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**ADVANCED REVIEW**

# Antarctica's vegetation in a changing climate

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**Abstract**

Antarctica plays a central role in regulating global climatic and oceanographic patterns and is an integral part of global climate change discussions. The functioning of Antarctica's terrestrial ecosystems is dominated by poikilohydric cryptogams such as lichens, bryophytes, eukaryotic algae, and cyanobacteria and there are only two native species of vascular plants. Antarctica's vegetation is highly adapted to the region's extreme conditions but, at the same time, it is potentially highly susceptible to climatic fluctuations. Biological responses to shifts in temperature, water availability, wind patterns, snow, and ice cover are complex, taxa-specific and act on different temporal and spatial scales. In maritime Antarctica, where warming and mass loss of outlet glaciers have been mainly observed, the vegetation is expected to show increases in productivity, abundance, and cover. In continental Antarctica, observational and experimental evidence is still sparse, but it is pointing toward even drier and harsher conditions for survival. We need more information on what the observed and predicted changes in Antarctic vegetation are for different regions and ecosystems. This will inform us how environmental change and human impact will shape the future of these ecosystems, and whether the speed and magnitude of change have habitat-specific effects and implications. Antarctica's unique ecosystems are changing and in this review, we describe the current situation, tools to measure, and evaluate change and how change is likely to look in the future.

This article is categorized under:

Climate, Ecology, and Conservation > Observed Ecological Changes

Assessing Impacts of Climate Change > Evaluating Future Impacts of Climate Change

Climate, Ecology, and Conservation > Modeling Species and Community Interactions

Assessing Impacts of Climate Change > Observed Impacts of Climate Change

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## KEYWORDS

Antarctica, climate change, lichen, terrestrial, vegetation

## 1 | INTRODUCTION

Antarctica, the world's most remote continent, is no longer pristine. Global climate change is affecting its marine and terrestrial ecosystems (Convey & Peck, 2019; Siegert et al., 2019), alongside the impact of researchers and tourists (Brooks, Jabour, et al., 2019; Liggett et al., 2017). In 2021, the IPCC assessment report on climate change (<https://www.ipcc.ch/report/sixth-assessment-report-working-group-ii/>, Chapter 12.4.9) specifically highlighted the first physical evidence of anthropogenic climate change in Antarctica.

Antarctica's biota is already responding to changing climate. In the marine realm, benthic and pelagic communities show complex responses to collapsing ice shelves and calving icebergs (Ingels et al., 2021). In the terrestrial realm, with a current area of potentially habitable ice-free ground of around 0.18% of the Antarctic continent (Burton-Johnson et al., 2016), biological responses are also multifaceted (Andriuzzi et al., 2018; Convey & Peck, 2019). Terrestrial ecosystems in Antarctica are unique because of the dominance of nonvascular vegetation like lichens, bryophytes, eukaryotic algae, and cyanobacteria (Green et al., 2007; Robinson et al., 2003; Rudolph, 1966). There are only two species of native vascular plants (the grass *Deschampsia antarctica* Desv. and the pearlwort *Colobanthus quitensis* [Kunth.] Bartl.). The nonvascular vegetation is poikilohydric, which means that they equilibrate their water content with the surrounding air humidity and moisture, allowing them to desiccate and reactivate only when conditions are favorable (Proctor & Tuba, 2002). Additionally, cryotolerant terrestrial algae in Antarctica have encystment phases, which enable them to remain dormant under certain conditions (Davey et al., 2019; Hoham & Remias, 2020). Therefore, the physiological state of nonvascular vegetation reflects their immediate environmental conditions. As a result, the distribution, biomass and diversity of vegetation in Antarctica can be interpreted as a direct reflection of the habitats' climatic conditions (Convey et al., 2014; Green et al., 2007).

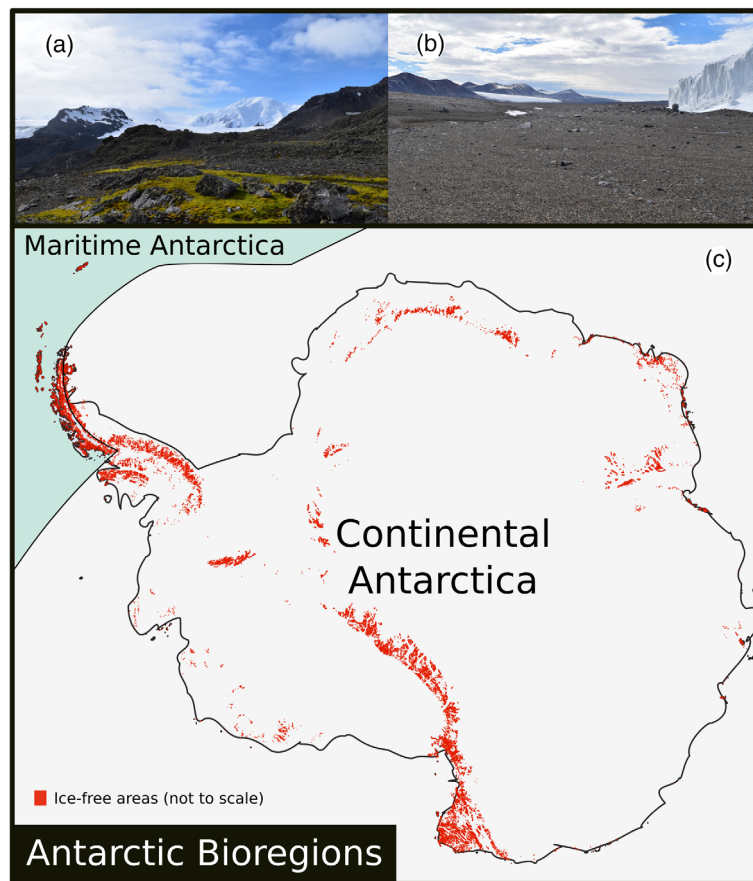
Biogeographically, Antarctica can be divided into two major regions (Figure 1c). The maritime Antarctic, including the west coast of the Antarctic Peninsula northwards from Alexander Island, through the island archipelagos of the Scotia Arc (South Shetland, South Orkney and South Sandwich Islands), to South Georgia. South Georgia, while being on the Scotia Arc, is defined as part of the sub-Antarctic. The climate in maritime Antarctica has a strong year-round maritime influence, resulting in a damping of seasonal temperature variation (Convey & Smith, 2006). The vegetation here is lush (Figure 1a) and the diversity is high with 386 known species of lichen (Øvstedal & Smith, 2001) and about 133 species of mosses and 27 species of liverworts (Ochyra et al., 2008; Smith, 2005). The two native species of vascular plants also occur here.

