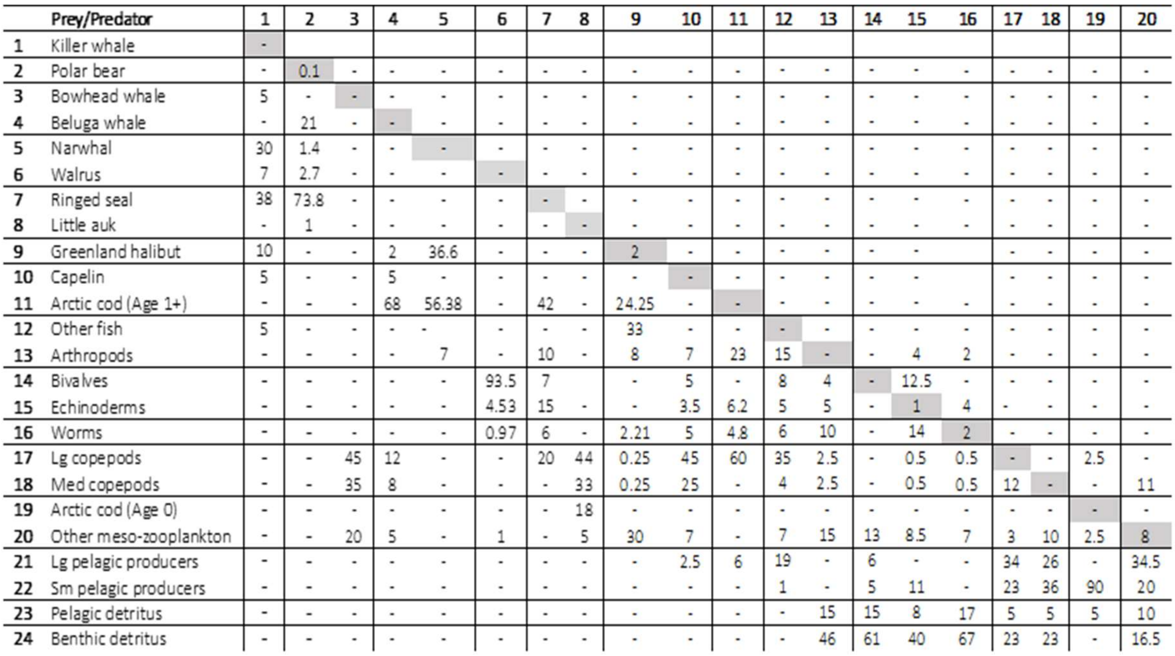
Functional group		***B***	***P/B***	***Q/B***	**Conversion factors**	**Diet matrix**
1	Killer whale	--------	(Pedro et al., 2023)	(Lefort et al., 2020)	--------	(Ferguson et al., 2012; Lefort et al., 2020; Pedro et al., 2023)
2	Polar bear	(York et al., 2016)	(Heide-Jørgensen et al., 2013; York et al., 2016)	--------	-------	(Hoover et al., 2021; Pedro et al., 2023)
3	Bowhead whale	(Boertmann et al., 2015; Heide-Jørgensen et al., 2013, 2016)	(Pedro et al., 2023)	(Banas et al., 2021)	-------	(Pedro et al., 2023)
4	Beluga whale	(Heide-Jørgensen et al., 2013)	(Hoover et al., 2021; NAMMCO, 2016)	(Hoover et al., 2021; Innes et al., 1987)	-------	(Hobson et al., 2002; Hoover et al., 2021; Thiemann et al., 2008)

5	Narwhal	(Heide-Jørgensen et al., 2013)	--------	(Pedro et al., 2023)	--------	
6	Walrus	(Witting & Born, 2005)	(NAMMCO, 2016; Witting & Born, 2013)	(Innes et al., 1987)	-------	(Born et al., 1995; Dietz et al., 2014; Mansfield, 1959; Outridge et al., 2003; Vibe, 1950)
7	Ringed seal	(Kingsley, 1998)	(Hoover et al., 2021; NAMMCO, 2016)	(Innes et al., 1987)	-------	(Hoover et al., 2021; Kelly et al., 2010; Kovacs, 2014)
8	Little auk	(Boertmann & Mosbech, 1998; Egevang et al., 2003)	(Mosbech et al., 2018)	(Tam & Bundy, 2019)	-------	(Fort et al., 2010; Karnovsky & Hunt, 2002; Montevecchi et al., 2002; Pedersen & Falk, 2001; Rosing-Asvid et al., 2013; Wojczulanis-Jakubas et al., 2022)
9	Greenland halibut	(Treble, 2005, 2013)	FishBase	FishBase	--------	(Giraldo et al., 2018; Pedro et al., 2023)
10	Capelin	--------	FishBase	FishBase	--------	(Hoover et al., 2021)
11	Arctic cod (Age 1+)	Max Geoffroy (pers. comm.)	FishBase	FishBase	-------	(Craig et al., 1982; Dodson et al., 2007; Hoekstra et al., 2003; Lacho, n.d.)
12	Other fish	-------	(Hoover et al., 2021)	(Hoover et al., 2021)	-------	(Harris et al., 2022; Scott & Scott, 1988)

13	Arthropods	Archambault lab (pers. comm.); (Mäkelä et al., 2017)	(Hoover et al., 2021)	(Jatte-Teichmann et al., 1997)	-------	(Arndt & Swadling, 2006; Carey Jr & Ruff, 1977; Pedro et al., 2023)
14	Bivalves	Archambault lab (pers. comm.); (Mäkelä et al., 2017)	(Hoover et al., 2021)	(Christensen et al., 2005)	-------	(Hoover et al., 2021; Pedro et al., 2023)
15	Echinoderms	Archambault lab (pers. comm.); (Mäkelä et al., 2017)	(Hoover et al., 2021)	(Jatte-Teichmann et al., 1997)	-------	(Hoover et al., 2021; Pedro et al., 2023)
16	Worms	Archambault lab pers. comm.; (Mäkelä et al., 2017)	(Hoover et al., 2021)	(Jatte-Teichmann et al., 1997)	-------	(Hoover et al., 2021; Pedro et al., 2023)
17	Lg copepods	Gérald Darnis (pers. comm.)	(Arnkværn et al., 2005; Breteler et al., 1995; Hirst & Kiørboe, 2002; Ohman & Wood, 1995)	(Hoover et al., 2021)	-------	(Hoover et al., 2021; Pedro et al., 2023; Tam & Bundy, 2019)
18	Med copepods	Gérald Darnis (pers. comm.)	(Arnkværn et al., 2005; Breteler et al., 1995; Hirst & Kiørboe, 2002; Ohman & Wood, 1995)	(Hoover et al., 2021)	-------	(Hoover et al., 2021; Pedro et al., 2023; Tam & Bundy, 2019)
19	Arctic cod (Age 0)	Max Geoffroy (pers. comm.)	(Tam & Bundy, 2019)	(Tam & Bundy, 2019)	-------	(Hoover et al., 2021)

20	Other meso-zooplankton	Gérald Darnis (pers. comm.)	(Arnkværn et al., 2005; Breteler et al., 1995; Hirst & Kiørboe, 2002; Ohman & Wood, 1995)	(Hoover et al., 2021)	-------	(Bouchard & Fortier, 2020; Pedro et al., 2023; Tam & Bundy, 2019)
21	Sm pelagic producers	(Ardyna et al., 2011)	(Hoover et al., 2021)	-------	(Pauly & Christensen, 1995)	-------
22	Lg pelagic producers	(Ardyna et al., 2011)	(Hoover et al., 2021)	-------	(Pauly & Christensen, 1995)	-------
23	Pelagic detritus	(Hoover et al., 2021)	-------	-------	-------	-------
24	Benthic detritus	(Hoover et al., 2021)	-------	-------	-------	-------

Table S5.2. Diet matrix for the NOW polynya Ecopath models (Killer whale only for Scenario 4). Diets are expressed as a relative proportion (%) of the total diet. Diets in gray shading indicate cannibalizing trophic groups. Columns are predators; rows are prey.



	Prey/Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20
1	Killer whale	-																			
2	Polar bear	-	0.1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
3	Bowhead whale	5	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
4	Beluga whale	-	21	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
5	Narwhal	30	1.4	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
6	Walrus	7	2.7	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
7	Ringed seal	38	73.8	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
8	Little auk	-	1	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-
9	Greenland halibut	10	-	-	2	36.6	-	-	-	2	-	-	-	-	-	-		-	-	-	-
10	Capelin	5	-	-	5	-	-	-	-	-	-	-	-	-	-	-		-	-	-	-
11	Arctic cod (Age 1+)	-	-	-	68	56.38	-	42	-	24.25	-	-	-	-	-	-	-	-	-	-	-
12	Other fish	5	-	-	-	-	-	-	-	33	-	-	-	-	-	-	-	-	-	-	-
13	Arthropods	-	-	-	-	7	-	10	-	8	7	23	15	-	-	4	2	-	-	-	-
14	Bivalves	-	-	-	-	-	93.5	7		-	5	-	8	4	-	12.5	-	-	-	-	-
15	Echinoderms	-	-	-	-	-	4.53	15	-	-	3.5	6.2	5	5	-	1	4	-	-	-	-
16	Worms	-	-	-	-	-	0.97	6	-	2.21	5	4.8	6	10	-	14	2	-	-	-	-
17	Lg copepods	-	-	45	12	-	-	20	44	0.25	45	60	35	2.5	-	0.5	0.5	-	-	2.5	-
18	Med copepods	-	-	35	8	-	-	-	33	0.25	25	-	4	2.5	-	0.5	0.5	12	-	-	11
19	Arctic cod (Age 0)	-	-	-	-	-	-	-	18	-	-	-	-	-	-	-	-	-	-	-	-
20	Other meso-zooplankton	-	-	20	5	-	1	-	5	30	7	-	7	15	13	8.5	7	3	10	2.5	8
21	Lg pelagic producers	-	-	-	-	-	-	-	-	-	2.5	6	19	-	6	-	-	34	26	-	34.5
22	Sm pelagic producers	-	-	-	-	-	-	-	-	-	-	-	1	-	5	11	-	23	36	90	20
23	Pelagic detritus	-	-	-	-	-	-	-	-	-	-	-	-	15	15	8	17	5	5	5	10
24	Benthic detritus	-	-	-	-	-	-	-	-	-	-	-	-	46	61	40	67	23	23	-	16.5

Table S5.3. Novel ecosystem hypotheses and supporting literature underlying Ecosim scenarios for the North Water (NOW) polynya.

Hypotheses and scenarios	**Supporting references**
1. Future climate change will impact primary production in the NOW Polynya. **Scenario 1.1:** Pelagic primary producer biomass increases due to longer growing season caused by increase in both the extent and duration of the open water season, enhancing average annual light availability for photosynthesis. **Scenario 1.2:** Pelagic primary producer biomass biomass decreases due to nutrient limitation caused by reduced mixing and/or upwelling, increasing stratification or reduced light penetration due to increased drifting of ice through the NOW polynya (no ice bridge condition).	1. (Hornby et al., 2021) Scenario 1.1: (Arrigo & van Dijken, 2011; Meredith et al., 2019) Scenario 1.2: (Buchart et al., 2022; Kyhn & Mosbech, 2019)
2. Zooplankton biomass and composition will be altered due to climate-induced environmental changes (e.g., increasing water temperatures, predation as new species invade from the south) **Scenario 2.1:** Shift in size composition structure in the *Calanus* community, due to increasing biomass of smaller and less fat calanoid copepod species (e.g., *Calanus finmarchicus*). **Scenario 2.2:** Biomass decrease due to mismatch caused by earlier onset of phytoplankton spring bloom, which escapes zooplankton grazing, and/or overall reduced primary production	2. (Hornby et al., 2021) Scenario 2.1: (Heneghan et al., 2023; Møller & Nielsen, 2020) Scenario 2.2: (Bélanger et al., 2013)
3. With the northward shift of forage fish into the NOW polynya, primarily due to warming waters, biomass of Arctic cod will be impacted. **Scenario 3:** Replacement of Arctic cod by capelin, a zooplankton predator in direct competition with Arctic cod for resources, due to climate-driven abundance increase of capelin in the NOW Polynya	Scenario 3: (Hornby et al., 2021; Kyhn & Mosbech, 2019)
4. Increased access for southern marine top predator due climate-driven sea ice reductions **Scenario 4:** Northward expansion of killer whales leads to greater predation pressure on other large arctic mammals, such as narwhal, beluga, and seals.	(Hornby et al., 2021)

Table S5.4. Ecosim sensitivity analysis parameter (B) changes compared to the initial scenarios.

