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Synthesis Paper

Antarctic terrestrial and freshwater biological responses to climate change

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Abstract

This review considers the current status, and highlights existing knowledge gaps, on Antarctic terrestrial and freshwater biological responses to climate change. Climate change is considered to be one of the major drivers of future ecosystem change in Antarctica. Understanding the biological responses, and associated shifts in biodiversity patterns, biotic interactions and processes, that are likely to occur under continued climate change is fundamental for predicting its consequences for the functioning of Antarctic ecosystems. However, quantifying changes in species abundance, biodiversity, community composition and biotic interactions, and how these are influenced by variations in a multitude of environmental variables, is challenging. All biological groups in the Antarctic terrestrial and freshwater domains currently show low species richness at higher latitudes, indicating that there should be scope for lower-latitude species to expand their distributions southwards under warming conditions. The northern, 'trailing edge' or lower altitudinal limits may also shift southwards or upwards, respectively. However, to date, only one report exists of increased diversity within field experimental warming studies, and none exist from the few available long-term monitoring sites. Similarly, while notable plant-cover expansions have been recorded at some localized sites, no clear large-scale vegetation response has been documented within recognized Antarctic biological regions, while organisms living within the vegetation show highly variable responses. There are still many knowledge gaps on this matter for various biological groups across and within Antarctic regions. While it is frequently posited that the potential for climate change-driven range expansion and biodiversity shifts is substantial, the biological responses reported to date indicate that current levels of climate change have not (yet) resulted in large-scale changes in abundance and biodiversity patterns across Antarctica.

Keywords: Ecosystems; monitoring; nutrients; primary producers; UV; warming; water

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Introduction

Antarctica is the least anthropogenically impacted continent on Earth (Carter *et al.* 2025) and therefore provides a unique opportunity to study how organisms and ecosystems respond to climatic changes in the absence of the strong confounding anthropogenic factors influencing most other continents. Antarctic terrestrial biota are exposed to large natural variations in micro-environmental conditions across diurnal and seasonal scales (Peck *et al.* 2006), upon which larger-scale climatic changes are likely to be superimposed in an as-yet undocumented manner (Convey *et al.* 2018). Beyond the main effects of changes in temperature and precipitation, projected climate change can influence many other environmental factors that impact Antarctic terrestrial and freshwater biota, including solar radiation receipt and composition, the frequency and magnitude of temperature extremes, freezing and thawing and the length of the active/growing season (Convey & Peck 2019, Siegert *et al.* 2019, Davies *et al.* 2026). In addition, nutrient limitation may come into play when temperature and water requirements have been met, as has also been shown for Arctic ecosystems (Hobbie *et al.* 2002). Furthermore, atmospheric CO_2 concentrations have risen by 51%, from 285 to 430 ppm (2025), since the 1800s (https://climate.nasa.gov/vital-signs/carbon-dioxide/), although, to our knowledge, the impacts of these increased CO_2 concentrations on Antarctic biota have not been tested, either under laboratory or field conditions. However, internal CO_2 concentrations appear to differ between cushion- and turf-forming mosses and influence growth (Tarnawski *et al.* 1992). The scale of these climatic and environmental changes will vary greatly across microhabitats and at regional scales depending on local climates and weather conditions. Biotic responses to climate change will, therefore, vary within and across Antarctic biogeographical regions. Although the cold and arid conditions encountered in most Antarctic ecosystems limit species physiological processes, growth and reproduction (Kennedy 1993, Block *et al.* 2009, Convey *et al.* 2014), contemporary climate warming may alleviate some of these restrictions. In addition, the melting and retreat of glaciers will expose new sites for Antarctic biota to colonize, as well as potentially linking local patches of biota currently isolated by snow

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and ice barriers, which may affect genetic diversity (Hall & Walton 1992, Chown & Convey 2007, Lee *et al.* 2017, Ruiz-Fernandez *et al.* 2019, Siegert *et al.* 2019, Beet *et al.* 2022).

Existing patterns of terrestrial and freshwater biota along latitudinal and temperature gradients (Yergeau *et al.* 2007, Convey *et al.* 2014, Chown *et al.* 2015, Nayaka & Rai 2022) and across small habitat scales (Powers *et al.* 1998, Sinclair 2001, Cannone *et al.* 2017, Wlostowski *et al.* 2018) suggest that the increasing temperature and water availability predicted under climate change scenarios are likely in many cases to increase the abundance and local distribution of native Antarctic biota (Convey 2011), although the converse can occur, especially when water availability becomes more limited (Robinson *et al.* 2018). In addition, many ecophysiological studies find that there is often ample physiological plasticity within Antarctic species to cope with predicted future climate change scenarios (Block & Convey 2001, Elnitsky *et al.* 2008, Everatt et al. 2013, 2014, Giovannini *et al.* 2018), but there are exceptions (Newsham 2024). Collectively, these patterns and physiological properties broadly support future predictions of Antarctic biota under climate change scenarios (Hogg & Wall 2011, Nielsen & Wall 2013, Convey & Peck 2019), but field evidence for such biological responses remains scarce. In part, this is driven by the typically slow growth rates and low physiological activity of most Antarctic biota (Peck *et al.* 2006), which makes quantifying biotic responses to climate change practically challenging and often beyond the scope of regular research funding.

Awareness of the occurrence and possible consequences of systematic anthropogenic climate change only started to receive increasing research and societal attention in the late 1980s (Smith 1990, Smith & Steenkamp 1990, Kennedy 1995a). Various experimental climate manipulation studies have been conducted in Antarctica with the intention of identifying the responses of species and ecosystems to the various environmental consequences associated with global climate change, in particular to warming. A large proportion of existing knowledge of the responses of Antarctic ecosystems and organisms to climate warming scenarios is based on these early experiments. Such climate manipulation studies are, however, often criticized for changing multiple environmental factors other than those ostensibly intended (Bornman *et al.* 2019), which makes it harder to identify the specific causes of any biotic responses observed. This critique is certainly justified, but, as long as appropriate micro-environmental conditions are accurately recorded, it remains realistic to identify potential drivers of change (Kennedy 1995b, Bokhorst *et al.* 2011).

In addition to experimental studies, some insights into potential climate change responses have been provided through observations *in situ*. For example, expansion of vascular plant populations has been reported at locations along the Antarctic Peninsula (Fowbert & Smith 1994), on the South Shetland Islands (Torres-Mellado *et al.* 2011) and South Orkney Islands (Cannone *et al.* 2016, 2022) and on some sub-Antarctic islands (Bergstrom *et al.* 2006, Mazibuko *et al.* 2024). Expansion of cryptogam populations is often dependent on sufficient water availability, with contractions seen where water has become scarce following local warming (Brabyn *et al.* 2006, Green *et al.* 2011, Cannone *et al.* 2017, Sancho *et al.* 2017, 2019). Laboratory studies have detected changes to microbial process rates in response to warming, freeze-thaw (FT) cycles and water and nutrient manipulations (Parsons *et al.* 2004, Wasley *et al.* 2006b, Yergeau & Kowalchuk 2008), and some field climate manipulation studies have shown similar responses (Kennedy 1996, Bokhorst *et al.* 2007a, Dennis *et al.* 2013). However, the responses of invertebrates, vegetation and soils often take many years or even decades to become apparent (Smith 1994, Bokhorst *et al.* 2016, Andriuzzi *et al.* 2018).

In this review, we provide an overview of the current state of knowledge regarding the responses of the main biotic groups present in Antarctic terrestrial and freshwater ecosystems to both experimentally manipulated climate scenarios and contemporary climate change. To achieve this, we compiled 209 published reports of biological responses to altered temperature, water (including snow) availability, ultraviolet (UV) radiation and nutrient availability. Where possible, biological responses are synthesized separately across primary producers, microbial communities and invertebrates (arthropods, nematodes, tardigrades). Evidence of biological responses are ordered by field observations from long-term monitoring studies and across environmental gradients, followed by experimental manipulations, information on physiological plasticity and historical records and proxies that indicate the scope for the response to climate change. Biological responses were obtained from peer-reviewed articles identified from Web of Science and forward and backward searches from key review papers. To ensure coverage, we performed separate literature searches using 'warming', 'temperature', 'water', 'snow', 'meltwater', 'precipitation', 'UV', 'nutrients', 'nitrogen' and 'phosphorus' in combination with broad taxonomic groups (algae, lichens, liverworts, mosses, bryophytes, flowering plants, collembola, springtails, acari, mites, tardigrades, nematodes, bacteria, fungi, flagellates, diatoms). The primary focus was on experimental studies and was mostly limited to work from the 1970s onwards. Papers were retained if they contained quantitative data of a biological response to altered conditions in temperature, water, UV radiation or nutrients, resulting in 377 biological responses from terrestrial (171) and freshwater (38) publications. We relied on reviews to identify older biological survey and grey literature not focusing on one of these four environmental drivers. However, it remains possible that some of this literature may have been missed. This information was used to map out from where records of biological climate change responses are derived, and a qualitative comparison is made between the biological responses of taxonomic groups from experimental studies, field observations and historical proxies (e.g. peat and lake coring) as well as any information (laboratory and field data) on physiological plasticity towards climatic changes. In addition, we identify where interactions between climate change drivers are relevant, and where this has played a role in biological interactions. We conclude by proposing an integrative way forward to tackle the various challenges raised.