Continental Antarctica includes the perpetually ice-free areas on the main body of the continent, such as the McMurdo Dry Valleys, the Windmill Islands and inland nunataks. Precipitation in continental Antarctica is often less than 100 mm year<sup>-1</sup> and is almost always delivered as snow. Exacerbating the extremely dry conditions are the sub-zero summer temperatures, making liquid water inaccessible. Here, water availability is limiting life to such an extent that even lichens and bryophytes are restricted to small suitable microhabitats (Figure 1b, Green et al., 2011).

The contrast between maritime and continental Antarctica is best visualized by the drop in lichen and bryophyte diversity (Peat et al., 2007; Sancho et al., 2019; Smith, 1984) and the significantly reduced lichen growth rates (Figure 2a,b, Sancho et al., 2007). While lichens from maritime Antarctica have previously been described among the fastest-growing (0.87 mm year<sup>-1</sup>), lichens from the continent have only grown 0.25 mm in 25 years, ranking them among the slowest-growing organisms on the planet (Sancho et al., 2007).

This relatively broad distinction between maritime and continental Antarctica has recently been noticeably refined through the identification of 16 biologically distinct "Antarctic Conservation Biogeographic Regions" (Terauds et al., 2012; Terauds & Lee, 2016), which provide a systematic framework for Antarctic conservation management.

Now, Antarctica's vegetation is facing different levels and rates of environmental change and human impact. Significant change in Antarctica's physical and living systems is ongoing and exacerbating (Chown et al., 2022; Turner et al., 2020; Turner, Phillips, et al., 2019), most recently very powerfully demonstrated by an amassment of unprecedented climatic extremes (Colucci, 2022; Jena et al., 2022; Robinson et al., 2020). However, regional effects are complicating continent-wide predictions. Over the last half of the 20th century, the western Antarctic Peninsula, and maritime Antarctica in general, has been one of the most rapidly warming regions on the planet, leading to substantial reductions in sea ice and mass loss of outlet glaciers (Chen et al., 2022; González-Herrero et al., 2022; Hobbs



**FIGURE 1** The two biomes of Antarctica. (a) Coastal terrestrial habitats in maritime Antarctica sustain often a lush vegetation dominated by cryptogamic organisms such as mosses. The picture here shows a moss carpet close to the Spanish Juan Carlos I research station (in the back) on Livingston Island. (b) In continental Antarctica, life is often restrained to microniches and the resulting habitats appear barren. Here, a landscape overview from Taylor Valley in the Antarctic McMurdo Dry Valleys. (c) A map outlining maritime and continental Antarctica with ice-free areas indicated in red. Photos credit: Claudia Colesie



**FIGURE 2** Lichen growth and diversity in Antarctica. (a) In many maritime Antarctic habitats, lichen diversity and growth rates are high. Here, a photograph of a lichen-dominated fellfield with a glove as scale. (b) In continental Antarctica, lichen form a major part of the vegetation but they are much less diverse and grow much slower than in maritime Antarctica. Here, a photograph showing very large lichen exemplars at Botany Bay in continental Antarctica with a 2 cm scale included (red). Photos credit: Claudia Colesie

et al., 2016). In contrast, the warming trends in continental Antarctica have been localized and inconsistent (Stenni et al., 2017; Turner et al., 2020). This is notably due to the difference in the response to the Antarctic Oscillation, the “periodical strengthening and weakening of the circumpolar vortex in the Southern Hemisphere” (Van Den Broeke & Van Lipzig, 2004). When the vortex is strong, the western and maritime part of Antarctica mostly experiences warming and higher precipitation rates, while areas on the main continent in the eastern parts of Antarctica experience cooling

and become drier. In response to those regional effects, it is likely that there will be contrasting effects of a changing climate on vegetation between maritime and continental Antarctica.

We will review our current understanding of the effects of climate change on Antarctica's unique vegetation. Organisms that have undergone selection for functional life-history traits over many generations that make them fit to survive and reproduce in one of the harshest environments on the planet (with examples given for lichens in Domaschke et al., 2012; for mosses in Hebel et al., 2018, and more general in Newman et al., 2009) are suddenly facing rapid and unpredictable change. With Antarctica being at the heart of considerable global concern in recent climate change discussions, it is imperative to summarize the current knowledge of the status, the risks and threats as well as evidenced and predicted change of these iconic ecosystems. This article aims to update on large-scale trends and emerging techniques to detect change, as well as summarize single findings that will help us gain a more complete understanding of the physiological, ecological, and abiotic processes that drive change in Antarctica's unique terrestrial ecosystems.

## 2 | ANTARCTIC VEGETATION, SELECTED FOR LIFE AT THE LIMITS

Extremely cold temperatures, high levels of UV radiation, drastic seasonal changes in day length, low water availability and physical isolation limit life in Antarctica. The physical isolation underlies the exceptionally strong bioregionalization with evidence now emerging from phylogeographic studies [e.g., for mosses (Biersma et al., 2018; Pisa et al., 2014), lichens (Lagostina et al., 2021; Ruprecht et al., 2012), or diatoms (Verleyen et al., 2021)]. Roughly, half of all Antarctic lichens are thought to be endemic to the continent (Øvstedal & Smith, 2001). This vegetation has evolved physiological traits, allowing them to survive and reproduce in the disparate and marginal ecosystems of Antarctica (Figure 3). Our understanding of their biology and functioning is now reasonably well established (Kennedy, 1995; Robinson et al., 2003; also see sections below for individual organism groups) but, the natural variability and plasticity, which determines ecosystem resilience, is still largely unknown. This is because survey periods have to span decades rather than years or seasons to allow for significant and accurate detection of growth and the establishment of robust baselines (Convey et al., 2018; Green et al., 2011; Turner et al., 2018). It is because of these complications, that so far, only three “long-term” baseline studies exist in and around Antarctica: two of them situated in the maritime Antarctic [Signy Island (Cannone et al., 2016, 2022), and Argentine Islands (Fowbert & Smith, 1994; Parnikoza et al., 2009)], and one in continental Antarctica (Brabyn et al., 2006; Colesie et al., 2022).