Scenario	Ecopath parameter changes	Initial scenarios	Increments for sensitivity analysis (%)	Assumptions and supporting literature
1.1	Increase *B* of large and small pelagic producers.	10% increase in large pelagic producers; 10% increase in small pelagic producers.	5%, 10%, 15%	(Tagliabue et al., 2021; Tittensor et al., 2021)
1.2	Decrease *B* of large and small pelagic producers.	15% decrease in large pelagic producers; 15% decrease in small pelagic producers	-10%, -15%, -20%, -25%	Based on CMIP6 ensemble mean in CHL-a projections (SSP1-RC8.5), and relative change (2080-2099 relative to 1981-2000) from Noh et al. (2023)
2.1	Increase *B* *r*atio between large and medium copepods.	Increase ratio by 10:90	20:80; 40:60; 50:50	(Heneghan et al., 2023; Møller & Nielsen, 2020)
2.2	Decrease *B* of large and medium copepods.	10% decrease (each) in large and medium copepods.	-15%, -20%, -25%	Maximum change based on projected CMIP6 SSP1-85 omnivorous zooplankton change (2080-2100 relative to 1980-2000) in the NOW region from Heneghan et al. (2023). This range covers the maximum and the average decrease for total zooplankton in the poles.
3	Increase *B* of capelin; decrease *B* of Arctic cod (Age 1+).	40% increase in capelin, 15% decrease in Arctic cod (Age 1+).	Capelin: 10%, 20%, 50%, 60%; Arctic cod: -5%, -10%, -20%, -25%	Based on assumption of trophic amplification, supported by Heneghan et al. (2023): Small pelagic change in response to lower trophic level changes is larger than changes in primary producers and zooplankton change.
4	Increase *B* of killer whale, capelin, and	20% increase in killer whale, 40% increase	Killer whale: 10%, 30%, 40%, 50%	

	Arctic cod (Age 1+).	in capelin, 15% decrease in Arctic cod (Age 1+).		

S5.5 Table. AUC results for the four species distribution modeling techniques (Generalized Additive Models (GAM), Boosted Regression Trees (BRT), Maximum Entropy (MaxEnt) and Random Forests (RF)) for the four species across each of the ten blocks.

Model type	**Block**	**AUC**			
		Mallotus villosus	***Boreogadus saida***	***Reinhardtius hippoglossoides***	***Orcinus orca***
GAM	1	0.985	0.955	0.984	0.890
	2	0.986	0.974	0.988	0.892
	3	0.990	0.972	0.992	0.940
	4	0.989	0.951	0.991	0.880
	5	0.990	0.969	0.982	0.907
	6	0.989	0.955	0.987	0.911
	7	0.984	0.949	0.984	0.894
	8	0.992	0.974	0.992	0.881
	9	0.981	0.961	0.989	0.906
	10	0.990	0.955	0.986	0.926
BRT	1	0.989	0.956	0.991	0.902
	2	0.988	0.967	0.985	0.897
	3	0.988	0.966	0.991	0.942
	4	0.987	0.963	0.993	0.901
	5	0.993	0.974	0.989	0.912
	6	0.990	0.959	0.993	0.917
	7	0.978	0.961	0.986	0.903
	8	0.995	0.981	0.993	0.891
	9	0.993	0.976	0.991	0.919
	10	0.992	0.949	0.990	0.933
MaxEnt	1	0.988	0.953	0.991	0.905

	2	0.986	0.971	0.986	0.905
	3	0.988	0.966	0.991	0.941
	4	0.987	0.961	0.992	0.904
	5	0.990	0.974	0.989	0.914
	6	0.992	0.956	0.993	0.915
	7	0.983	0.959	0.988	0.895
	8	0.995	0.980	0.993	0.888
	9	0.987	0.975	0.991	0.921
	10	0.991	0.964	0.989	0.938
RF	1	0.992	0.967	0.994	0.935
	2	0.993	0.974	0.992	0.947
	3	0.989	0.974	0.992	0.953
	4	0.991	0.969	0.996	0.938
	5	0.994	0.984	0.991	0.934
	6	0.991	0.970	0.995	0.946
	7	0.990	0.971	0.993	0.938
	8	0.997	0.990	0.995	0.928
	9	0.991	0.985	0.995	0.943
	10	0.990	0.983	0.992	0.960

Table S5.6. Data pedigree quality classification (Christensen et al., 2005). *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio.

Index	***B***	***P/B* and *Q/B***	**Diet composition**
1	Estimated by Ecopath	Estimated by Ecopath	General knowledge of related group/species
2	From other model	Guesstimate	From other model
3	Guesstimate	From other model	General knowledge for same group/species
4	Approximate or indirect method	Empirical relationship	Qualitative diet composition study
5	Sampling/locally, low precision	Similar species, similar system, low precision	Quantitative but limited diet composition study
6	Sampling/locally, high precision	Similar species, same system, low precision	Quantitative, detailed, diet composition study

7	-	Same species, similar system, high precision	-
8	-	Same species, same system, high precision	-

Table S5.7. Data pedigree indices for the NOW polynya ecosystem models with confidence intervals (+/-%). *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio. Orange shading indicates parameters with highest uncertainty. Sources were assigned an index based on the criteria in Table S2.

Functional group	***B***	***P/B***	***Q/B***	**Diet**
Killer whale	3 (80)	3 (60)	3 (60)	2 (80)
Polar bear	4 (50)	4 (50)	4 (50)	2 (80)
Bowhead whale	4 (50)	3 (60)	7 (20)	2 (80)
Beluga	5 (30)	4 (50)	3 (60)	5 (30)
Narwhal	5 (30)	1 (80)	5 (40)	3 (60)
Walrus	4 (50)	4 (50)	7 (20)	3 (60)
Ringed seal	4 (50)	4 (50)	7 (20)	2 (80)
Little auk	6 (10)	3 (60)	3 (60)	3 (60)
Greenland halibut	5 (30)	4 (50)	4 (50)	2 (80)
Capelin	1 (80)	4 (50)	4 (50)	2 (80)
Arctic cod (Age 1+)	6 (10)	4 (50)	4 (50)	4 (50)
Other fish	1 (80)	5 (40)	5 (40)	1 (80)
Arthropods	5 (30)	3 (60)	3 (60)	2 (80)
Bivalves	5 (30)	3 (60)	3 (60)	2 (80)
Echinoderms	5 (30)	3 (60)	3 (60)	2 (80)
Worms	5 (30)	3 (60)	3 (60)	2 (80)
Large copepods	6 (10)	3 (60)	3 (60)	2 (80)
Medium copepods	6 (10)	3 (60)	3 (60)	2 (80)
Arctic cod (Age 0)	6 (10)	4 (40)	3 (60)	6 (10)
Other meso-zooplankton	1 (80)	2 (70)	2 (70)	2 (80)
Large pelagic producers	6 (10)	6 (30)	-	-
Small pelagic producers	6 (10)	6 (30)	-	-
Pelagic detritus	2 (80)	-	-	-
Benthic detritus	2 (80)	-	-	-

Table S5.8. Magnitude of changes in parameter estimates (%) from initial unbalanced model to balanced model. *B* = Biomass; *P/B* = Production/biomass ratio; *Q/B* = Consumption/biomass ratio.

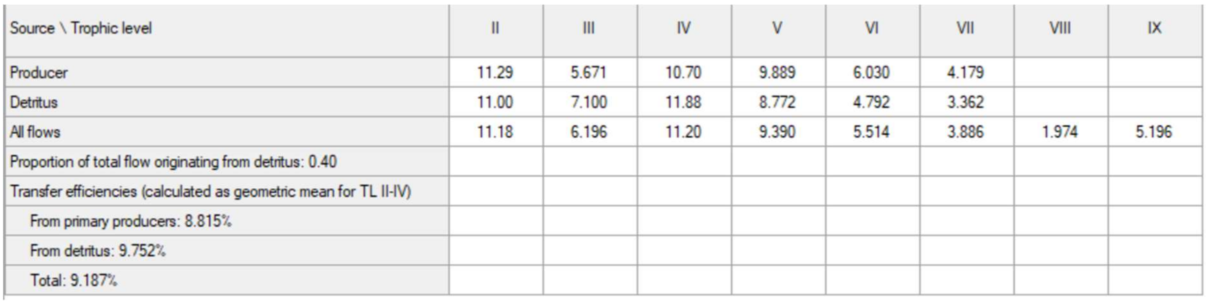
Functional group		***B***	***P/B***	***Q/B***
2	Bowhead whale	+310%	-	-
8	Greenland halibut	+30.92%	-	-
10	Arctic cod (Age 1+)	+18.73%	+25%	-

Table S5.9. Trophic levels reported for the functional groups in the NOW polynya ecosystem and other high Arctic marine ecosystems. TL = trophic level; SE = standard error.

Functional group	**Species**	**Scientific name**	**TL (+/- SE)**	**Source**
Polar bear	Polar bear	*Ursus maritimus*	5.1; 5.5	(Hobson et al., 2002; Hobson & Welch, 1992)
Bowhead whale	Bowhead whale	*Balaena mysticetus*	3.4: 2.8; 2.8 (+/- 0.1); 3.34 (+/- 0.56)	(Hobson et al., 2002; Hoekstra et al., 2003); SeaLifeBase
Beluga whale	Beluga whale	*Delphinapterus leucas*	4.1-4.4	(Hobson et al., 2002)
Narwhal	Narwhal	*Monodon monoceros*	3.7; 4.1	(Hobson et al., 2002; Hobson & Welch, 1992)
Walrus	Atlantic walrus	*Odobenus rosmarus rosmarus*	2.9; 3.2	(Hobson et al., 2002; Hobson & Welch, 1992)
Ringed seal	Ringed seal	*Pusa hispida*	4.4-4.6	(Hobson et al., 2002)
Little auk	Little auk	*Alle alle*	3.2	(Hobson et al., 2002)
Greenland halibut	Greenland halibut	*Reinhardtius hippoglossoides*	4.4 (+/- 0.14 3.9)	FishBase
Capelin	Capelin	*Mallotus villosus*	3.15 (+/- 0.9); 3.19 (+/-0.4)	FishBase
Arctic cod	Arctic cod (Age 1+)	*Boreogadus saida*	3.6; 3.1 (+/- 0.11)	(Hobson et al., 2002); FishBase
Other fish	Arctic char; Lumpfish; Gelatinous seasnail; Thorny skate	*Salvelinus alpinus*; *Cyclopterus lumpus;* *Liparis fabricci;* *Amblyraja radiata*	4.4 (+/- 0.51); 3.3 (+/- 0.42); 3.8; 4.5 +/-0.27	FishBase; FishBase; FishBase; (Hobson et al., 2002), FishBase