Terrestrial ecosystems

Initial field studies simulating climate warming were conducted using closed Perspex chambers (Kennedy 1994, Smith 1994). However, these studies were quickly criticized for their artificial nature and the complexity in disentangling the effects of warming from other microclimate impacts (Kennedy 1995b). The use of various types of open-top chambers (OTCs; Fig. 1) in Antarctica, based on the Arctic ITEX (International Tundra EXperiment) model (Molau & Molgaard 1996), improved upon aspects of the microclimate simulation achieved and reduced the occurrence and scale of unrealistic temperature extremes (Bokhorst *et al.* 2011, 2013). Later, active heating, using infrared heaters above vegetation, was included in experiments on Anvers Island (Day *et al.* 2009), which has the benefit of focusing on only one environmental driver. However, this experimental approach remains impractical for most

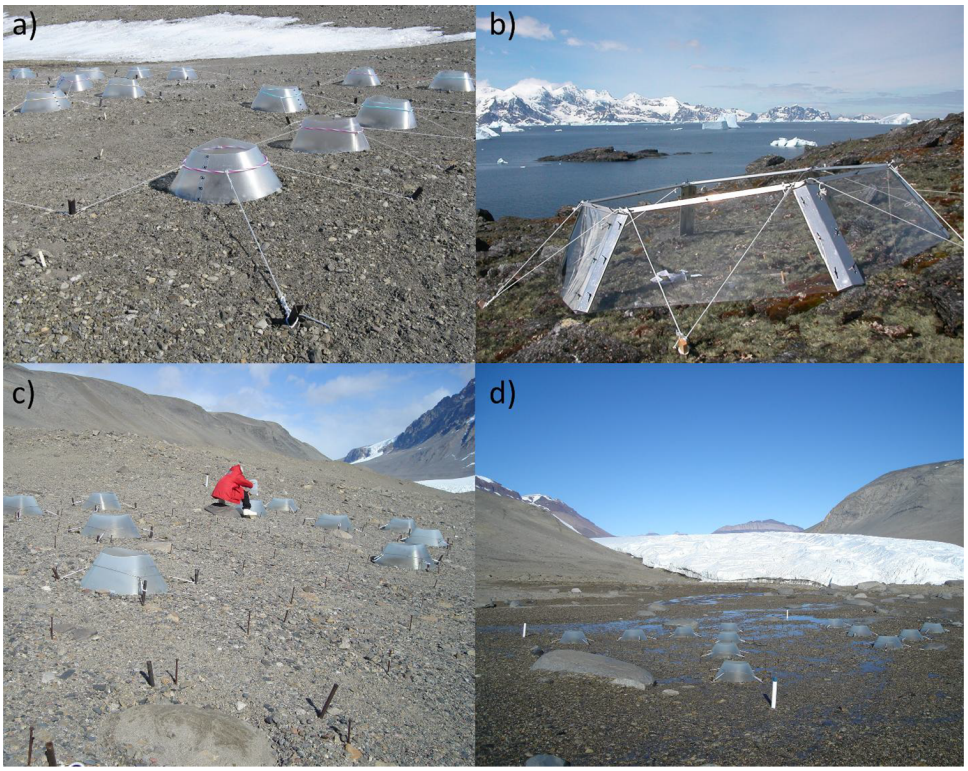

Figure 1. Examples of passive open-top chamber warming methodologies employed in the Antarctic: (a) Mars Oasis, Alexander Island (Newsham *et al*. 2019), (b) Signy Island (Bokhorst *et al*. 2007b), (c) the McMurdo Dry Valleys and (d) a warming experiment that flooded due to an extreme melt event in the McMurdo Dry Valleys (Nielsen *et al.* 2012).

Antarctic field sites due to its requirement for a continuous power supply. To date, more than 350 biological effects of warming in Antarctic terrestrial ecosystems have been recorded (Figs 2 & S1), but with differences in the direction of response and many species-specific effects.

Observed responses of Antarctic terrestrial communities to temperature change

Primary producers: field observations

Bank-forming moss species on Signy Island (60°S) have expanded over the last 50 years (Cannone *et al.* 2017), while colonization following glacial retreat on Livingston Island (62°S) has been surprisingly slow, with only 0.04 ha of land showing signs of new vegetation cover since 1956 (Ruiz-Fernandez *et al.* 2017). Lichen assemblages in deglaciated areas of King George Island show loss of some species due to desiccation, while pioneer species have emerged on the youngest moraines (Olech & Slaby 2016, Rodriguez *et al.* 2018). No changes in lichen abundance and diversity were found in Dronning Maud Land (73°S) between 1991 and 2002 (Johansson & Thor 2008), nor at Cape Hallett (72°S) between 1961 and 2018 (Colesie *et al.* 2022), indicating that current levels of regional change have been insufficient to affect the cover of lichen communities. Vegetation monitoring in Victoria Land (73–75°S) since 2000 suggests that permafrost warming has supported the expansion of moss communities with sufficient water supply, while lichen communities expand at drier microsites (Guglielmin *et al.* 2014). Colder and drier summers have caused declines in moss health in the East Antarctica Antarctic Conservation Biogeographic Region (ACBR; Robinson *et al.* 2018).

Local distribution expansions of the native Antarctic vascular plant species *Colobanthus quitensis* (Kunth.) and *Deschampsia antarctica* (Desv.), and changes in their reproductive output, have been reported at various locations in the Maritime Antarctic (Fowbert & Smith 1994, Smith 1994, Convey 1996, Grobe *et al.* 1997, Torres-Mellado *et al.* 2011, Cannone *et al.* 2016, 2022). In the Argentine Islands, there is a suggestion that the rapid expansion documented between the 1960s and mid-1990s (Fowbert & Smith 1994) subsequently plateaued (Parnikoza *et al.* 2009), consistent with the temporary cessation of the regional mean air temperature warming trend documented for the western Antarctic Peninsula region since the late 1990s (Turner *et al.* 2016). Similar temperature- and moisture-driven vascular plant responses have been reported from sub-Antarctic islands (Chown & Smith 1993, Frenot *et al.* 1993, Bergstrom *et al.* 2006, le Roux & McGeoch 2008, Robin *et al.* 2011, van der Merwe *et al.* 2024). There are no known field observations of increased terrestrial algal growth over time.

Primary producers: environmental gradients

There are consistent species richness declines across latitudinal gradients in Antarctica (Peat *et al.* 2007, Green *et al.* 2011) that also correlate with physiological activity patterns (Sancho *et al.* 2019, Shelyakin *et al.* 2020, Beltrán-Sanz *et al.* 2022). However, physiological work on isolated lichen photo- and mycobionts suggests that responses to warming may vary widely between species depending on their acclimation ability and due to the fact that species with a broad ecological amplitude may be favoured (Colesie *et al.* 2018, Marín *et al.* 2022).

A comparison of vegetation types along elevation gradients on Marion Island indicates that warming-induced changes will probably be mediated by water availability (Smith *et al.* 2001).

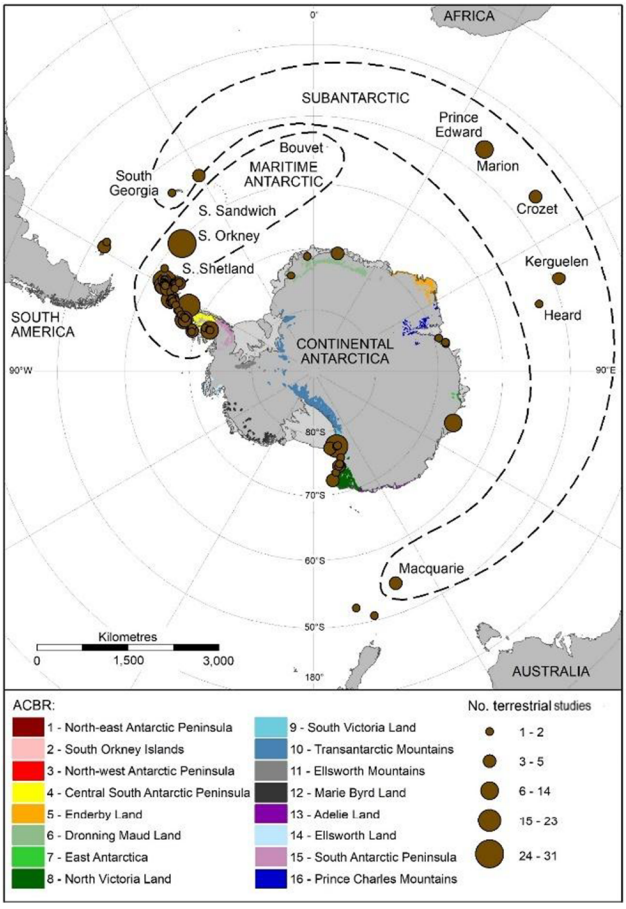

Figure 2. Summary of climate change studies performed in the Antarctic, indicating the numbers of studies focused on terrestrial species, communities or ecosystem processes. Coloured regions within the continent delimit the current Antarctic Conservation Biogeographic Regions (ACBRs; Terauds & Lee 2016). Note that multiple publications relating to the same study site were not incorporated within the numbers given here unless they were reporting responses from different biological groups. Physiological work based on laboratory studies was not included in the figure. Data obtained from Web of Science, including backward and forward searches of temperature, water (including snow), ultraviolet radiation, nutrients and relevant taxonomic groups.

Notably, there were no abundance differences of *D. antarctica* or *C. quitensis* along a 147 m elevation gradient on Livingston Island (Vera 2011). Local elevation studies have also shown clear species differentiation of crustose lichen communities in the McMurdo Dry Valleys, indicating species niche differences and, hence, scope for climate change impacts (Wagner *et al.* 2020). Reconstruction of lichen growth rates also indicates a match between radial growth and glacier retreat on South Georgia (Roberts *et al.* 2010).

Primary producers: experimental studies

Moss and algae rapidly covered entire experimental plots within 1–3 years of treatment with completely enclosed cloches on Signy Island (Kennedy 1996), while the response in OTCs was limited following 10 year field experimental manipulations (Bokhorst *et al.* 2016). However, moss cover expanded and gametangia production increased after only 2–6 years of treatment with OTCs on Fildes Peninsula (King George Island; Casanova-Katny *et al.* 2016, Shortlidge *et al.* 2017, Prather *et al.* 2019). Lichen photosynthetic capabilities appear diminished within OTCs due to increased desiccation (another micro-environmental consequence of OTCs; Casanova-Katny *et al.* 2019). Lichen community responses to experimental warming also appear to be highly species-specific (Bokhorst *et al.* 2007b, 2016), in line with species ecophysiological characteristics (Colesie *et al.* 2018, Marín *et al.* 2022). Field and laboratory incubations of Antarctic soils under increased temperature show accelerated growth of algae, mosses and microbial soil crusts (Kennedy 1996, Wynn-Williams 1996, Teoh *et al.* 2004, Wong *et al.* 2015), indicating that there is scope for increased growth of these organisms and assemblages under climate change scenarios.

Primary producers: physiological plasticity

The response of vascular plant leaf respiration to warming at sub-Antarctic Heard Island was stronger at high elevation compared with at low elevation (Schortemeyer *et al.* 2015). However, experimental warming using OTCs for 12 years did not result in species-specific responses or changes in the community composition of vascular plants on the Falkland Islands (Bokhorst *et al.* 2017). Increased growth of *D. antarctica* and *C. quitensis* was reported on Anvers Island under infrared heaters (Day *et al.* 2009) and in passive warming chambers (Day *et al.* 1999, 2008). These responses are further supported by the photosynthetic temperature response appearing to be suboptimal for *D. antarctica* and *C. quitensis*, with optimum rates at 10–14°C, suggesting that warming may promote greater carbon acquisition (Xiong *et al.* 1999). However, warming with OTCs on King George Island resulted in no effect on the growth or photosynthesis of *D. antarctica*, while *C. quitensis* showed increased photosynthetic performance and growth (Saez *et al.* 2018a). Antarctic vascular plants exposed to field warming within OTCs showed reduced freezing resistance on King George Island (Sierra-Almeida *et al.* 2018). Laboratory studies on the photosynthetic performance of *D. antarctica* indicate increased photochemical activity and decreased thermal dissipation activity and specific leaf mass with warming (Saez *et al.* 2019). However, increased growth under warming may be limited by mesophyll conductance, indicating that water limitation may counteract warming effects (Fuentes-Lillo *et al.* 2017, Saez *et al.* 2018b). In addition, there is little evidence for photosynthetic temperature acclimation across temperatures from 7°C to 20°C (Xiong *et al.* 2000).