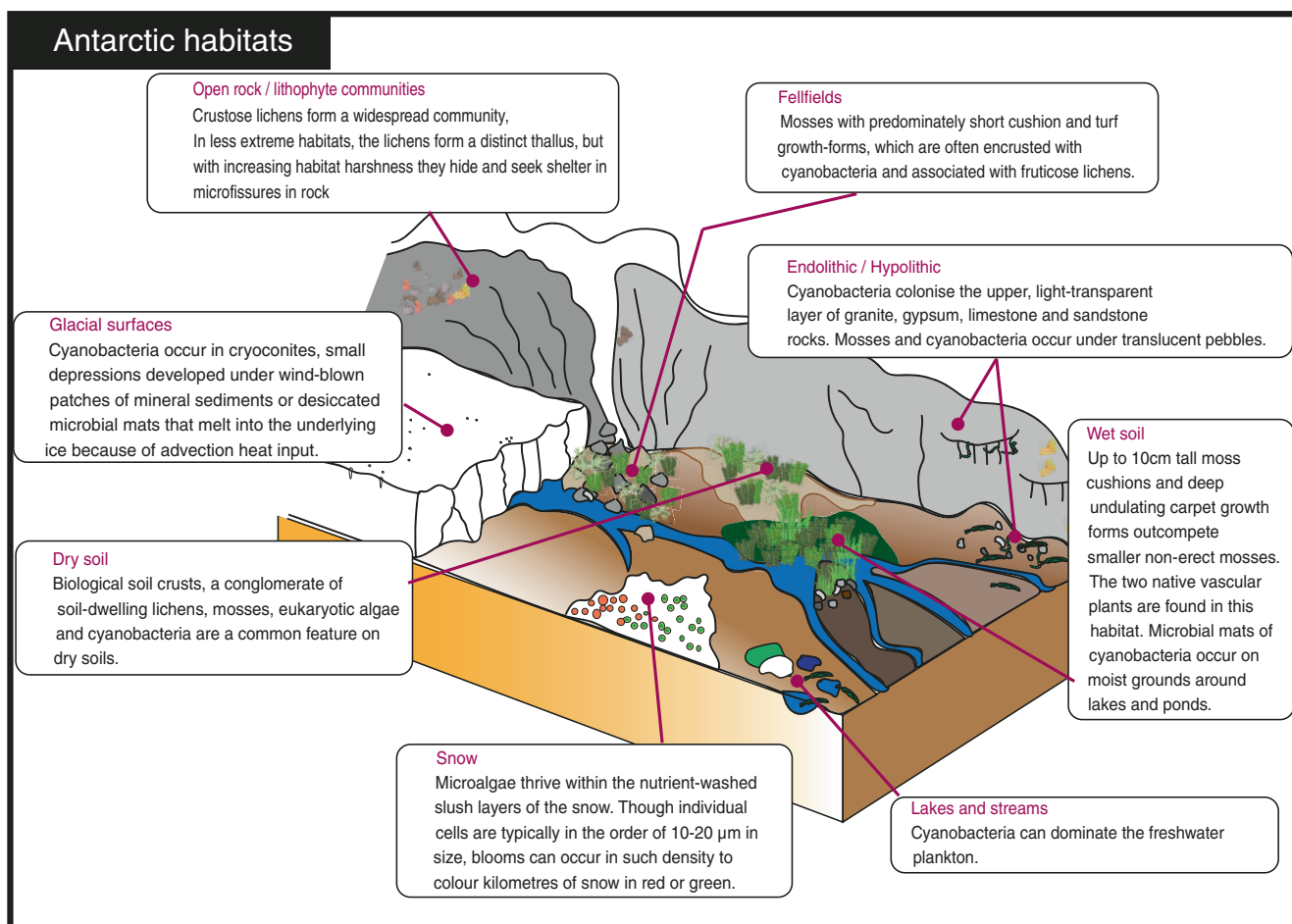
### 2.1 | Bryophytes

A total of 109 taxa of moss (107 species +2 varieties) are currently described to occur in maritime Antarctica, and 24 taxa (23 species +1 variety) in the continental Antarctic region (Smith, 2005; Ochyra et al., 2008; Royles & Griffiths, 2015). There are 27 species of liverwort known from Antarctica and only one, the leafy liverwort *Cephaloziella varians* (Gottsche) Steph., occurs in continental Antarctica (Bednarek-Ochyra et al., 2000; Newsham, 2010). As a dominant element of the vegetation (Figure 4a,b, Cannone et al., 2017), Antarctic mosses have well-developed stress tolerance features. They grow and survive even at temperatures around 0°C (Folgar-Cameán & Barták, 2019; Pannewitz et al., 2005; Perera-Castro et al., 2020), although their optimal physiological response temperature is much higher at 20–30°C (Perera-Castro et al., 2020). Mosses have traits that have been selected to withstand exposure to high light and UV (Li et al., 2019; Snell et al., 2009; Turnbull & Robinson, 2009; Wang et al., 2021; Waterman et al., 2018), and they can resist repeated high drying pressure (Perera-Castro et al., 2021; Pizarro et al., 2019; Robinson et al., 2000; Takezawa, 2018). Cryptobiosis (a metabolic state of desiccation and freezing-induced dormancy, which can be reversed when environmental conditions become hospitable again), can allow for millennial-scale survival and viability (Pisa et al., 2014; Roads et al., 2014).

### 2.2 | Lichens

Lichens as symbiotic organisms between a fungus and a photobiont (eukaryotic algae or cyanobacteria), have the greatest number of species in Antarctica (386 species; Øvstedal & Smith, 2001). They are able to colonize all types of solid substrata (Figure 4c,d) and have a low mineral nutrient demand (Kappen, 2000). Their physiological vigor is derived from high freezing tolerance (Barták et al., 2007; Hájek et al., 2016; Harańczyk et al., 2003) and the ability to be photosynthetically