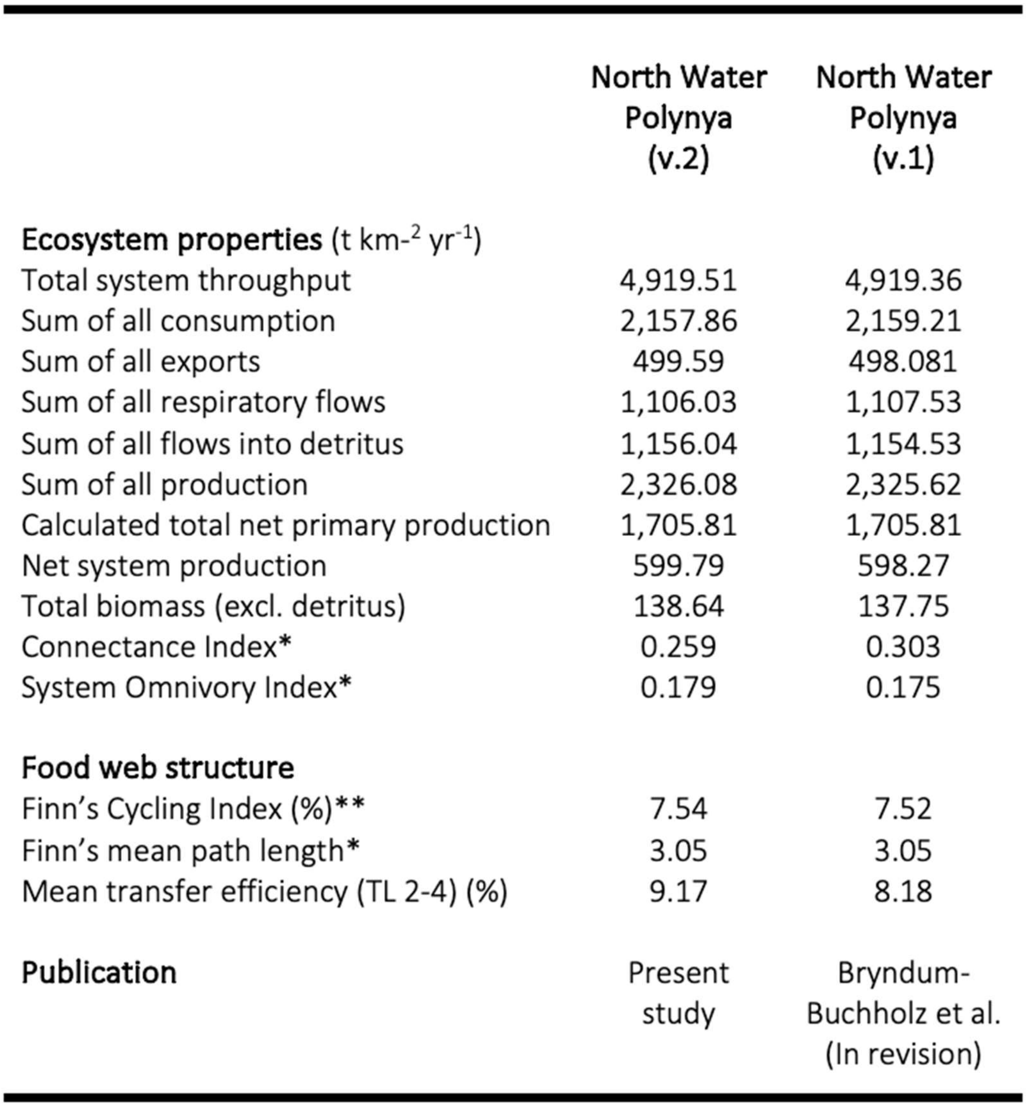
Arthropods	Amphipods; Mysis shrimp; Cold-water prawn	*Acanthostepheia spp.;* *Anonyx nugax;* *Atylus carinatus;* *Mysis oculata ;* *Onisimus sp.;* *Pandalus sp.;* *Themisto abyssorum;* *Themisto libellula*	2.6; 3.4; 2.3; 2.7; 2.6; 3.4; 2.6; 2.5	(Hobson et al., 2002)
Bivalves	Elliptical astarte; Narrow-hinge astarte; Saltwater clams; Broad yoldia; Northern blind limpet	*Astarte elliptica;* *Astarte montagui;* *Macoma sp.;* *Yoldia thraciaeformis;* *Lepeta caeca*	2.2; 3; 1.8; 2; 1.8	(Hobson et al., 2002)
Echinoderms	Sea lilies/Feather stars; Common mud star; Pale urchin; Basket star; Brittle star; Notched brittle star	*Heliometra glacialis;* *Ctenodiscus crispatus;* *Strongylocentrotus pallidus;* *Gorgonocephalus arcticus;* *Ophiophthalmus sp.* *Ophiura sarsi*	3; 3.3; 2.1; 3.1; 3.5; 2.5	(Hobson et al., 2002)
Worms	Bristle worms	*Lumbrineris sp.;* *Phyllodoce mucosa*	3.6; 3.2	(Hobson et al., 2002)
Large copepods	Copepods	*Calanus glacialis;* *Calanus hyperboreus*	2.3; 2	(Hobson et al., 2002)
Medium copepods	Copepods	*Pseudocalanus sp.;* *Calanus finmarchicus*	2.2; 2.37	(Hobson et al., 2002); SeaLifeBase
Arctic cod (Age 0)	Arctic cod (larvae)	*Boreogadus saida*	2.7	(Hobson et al., 2002)
Other meso-zooplankton	Copepod Copepod	*Chiridius obtusifrons* *Metridia longa*	2.6; 2.5	(Hobson et al., 2002)

Table S5.10. Transfer efficiency in the NOW polynya food web.



Source \ Trophic level	II	III	IV	V	VI	VII	VIII	IX
Producer	11.29	5.671	10.70	9.889	6.030	4.179		
Detritus	11.00	7.100	11.88	8.772	4.792	3.362		
All flows	11.18	6.196	11.20	9.390	5.514	3.886	1.974	5.196
Proportion of total flow originating from detritus: 0.40								
Transfer efficiencies (calculated as geometric mean for TL II-IV)								
From primary producers: 8.815%								
From detritus: 9.752%								
Total: 9.187%								

Table S5.11. Comparison of the NOW polynya with other Arctic ecosystem models. TL: trophic level; TST: total system throughput.



	North Water Polynya (v.2)	North Water Polynya (v.1)
Ecosystem properties (t km-^{2} yr^{-1})		
Total system throughput	4,919.51	4,919.36
Sum of all consumption	2,157.86	2,159.21
Sum of all exports	499.59	498.081
Sum of all respiratory flows	1,106.03	1,107.53
Sum of all flows into detritus	1,156.04	1,154.53
Sum of all production	2,326.08	2,325.62
Calculated total net primary production	1,705.81	1,705.81
Net system production	599.79	598.27
Total biomass (excl. detritus)	138.64	137.75
Connectance Index*	0.259	0.303
System Omnivory Index*	0.179	0.175
Food web structure		
Finn's Cycling Index (%)**	7.54	7.52
Finn's mean path length*	3.05	3.05
Mean transfer efficiency (TL 2-4) (%)	9.17	8.18
Publication	Present study	Bryndum-Buchholz et al. (In revision)

Table S5.12. Sensitivity analysis results for each scenario. Showing direction of change of biomass for each functional group.

Functional group		**TL**	**Direction of biomass change for Scenario 1.1.**			**Direction of biomass change for Scenario 1.2.**			
			+5%	**+10%**	**+15%**	**-10%**	**-15%**	**-20%**	**-25%**
1	Killer whale	4.77	/	/	/	/	/	/	/
2	Polar bear	4.73	↑	↑	↑↑	↓	↓↓	↓↓	↓↓↓
3	Bowhead whale	3.16	↑	↑	↑	↓	↓	↓	↓
4	Beluga	3.95	↑	↑	↑↑	↓	↓↓	↓↓	↓↓
5	Narwhal	4.35	↑	↑	↑	↓	↓	↓	↓
6	Walrus	3.18	↑	↑	↑	↓	↓	↓↓	↓↓
7	Ringed seal	3.68	↑	↑	↑	↓	↓	↓↓	↓↓
8	Little auk	3.14	↑	↑	↑	↓	↓	↓	↓
9	Greenland halibut	3.77	↑	↑	↑	↓	↓	↓	↓↓
10	Capelin	3.17	↑	↑	↑	↓	↓	↓	↓
11	Arctic cod (Age 1+)	3.20	↑	↑	↑	↓	↓	↓↓	↓↓
12	Other fish	3.00	↓	↓	↓	↑	↑	↑	↑
13	Arthropods	2.48	↑	↑	↑	↓	↓	↓	↓
14	Bivalves	2.16	↑	↑	↑	↓	↓	↓	↓
15	Echinoderms	2.50	↑	↑	↑	↓	↓	↓	↓
16	Worms	2.21	↑	↑	↑	↓	↓	↓	↓
17	Lg copepods	2.17	↑	↑	↑	↓	↓	↓	↓
18	Med copepods	2.12	↑	↑	↑	↓	↓	↓	↓

19	Arctic cod (Age 0)	2.06	↑	↑	↑	↓	↓	↓	↓
20	Other meso-zooplankton	2.22	↑	↑	↑	↓	↓	↓	↓
21	Lg pelagic producers	1.00	↑	↑	↑	↓	↓	↓	↓
22	Sm pelagic producers	1.00	↑	↑	↑	↓	↓	↓	↓
23	Pelagic detritus	1.00	↑	↑	↑	↓	↓	↓	↓
24	Benthic detritus	1.00	↑	↑	↑	↓	↓	↓	↓

Functional group		**TL**	**Direction of biomass change for Scenario 2.1.**			**Direction of biomass change for Scenario 2.2.**			
			20:80	**40:60**	**50:50**	**-10%**	**-15%**	**-20%**	**-25%**
1	Killer whale	4.77	/	/	/	/	/	/	/
2	Polar bear	4.73	↓↓↓	↓↓↓	↓↓↓	↓	↓	↓↓	↓↓
3	Bowhead whale	3.16	↑↑↑	↑↑↑	↑↑↑	↓	↓	↓↓	↓↓
4	Beluga	3.95	↓↓	↓↓	↓↓	↓	↓	↓↓	↓↓
5	Narwhal	4.35	↓	↓	↓	↓	↓	↓	↓
6	Walrus	3.18	↓	↓	↓	↑	↑	↑	↑
7	Ringed seal	3.68	↓↓↓	↓↓↓	↓↓	↓	↓	↓	↓
8	Little auk	3.14	↑↑↑	↑↑↑	↑↑↑	↓	↓	↓↓	↓↓
9	Greenland halibut	3.77	↓	↓	↓	↓	↓	↓	↓
10	Capelin	3.17	↑↑↑	↑↑↑	↑↑↑	↓	↓	↓	↓
11	Arctic cod (Age 1+)	3.20	↓↓↓	↓↓↓	↓↓↓	↓	↓	↓	↓

12	Other fish	3.00	↑	↑	↑	↑	↑	↑	↑
13	Arthropods	2.48	↑↑↑	↑↑	↑↑	↑	↑	↑	↑
14	Bivalves	2.16	↑	↑	↑	↑	↑	↑	↑
15	Echinoderms	2.50	↑	↑	↑	↑	↑	↑	↑
16	Worms	2.21	↑	↑	↑	↑	↑	↑	↑
17	Lg copepods	2.17	↓↓↓	↓↓↓	↓↓	↓	↓	↓	↓
18	Med copepods	2.12	↑↑↑	↑↑↑	↑↑↑	↓	↓	↓	↓
19	Arctic cod (Age 0)	2.06	↓	↓	↓	↑	↑	↑	↑
20	Other meso-zooplankton	2.22	↑↑↑	↑↑	↑↑	↑	↑	↑	↑
21	Lg pelagic producers	1.00	↑	↑	↑	↑	↑	↑	↑
22	Sm pelagic producers	1.00	↑	↓	↓	↑	↑	↑	↑
23	Pelagic detritus	1.00	↑	↑	↑	↑	↑	↑	↑
24	Benthic detritus	1.00	↑	↑	↑	↑	↑	↑	↑

Functional group		**TL**	**Direction of biomass change for Scenario 3**			
			+10 Capelin -5% Arc. cod (Age 1+)	**+20 Capelin -10% Arc. cod (Age 1+)**	**+50 Capelin -20% Arc. cod (Age 1+)**	**+60 Capelin -25% Arc. cod (Age 1+)**
1	Killer whale	4.77	/	/	/	/
2	Polar bear	4.73	↓	↓↓	↓↓	↓↓↓
3	Bowhead whale	3.16	↑	↑	↑	↑
4	Beluga	3.95	↓	↓	↓↓	↓↓