Primary producers: historical proxies

Various studies using historical proxies indicate that changes in moss growth during the last 50 years along the Antarctica Peninsula have been exceptional in a historical context, and they are expected to increase further with future climate warming (Royles *et al.* 2013, Amesbury *et al.* 2017, Charman *et al.* 2018). However, this is contingent on topography controlling suitable microclimatic conditions, including water availability in particular (Stelling *et al.* 2018). Similar evidence has been reported from sub-Antarctic islands such as Iles Crozet (Van der Putten *et al.* 2008). Additionally, lake sediment cores show increased moss remains during the Holocene 'climate optimum' (*c.* 3800–1300 years BP) at Signy Island (Jones *et al.* 2000). The remains of a peatland ecosystem re-exposed from ice cover have been found near Cape Rasmussen, Graham Coast (65°S), an ecosystem type not currently present in the Maritime Antarctic, indicating that warm periods have occurred along the Antarctic Peninsula during the last 2500 years and that future climate warming may facilitate the re-establishment and spread of such ecotypes (Yu *et al.* 2016, Loisel *et al.* 2017).

Microbial responses: environmental gradients and proxies

Fungal community composition did not change with latitude across a 54–72°S gradient along the Scotia Arc and Antarctic Peninsula, with changes instead being associated with vegetation, microclimate and edaphic factors (Yergeau *et al.* 2007, Dennis *et al.* 2012), and vegetation-soil associations for microbes have also been found in the McMurdo Dry Valley ecosystems (Lee *et al.* 2019). Fungal and bacterial diversity were positively correlated with mean annual surface air temperature across the 54–72°S gradient (Newsham *et al.* 2016, Dennis et al. 2019). Comparisons across large latitudinal scales indicate the loss of microbial diversity in colder environments (Dragone *et al.* 2025). Moss-inhabiting diatom species richness similarly declines with elevation on sub-Antarctic Iles Kerguelen (Gremmen *et al.* 2007). Records of testate amoebae obtained from moss bank archives indicate increases in the abundance of these organisms associated with rising air temperatures since the 1950s (Royles *et al.* 2013, 2016). Diatom community changes have also been used to reconstruct historic climates on Ile de la Possession and Iles Crozet (Ooms *et al.* 2011).

Microbial responses: experimental studies

Warming with OTCs induced consistent increases in the abundance of fungi and bacteria, and in the Alphaproteobacteria-to-Acidobacteria ratio, in a study spanning from the Falkland Islands (54°S) to Anchorage Island (67°S) in both moss and fellfield vegetation (Yergeau *et al.* 2012). Similarly, a 20% increase in bacterial and fungal biomass was reported at Fildes Peninsula following warming over 7 years (Kim *et al.* 2018), while plant-associated microbial communities declined in OTCs on King George Island (Perazzolli *et al.* 2022). OTC impacts on the concentrations of Gram-positive bacterial markers in soil were negative at Mars Oasis on Alexander Island (72°S), while no such response was observed at Signy Island (60°S), probably owing to the weaker effects of OTCs on soil temperatures at the latter site (Dennis *et al.* 2013). However, using Illumina sequencing, Newsham *et al.* (2019) reported strong responses of soil bacterial communities to nutrient additions but no effects of warming with OTCs at Mars Oasis after 4 years, as well as no effects of OTCs on the Alphaproteobacteria-to-Acidobacteria ratio. Warming-induced stress, using miniature closed cloches, resulted in reduced fungal diversity and the dominance of a few species in Victoria Land (74°S; Tosi *et al.* 2005). Soils from the McMurdo Dry Valleys showed declines in bacterial cell numbers in response to warming and increased FT frequency under laboratory conditions (Knox *et al.* 2017). In contrast, laboratory studies using soils from Signy Island (60°S) showed that bacteria were more affected by warming than changes in FT frequency, while fungal abundance and community structure were most affected by FT frequency (Yergeau & Kowalchuk 2008). Laboratory studies of Antarctic algal species show increased growth rates at higher temperatures (Teoh *et al.* 2004, Wong *et al.* 2015).

Microbial responses: physiological flexibility

The temperature sensitivity of Antarctic microbial process rates, as measured through Q_{10} values quantified under laboratory conditions, has been shown to increase with mean annual soil temperature. This has been used to suggest that bacterial communities from colder regions are less temperature sensitive than those from warmer regions, although warming with OTCs for 3 years had no effect on the temperature relationships of the soil bacterial community in question (Rinnan *et al.* 2009). Laboratory studies of soil microbial process rates, such as respiration and nitrogen mineralization, often report increased rates with higher temperatures (Bokhorst *et al.* 2007a, Sun *et al.* 2014, Laudicina *et al.* 2015, Khan & Ball 2024). However, conversely, cotton strip decomposition was not affected by experimental warming in the McMurdo Dry Valleys (Treonis *et al.* 2002). Increased temperature fluctuation, associated in the natural environment with clear skies and high solar radiation during the summer, reduces fungal growth under laboratory conditions (Newsham 2024).

Invertebrate responses: field observations

Some non-native invertebrates (e.g. the beetles *Merizodus soledadinus* (Guerin-Méneville) and *Trechisibus antarcticus* (DeJean)) have expanded their ranges on South Georgia (Convey et al. 2011, Tichit *et al.* 2024) and Iles Kerguelen (Ouisse *et al.* 2020), which may in part have been facilitated by local environmental warming. Similarly, Ectemnorhinini weevil colonization and speciation rates appear to be linked to long-term climate variability across Southern Ocean islands along the Antarctic Polar Front (Baird *et al.* 2021). However, there are no repeat descriptions or long-term monitoring studies of terrestrial invertebrate communities in Antarctica except for nematode populations in the McMurdo Dry Valleys (Andriuzzi *et al.* 2018). Large egg aggregations of the springtails *Cryptopygus antarcticus* (Willem) and *Friesea grisea* (Schäffer) (now reclassified to *Friesea antarctica* (Greenslade 2018)) have been linked with very early commencement of the growing season near Palmer Station (Schulte *et al.* 2008).

Invertebrate responses: environmental gradients

Arthropod species richness and abundance declined with elevation on Marion Island, indicating that warming may result in increased abundance and richness (Lee *et al.* 2012, Hugo-Coetzee & le Roux 2018, Treasure *et al.* 2019). Seasonality and resource availability explain the size differences of weevils with elevation between Marion Island and Heard Island (Chown & Klok 2003), indicating that lengthening of the growing season may lead to larger-sized animals with consequential outcomes for life history features such as overall egg production or offspring size. A latitudinal comparison of nematode abundance, based on gene abundance, did not indicate a consistent pattern along the Antarctic Peninsula except for considerably lower abundance on southern Alexander Island (71°S; Yergeau *et al.* 2007). However, this location supports a strikingly higher and distinct nematode diversity compared to the rest of the Maritime Antarctic region (Maslen & Convey 2006).

Invertebrate responses: experimental studies

Springtail abundance and alpha diversity decline under experimental warming on sub- and peri-Antarctic islands (McGeoch *et al.* 2006, Bokhorst *et al.* 2017), while the response of the dominant Maritime Antarctic springtail, *C. antarcticus*, shows a mixed response to experimental warming. Increased abundance was reported from active warming in combination with increased water input on Anvers Island near Palmer Station (64°S; Day *et al.* 2009), whereas declines in abundance were found under a passive warming manipulation experiment at the same location after 4 years (Convey *et al.* 2002). These responses mostly reflect differences in warming intensity and increased growth under active warming compared to passive warming. At Signy Island (60°S), *C. antarcticus* increased in abundance after 8 years of warming in closed cloches (Kennedy 1994) but showed a decreasing abundance trend following 2 years of warming with OTCs (Bokhorst *et al.* 2008). However, the latter pattern was not maintained, and no effect on abundance was found after 10 years of warming

(Bokhorst *et al.* 2016), possibly reflecting the timescale required for such field manipulation experiments in the Antarctic to stabilize and generate reliable community and abundance profiles. Microarthropod abundance increased in mosses warmed by OTCs over 8 years at Fildes Peninsula (62°S; Prather *et al.* 2019), while no effect on microarthropod abundance associated with OTC warming over 2 years was reported on Anchorage Island (67°S; Bokhorst *et al.* 2008). Warming through the use of closed cloches at Cape Bird on Ross Island for 3 years also did not result in changes in the abundance of microarthropods (Sinclair 2002).

In the McMurdo Dry Valleys, while nematode abundance did not show a response to 2 years of passive warming using OTCs (Treonis *et al.* 2002), a 42% decline in the abundance of *Scottnema lindsayae* (Timm), the dominant species in this community, was reported after 8 years of warming (Simmons *et al.* 2009). In a ventilated cloche study at Mars and Ares oases, Alexander Island (72°S), there were very rapid increases of two to three orders of magnitude in soil nematode population density after only 1 year of manipulation, although in subsequent years this dropped back to only two- to five-fold increases (Convey & Wynn-Williams 2002, Convey 2003). These changes appear mostly driven by the bacterivorous genus *Plectus* (Bastian) in response to the rapid development of surface microbial and moss communities. Although warming-induced increases in the population density of *Plectus* inhabiting hydrated vegetation have similarly been recorded in a 3 year study on Adelaide Island (Newsham et al. 2021), no effect of OTCs was found on total tardigrade and nematode abundances after 10 years of warming on Anchorage Island (S. Bokhorst, unpublished data 2016) and after 8 years of warming on Fildes Peninsula (Prather *et al.* 2019).

An exceptional warming event in the McMurdo Dry Valleys, which resulted in widespread flooding (Fig. 1d), led to the decreased abundance of the microbivorous nematode *S. lindsayae*, while the omnivorous *Eudorylaimus* spp. increased in abundance (Barrett *et al.* 2008, Simmons *et al.* 2009). However, 2 decades of monitoring of the soil community in the McMurdo Dry Valleys has not revealed consistent patterns in nematode abundances with respect to mean summer temperatures, although the community did respond to extreme events related to water availability, as described earlier (Andriuzzi *et al.* 2018, Barrett *et al.* 2024). Antarctic nematode responses to climate change will be largely contingent on local soil moisture and vegetation patterns (Nielsen *et al.* 2011, Nielsen & Wall 2013, Snyder *et al.* 2025).