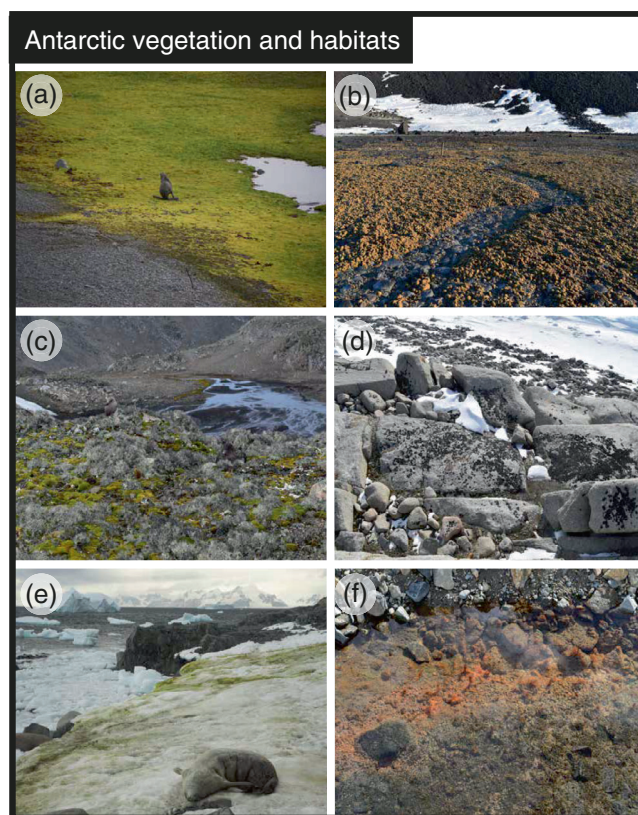


**FIGURE 3** Habitats and the corresponding vegetation communities. This stylised model shows different vegetation types occurring in various Antarctic terrestrial habitats. Relevant habitat descriptors can be found here (Alger et al., 1997; Bonani et al., 1988; Bottos et al., 2014; Büdel et al., 2008; Cameron et al., 2012; Casanova-Katny & Cavieres, 2012; Cockell & Stokes, 2004; Colesie, Gommeaux, et al., 2014; Convey et al., 2011; Cowan et al., 2011; Davey et al., 2019; De Los Rios et al., 2004; Ellis-Evans, 1996; Friedmann & Ocampo, 1976; Gray et al., 2020; Hawes, 1990; Hodson et al., 2017; Hoham & Remias, 2020; Hughes & Lawley, 2003; Jungblut et al., 2010; Lacap-Bugler et al., 2017; Lagostina et al., 2021; Le et al., 2016; Ling & Seppelt, 1993; Makhalyanyane et al., 2015; McKnight et al., 1999, 2004; Mergelov et al., 2012; Niederberger et al., 2012; Ochyra et al., 2008; Remias, Jost, et al., 2013; Segawa et al., 2018; Suman et al., 2010; Sun & Friedmann, 2005; Sumner et al., 2016; Velichko et al., 2021; Vincent, 2007; Vincent & Quesada, 2012; Wagner et al., 2020; Wei et al., 2016; Wierzchos et al., 2005; Williams et al., 2017).

activated by liquid water or water vapor uptake (Colesie et al., 2016; Schroeter et al., 2021). The optimum temperature for photosynthesis of Antarctic lichens typically lies between 10 and 17°C (Laguna-Defior et al., 2016). In their natural habitats, photosynthetic activity often takes place at an optimal combination of temperature and irradiance (Sancho et al., 2019) which can also happen under snow (Pannewitz et al., 2003). However, the small window of optimal growing conditions can easily be surpassed as shown, for example, for the lichen species *Himantormia lugubris*, which performs at an optimum temperature of 0–10°C only (Sancho et al., 2020). This happens mostly when a lichen grow on open rock surfaces, where strong light exposure creates additionally challenging conditions (Schroeter et al., 2010). However, Antarctic lichens have evolved mechanisms to resist damage from high light exposure (Barták et al., 2012; Determeyer-Wiedmann et al., 2019; Vráblíková et al., 2005) and can recover quickly from light-induced stress (Balarinová et al., 2014).

## 2.3 | Vascular plants

The only two native Antarctic vascular plants, *D. antarctica* and *C. quitensis* occur along the Antarctic Peninsula, with their southernmost distribution limits currently at the Terra Firma Islands (Komárková et al., 2018) and the



**FIGURE 4** Functional groups of vegetation in Antarctica. (a) Dense carpets of moss and vascular plants on wet soils on Livingston Island, maritime Antarctica. (b) the dry small turf moss *Bryum argenteum* along a dry meltwater river at Cape Hallett, continental Antarctica. (c) Lichen and mosses form diverse communities in the form of biological soil crusts on Livingston Island, maritime Antarctica. (d) Crustose lichen covering large boulders and rocks at Botany Bay, continental Antarctica. (e) Snow algae bloom in a snow patch near Rothera point, maritime Antarctica. (f) Cyanobacterial mats in a meltwater lake in Taylor Valley, continental Antarctica. Photo credit: (a), (b), (c), (d), (f) Claudia Colesie; (e) Andrew Gray

Lazarev Bay (Convey et al., 2011). Both *D. antarctica* and *C. quitensis* are able to grow, photosynthesise and reproduce at low temperatures (Xiong et al., 1999) with a net annual production of the above-ground parts of *D. antarctica* measured between 294.41 and 1256.62 g dry weight m<sup>-2</sup> year<sup>-1</sup> (Barcikowski et al., 1999). The optimal temperature for photosynthesis in *C. quitensis* and *D. antarctica* was found to be 14 and 10°C, respectively, but they are operating at sub-optimal temperature conditions for most of their growing season (86% of the total time, Xiong et al., 1999). The photosynthetic water-use efficiency, a factor demonstrating the presence of mechanisms facilitating the functioning of the plants in nonoptimal conditions, is significantly higher in the Antarctic population of *D. antarctica* when compared with nonpolar counterparts or other C3 plants (Bystrzejewska-Piotrowska & Urban, 2009; Montiel et al., 1999), which is a feature to avoid heat loss (Mantovani & Vieira, 2000). Both species also show high levels of freezing (Alberdi et al., 2002), and UV exposure, tolerance (Köhler et al., 2017). However, the day length is probably the most important environmental factor limiting their success in Antarctica because assimilates can only be used as structural growth components with sufficient day length (Bravo et al., 2001). Bravo et al. (2001) suggest that the 21-h day length most likely represents the critical photoperiod threshold for stimulating growth.

## 2.4 | Eukaryotic algae and cyanobacteria

Eukaryotic algae are an important component of the soil microbiota (Broady, 1981, 1996, 2005). Snow algae, in particular, have recently experienced a high level of attention in Antarctic terrestrial ecology research (Davey et al., 2019; Soto et al., 2022). Snow algal blooms have been identified in summer coastal snows across many regions both in maritime and continental Antarctica (Gray et al., 2020; Ling & Seppelt, 1993; Remias, Wastian, et al., 2013; Segawa et al., 2018).

Many snow algal communities consist of either a vegetative stage, seen as green patches in the snow, or an encystment phase, in which the cells have accumulated the keto-carotenoid astaxanthin, giving rise to red snow patches (De Wever et al., 2009; Hoham & Duval, 2001; Komárek & Nedbalová, 2007; Leya, 2013). The term snow algae covers a broad number of green and red-colored algal species, in Antarctica, these are commonly identified as *Chlorominia* sp. (Gálvez et al., 2021); *Chloromonas* or *Chlamydomonas* sp. (Davey et al., 2019) with the red and/or orange snow algae bloom species typically being *Sanguina* sp., *Chloromonas polyptera*, or *Hydrurus* sp. (Procházková et al., 2019; Remias, Jost, et al., 2013; Remias, Wastian, et al., 2013).

Under laboratory conditions, different snow algal species grow across a range of temperatures with various growth optima around 10°C is commonplace, however, our understanding of the physiology and genetics of these organisms isolated from Antarctica is still limited to a few experimental studies (e.g., Gálvez et al., 2021; Zhang et al., 2020). Initial estimates show that green snow algae blooms (Figure 4e) can cover up to 1.95 km<sup>2</sup> seasonally in the West Antarctic Peninsula (Gray et al., 2020), but with better and higher resolution satellite detection, the total value may be 17.5x greater (Gray et al., 2021). On one Antarctic maritime island, the area of the snow algae blooms was measured to be similar to that of other moss and lichen vegetation ( $1.57 \times 10^5$  vs.  $1.37 \times 10^5$  m<sup>2</sup>; Gray et al., 2020), meaning that although they are more spatially and temporally transient, the snow algae blooms do have a significant ecological role to play to local ecosystem primary productivity. One of the interesting habitat features, or consequences, of the snow algae blooms, is that they can be responsible for decreasing surface albedo (Huovinen et al., 2018; Lutz et al., 2016) and therefore slightly accelerate the melting of snow (Ganey et al., 2017; Khan et al., 2021).