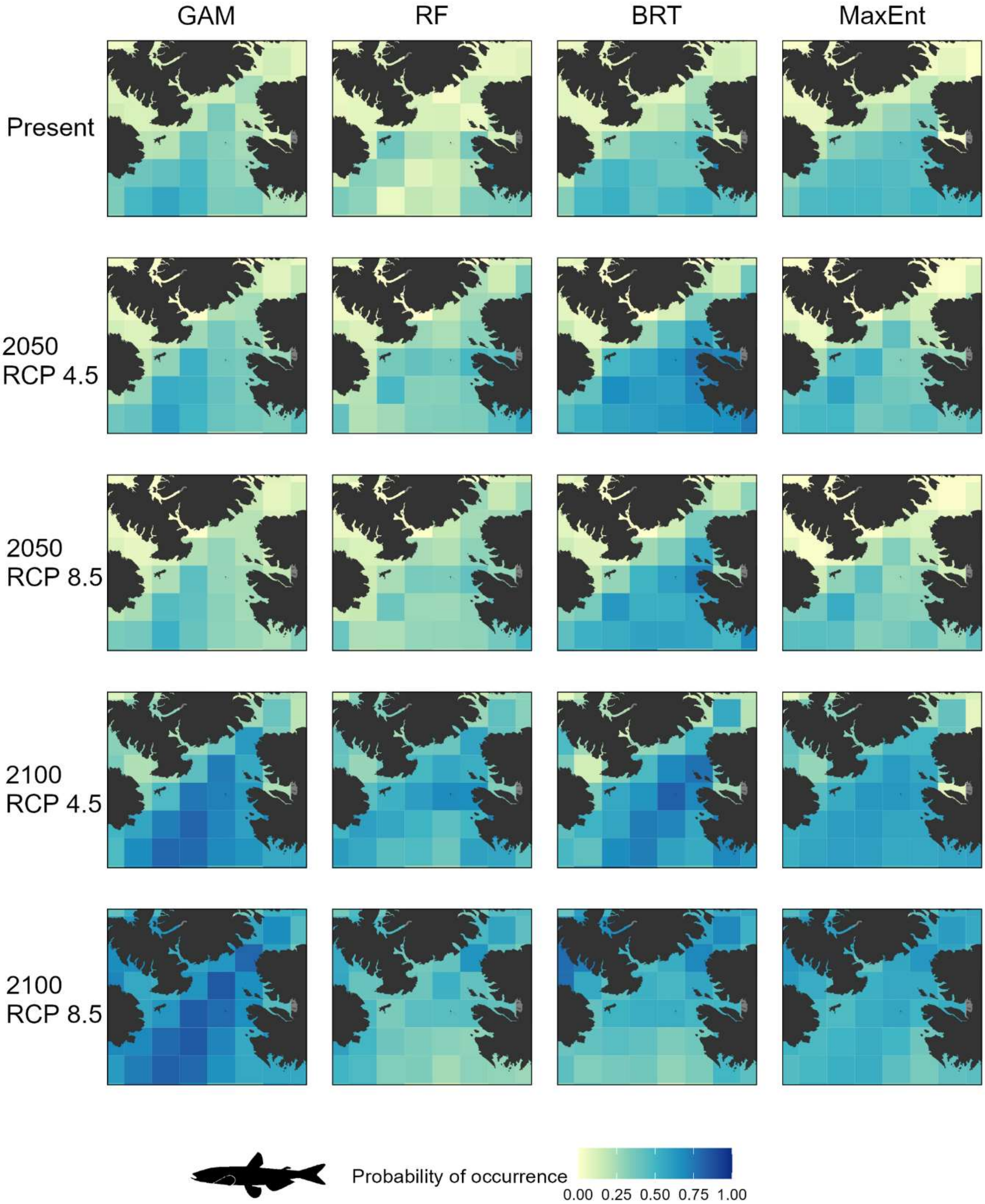
5	Narwhal	4.35	↓	↓	↓	↓
6	Walrus	3.18	↓	↓	↓	↓
7	Ringed seal	3.68	↓	↓	↓↓	↓↓
8	Little auk	3.14	↑	↑	↑	↑
9	Greenland halibut	3.77	↓	↓	↓	↓
10	Capelin	3.17	↑	↑↑	↑↑↑	↑↑↑
11	Arctic cod (Age 1+)	3.20	↓	↓	↓↓	↓↓
12	Other fish	3.00	↑	↑	↑↑	↑↑
13	Arthropods	2.48	↑	↑	↑	↑
14	Bivalves	2.16	↓	↓	↓	↓
15	Echinoderms	2.50	↓	↓	↓	↓
16	Worms	2.21	↓	↓	↓	↓
17	Lg copepods	2.17	↑	↑	↑	↑
18	Med copepods	2.12	↓	↓	↓	↓
19	Arctic cod (Age 0)	2.06	↑	↑	↑	↑
20	Other meso-zooplankton	2.22	↓	↓	↓	↓
21	Lg pelagic producers	1.00	↓	↓	↓	↓
22	Sm pelagic producers	1.00	↑	↑	↑	↑
23	Pelagic detritus	1.00	↓	↓	↓	↓

24	Benthic detritus	1.00	↑	↑	↑	↑

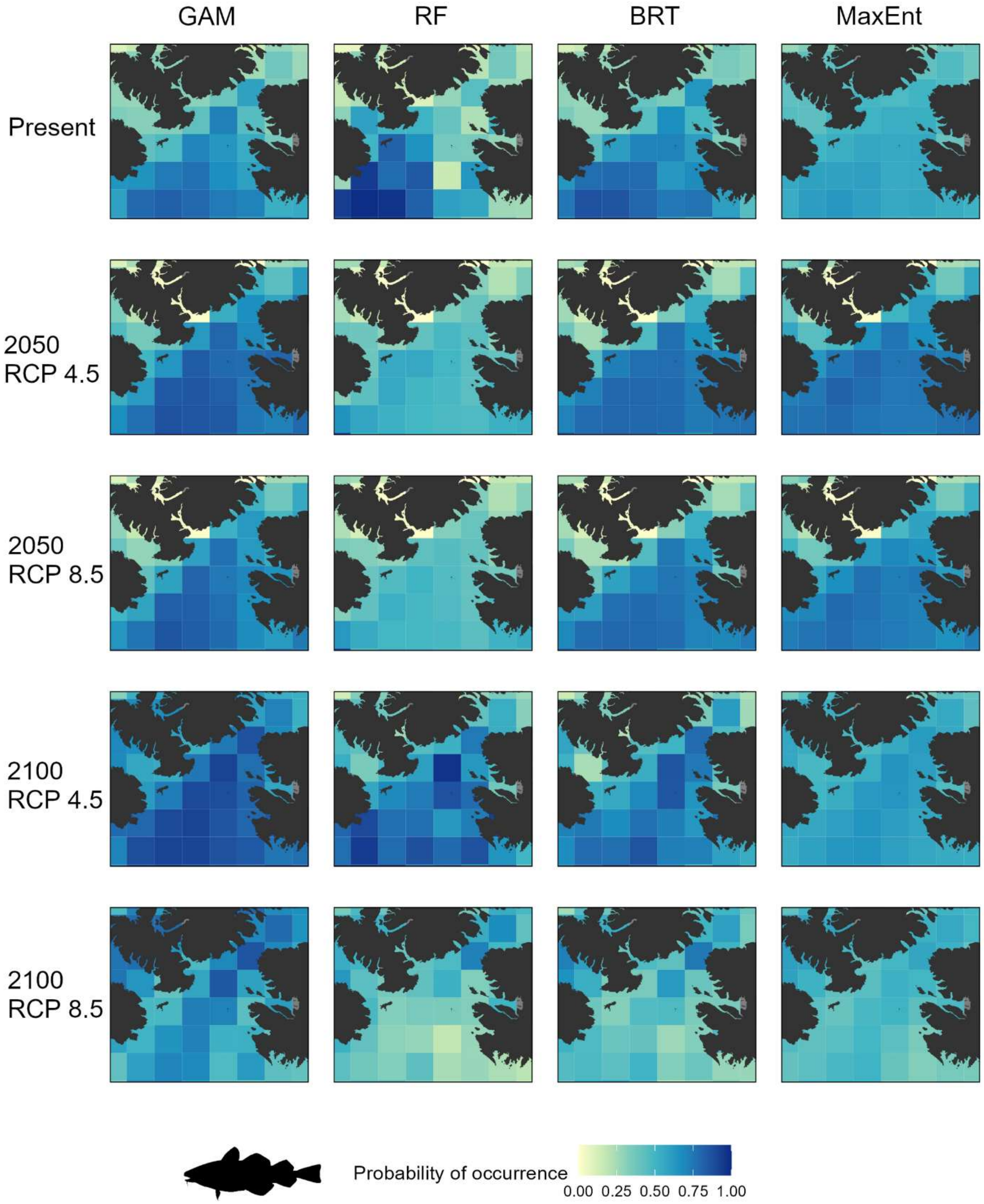
Functional group		**TL**	**Direction of biomass change for Scenario 4**			
			10%	**+30%**	**+40%**	**+50%**
1	Killer whale	4.77	↑	↑	↑	↑
2	Polar bear	4.73	↓↓	↓↓	↓↓	↓↓
3	Bowhead whale	3.16	↑↑↑	↑↑↑	↑↑↑	↑↑↑
4	Beluga	3.95	↓↓	↓↓	↓↓	↓↓
5	Narwhal	4.35	↓	↓	↓	↓
6	Walrus	3.18	↓	↓	↓	↓
7	Ringed seal	3.68	↓↓	↓↓	↓↓	↓↓
8	Little auk	3.14	↑	↑	↑	↑
9	Greenland halibut	3.77	↓	↓	↓	↓
10	Capelin	3.17	↑↑	↑↑	↑↑	↑↑
11	Arctic cod (Age 1+)	3.20	↓	↓	↓	↓
12	Other fish	3.00	↓	↓	↓	↓
13	Arthropods	2.48	↑	↑	↑	↑
14	Bivalves	2.16	↓	↓	↓	↓
15	Echinoderms	2.50	↓	↓	↓	↓
16	Worms	2.21	↓	↓	↓	↓
17	Lg copepods	2.17	↑	↑	↑	↑

18	Med copepods	2.12	↓	↓	↓	↓
19	Arctic cod (Age 0)	2.06	↑	↑	↑	↑
20	Other meso-zooplankton	2.22	↓	↓	↓	↓
21	Lg pelagic producers	1.00	↓	↓	↓	↓
22	Sm pelagic producers	1.00	↑	↑	↑	↑
23	Pelagic detritus	1.00	↓	↓	↓	↓
24	Benthic detritus	1.00	↑	↑	↑	↑