Invertebrate responses: physiological plasticity

Laboratory studies on the upper and lower thermal limits of native and invasive invertebrate species on sub-Antarctic islands (Kerguelen and Marion islands) indicate that these are likely to be exceeded more frequently in short-term events under climate warming (Klok & Chown 1997, van der Merwe *et al.* 1997, Klok & Chown 1998, Klok & Chown 2001, Sinclair & Chown 2002, 2003, Smith 2002, Sinclair *et al.* 2004, 2006, Deere *et al.* 2006, Slabber *et al.* 2007, Lalouette *et al.* 2012, Haupt *et al.* 2017). Increased population growth of *C. antarcticus* from Anchorage Island (67°S) was reported with warming in controlled laboratory experiments (Martin *et al.* 2023). Various invertebrates show great interannual variation in supercooling point, in part driven by avoidance and glycerol/glucose production (Sinclair & Sjursen 2001a, Worland & Convey 2001, Sjursen & Sinclair 2002), which should allow them to survive unseasonal temperature extremes. Laboratory studies into the impact of FT cycle frequency on Continental Antarctic nematodes showed that increased FT cycles resulted in greater mortality among smaller nematodes and reduced bacterial cell numbers (Knox *et al.* 2017). A similar response was observed in the field for the nematode *S. lindsayae* in Taylor Valley (Knox *et al.* 2016). Laboratory incubation of the tardigrade *Acutuncus antarcticus* indicated more rapid development at 15°C, but that those reared at 5°C lived longer and produced more offspring (Giovannini *et al.* 2023). Metabolic activity of the Continental Antarctic nematode *Plectus murrayi* increased when cultured up to 40°C under laboratory conditions, indicating a large temperature range and resource demand under future climate warming (Robinson *et al.* 2023).

Invertebrate responses: historical records and proxies

Population expansions and declines have been reported for the oribatid mites *Alaskozetes antarcticus* (Michael) and *Halozetes belgicae* (Michael) in conjunction with a warming period in the Holocene through analysis of lake sediment cores at Signy Island (Hodgson & Convey 2005).

Summary of biotic responses to temperature

Primary producer distribution patterns and physiological activity across large-scale latitudinal gradients, along with historical proxies, indicate that there is scope for community change if temperatures keep rising. However, to date, no such changes have been reported and only a limited number of local-scale primary producer population increases have been documented. Field experimental warming studies show a mixed response within and across biological groups, highlighting the context dependency of climate warming impacts (Fig. 3). While parts of Antarctica have warmed, there is as yet relatively little direct evidence of terrestrial biological responses to these changes to the climate in the natural environment. This suggests that biotic responses to warming may take longer than we anticipate to emerge, which is not unsurprising given the low physiological activity of most affected organisms, or it suggests that warming levels to date have been insufficient to generate measurable biological responses.

Response to changes in water availability

Despite the fact that water is considered to be the main limiting factor for the metabolism of most Antarctic terrestrial biota (Kennedy 1993, Schroeter *et al.* 2017) and the driver of overall terrestrial biodiversity on the continent (Convey *et al.* 2014), water addition or snow amendments through snowfence experiments have been conducted at relatively few locations (Convey *et al.* 2002, Wasley *et al.* 2006a, Day *et al.* 2009, Ayres *et al.* 2010, Sylvain *et al.* 2014). Water-impact studies on terrestrial biota have focused on cryptogams between 62°S and 75°S (Fig. S2), while drought effects have been the focus on sub-Antarctic islands.

Primary producers: environmental gradients

Comparison of cryptogam physiological activity shows an increase from the cold and dry McMurdo Dry Valleys to the wetter Antarctic Peninsula (Sancho *et al.* 2007, Schroeter *et al.* 2017). A key aspect here is that lichen activity in the McMurdo Dry Valleys is activated by water concurrently with potentially damaging light levels, whereas, along the Antarctic Peninsula, activity can occur throughout the year but often at lower levels. Similar contrasts in the activity levels of cryptogams have been reported from xeric and mesic sites along the Antarctic Peninsula (Schlensog *et al.* 2013). Comparisons along an elevation gradient indicate that water supply

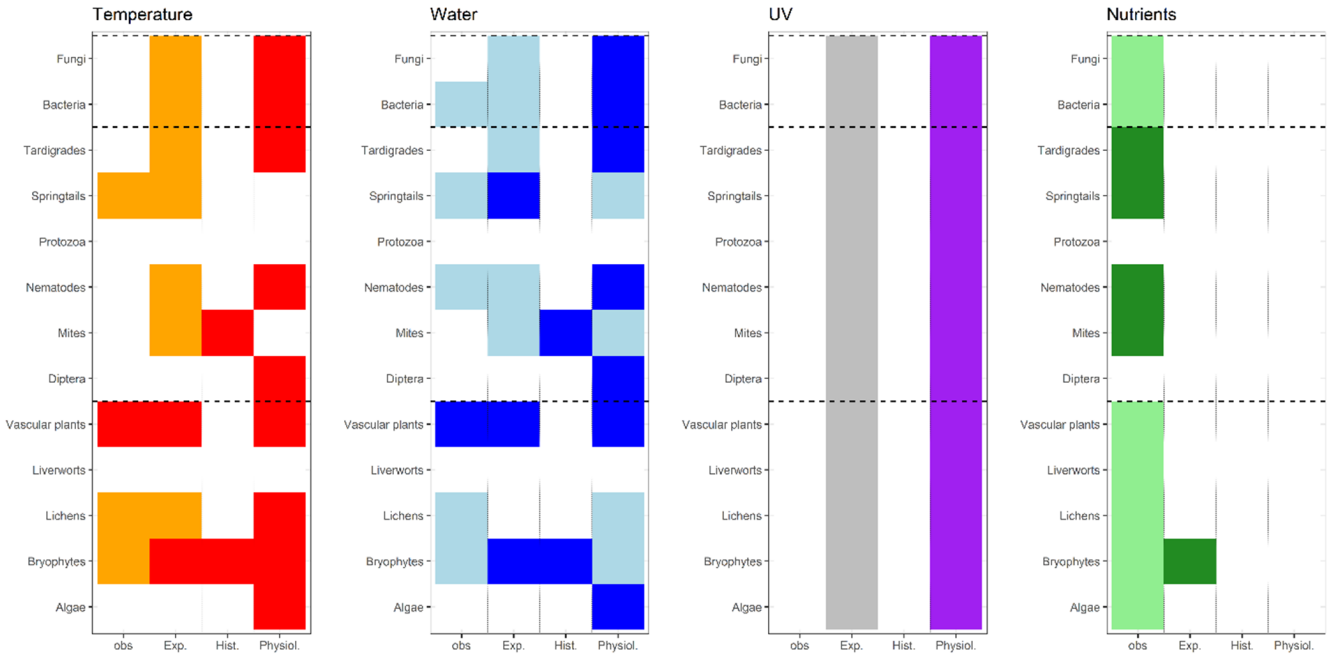

Figure 3. Heatmap of biological responses to altered levels of temperature, water, ultraviolet (UV) radiation exposure and nutrients in Antarctica. Biological responses across taxonomic groups (microbial, invertebrate and primary producers) are reported from field observational studies (obs), experimental studies (Exp.) in both field and laboratory settings, historical evidence for change (Hist.) and indications of sufficient physiological flexibility (Physiol.). Grey indicates negative impacts and white represents a lack of data. Dark colours indicate increased growth/population size or sufficient physiological flexibility and light colours indicate a mixed response (both positive and negative).

has a greater influence on lichen activity than temperature on Livingston Island (Schroeter *et al.* 2021). Physiological adaptations to submergence and desiccation tolerance correspond with the distribution of moss species (Longton 1988, Wasley *et al.* 2006b, 2012).

Primary producers: experimental studies

Experimental drying and field-water deficits have increased the mortality of *Azorella* species on sub-Antarctic Marion Island and Macquarie Island (le Roux *et al.* 2005, Bergstrom *et al.* 2015, Dickson et al. 2019). Similarly, drying in parts of coastal East Antarctica has led to the deterioration of moss vegetation (Robinson *et al.* 2018), while experimental water addition to moss communities increased productivity (Wasley *et al.* 2006a). A similar response to water amendment was reported for moss and vascular plant biomass at Palmer Station on Anvers Island (Day *et al.* 2009). Increased moss and algal abundance in response to increased water availability was reported after long-term monitoring at Cape Hallett (Brabyn *et al.* 2006), but the biological response was not sustained (Colesie *et al.* 2022).

Primary producers: physiological plasticity

The algal genus *Trebouxia* (Hildreth & Ahmadjian), a photobiont of some lichens, has been found to be susceptible to drought stress, but it recovers rapidly from freezing (Sadowsky & Ott 2012). However, large differences exist in desiccation resistance between the photobionts of various lichens (Sadowsky *et al.* 2016). The growth response of *C. quitensis* was found to be stronger to water additions than to warming under laboratory incubations (Fuentes-Lillo *et al.* 2017). Species-specific morphological characteristics affect the influence of vapour pressure differences of moss and lichen species on their carbon uptake and loss (Stanton *et al.* 2014, 2023).

Primary producers: historical proxies

Increases in moss growth have been reported from historical archives (70–2700 years BP) in relation to greater water availability along the Antarctic Peninsula (Royles *et al.* 2013, Royles & Griffiths 2015, Amesbury *et al.* 2017, Charman *et al.* 2018, Stelling *et al.* 2018).

Microbial and invertebrate responses: environmental gradients

Microbial biomass and respiration rates were enhanced in the proximity of drainage lines in the McMurdo Dry Valleys, but these patterns were also affected by soil conditions and salinity effects, indicating that the impact of water was not consistent across the landscape (Ball & Levy 2015, Lee *et al.* 2018). Similar patterns have been reported for soil communities during extreme melt events in this region (Ball *et al.* 2011, Nielsen *et al.* 2012, Gooseff *et al.* 2017).

Microbial and invertebrate responses: experimental studies

Sylvain et al. (2014) reported lower nematode abundances at wetter sites in the McMurdo Dry Valleys and also in response to water additions. This response contrasts with other reports from the same location, probably reflecting differences in watering intensity and species-specific tolerance limits (Nielsen *et al.* 2012). The abundance of the springtail *C. antarcticus* increased in response to water additions in the field at Palmer Station (Day *et al.* 2009), which corresponds with its poor control over water loss, which is broadly characteristic of springtails (Block & Convey 2001, Convey *et al.* 2003, Elnitsky *et al.* 2008).