With respect to algal cells and cyanobacteria on glaciers, cryoconite holes in maritime Antarctica appear analogous to those of Arctic glaciers, being open to the atmosphere during the summer months (Buda et al., 2020). As such, they tend to be hydraulically linked, receiving nutrients from meltwater and precipitation and are more susceptible to disturbance and melt-out (Telling et al., 2012). Cryoconite holes on colder continental Antarctic glaciers are mostly covered by ice lids, which isolate them from allochthonous inputs of meltwater and nutrients, yet provide some protection from physical disturbance during the melt season (Bagshaw et al., 2016; Porazinska et al., 2004; Weisleitner et al., 2020).

Cyanobacteria can be found in ice and snow (Cameron et al., 2012), in streams or lakes (Figure 4f, Vincent & Quesada, 2012), in soil (Bottos et al., 2014) and on rocks (Golubič & Schneider, 2003). Most of the cultured Antarctic cyanobacteria are considered psychrotolerant because their optimal growth temperature lies above those found in the local environment (Pandey et al., 2004; Zakhia et al., 2008). Varin et al. (2012) and Pointing et al. (2014) describe various regulators and mechanisms that allow for growth and survival under the harshest environmental conditions in terms of temperature and water availability extremes (also see Wei et al., 2015; Vincent, 2007; Christmas et al., 2015; De Los Rios et al., 2004). Antarctic cyanobacteria are also well-equipped against damage from high UV radiation (Proteau et al., 1993; Quesada & Vincent, 1997).

### 3 | THE ENVIRONMENT IS CHANGING

#### 3.1 | Climatic factors

It is getting warmer in Antarctica. In maritime Antarctica, previous temperature trend estimates have been complicated by natural variability and short-term cooling trends reported during 1999–2016 (Turner et al., 2016). However, a consistent warming trend has been emerging since 1950 and is now evident based on field station data (Jones et al., 2019; Turner et al., 2020) and century-scale based reconstructions (Lyu et al., 2020; Stenni et al., 2017; Zagorodnov et al., 2012). In continental Antarctica, trend estimates are less significant (Jones et al., 2019). Based on ice-core reconstructions, the century-scale warming in Queen Maud Land Coast, for example, lies within the range of centennial internal variability (Stenni et al., 2017). This, however, is set to change and there is high confidence in future warming across all of the continent (Meredith et al., 2019), especially in coastal areas due to stronger relative Southern Ocean warming and relatively stronger effects of ozone recovery (Bracegirdle et al., 2020). Heatwaves are an additional concern and high-temperature records have been recently documented from several locations all across Antarctica (González-Herrero et al., 2022; Robinson et al., 2020; Wille et al., 2019).

Projection of future climates can be a useful tool to forecast how the climate will impact Antarctic biodiversity if data challenges can be overcome and modeling is carefully implemented (Koerich et al., 2022). Some of the most relevant, current climate scenarios for terrestrial Antarctica make projections for the end of the 21st century under two of the Representative Concentration Pathways (RCP4.5 and 8.5; Lee et al., 2017). Under the strongest forcing scenario,



these projections predict a tripling (300% increase) of ice-free areas over parts of the Antarctic Peninsula as a result of more than 50 additional-degree days above freezing (Lee et al., 2017). The manifold consequences of a 1.5°C warming scenario, for example, are described by Siegert et al. (2019) for the Antarctica Peninsula with particularly alarming notes, given that the northernmost region of the Peninsula has already exceeded the 1.5°C warming. In this scenario, precipitation along the Peninsula is likely to increase by 10%–20% (relative to the pre-industrial period) with an intensification of extreme precipitation events (Hoegh-Guldberg et al., 2018).

Under a 2°C global warming scenario, CMIP6 models predict a 15% and 12% increase in annual maximum daily precipitation and a 15% and 10% increase in maximum 5-day precipitation for maritime and continental Antarctica respectively (Boening et al., 2012). The increases in precipitation are largely attributed to the contribution of extreme snowfall events mainly in coastal areas (Turner, Phillips, et al., 2019) which, especially along the Antarctic Peninsula, will result in increased rainfall in comparison to snow (Scarchilli et al., 2020). Besides precipitation, other factors such as permafrost play a significant role in local water availability changes. In maritime Antarctica, dense moss covers buffer against radiation-driven active layer thickening (thaw depth of the permafrost; Guglielmin et al., 2012; Hrbáček et al., 2020; Hrbáček et al., 2021), which means that ground water will remain available in the upper part of the soil throughout the season. In continental Antarctica, this process might be opposite. With less vegetation cover in general, a thickening of the active layer leads to a decrease in groundwater, due to better drainage (Guglielmin et al., 2014), which consequentially can cause lake reduction and increased soil moisture deficits matching with projections of future drought increase (Spinoni et al., 2019). Regional drying trends have already been observed for example in the Windmill Islands in continental Antarctica (Robinson et al., 2018). Additionally, the Southern Annular Mode is strengthening, leading to decreased easterlies along Antarctica's coast (Bintanja et al., 2014) and global sea-level rise also significantly increases the possibility for coastal flooding and erosion all across the continent (Bamber et al., 2019).

### 3.2 | Biotic factors

The changing climate is not the only challenge for Antarctica's terrestrial vegetation. It is also getting busier (Box 1). In 2005, Frenot et al. listed a total of 108 alien, invasive vascular plant species for Antarctica, although the highest establishment success was then found to be on the sub-Antarctic Islands (95% of all the listed species). Ten years later, in 2015, Hughes et al. (2015) summarizes the successful establishment of vascular plant species also further south, along the Antarctic Peninsula. Invasion risks are likely to be enhanced by human activities from both tourism and research activities (Huiskes et al., 2014; Smith & Richardson, 2011) and mostly dominated by grasses of the Poaceae family

#### BOX 1 Take only pictures, (do not) leave footprints

Due to their slow growth rates, most of Antarctica's vegetation is particularly vulnerable to disturbance (Figure 5). From a review of 31 studies, 83% confirmed impacts in areas of visible disturbance (Brooks, Tejedo, & O'Neill, 2019). Disturbance was found to modify the physical environment, consequently reducing habitat suitability as well as directly damaging biota. Trampling is one of the most significant disturbances in this context. Trampling can change the substrate's physiochemical properties (such as the bulk density and penetration resistance [Tejedo et al., 2005; O'Neill et al., 2015]), biology (mostly through direct plant cover decrease [Cajiao et al., 2020]), and nutrient availability (Perterra et al., 2013). Most intense trampling and disturbance occur in the vicinity of research stations or field camps and at key tourist sites. For example, the summit ridge of Caliente Hill on Deception Island (South Shetland Islands) is a famous tourist spot as it includes a physically small geothermally heated area and associated unusual vegetation community. Here, severe trampling damage to the moss assemblages growing in association with the localized geothermal activity was observed (Perterra et al., 2018). The range of species affected included the entire known population of *Schistidium deceptionense*, an endemic moss known only from this site, as well as other very rare Antarctic mosses (Perterra et al., 2018). Disturbingly, it was now reported that disturbance associated with infrastructure can now be found in more than half of all large ice-free areas in Antarctica and that the disturbance footprint for every person at an Antarctic research station equates to an area of nearly 1000 football fields (Brooks, Jabour, et al., 2019).