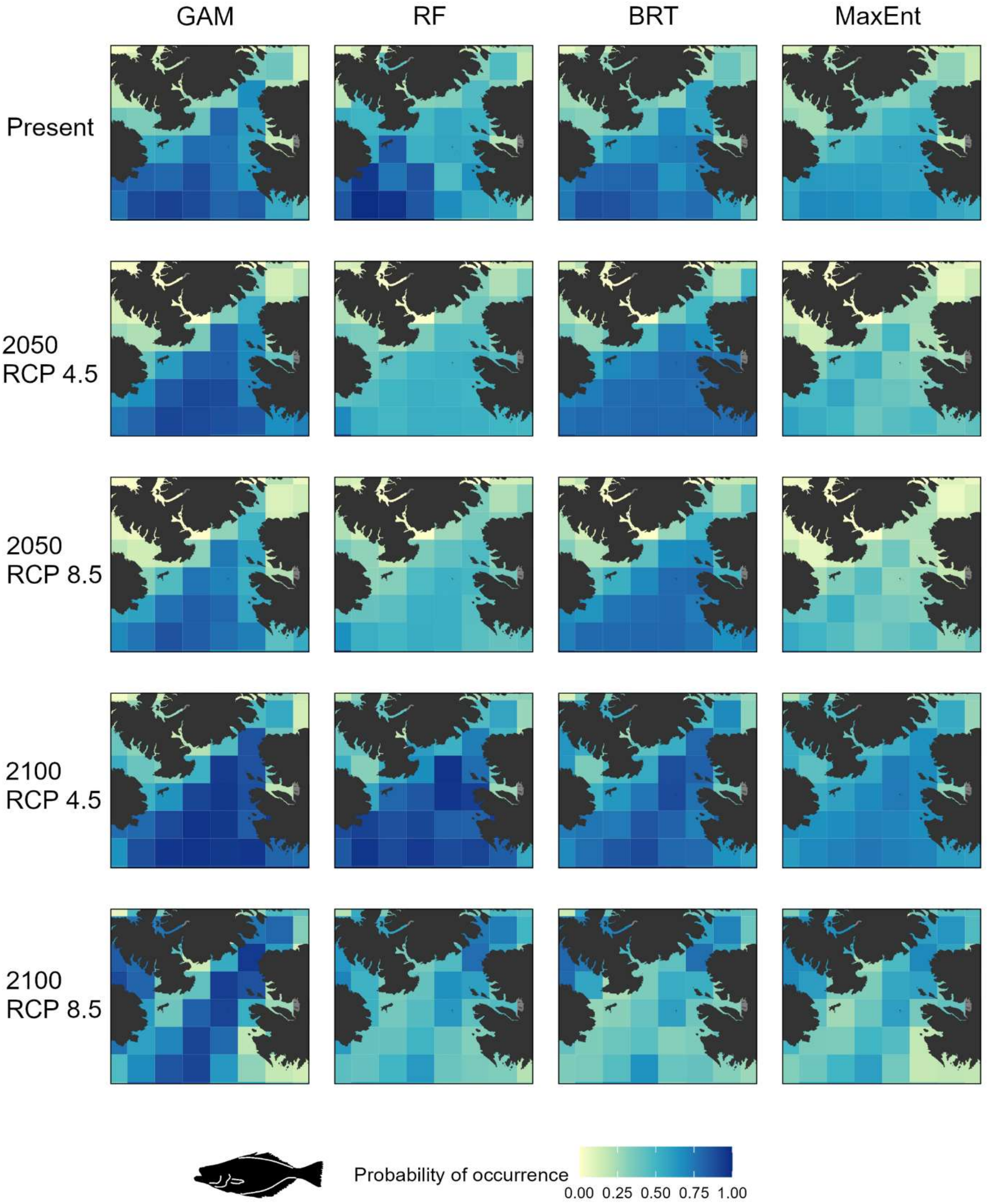
Supplementary figures



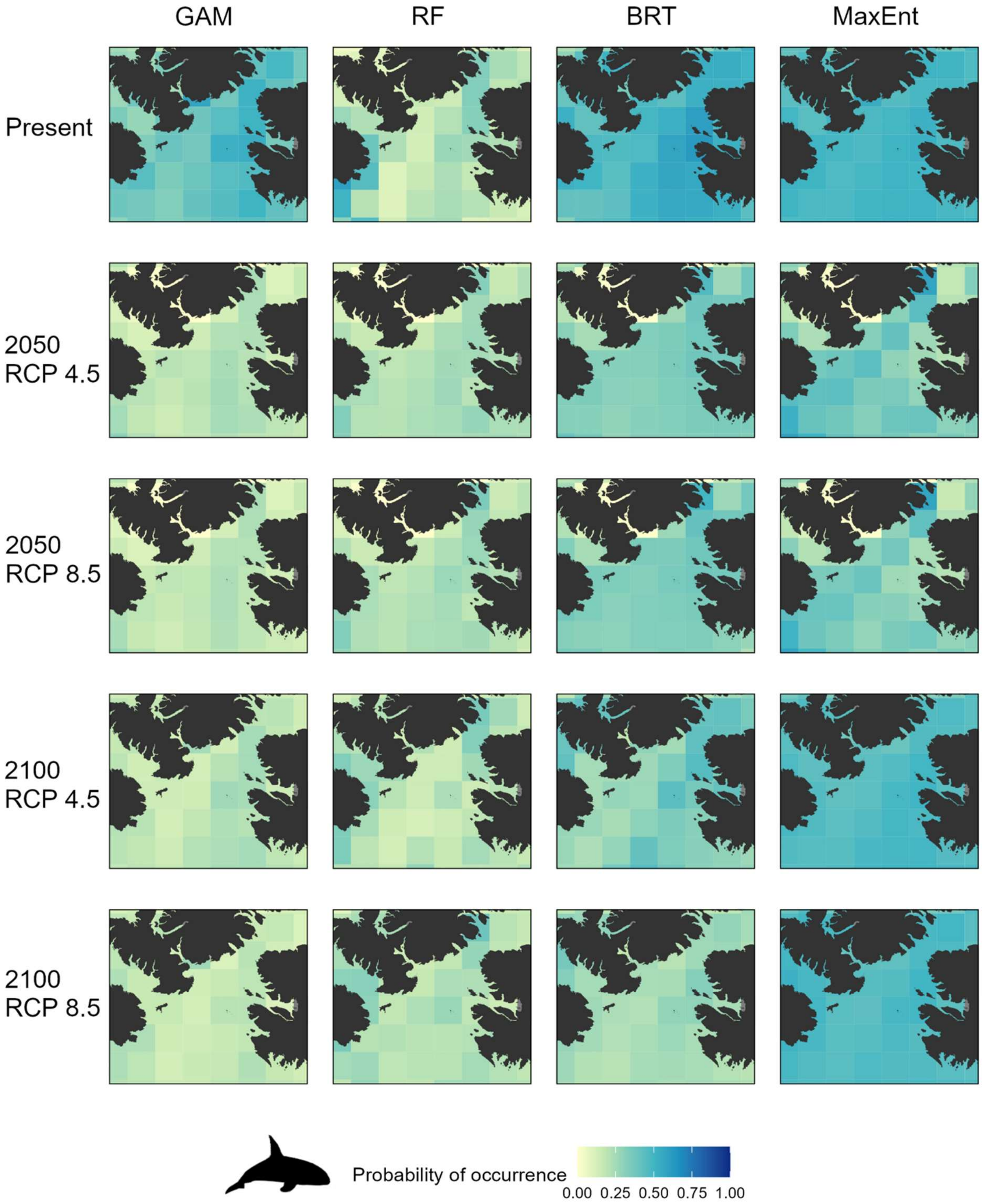
S5.1 Fig. Median projections (across 10 blocks) for each modeling approach for capelin (Mallotus villosus) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Public domain silhouette image is by xgirouxb, via PhyloPic (www.phylopic.org).



S5.2 Fig. Median projections (across 10 blocks) for each modeling approach for Arctic cod (*Boreogadus saida*) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Public domain silhouette image is by Milton Tan, via PhyloPic (www.phylopic.org).



S5.3 Fig. Median projections (across 10 blocks) for each modeling approach for Greenland halibut (Reinhardtius hippoglossoides) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Public domain silhouette image is by Tessa Rehill, via PhyloPic (www.phylopic.org).



S5.4 Fig. Median projections (across 10 blocks) for each modeling approach for killer whales (*Orcinus orca*) for present-day, 2050 and 2100 (under RCP4.5 and RCP8.5 emissions scenarios). Icon created by authors.

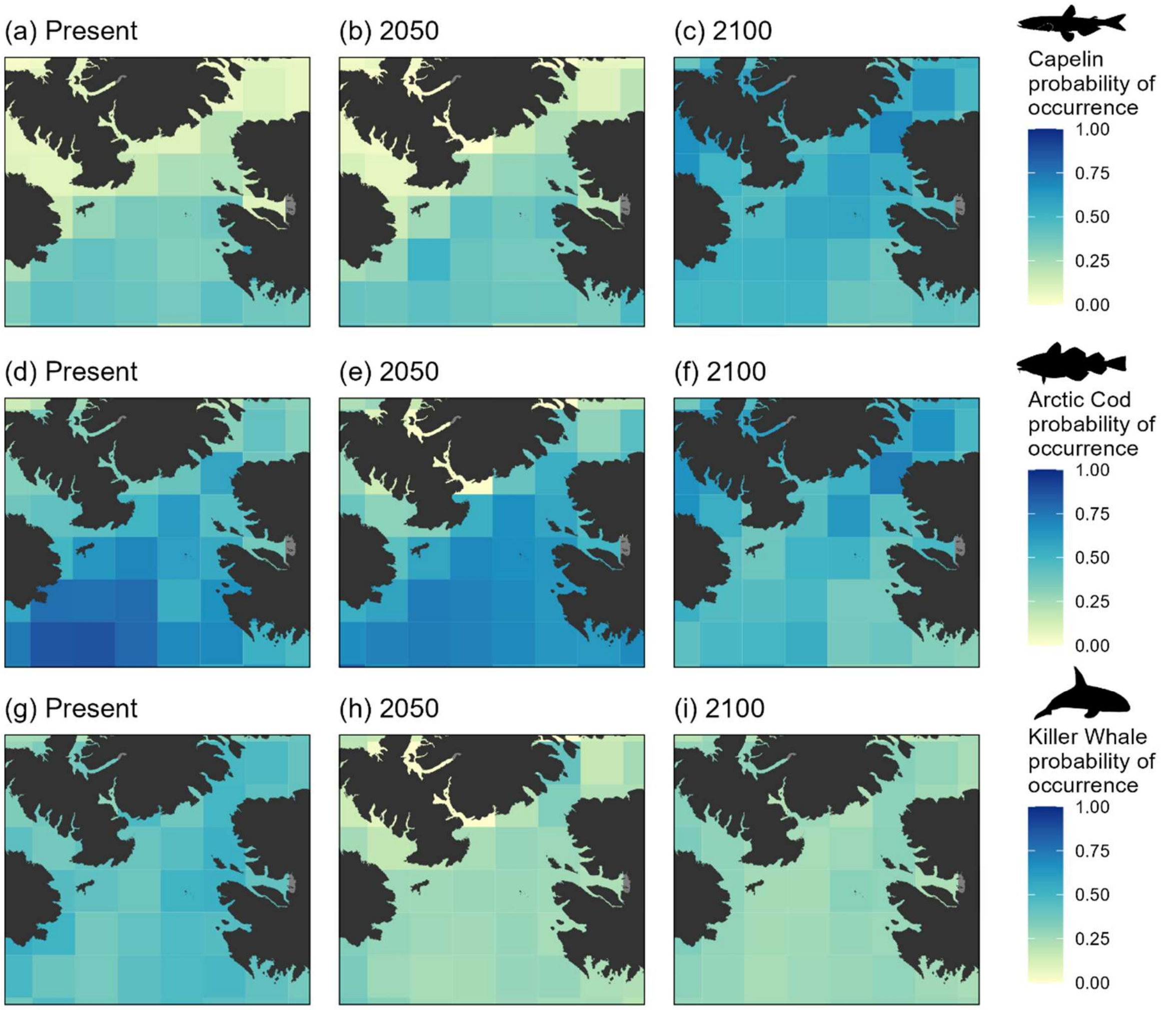


Figure S5.5. Projected distribution of Capelin (*Mallotus villosus*), Arctic Cod (*Boreogadus saida)* and Killer Whale (*Orcinus orca*) in the NOW polynya from present-day to 2100 under RCP8.5 emissions scenario. Capelin (a) present, (b) 2050 and (c) 2100. Arctic cod (d) present, (e) 2050 and (f) 2100. Killer whale (g) present, (h) 2050 and (i) 2100. Killer whale icon created by authors, other icons are public domain silhouette images by Milton Tan (*Gadus morhua*) and xgirouxb (*Thaleichthys pacificus*), via PhyloPic (www.phylopic.org).