Microbial and invertebrate responses: physiological plasticity

Water additions to Antarctic biological soil crusts increased nitrogen fixation rates under laboratory conditions (Perez *et al.* 2017). They also increased soil respiration, nitrification and the decomposition of cotton strips in McMurdo Dry Valley soils in the

Figure 4. Snow-filled open-top chambers on Signy Island (left, summer 2004) and Anchorage Island (right, winter 2005), where the thicker winter snowpack insulates the contained vegetation against freezing temperatures, with detrimental consequences for lichens such as *U. antarctica* (Bokhorst *et al*. 2016).

laboratory (Treonis *et al.* 2002). However, extracellular enzyme activities can be impaired under enhanced water and temperature conditions (Misiak *et al.* 2021).

Snow manipulations

In contrast with Arctic and alpine regions, snow manipulation experiments are scarce in Antarctica (Wipf & Rixen 2010, Cooper 2014). Ayres *et al.* (2010) reported shifts in the nematode communities of the McMurdo Dry Valleys, where increased snow depth resulted in altered moisture conditions. The native vascular plant flora appears to be negatively affected by deeper and more prolonged snow cover (Edwards 1972, Park *et al.* 2013). Year-round placement of OTCs and consequential (unintended) accumulation of snow (Fig. 4) have been implicated in the decline of the lichen *Usnea antarctica* (Du Rietz) on Signy Island (Bokhorst *et al.* 2016). The presence of *Usnea* is also used as a proxy for thinner snowpacks along the Antarctic Peninsula (Vieira *et al.* 2014). Bacterial activity levels are strongly regulated by snow and ice cover, as the thickness of these layers regulates light levels and UV radiation exposure (Cockell *et al.* 2002).

Summary of biotic responses to water

Primary producer distribution patterns and physiological activity are strongly driven by water availability across Antarctica, as is apparent across current environmental gradients and historical proxies. Most primary producers will benefit from increased moisture levels or duration of water availability, except at locations that are already saturated. Although experimental evidence is limited, the same applies for associated microbial and invertebrate communities (Fig. 3). Despite being a continent almost completely covered by snow and ice, very few studies relating to snow and ice cover have been made in Antarctic terrestrial ecosystems, indicating that the role of snow and ice on organism physiology, growth and population sizes is largely unknown.

Responses to UV radiation

The discovery of the Antarctic ozone hole in the 1980s (Farman *et al.* 1984), caused by anthropogenic atmospheric pollution, catalysed a surge in research on the potential impacts of increased

Figure 5. Ultraviolet radiation enhancement of Antarctic moss vegetation on Signy Island, South Orkney Islands (Boelen *et al.* 2006).

UV-B radiation (280–315 nm) on Antarctic biota (Roberts 1989). Such studies typically used filters to exclude UV radiation in the field (Montiel *et al.* 1999, Huiskes *et al.* 2001) or used lamps (Fig. 5) to enhance UV exposure (George *et al.* 2001, Rozema *et al.* 2001, Boelen *et al.* 2006). UV impact studies of terrestrial biota have primarily focused on cryptogam and microbial responses at locations from 60°S to 72°S (Fig. S1).

Primary producer responses to UV: environmental gradients

There appears to be a considerable shift in the type of lichen secondary compounds produced naturally, which help in protection against UV radiation, among lichen species from the northern Maritime Antarctic compared to those inhabiting more southern locations (de Jonge *et al.* 2025), indicating that UV exposure and lichen chemistry may affect species distribution patterns.

Primary producer responses to UV: experimental studies

Newsham & Robinson (2009) carried out a meta-analysis of studies into the responses of Antarctic and Arctic bryophytes and

vascular plants to UV radiation, concluding that enhanced levels of UV increased pigmentation levels and DNA damage and reduced biomass. The underlying repair mechanisms have yet to be completely resolved (Contreras & Zúñiga 2025). The lichens *Turgidosculum complicatulum* (Nyl), *Stereocaulon alpinum* (Laurer) and *U. antarctica* did not show any physiological response to 2 years of reduced UV levels on Léonie Island (Huiskes *et al.* 2001, Lud *et al.* 2001a). UV filtering reduced the concentration of UV-absorbing compounds present in moss and lichen species in East Antarctica (Gautam *et al.* 2011, Singh *et al.* 2012). Antarctic mosses show UV screening capabilities, although endemic species appear to be poorly protected compared to cosmopolitan species (Dunn & Robinson 2006, Turnbull & Robinson 2009). The thalli of the liverwort *Cephaloziella varians* (Gottsche) lost their dark colour when placed underneath UV-filtering Mylar screens, and pigmentation was induced within 48 h of removing the screens (Snell *et al.* 2009). Ambient UV levels have been implicated in affecting rhizosphere microbial communities associated with *D. antarctica* (Avery *et al.* 2003), while fungal symbionts appear to help protect *C. quitensis* against UV damage (Barrera *et al.* 2020, Acuña-Rodríguez *et al.* 2024). Historical ozone concentrations have been tracked through flavonoid levels in herbarium specimens of the Antarctic moss *Bryum argenteum* (Ryan *et al.* 2009).

Primary producer responses to UV: physiological plasticity

Physiological plasticity responses of primary producers to UV radiation exposure have not been widely studied. However, laboratory studies show increased membrane damage and photoinactivation in *C. quitensis* with exposure to high UV levels (Navarrete-Gallegos *et al.* 2012).

Microbial responses to UV radiation: experimental studies

Strong microalgal colonization was reported in ventilated cloches that also reduced UV radiation on Signy Island (Wynn-Williams 1996). Algae of the genus *Zygnema* (Bessey) showed reduced levels of photosystem II activity under high-UV conditions, while phenolic compound concentrations at the cell periphery increased (Pichrtova *et al.* 2013). The terrestrial microalga *Stichococcus bacillaris* (Nägeli) showed reduced cell viability and maximum quantum yield of photosystem II under increased UV conditions (Hughes 2006). In contrast, the terrestrial alga *Prasiola crispa* (Kützing) showed limited and transient response differences between UV-sheltered and -exposed treatments (Lud *et al.* 2001b), although increased UV resulted in reduced photosynthetic performance (Post & Larkum 1993). Cyanobacterial communities showed more species-specific responses to UV exposure (George *et al.* 2001). Fungal communities showed increased growth under reduced UV irradiance in Victoria Land (Tosi *et al.* 2005), and bacterial communities similarly performed better underneath ultrathin soil layers (500 µm) compared with bacterial communities exposed to ambient UV levels (Cockell *et al.* 2003).

Microbial responses to UV radiation: physiological plasticity

Laboratory studies on a strain of the freshwater alga *Chlorella* (UMACC 237) showed that high UV levels impaired the return of optimal photosystem II activity at higher temperatures (Wong *et al.* 2015). Young vegetative algal cells adapt better to experimental UV stress exposure than older cells (> 6 months) under laboratory conditions (Holzinger *et al.* 2018). Pigmentation in various bacteria and fungi isolated from Antarctic environments increases resistance to environmental stressors such as high light and UV exposure (Arcangeli *et al.* 1997, Wong *et al.* 2007, Mojib *et al.* 2013, Reis-Mansur *et al.* 2019). The fungus *Arthrobotrys ferox* (Onofri & Tosi) isolated from Antarctic soil showed better protection against UV radiation compared to temperate species (Zucconi *et al.* 2002). Ice layers protect microbial communities of cryoconite and cryo-lake ecosystems from high light intensity (Bagshaw *et al.* 2016).

Invertebrate responses to UV

Field experimental enhancements of UV radiation resulted in decreased microarthropod abundance in a study on Anvers Island, but this response may have been mediated through changes in the biochemical composition of the vegetation or litter formed (Convey *et al.* 2002). The Continental Antarctic Collembola species *Gomphiocephalus hodgsoni* (Carpenter) showed reduced survival and moult rates when exposed to UV radiation compared to darkness and also showed upregulation of DNA repair mechanisms (Hawes *et al.* 2012).

Summary of biotic responses to UV radiation

Antarctic vegetation appears relatively well protected against UV radiation, but there are costs associated with this protection, which may to some extent impair physiology, growth, reproduction and distribution patterns. Similar observations have been made for microbes and invertebrates, but with fewer studies made on these organisms (Fig. 3). There have been limited comparisons across environmental gradients, local and latitudinal comparisons and historic proxies.

Responses to changing nutrient availability

Terrestrial biological studies relating to nutrient availability from the sub-Antarctic to the continent include more than 40 biological responses (Fig. S1). The largest local nutrient input for Antarctic terrestrial ecosystems along the coast (and in some instances inland) is derived from the marine environment through faecal deposition by penguins, other birds and seals.

Primary producer responses to nutrients

Except for nitrophilous algae, hardly any vegetation grows in seal and penguin colonies due to trampling and extreme levels of nutrients (Smykla *et al.* 2007, Favero-Longo *et al.* 2011). Around the periphery of such colonies, increased vegetation development can sometimes be observed where suitable habitats are present (Zwolicki *et al.* 2015), although there is no Antarctic equivalent to the sometimes spectacular 'bird cliff' vegetation that characterizes some parts of the High Arctic (Zwolicki *et al.* 2019). Sub-Antarctic islands show lusher and nutrient-enriched vegetation in proximity to penguin and seal colonies (Erskine *et al.* 1998, Smith *et al.* 2001, Vidal *et al.* 2003). Cryptogam abundance and diversity was also increased near petrel nests in the Vestfold Hills and Dronning Maud Land in Continental Antarctica (Ryan & Watkins 1989, Leishman & Wild 2001). Lichen physiological activity is affected by nutrients from penguin colonies (Crittenden *et al.* 2015). However, aside from such observational studies on vegetation development in the proximity of vertebrate aggregations, nutrient addition studies on vegetation are scarce, although mosses respond more strongly to nutrient additions than water amendments in East Antarctica (Wasley *et al.* 2006a). Moss-inhabiting diatom communities are often dominated by different taxa in the proximity of nutrient inputs from vertebrate species along the Antarctic Peninsula (Kopalova *et al.* 2014).

Microbial responses to nutrients

Marine-derived nutrients promote soil microbial abundance (Smith & Steyn 1982), microbial processes and decomposition on sub-Antarctic islands (Smith *et al.* 1993, Smith 2003, 2005, 2008) and at sites along the Antarctic Peninsula (Bokhorst *et al.* 2007a, Park *et al.* 2007, Zhu *et al.* 2008, 2009, Teixeira *et al.* 2013, 2014, Rampelotto *et al.* 2015, Guo *et al.* 2018, 2019, Ramírez-Fernández *et al.* 2019, Wang *et al.* 2019), as well as at colder sites such as Ross Island (Ball *et al.* 2015) and Dronning Maud Land (Cocks *et al.* 1998). However, field manipulation studies in the McMurdo Dry Valleys suggest that the impacts of nutrients are limited by water availability (Ball *et al.* 2018), and high nutrient levels can result in reduced microbial biomass, process rates and bacterial diversity and community composition (Ball & Virginia 2014). There is also evidence that warming can both constrain and enhance certain microbial responses to additional nutrients (Dennis *et al.* 2013, Newsham *et al.* 2022).