(Malfasi et al., 2020; Olech & Chwedorzewska, 2011; Rew et al., 2020; Rudak et al., 2019). The non-native grass *Poa pratensis*, for example, persisted at Cierva Point for 58 years (Pertierra et al., 2017). The fast-growing, ruderal opportunist *Poa annua* has rapidly spread from South America and Europe (Chwedorzewska, 2008) to the sub-Antarctic islands over the last two centuries, and into the maritime Antarctic in recent decades (Convey & Lebouvier, 2009; Frenot et al., 2005; Molina-Montenegro et al., 2012). There is increasing evidence that the adaptive plasticity and competitiveness of growth of *P. annua* are greater than those of the native grass *D. antarctica* (Davidson et al., 2011; Molina-Montenegro et al., 2015).

However, for successful establishment at most sites along the Antarctic Peninsula and the main continent, the environment still represents a strong environmental filter (Rudak et al., 2018). The strong geographical barrier, the low potential bioclimatic suitability and resource availability generally reduce the likelihood of biological invasion (Galera et al., 2018), especially in continental Antarctica.

Vascular plants are not the only potential invaders of Antarctic terrestrial ecosystems. Alien lichen, moss, algal propagules and fragments have been reportedly found to be distributed across the Antarctic by tourists and scientists (Hughes et al., 2018; Huiskes et al., 2014; Kirtsideli et al., 2018; Laichmanová & Sedláček, 2019; Osyczka, 2010; Osyczka et al., 2012), but reports on their establishment and growth are rare (e.g., Archer et al., 2019; Câmara et al., 2020, 2022; Hughes et al., 2018; Vlasov et al., 2020). There are few reports on new establishments of bryophytes, such as *Polytrichum piliferum*, on Signy Island (Convey & Smith, 1993) but despite the ever-growing knowledge on diversity and species distribution in Antarctica, the baseline for species turnover is still largely unknown. This is because many sites have never been revisited with the particular purpose of describing the new establishment of vegetation or evaluating change. For lichens, species with an already diverse population and high levels of gene flow are less at risk, while those with highly differentiated populations are at risk of the introduction of alien genotypes and gene pool homogenization (Lagostina et al., 2021).

Besides invasions, altered nutrient regimes are another factor in Antarctica's changing environment that can be linked to biotic influence. Although native terrestrial vertebrates are absent, breeding and molting populations of marine mammals and birds are a key source of marine-derived nutrient supplies (Bokhorst et al., 2019). It is very likely that these marine animals will alter their movements with the changing climate (McCarthy et al., 2019), which can have significant implications for terrestrial nutrient availability (Bokhorst et al., 2022).

## 4 | HOW DOES THE VEGETATION RESPOND TO THE CHANGING ENVIRONMENT?

### 4.1 | Bryophytes

Due to the high diversity of physiological traits in Antarctic bryophytes, generalized predictions on climate change-related changes in performance are difficult. Ultimately, the length of the growing season is the critical determinant for moss growth rate (Royles & Griffiths, 2015) and warmer conditions can lead to increased growth and fitness (Shortlidge et al., 2017, Table 1). Sexual reproduction in Antarctic mosses is currently constrained by the cold environmental conditions (Convey & Smith, 1993), but initial studies have shown the number of sporophytes to increase with experimental warming (Casanova-Katny et al., 2016) and where favorable microclimatic conditions persist locally (Smith & Convey, 2002). The lack of baseline knowledge on moss growth and its natural variability is still limiting our ability to evaluate change. The only study, to date, to report the long-term baseline ecology of Antarctic mosses is reporting strong seasonal phenology, distribution patterns that are driven by water availability, and steady perennial growth of moss at Cape Hallett in continental Antarctica (Colesie et al., 2022). Amesbury et al. (2017) have shown that with the Antarctic Peninsula becoming warmer and wetter, moss growth rates have quadrupled. Vice versa, at some sites on the continent such as the Windmill Islands moss "heath" has been shown to deteriorate with the ongoing drying trend (Robinson et al., 2018). For the moss *Sanionia uncinata*, for example, a simulation model has predicted a reduction in overall carbon gain with warming, especially for populations subject to repeated desiccation cycles (Nakatsubo, 2002).

TABLE 1 Summary of changes to different Antarctic terrestrial habitats









Habitat	Maritime Antarctica	Continental Antarctica	References
	Change	Change	
Universal	Invasive species compete with native communities <sup>1,2,3</sup> Photoautotrophic productivity increases <sup>5,7,8,10</sup> Newly deglaciated land gets colonized <sup>4,6</sup>	Increased drying pressure shortens activity periods for organisms <sup>9</sup> Newly deglaciated land gets colonized <sup>4,6</sup>	<sup>1</sup> Bokhorst et al., 2021 <sup>2</sup> Cannone et al., 2016 <sup>3</sup> Cannone et al., 2022 <sup>4</sup> Favero-Longo et al., 2012 <sup>5</sup> Hughes et al., 2015 <sup>6</sup> Lee et al., 2017 <sup>7</sup> Malfasi et al., 2020 <sup>8</sup> Molina-Montenegro et al., 2019 <sup>9</sup> Sancho et al., 2007 <sup>10</sup> Sancho et al., 2019
Wet soil 	Increased rainfall and snow increases soil moisture <sup>2</sup> Longer activity periods for organisms <sup>1,3</sup>	Drying due to a decrease in groundwater levels <sup>4,5</sup> Shorter activity periods for organisms <sup>6</sup> Earlier snowmelt affects phenology <sup>7</sup>	<sup>1</sup> Amesbury et al., 2017 <sup>2</sup> Boening et al., 2012 <sup>3</sup> Cavieres et al., 2016 <sup>4</sup> Guglielmin et al., 2014 <sup>5</sup> Guglielmin et al., 2012 <sup>6</sup> Sancho et al., 2007 <sup>7</sup> Scarchilli et al., 2020
Dry soil 	Vascular plant encroachment reduces insulating moss cover and leads to increased active layer thickness and soil drying <sup>2</sup>	Higher evapotranspiration increases soil moisture deficits <sup>1,3,4</sup> Pulsed melt-water events from heatwaves stimulate soil biota <sup>5,6</sup>	<sup>1</sup> Barrett et al., 2008 <sup>2</sup> Guglielmin et al., 2012 <sup>3</sup> Perera-Castro et al., 2021 <sup>4</sup> Robinson et al., 2018 <sup>5</sup> Robinson et al., 2020 <sup>6</sup> Wall, 2007
Fellfield 	Community homogenization with specialist species being outcompeted by fast-growing generalists with high plasticity <sup>1</sup>	More evidence needed	<sup>1</sup> Colesie et al., 2018
Open Rock 	Increased lichen productivity and growth with higher water availability <sup>2,4</sup> Increased lichen mortality through snowkill <sup>3</sup>	Decreased lichen productivity due to higher evapotranspiration and dryer conditions <sup>1</sup>	<sup>1</sup> Colesie, Green, et al., 2014 <sup>2</sup> Laguna-Defior et al., 2016 <sup>3</sup> Sancho et al., 2019 <sup>4</sup> Sancho et al., 2007
Snow 	Loss of low-lying summer snowfields on islands <sup>2</sup> Upward expansion of snow algae onto glacial snow packs <sup>1</sup>	Increased amount of habitable snow <sup>3</sup>	<sup>1</sup> Gray et al., 2020 <sup>2</sup> Hodson et al., 2017 <sup>3</sup> Hoham & Remias, 2020
Endolithic/hypolithic 	More evidence needed	Any unfavorable change in external conditions can result in the death and disappearance <sup>1</sup>	<sup>1</sup> Wierzchos & Ascaso, 2001