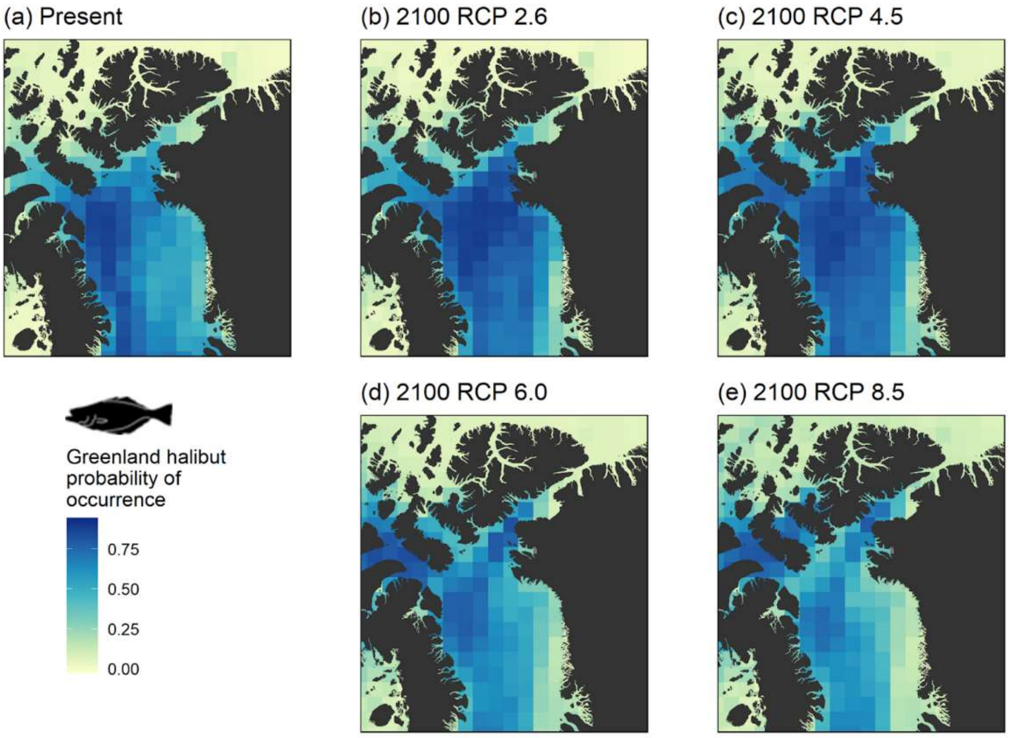


Figure S5.6. Projected current (2000-2014) and future (2100) distributions of Greenland halibut (*Reinhardtius hippoglossoides*) in the NOW polynya under each emissions scenario. Public domain silhouette image by Tessa Rehill, via PhyloPic (www.phylopic.org).

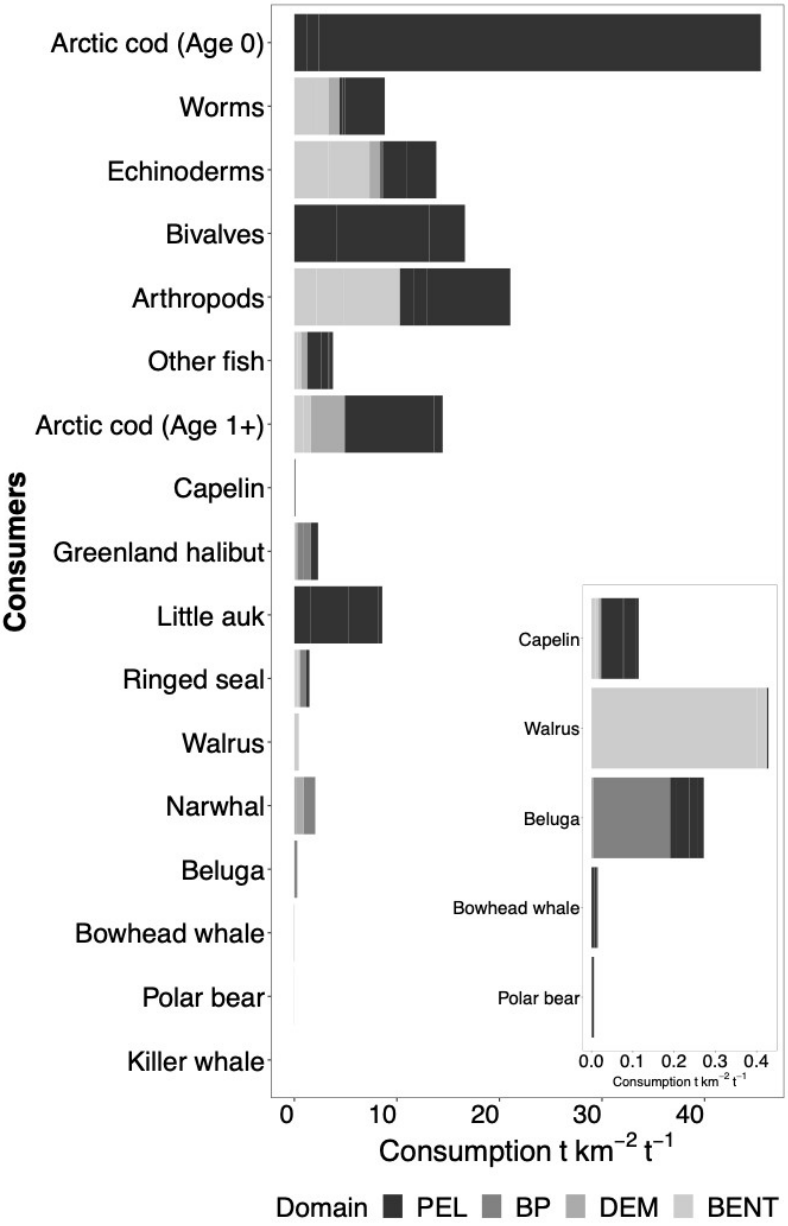


Figure S5.7. Benthic-Pelagic coupling represented by consumption rates of consumers on specific prey domains in the North Water polynya food web. PEL = Pelagic; BP = Bentho-pelagic; DEM = Demersal; BENT = Benthic. The consumption rate for killer whales is very low and not visible: Killer whales consume functional groups from the pelagic, bentho-pelagic and demersal domain (total rate is 9.11e^{-07} t km^{-2} t^{-1}).

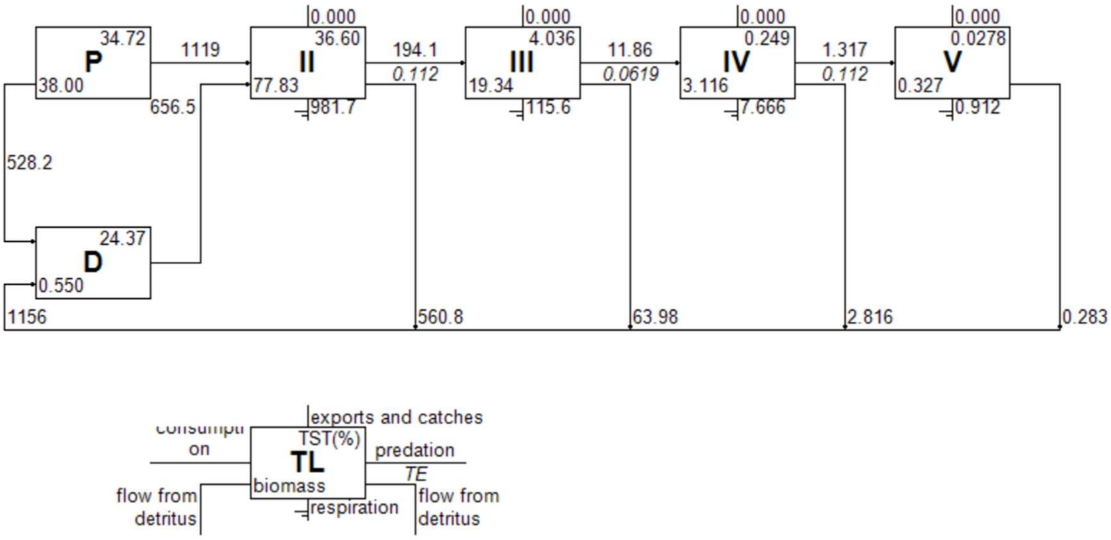


Figure S5.8. Lindeman spline of trophic flows (t km2/yr) in the NOW polynya ecosystem base model for 2005−2007. Flows to detritus are recycled through the detritus (D) and primary production (P) compartment at trophic level (TL) I. P: primary producers; D: detritus; TL: trophic level; TE: trophic efficiency; TST: total system throughput.

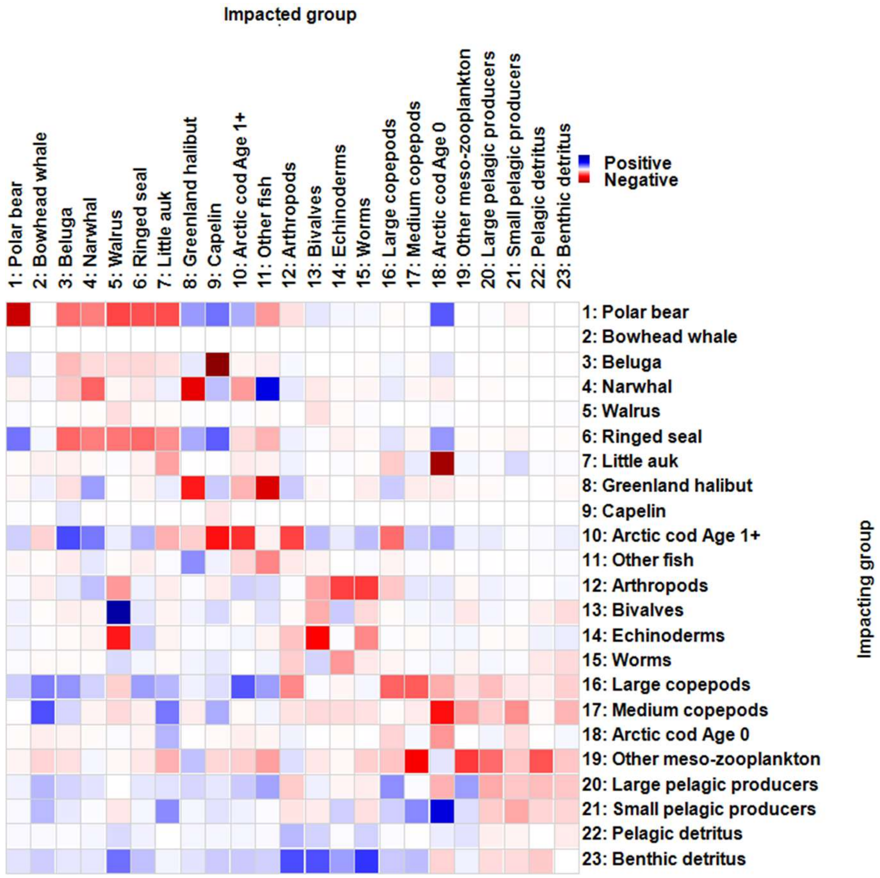


Figure S5.9. Mixed trophic impact analysis of the NOW polynya ecosystem base model in 2005−2007. Diagram shows the positive (blue) and negative (red) impact of an increase in the biomass on the impacting group on the impacted group.