Invertebrate responses to nutrients

Field surveys in the proximity of nitrogen sources from penguins and elephant seals indicate that invertebrate abundance and diversity are greatly increased compared to sites without nitrogen input along the Antarctic Peninsula and Scotia Arc (Bokhorst & Convey 2016, Bokhorst *et al.* 2019). Similar patterns have been observed in Dronning Maud Land near nesting petrels (Ryan & Watkins 1989). However, nematode communities within penguin colonies at much colder and drier sites on Ross Island were dominated by a single species (Porazinska *et al.* 2002).

Summary of biotic response to nutrients

The abundance and physiological activity of plants and associated organisms tend to respond positively to nutrient inputs, indicating that most Antarctic terrestrial ecosystems are nutrient limited. Only in some of the coldest and driest regions are nutrients not the most limiting resource. However, most such knowledge is derived from environmental gradient studies, and there is a lack of controlled field and laboratory experimentation to better understand underlying mechanisms (Fig. 3). Given the strong impacts that external nutrients tend to have on population size, any changes in marine-derived nutrient inputs from penguins, birds and seals may affect local terrestrial biodiversity patterns.

Freshwater ecosystems

Freshwater ecosystems are greatly under-researched compared to terrestrial ecosystems in Antarctica (Hawes *et al.* 2023, Pertierra *et al.* 2025). This is reflected in the number of climate change studies that emerged from the literature searches, with just over 60 locations (Fig. 6).

Freshwater ecosystem responses to warming

Climate-impact studies on freshwater ecosystems have been carried out at > 60 locations from the sub-Antarctic islands to Dronning Maud Land and North and South Victoria Land (Fig. S2). Reductions in lake ice and snow cover were reported across Signy Island between 1980 and 1995 (when the previous long-term year-round monitoring programme was discontinued) as a result of climate warming trends, thereby extending the open water period by up to 4 weeks and with 2- to 10-fold increases in chlorophyll concentrations in lake water (Quayle *et al.* 2002, 2003). In the same vein, periodic cooling trends resulted in decreases in primary production in lakes in the McMurdo Dry Valleys (Doran *et al.* 2002), indicating that these lakes are extremely sensitive to small changes in temperature. Warmer temperatures have been associated with fungal outbreaks in microbial mats of freshwater ecosystems, resulting in declines in structural properties and photobionts and nitrogen depletion (Velazquez *et al.* 2016). Experimental warming of cyanobacterial mats in the Maritime Antarctic resulted in higher diversity, but also an increased presence of cyanobacterial toxins (Kleinteich *et al.* 2012). Photosynthesis and nitrogen fixation in cyanobacterial mats responded positively to increased temperatures on Livingston Island (Velazquez *et al.* 2011).

Oxygen consumption of the crustacean *Branchinecta gaini* (Daday) increased at higher temperatures under laboratory conditions (Peck 2004, Pociecha 2007), while flagellate growth was also increased by experimental warming under laboratory conditions (Newsham & Garstecki 2007). Laboratory studies imply that predatory *Lancetes* (Curtis) water beetles could switch from their current biennial to an annual life cycle with as little as 1°C warming on South Georgia, which would allow for rapid population increases (Arnold & Convey 1998). Benthic diatoms show different temperature growth optima in McMurdo Dry Valley

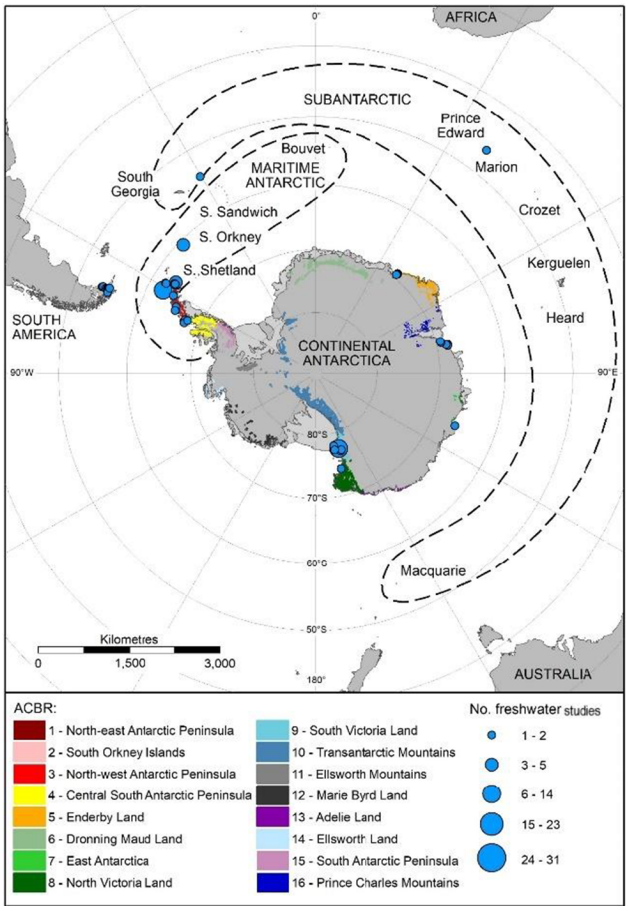

Figure 6. Summary of climate change studies performed in the Antarctic, indicating the numbers of studies focused on freshwater species, communities or ecosystem processes. Coloured regions within the continent delimit the current Antarctic Conservation Biogeographic Regions (ACBRs; Terauds & Lee 2016). Note that multiple publications relating to the same study site were not incorporated within the numbers given in this figure unless reporting responses from different biological groups.

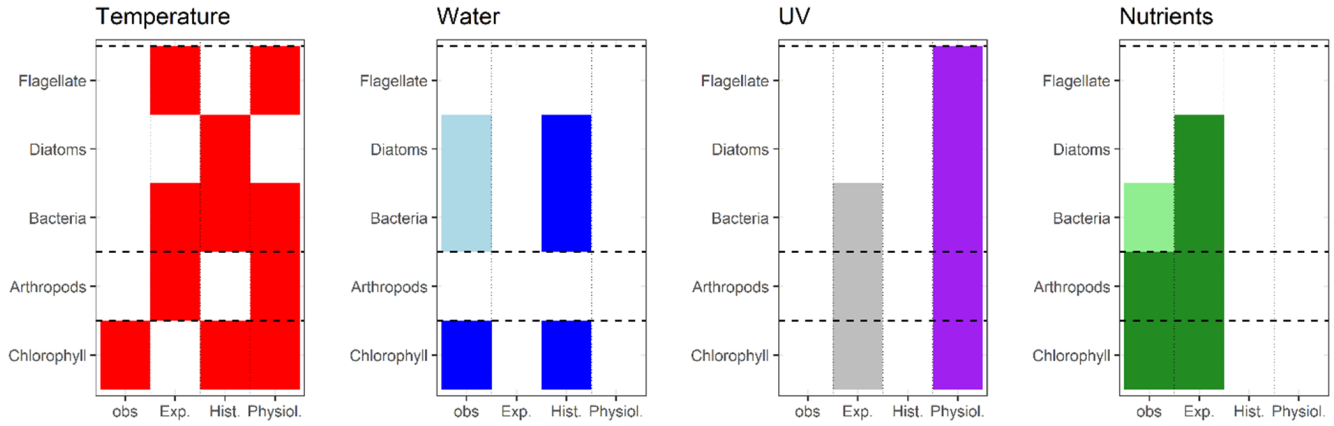

Figure 7. Heatmap of biological responses in freshwater ecosystems to enhanced levels of temperature, water, ultraviolet (UV) radiation exposure and nutrients in Antarctica. Biological responses across taxonomic groups including unicellular organisms, invertebrates and chlorophyll as a measure of productivity are reported from field observational studies (obs.), experimental studies (Exp.) in both field and laboratory settings, historical evidence for change (Hist.) and indications of sufficient physiological flexibility (Physiol.). White represents a lack of data, while dark colours indicate increased growth/population size or sufficient physiological flexibility, and light colours indicate a mixed response (positive and negative).

rivers, which may affect future community composition under warming (Darling *et al.* 2017).

Bacterioplankton abundance declined at increasing latitudes along a transect from southern Argentina to the Maritime Antarctic across 45 freshwater lakes, with latitude and declines in phosphate and light attenuation playing large roles (Schiaffino *et al.* 2011). Algal biomass and pigments showed declining trends with latitude in Victoria Land lakes (Borghini *et al.* 2016). However, there were no latitudinal trends of viral diversity in lake ecosystems along the Antarctic Peninsula (de Carcer *et al.* 2016). Across 37 lakes in the McMurdo Dry Valleys, microbial mat communities appear to be structured by salinity, lake water depth and nutrient concentrations - variables that are all likely to be affected by climate change (Verleyen *et al.* 2010).

Biogenic productivity quantified from lake core samples on Vega Island (off the north-east Antarctic Peninsula) corresponded with climatic changes during the Holocene (Píšková *et al.* 2019, Čejka *et al.* 2020). High carotenoid and chlorophyll concentrations in lake sedimentary records (Beak Island) have similarly been linked to the Holocene climate optimum, again indicating that the cyanobacterial flora is sensitive to climate warming (Fernandez-Carazo *et al.* 2013). Environmental and climatic changes and associated diatom communities in various lakes of East Antarctica have been tracked over the Holocene period, with occasional incursions of marine diatom communities indicative of sea ice-free coastal zones (Verkulich *et al.* 2002, Tavernier *et al.* 2014).

Summary of freshwater biotic responses to temperature

There is clear evidence from different methodological approaches that increased temperature results in increased physiological activity and growth in freshwater ecosystems (Fig. 7). However, this creates opportunities for algal blooms and increased cyanobacterial toxins, which could severely impact local diversity.