TABLE 1 (Continued)

Habitat	Maritime Antarctica	Continental Antarctica	References
	Change	Change	
Glaciers 	Increase in cryoconite productivity as earlier snow melt exposes glacier surface to longer seasons <sup>1,2</sup> Losses of cryoconite lids results in greater hydrological connectivity and nutrient availability <sup>3</sup>	Increase in cryoconite productivity as earlier snow melt exposes glacier surface to longer seasons <sup>1,2</sup> Losses of cryoconite lids results in greater hydrological connectivity and nutrient availability <sup>3</sup>	<sup>1</sup> Foreman et al., 2004 <sup>2</sup> Takeuchi et al., 2018 <sup>3</sup> Weisleitner et al., 2020
Lakes/Streams 	Increase in productivity as covering snow/ice disappears <sup>2</sup> Nutrient inputs from direct precipitation <sup>3</sup>	Overall lake reduction due to drought <sup>1</sup> Increase in productivity as covering snow/ice disappears <sup>2</sup>	1 Hawes et al., 2013 2 Lyons et al., 2006 3 Verleyen et al., 2012

## 4.2 | Lichen

Antarctica's lichens are known to be excellent integrators of the local climate. Their growth rates have been shown to link directly with the local temperature, which makes them ideal biomonitors of temperature change (Sancho et al., 2019). On Livingston Island, mean summer temperatures between 1991 and 2002 rose by 0.42°C and four out of six monitored lichens species increased their growth rates by 124% (Sancho et al., 2019). Several lines of evidence are indicating that Antarctic lichens, *in situ*, operate at suboptimal temperatures and that warming could benefit the lichens' carbon balance (Laguna-Defior et al., 2016; Pannowitz et al., 2005; Sancho et al., 2003). However, such predictions are more complicated, especially in the lichen context. As mostly bipartite symbionts, any adjustments to warmer growing conditions must involve meticulous adjustments of the mutualistic relationships (Colesie et al., 2018; Wagner et al., 2021). It is known that the ratio of fungal hyphae and photosynthetic algae in the thallus represents a state of equilibrium at the temperature of the environment and that, at lower temperatures, fewer algae per unit lichen are present to sustain a functional lichen thallus (Friedmann & Sun, 2005; Sun & Friedmann, 2005). With increasing growth temperature, the respiratory demand of the fungal partner increases exponentially, and a higher proportion of algal cells is needed to allow for survival and carbon gain. Such adjustments are possible within lichen thalli (Lange & Green, 2005) but are subject to consistent, predictable and gradual change. However, the changes in frequency and magnitude of warming events that Antarctica is currently experiencing might be too fast and unpredictable for some lichen species (Table 1, Bokhorst et al., 2016; Colesie et al., 2018) and the integrity of their symbiosis or carbon allocation traits (Colesie, Green, et al., 2014) could be compromised as a consequence. Besides changes in temperature, another major threat for lichen in Antarctica can be snowkill. This is when lichen survival and growth is reduced due to increased snowfall and longer-lasting snow cover (Benedict, 1993; Bidussi et al., 2016; Sancho et al., 2017). Attributed to increased spring snows, declines in area coverage of lichens have already been observed in the South Shetland Islands (Miranda et al., 2020; Shin et al., 2014; Vieira et al., 2014).

## 4.3 | Vascular plants

Both native Antarctic vascular plant species have exhibited significant increases in the number of occupied sites and the percent cover since the 1960s, and these changes likely occurred in response to an increase of 1.2°C in summer air temperature (Cannone et al., 2016, 2022) and efficient nitrogen acquisition (Hill et al., 2011). Both species were predicted to show increased growth due to greater biomass allocation to the leaf-area production (Cavieres et al., 2016). However, it is now becoming clearer that in *C. quitensis*, the photosynthetic response to warming relied on specific adjustments in the anatomical determinants, which promote higher leaf carbon gain and overall plant growth, while *D. antarctica* showed no response to warming in open-top chamber experiments (Sáez et al., 2018). This species-specific response was supported by other experimental findings showing that *D. antarctica* was more sensitive to short-term changes in temperature than *C. quitensis*, associated with contrasting overall thermal acclimation in the two species (Sanhueza et al., 2019; Xiong et al., 2000). What was not found to differ between the two species was that both showed



increased vulnerabilities to freezing damage when exposed to an overall increased growing temperature, which, in the long-term, can affect their survival capacity (Sierra-Almeida et al., 2018).

There are facilitative effects between native Antarctic vascular plants and mosses (Atala et al., 2019; Casanova-Katny & Cavieres, 2012; Cavieres, Vivas, et al., 2018). However, this fragile equilibrium might be put at peril (Table 1) with the establishment of new and invasive competitors. *P. annua*, for example, has been shown to have negative impacts on the growth and survival of both native vascular plant species (Cavieres, Sanhueza, et al., 2018; Molina-Montenegro et al., 2019). At least 16 additional, non-native species can germinate and develop in warmer Antarctic soils and the thermal germination requirement and field soil temperature would allow invasive species to establishment as far south as 72°S (Bokhorst et al., 2021).