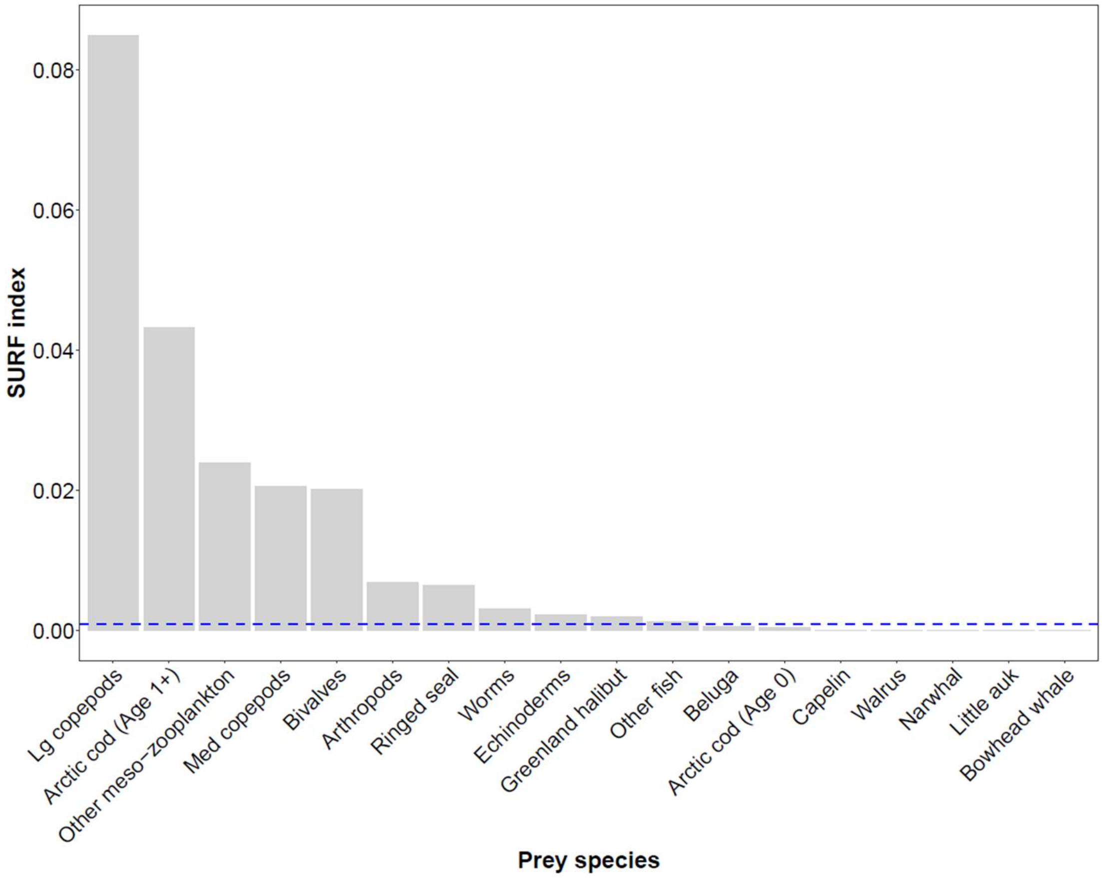


Figure S5.10. SUpportive Role to Fishery ecosystems index (SURF; Essington & Plagányi (2014)) calculated for prey species in the NOW polynya food web. SURF index calculations include consumers only; top predators and primary producers were excluded. Dashed blue line represents the threshold (0.001) above which functional groups are considered key prey species in the ecosystem.

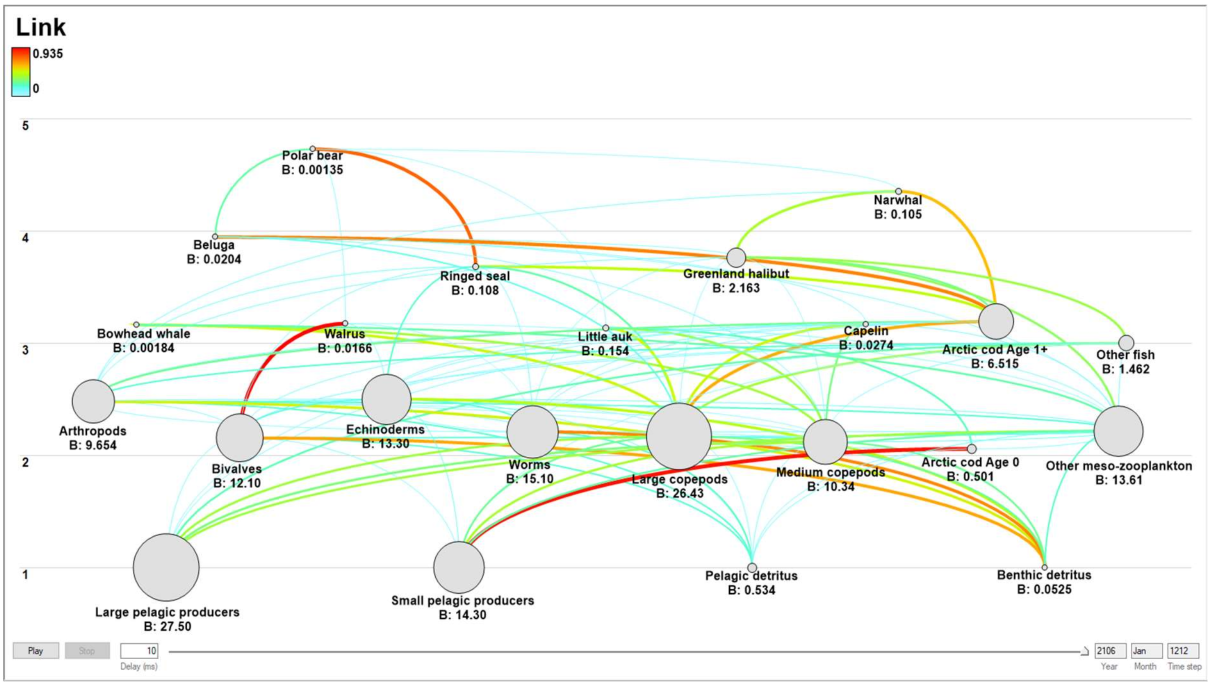


Figure S5.11. Ecosim flow diagram for Scenario 1.1. The size of circles is proportional to the amount of biomass. Numbers below circles: Biomass of the functional group in t km^2. Numbers on the left indicate the trophic level. Direction of energy flow defined by position of line in relation to circles; flows positioned on the top of a trophic group indicate biomass outgoing, flows positioned on the side indicate entering biomass. Weight and colour of the lines indicate the amount of energy flowing between nodes.

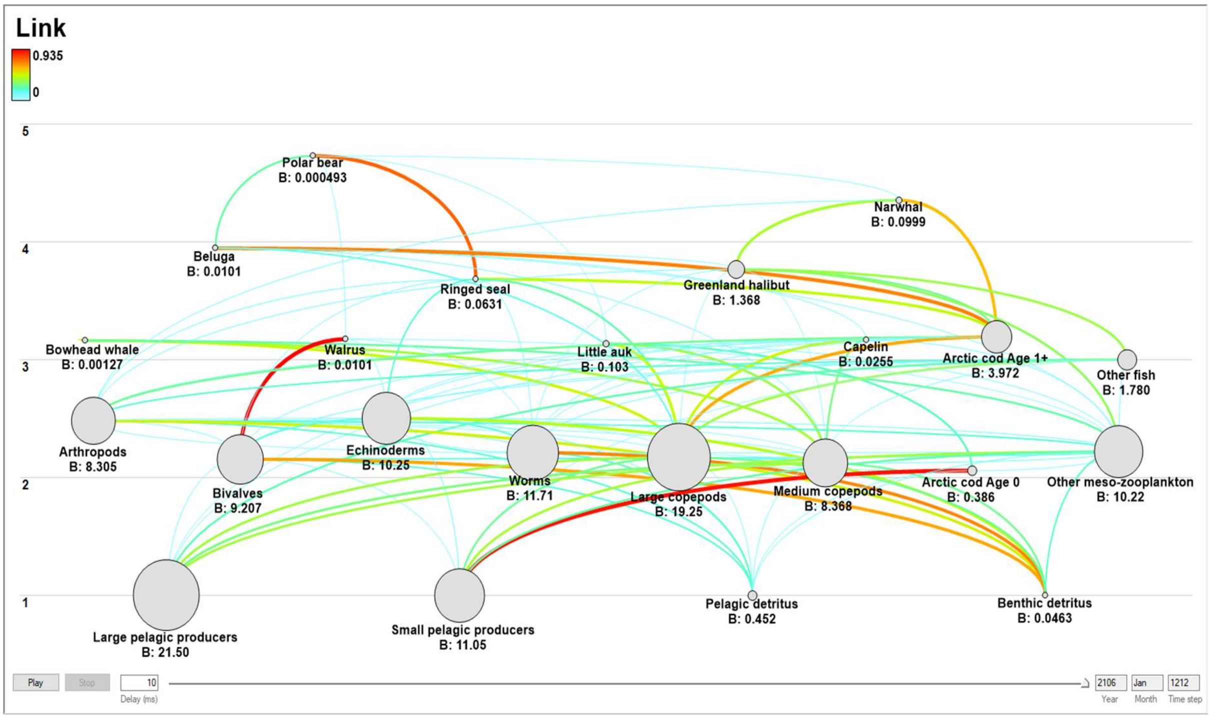


Figure S5.12. Ecosim flow diagram for Scenario 1.2. See Figure S5.7 for detailed captions.

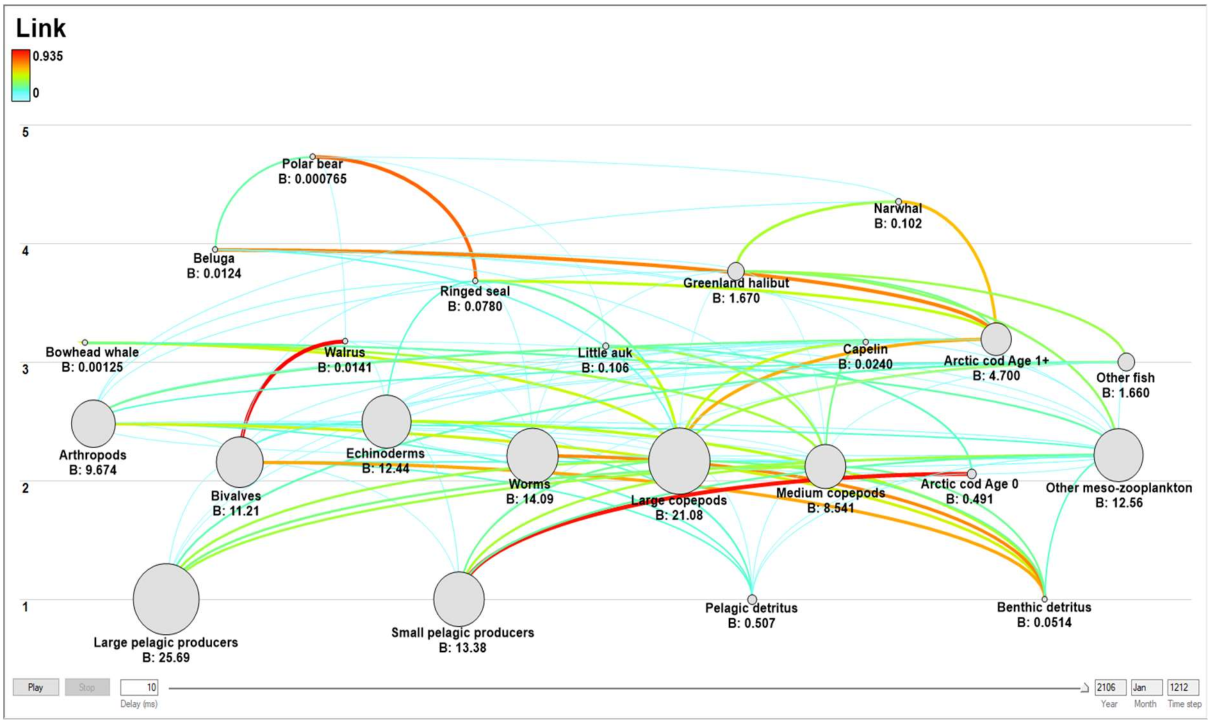


Figure S5.13. Ecosim flow diagram for Scenario 2.2. See Figure S5.7 for detailed captions.