Freshwater ecosystem responses to water availability

Freshwater habitats have been infrequently studied in the context of water impacts (Fig. S2). Freshwater ecosystem responses to increased or decreased water availability mostly reflect changes in nutritional/mineral availability (dilution or concentration), which can feed back to biological responses, but this has not been addressed across multiple sites. Most Antarctic freshwater ecosystems show marked differences in community structure between winter and summer due to differences in temperature and light availability/photoinhibition (Laybourn-Parry *et al.* 1996, Butler 1999). Intermittent flow can strongly influence diatom communities (Stanish *et al.* 2012), while microbial planktonic groups appear stable across the diurnal cycle in Maritime Antarctic lakes (Pearce & Butler 2002). Long-term monitoring of microbial mats in the McMurdo Dry Valleys indicates a clear growth response with increased water availability (Kohler *et al.* 2015), but comparable studies from the Antarctic Peninsula are lacking. Experimental manipulations of the hydrological cycle in freshwater ecosystems are impractical considering the scale of most lakes or catchment areas. However, natural intermittent stream flows provide insights into biotic responses to increased/decreased water availability (Stanish *et al.* 2012), while catastrophic draining of lakes due to melting of permafrost catchments or loss of ice dams can result in large phytoplankton community composition shifts (Izaguirre *et al.* 2012). Although such observations provide valuable insights, they are highly dependent on opportunistic sampling, which in itself is challenging and most often impractical given permitting protocols and limited logistical support.

Seasonal or short-term sampling indicates that dilution of ions in stream waters occurs following precipitation events on sub-Antarctic Marion Island (Stowe *et al.* 2019), but no biological responses were measured. Evaporative losses resulted in increased ion concentrations and reduced phytoplankton biomass, through photoinhibition, in the lakes of East Antarctica (Borghini *et al.* 2008, 2013). High levels of mercury (Hg) in lake sediment cores have been associated with melting periods on Livingston Island (Perez-Rodriguez *et al.* 2019), which could have ecological consequences if concentrations exceed physiological thresholds.

Summary of freshwater biotic responses to water availability

The impacts of changes in water supply to freshwater ecosystems mostly influence biota through the dilution of nutrients and minerals, which can limit physiology and growth, depending on local availability. Most knowledge on this subject derives from opportunistic sampling, and more insights could be derived from the application of (field) experimental approaches (Fig. 7).

Freshwater ecosystem responses to UV radiation

The response of freshwater ecosystems to UV-B radiation exposure has mainly been quantified under laboratory conditions or through comparisons between lake ecosystems. Studies of freshwater responses to UV impacts are restricted to eight locations mostly south of 69°S (Fig. S2). The research on UV impacts on primary production in Antarctic coastal and marine habitats has been extensive (Smith *et al.* 1992, Holm-Hansen *et al.* 1993, Hader *et al.* 2014), but freshwater ecosystems have been relatively little-studied (Vincent *et al.* 1998). Mat-forming benthic cyanobacteria decline under increased UV radiation (Quesada *et al.* 1995, Quesada & Vincent 1997), and similar results have been reported from phytobenthic organisms from lake beds near Syowa Station in Continental Antarctica (Kudoh *et al.* 2009, Tanabe *et al.* 2019). Greater pigmentation in bacteria increases resistance to environmental stressors such as high light and UV exposure (Dieser *et al.* 2010). Freshwater communities under high UV and photosynthetic active radiation conditions developed firm mat textures that were less transparent and characterized by high UV/photoprotective substance ratios with reduced photochemical efficiency (Tanabe *et al.* 2010). The Antarctic copepod *Boeckella poppei* (Mrázek) accumulates mycosporine-like amino acids as a form of protection against UV radiation (Rocco *et al.* 2002). Warming impacts were inversely related to those of UV radiation on bacterial functioning in Antarctic stream ecosystems (Roos & Vincent 1998).

Summary of biotic responses to UV radiation

UV exposure is harmful for most organisms and is evident in reduced abundance or the adaptations reported for various freshwater organisms (Fig. 7). However, it is unclear whether all such adaptations also affect growth and reproductive output for all freshwater organisms.

Freshwater ecosystem responses to nutrient availability

Assessments of freshwater biological responses to nutrients are limited to eight locations predominantly on sub-Antarctic islands and at low-latitude Maritime Antarctic sites (Fig. S2). Antarctic and sub-Antarctic freshwater ecosystems have shown large responses to eutrophication by marine vertebrates, leading to high bacterioplankton population density, increased productivity, reduced species richness and increased evenness among key groups, as well as changes in seasonal community patterns (Grobbelaar 1974, Hawes 1983, Smith 1985, Ellis-Evans 1990, Hansson *et al.* 1993, Butler 1999, Pearce *et al.* 2005). Lower bacterial diversity was reported from eutrophic lakes compared to oligotrophic lakes on Livingston Island (62°S; Villaescusa *et al.* 2010), and similar patterns were observed for fungal communities on James Ross Island (64°S; Gonçalves *et al.* 2022). Nutrient (N and P) additions to meltwater streams in the McMurdo Dry Valleys (78°S) resulted in greater chlorophyll *a* concentrations, total algal bio-volume and filamentous cyanobacteria and higher proportions of diatoms and species richness (Kohler *et al.* 2016). Lake plankton communities also showed increased growth responses to nutrient additions at Lake Chico in Hope Bay (63°S; Allende 2009).

Summary of biotic responses to nutrient availability

From sub-Antarctic islands to the McMurdo Dry Valleys, freshwater chlorophyll content, algal growth and microbial communities tend to respond positively to nutrient inputs, indicating that most, if not all, Antarctic freshwater ecosystems are nutrient limited (Fig. 7). This limitation may impair biological responses to climate change. More field experimental work is needed to unravel the underlying mechanisms, limitations and physiological plasticity of freshwater organism responses to nutrient inputs.

Interactions among climate change drivers

Climate change alters a range of environmental conditions other than temperature. Therefore, assessments of species and community responses to simulations of future climatic change scenarios should include multiple environmental variables. The tremendous growth of primary producers observed in the first Antarctic warming studies was in part driven by the high humidity within the closed cloches used (Kennedy 1996, Wynn-Williams 1996), indicating that primary production can increase with higher temperature, but only under conditions of sufficient water availability (Day *et al.* 2009). This is further supported by evidence from historical archives in sediment and peat cores from the Antarctic Peninsula region (Royles & Griffiths 2015). However, negative impacts of environmental combinations have also been reported. For instance, Dennis *et al.* (2013) found reduced microbial responses to nutrient additions under warmed conditions, while Convey *et al.* (2002) inferred that some species of microarthropods were less abundant under OTC warming treatments, probably as a result of increased desiccation. Warmer temperatures have been associated with fungal outbreaks in microbial mats in freshwater ecosystems, resulting in negative impacts on the physical characteristics of the microbial mat and nitrogen depletion (Velazquez *et al.* 2016). This possibility has also been raised for the occurrence of oomycete- and fungal-associated 'fairy ring' disease in Maritime Antarctic mosses and associated epiphytic algal communities, although this has not definitively been proven (Rosa *et al.* 2020, Câmara *et al.* 2021), with the high water contents of moss tissues emerging from snowpack being a probable explanation for the disease (Tojo & Newsham 2012). Increased emphasis is required on the application of multiple-factor studies to simulate more realistic future climate scenarios (Wall *et al.* 2011, Nielsen & Wall 2013). These aspects are even more important in light of the potential for the establishment of non-native species (Baird *et al.* 2019, Hughes *et al.* 2020, Bokhorst *et al.* 2021), which may be better suited to coping with warmer Antarctic environments. Laboratory studies show that non-native vascular plants benefit greatly from nutrient additions by penguins at 7°C, while they cannot do so at 2°C (Bokhorst *et al.* 2022, 2025).

Biotic interactions and climate change

Biotic interactions have received limited attention in Antarctic ecosystems due to the environmental restrictions imposed on Antarctic biota, although that concept has been increasingly challenged (Hogg *et al.* 2006, Caruso *et al.* 2013, 2019, Lee *et al.* 2019, Huisman *et al.* 2026), and vegetation models appear to achieve greater accuracy when incorporating species interactions (Rocha *et al.* 2024). Increasing temperatures may release some current abiotic restrictions and allow for more species interactions (Wall 2007). This field of research requires expansion, especially again in the context of the ever-increasing pressure that non-native species will exert on species interactions (Chown & Smith 1993, Molina-Montenegro *et al.* 2019, Hughes *et al.* 2020, Martin *et al.* 2023, Bokhorst *et al.* 2024a).

Warming of experimental microcosms reduced bacterial abundances by 75% and doubled NH_4^+ concentrations in mixtures

inoculated with four to six flagellate species compared with mixtures of only two flagellate species, indicating that climate warming is capable of affecting Antarctic species interactions in experimental settings (Newsham & Garstecki 2007). Warming with OTCs led to a doubling in the frequency of fungal hyphal coils in liverwort tissues on Adelaide Island (Newsham 2021). The photobiont of the lichen *U. antarctica* declined in OTCs, which led to the complete disappearance of the lichen (Bokhorst *et al.* 2016). Antarctic hairgrass (*D. antarctica*) grew more frequently and to larger sizes within moss carpets compared to bare ground on the South Shetland Islands (Casanova-Katny & Cavieres 2012). However, on islands near the coast of Anvers Island, field observations indicate that *D. antarctica* performed worse when in the presence of a neighbouring plant (moss, *C. quitensis* or itself) compared to growth in isolation (Krna *et al.* 2009). On sub-Antarctic Marion Island, more species occurred at higher elevation and in a consequently colder climate when grown next to the cushion plant *Azorella selago* (Raath-Kruger *et al.* 2019).

Increasing fur seal numbers have had generally detrimental impacts on coastal cryptogam and vascular plant communities through trampling and eutrophication (Bonner 1985, Smith 1988, Smith *et al.* 2001, Favero-Longo *et al.* 2011, Cannone *et al.* 2016, Convey & Hughes 2022), although positive effects have been reported where nutrient input and disturbance were more limited (Cannone *et al.* 2016), analogous to the situation in the vicinity of, but not within, the core of penguin colonies, as well as on the occurrence of some specifically coprophilic lichens (Favero-Longo *et al.* 2011). Considering the strong effect of eutrophication/manuring by marine vertebrates for Antarctic terrestrial and freshwater ecosystems, any changes in the abundance and distribution of these marine animals resulting from climate change or human activities (Trathan & Reid 2009, Clucas *et al.* 2014) will affect Antarctic terrestrial biota. In addition, invasive species may benefit more from high nutrient inputs than native biota (Bokhorst *et al.* 2022), but the order in which species arrive and germination speed can influence plant community composition (Bokhorst *et al.* 2024a). Understanding the interactions between nutrient availability and climate warming will require increased application of more complex multiple-factor experiments.

Future perspectives to quantify climate change impacts

Use of existing gradients

Comparative studies along elevational and latitudinal gradients are relatively scarce in the Antarctic but could provide valuable insights into the limits on, for instance, species distributions (Cannone *et al.* 2017, Sancho *et al.* 2019, Ouisse *et al.* 2020) and long-term ecosystem responses to climatic variables (Sundqvist *et al.* 2013, Horrocks *et al.* 2020, Bokhorst *et al.* 2024b). These are difficult to achieve with experimental manipulation studies. In line with this, there is ample scope for studies on the smaller scale (centimetres to metres) and taking advantage of temporal heterogeneity in terms of microclimate conditions (Rochera *et al.* 2010, Convey *et al.* 2018, Randall *et al.* 2025), which shape biotic responses (Sinclair & Sjursen 2001b). For example, sun-exposed lichens and bryophytes often have darker thalli than those growing in the shade (Kappen 1983, Sojo *et al.* 1997), but the implications of this plasticity for ecosystem functioning and potential climate change impacts have been rarely addressed (Snell *et al.* 2009), while these adaptations appears to drive species' latitudinal distribution patterns (de Jonge *et al.* 2025).

Species distribution modelling

An important approach to predicting species responses to climate change is that of species distribution modelling based on fitness (e.g. survival, reproduction) in relation to climatic parameters (Elith & Leathwick 2009, Jimenez-Valverde *et al.* 2011, Booth 2018). These approaches are now starting to be used to estimate both range changes in native species and the threat of invasive species establishment and expansion of their range across Antarctic ecosystems (Chown *et al.* 2012, Duffy *et al.* 2017, Baird *et al.* 2019, Bartlett *et al.* 2020, Contador *et al.* 2020, Pertierra *et al.* 2020, Vega *et al.* 2020). Distribution modelling or niche partitioning of native Antarctic terrestrial and freshwater species based on physiological optima has been a research focus for several years (Caruso *et al.* 2010, Lee *et al.* 2013, Ashcroft *et al.* 2016), but past glaciation events often affect distribution patterns in unexpected ways, thereby complicating model approaches (Caruso *et al.* 2009, Czechowski *et al.* 2016, Collins *et al.* 2019). In addition, environmental variability does not necessarily change consistently with latitude, complicating the use of proxies such as latitude (Howard-Williams *et al.* 2010, Hughes *et al.* 2013). To improve the distribution modelling of Antarctic species in the light of climate change, there is a need for more detailed understanding of species associations (Longton 1967, Mieczan & Adamczuk 2015, Cannone *et al.* 2017) and ecologically relevant microclimatic conditions (Convey *et al.* 2018, Randall *et al.* 2025). In addition, such distribution models require solid experimental data to support temperature-distribution associations, as experimental studies may indicate a different/greater latitudinal species range than those based on modelled assumptions (Bokhorst *et al.* 2021). A stronger collaboration between species modellers and field ecologists is required to address the mismatch between assumed environmental envelopes for Antarctic terrestrial and freshwater biota and realistic field conditions.

Long-term monitoring

Long-term monitoring has provided reliable data on species and ecosystem responses to contemporary climate change on the sub-Antarctic Kerguelen archipelago (Robin *et al.* 2011) and Marion Island (van der Merwe *et al.* 2024) and in some aquatic systems in Maritime and Continental Antarctica (Quayle *et al.* 2002, Laybourn-Parry & Bell 2014, Kohler *et al.* 2015). However, this approach has only been applied at a few sites and to a limited set of organisms, and most such programmes have regrettably been discontinued. Although not representing true monitoring programmes as such and, rather, serendipitous opportunity, elements of flowering plant and moss distributions and abundance have been resurveyed three times over a *c.* 60 year timespan in the Argentine Islands (Fowbert & Smith 1994, Parnikoza *et al.* 2009) and on Signy Island (Cannone *et al.* 2016, 2017, 2022), and similarly for mosses and lichens at Cape Hallett (Colesie *et al.* 2022). These remain the only long-term integrations available across Antarctica, although shorter time series at locations in the South Shetland Islands and James Ross Island are in place. A notable exception here is the Long Term Ecological Research (LTER) programme funded by the US National Science Foundation in the McMurdo Dry Valleys (https://mcm.lternet.edu/), although its extremely low-biodiversity ecosystems and particularly extreme conditions do not represent the large majority of Antarctic terrestrial biodiversity, and its continuation appears to be under real threat due to contemporary internal political influences in the USA. As a baseline future requirement, long-term monitoring of various groups across contrasting habitats and ACBRs would

provide a highly valuable contribution, such as that being proposed within the Scientific Committee on Antarctic Research's (SCAR) Antarctic Near-Shore and Terrestrial Observation System (ANTOS) programme, to understanding temporal and spatial variability in Antarctic ecosystems and their responses to climate change (Robinson *et al.* 2024).

Remote sensing of vegetation trends

Recent technological advances and the increased availability of satellite imagery across various regions of Antarctica should, in theory, allow for greater assessment of current vegetation status (Walshaw *et al.* 2024) and, over time, of the expansion or retraction of vegetation cover. However, such approaches require robust and validated ground truthing, especially if attempting to backdate the data to before 2014, when the availability of relatively low-resolution snow- and cloud-free Landsat 8 images was both limited and highly fragmented across regions of Antarctica. Interpreting satellite imagery in the context of Antarctica's predominantly small-extent (sub-pixel) cryptogamic vegetation is complex and challenging, and accurate or even plausible reconstructions across the satellite data era may not realistically be possible; see Colesie *et al.* (2025) for a detailed consideration.

Summary

Predicting future Antarctic species and ecosystem responses in relation to climatic and other environmental changes remains a challenge, although the field has progressed considerably since the onset of manipulation studies in the 1990s. Warming-induced expansion of vegetation typically leads to increases in associated microbial and invertebrate populations, which is also reflected in latitudinal studies along the Antarctic Peninsula. While microbial communities and process rates often respond to passive warming approaches in the field (mean increases of ~1–2°C above ambient), invertebrate communities are mostly non-responsive, or not on a scale that is detectable, indicating that there is group-specific temperature sensitivity. Laboratory studies of simulated climate change impacts on Antarctic microarthropod populations are missing from the literature (but see Martin *et al.* 2023), as is long-term field monitoring to assess population changes through time, with the exception of a programme monitoring the presence of non-native microarthropods on Deception Island between 2011 and 2017 (Enriquez *et al.* 2019). Experimental warming approaches for freshwater ecosystems using heating elements (e.g. Clark *et al.* 2019 in marine ecosystems) should be feasible and may provide valuable insights into freshwater ecosystem responses to climate change.

Water additions typically benefit Antarctic cryptogams and plants, except for typically dry-adapted species. Although the influence of water availability on the physiology of primary producers is well-studied in the Antarctic, laboratory and field-based studies on the impacts of water availability in combination with warming on the growth of Antarctic cryptogams and plants are lacking. Long-term monitoring of freshwater ecosystems indicates a strong dependence on water flow by microbial mats in the McMurdo Dry Valleys, but standardized studies within the context of climate change impacts have not been conducted. Antarctic biota experience long-term but also highly variable cover by snow, which is likely to be altered by current climate change. Experimental manipulations of snow thickness and cover duration, similar to Arctic approaches (Wipf & Rixen 2010, Cooper 2014), will provide more insights into the role of snow in shaping Antarctic communities. Manipulation of snow thickness and cover duration may also be relevant to freshwater ecosystems due to its regulatory effect on light and temperature. Stronger cross-disciplinary links between ecologists and snow scientists would improve ecologically relevant physical parameterizations of snow metamorphism and snow microstructure, which determine energy exchanges at the snow/soil and snow/air interfaces.

Most Antarctic terrestrial biota show physiological plasticity in relation to ambient and experimental UV exposure (Newsham & Robinson 2009). However, there is currently little knowledge on response trends across latitudinal or elevation gradients in Antarctica with respect to UV exposure. Considering that the annual ozone hole will continue to form for multiple decades (Oram *et al.* 2017, Montzka *et al.* 2018) and the strong effects of snow and ice on light transmission, field experimental approaches that manipulate snow-ice properties and thickness (e.g. by using snow fences) may provide useful insights into the sensitivity of terrestrial and freshwater ecosystems to changes in UV exposure. In addition, most of the available studies on UV impacts deal with organismal-level responses, while the consequences for biotic interactions and ecosystem process rates have rarely been addressed, except for indirect links through litter quality traits on arthropod responses (Convey *et al.* 2002), despite clear evidence of UV radiation affecting ecosystem processes in temperate regions (Moody *et al.* 2001, Austin & Vivanco 2006, Zaller *et al.* 2009).

Considering the large differences in climate variability between the three broad Antarctic biological regions (sub-Antarctic, Maritime Antarctic and Continental Antarctic) and the rates of environmental change experienced to date (Siegert *et al.* 2019, Nel *et al.* 2023, Kurita *et al.* 2025), there are major differences in responses to various aspects of climate change between these regions, as well as differences in the form(s) of changes being experienced. However, the geographical spread of simulated climate change manipulations is heavily biased towards the Antarctic Peninsula and Scotia Arc archipelagos, the McMurdo Dry Valleys and the Windmill Islands near Casey Station (Fig. 2). These locations are not fully representative of the currently recognized 16 distinct ACBRs within the Antarctic continent and peninsula region (Terauds & Lee 2016). Biotic responses to climate manipulations from studies on the Antarctic Peninsula are often not representative of Victoria Land, while studies carried out on sub-Antarctic islands are biased towards vascular plants, with little focus on cryptogams, which complicates comparisons between biogeographical regions. Any future starting up or extension of climate change manipulations would benefit from an international approach where the same methodology is used across different sites and ACBRs, as demonstrated through the long-running ITEX programme in the Arctic (e.g. Elmendorf *et al.* 2012).

Conclusions

In conclusion, current levels of climate change experienced across Antarctica have not led to large or consistent changes in local and regional biodiversity patterns or shifts in population sizes in Antarctic terrestrial and freshwater ecosystems. While there are clear cases of local vegetation expansion or temporal shifts in freshwater primary productivity, and experimental work indicates that there is scope for expansion (physiology, growth, population size and range distributions) under various climate change scenarios, current Antarctic climatic conditions still appear to be too limiting for species to expand, in contrast to the rapid vascular plant expansion across Nordic biomes (Myers-Smith *et al.*

2020). However, there is a significant chance that we are simply not noticing these changes, as very few long-term monitoring or repeat visit projects are active in Antarctica. As air temperatures in Antarctica are likely to keep rising during the remainder of this century (Tewari *et al.* 2022), it is even more important that we retain the opportunity to monitor such changes, especially in light of upcoming techniques that rely on proxies or machine learning (e.g. Sandino *et al.* 2025), but which are not necessarily ground-validated (Colesie *et al.* 2025), to infer changes in Antarctic biota patterns. Future research activities should ideally include standardization of experimental methodologies between Antarctic regions and continue monitoring them for a number of decades. In addition, climate change is likely to be accompanied by a greater frequency and intensity of weather extremes (Davies *et al.* 2026), which even Antarctic organisms may not be able to cope with (Bahrndorff *et al.* 2025).

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