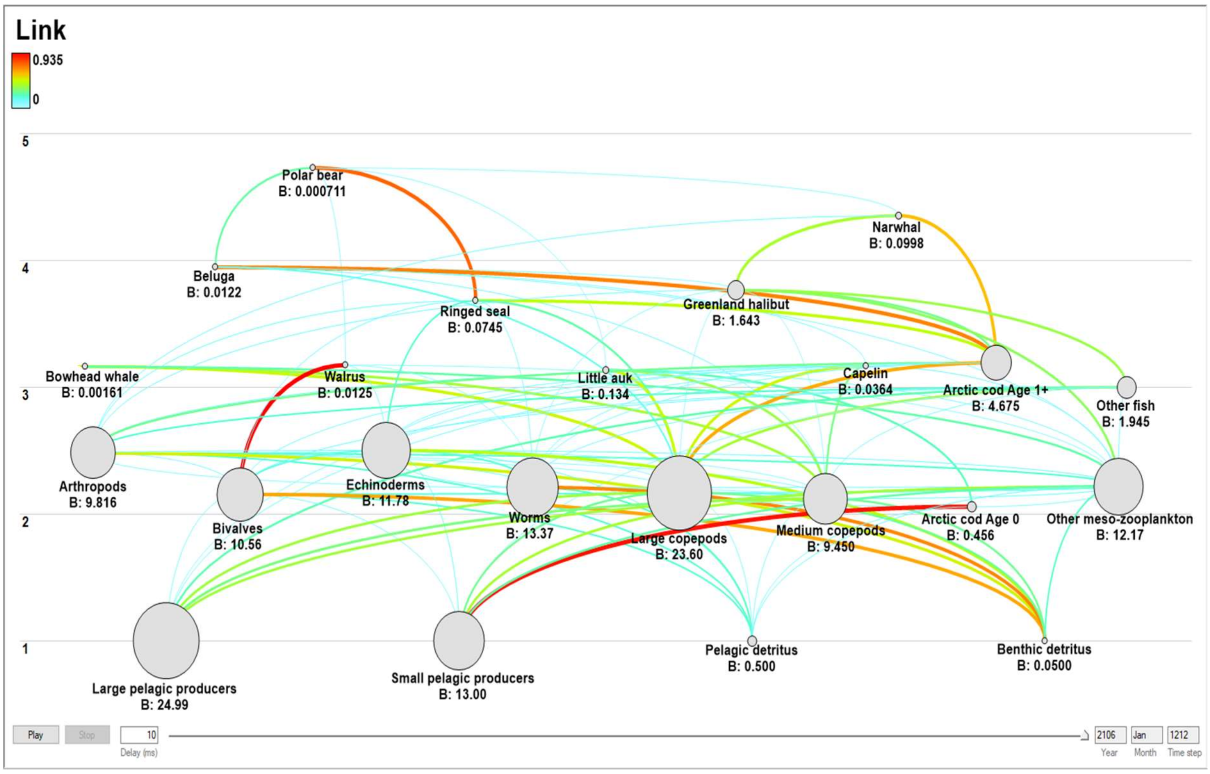


Figure S5.14. Ecosim flow diagram for Scenario 3. See Figure S5.7 for detailed captions.

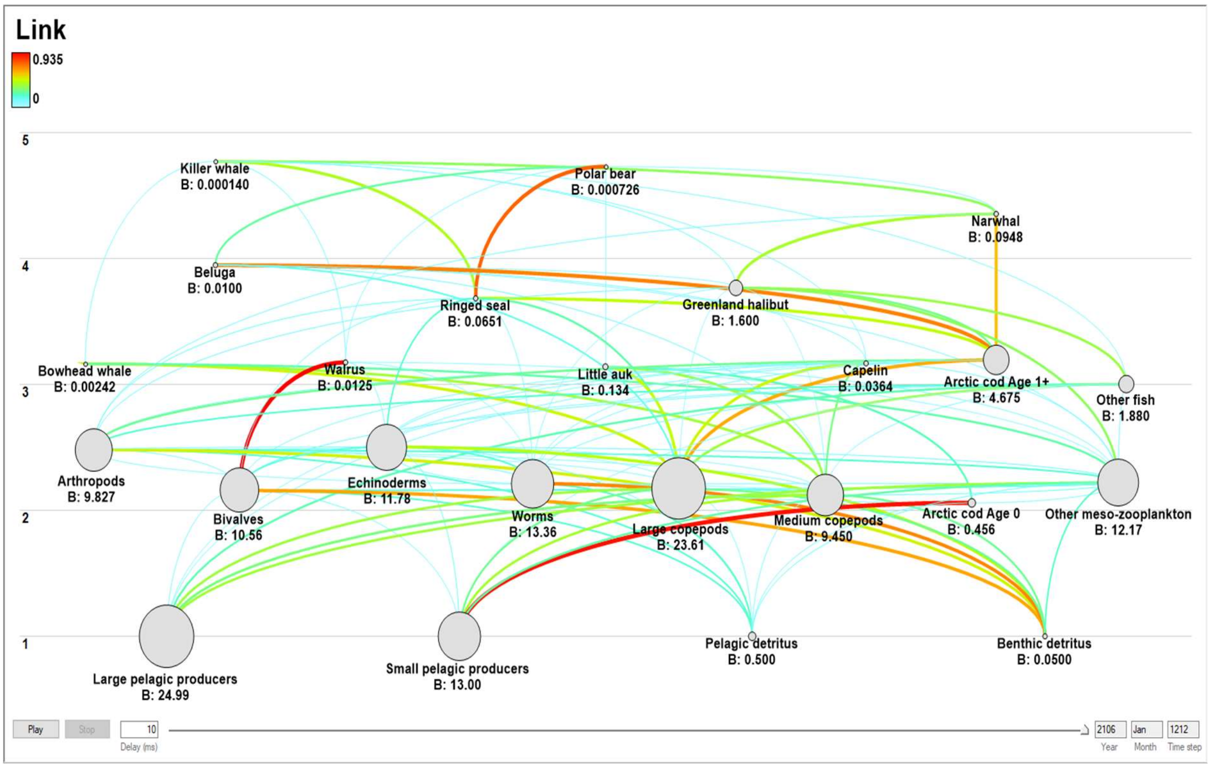


Figure S5.15. Ecosim flow diagram for Scenario 4. See Figure S5.7 for detailed captions.

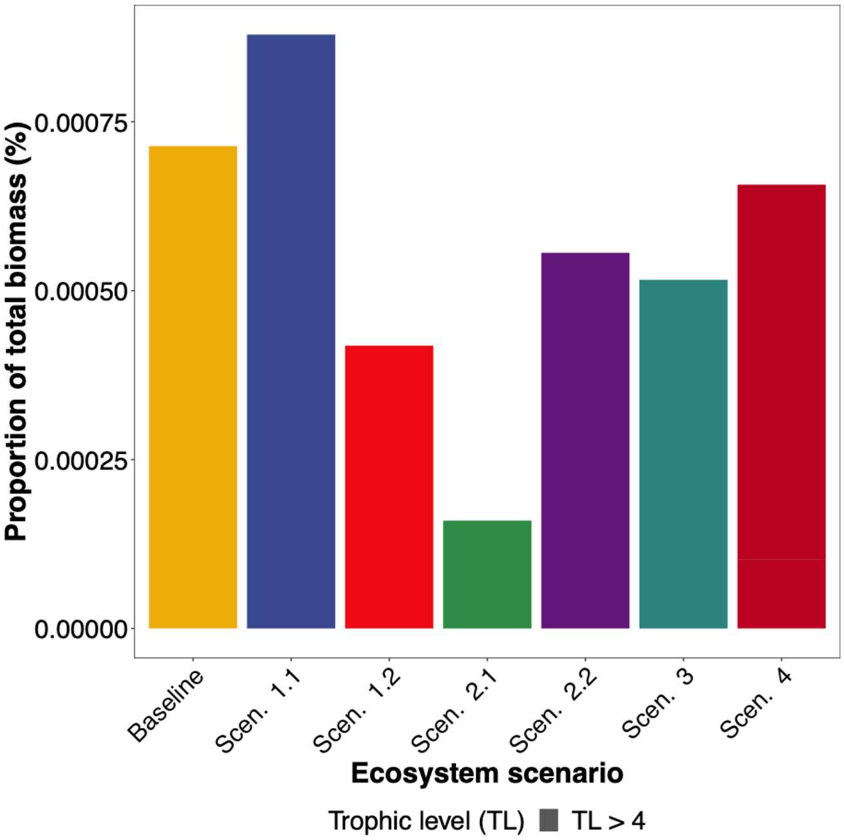


Figure S5.16. Biomass proportion relative to the total biomass in the North Water polynya food web for TL >4.

Appendix E: Supporting material for Chapter 6

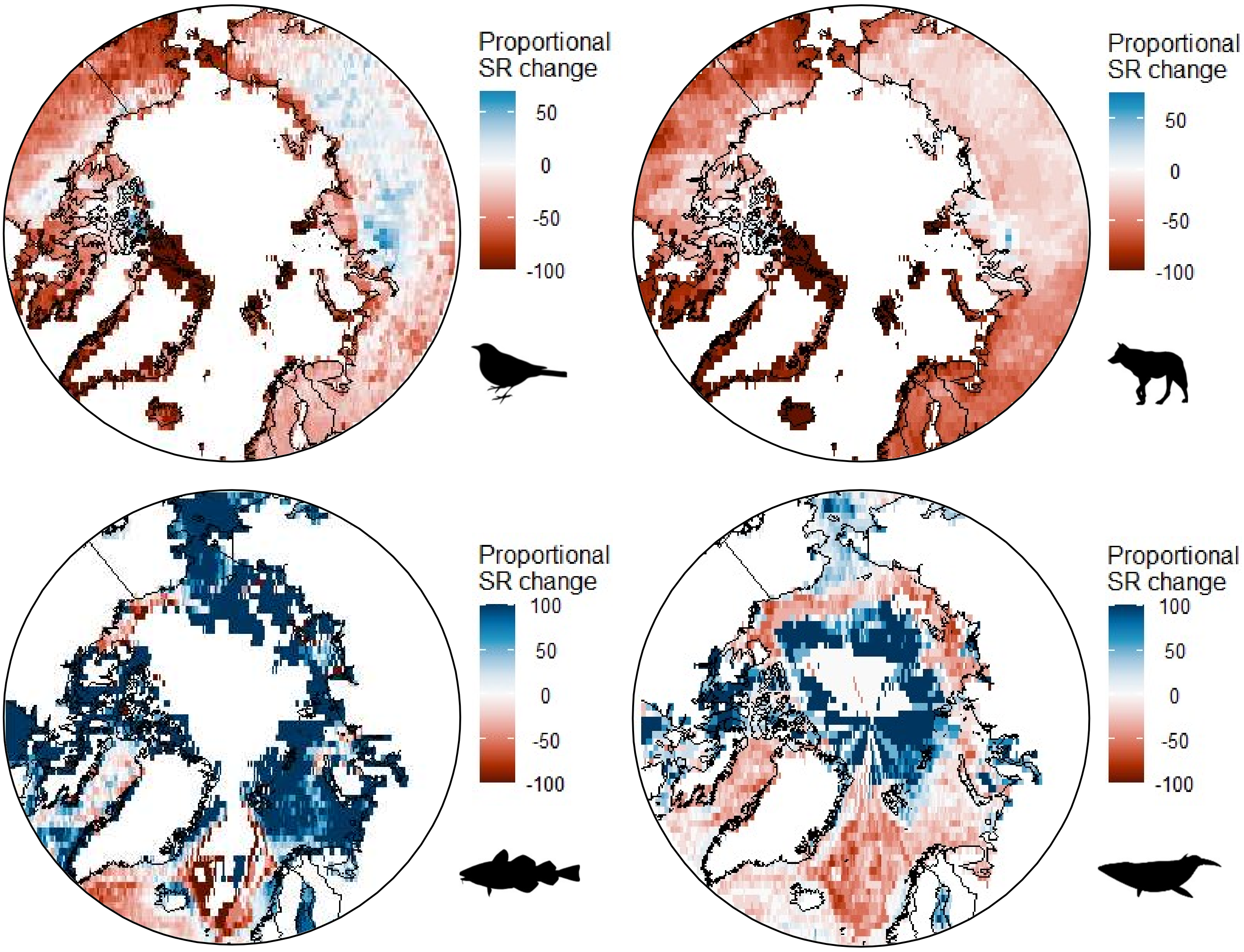


Figure S6.1. Proportional changes in species richness (SR) per two terrestrial taxa (birds and mammals) and two marine taxa (fish and mammals) of important trade species in the Arctic. SR increases are capped by 100% for fish and marine mammals. Future changes are projected to 2080 under SSP3.70 for terrestrial taxa and 2100 under RCP6.0 for marine taxa.

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