#### 4.4 | Eukaryotic algae/cyanobacteria

Snow algal blooms have been observed to grow higher up on glacial snows in the South Shetland Islands (Gray et al., 2020; Hodson et al., 2017), and upward range expansion may be possible (Gray et al., 2020) given sufficient nutrient supply away from the guano-rich coast (Bokhorst et al., 2019; Ji et al., 2022; Nowak et al., 2018). Constantly bathed in snow melt and slush, the temperatures around algal cells in the snowpack vary little with respect to changes in ambient temperature and warming in Antarctica is unlikely to be a direct selection pressure beyond the loss of habitat. Should increase temperatures or rainfall melt summer snow patches, then algal cells may not have long enough to grow to form visible blooms. Alternatively, slightly warmer temperatures may increase the availability of liquid water in the snow, resulting in an increase in the suitable habitat for snow algae to bloom (Davey et al., 2019). Alongside the challenges of the detection of these blooms the dispersal mechanisms of these species is still little understood. We know for example that the snow algae species are detected in airborne studies (Marshall & Chalmers, 1997), but further studies need to be completed so a comprehensive assessment of the risk and changes in this ecosystem can be made. Change is also to be expected for algae and cyanobacteria growing in cryoconites. The collapse of cryoconite holes has been attributed to warming events in Greenland (Takeuchi et al., 2018), and it may be that such disturbance events will become more commonplace on Antarctic glaciers also (Buda et al., 2020). Episodic warming events in continental Antarctica have previously caused cryoconite holes on glaciers around the McMurdo Dry Valleys to lose their ice lids (Foreman et al., 2004). The predicted heatwaves in continental Antarctica may, therefore, cause a switch from ice-lidded cryoconite holes to a perennially uncovered and hydraulically connected glacial surface. This disturbance will likely impact the stable microbial communities formed in the isolated cryoconite holes (Weisleitner et al., 2020).

#### 4.5 | Ecosystem-wide and large-scale responses

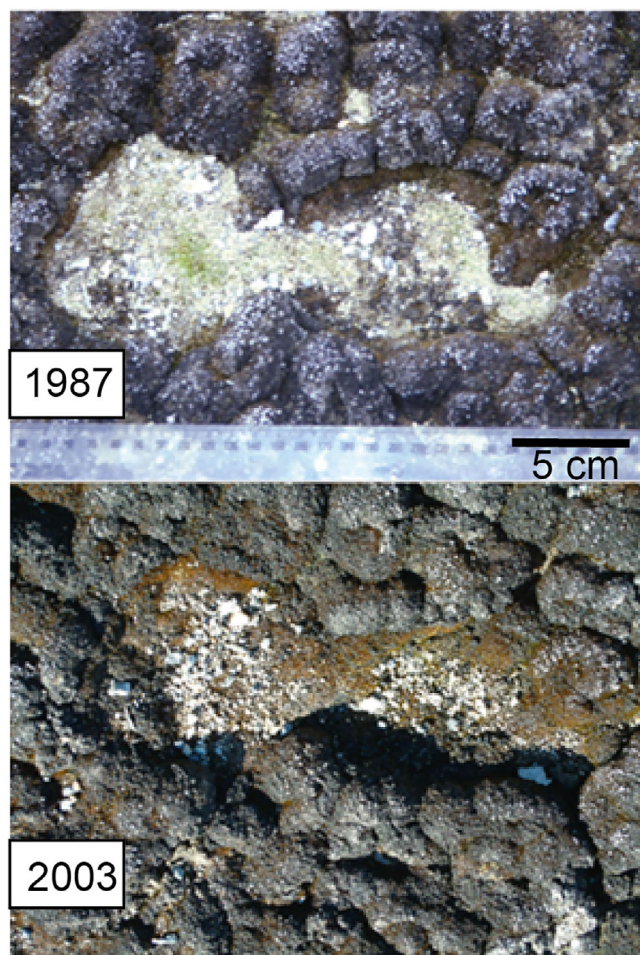
Antarctic ecosystems are often considered as “simple” due to a relatively low number of trophic interactions and a strong prevalence of abiotic ecosystem drivers (Hogg et al., 2006; Lee et al., 2019). However, it is this simplicity of biological communities and the sharp thermal gradients found in terrestrial Antarctica that can provide insights into how species may dwell in a changing climate and how biogeochemical cycles and food webs might look like in the future (Koerich et al., 2022).

The limits within which Antarctica's vegetation can function effectively are going to change. Newly deglaciated terrains can be colonized rapidly (Table 1), supporting an increasing diversity and abundance of bacteria, lichens, and bryophytes (Bajerski & Wagner, 2013; Favero-Longo et al., 2012; Le et al., 2016) and on an ecosystem scale, the expansion of vegetation could be accompanied by shifts in the soil microbiome ultimately changing the physicochemical soil environment (Ball et al., 2022). Snow algal blooms can increase in area and elevation (Gray et al., 2020) and cell and nutrient export from warming and flushing of the glacial surface have been shown to impact downstream community structure and increase productivity on glacial forefields and freshwater Antarctic ecosystems already (Bagshaw et al., 2016; Weisleitner et al., 2020).

However, the detection of such large scale, ecosystem relevant shifts in Antarctica remains difficult. Remote sensing offers the technological advancement to detect such changes in vegetation distribution and could provide a powerful tool for vegetation monitoring in the future (Box 2). For now, however, the majority of research incorporating a remote sensing element (listed in Table 2) still focuses on method development or on establishing a baseline distribution

TABLE 2 Optical sensors used or useful for ecological/human impact studies in Antarctica

Sensor (operator)	Temporal range	Temporal resolution	Pixel footprint	Number of bands	Cost	Studies
Landsat satellites (NASA)	1973 (Landsat 1) to present (Landsat 9)	Every 2 days (Landsat 8 and 9); Every 18 days (Landsat 1)	30 m (60 m Landsat 1 and 2)	11 (Landsat 8 and 9) Covering VNIR, SWIR and TIR	Free	Koch et al., 2008; Fretwell et al., 2011; Casanovas et al., 2015; Brooks, Tejedo, & O'Neill, 2019; Hossain & Hashim, 2020; Sotille et al., 2020
Sentinel 2 (ESA)	2015 to present	Every 4/5 days (Sentinel 2A and 2B)	10 m/20 m (band dependent)	13. Covering VNIR and SWIR	Free	Huovinen et al., 2018; Gray et al., 2020; Sotille et al., 2020
Worldview 2 or 3; Quickbird (MAXAR)	2001–2015 (Quickbird) 2009 to present (WV 2 and 3)	1.24 m multispectral, 0.3 m panchromatic, 3.7 m SWIR (WV3); 2 m multispectral, 0.5 m panchromatic (WV2); 2.4 m (Quickbird)	8 bands (VNIR); WV3 has an extended range SWIR sensor with an additional 8 bands. Quickbird has 4 bands covering the VNIR	Commercials, can task imagery over a specific location		Shin et al., 2014; Vieira et al., 2014; Malenovsky et al., 2017; Andrade et al., 2018; Jawak et al., 2019; Miranda et al., 2020; Power et al., 2020; Gray et al., 2021; Sun et al., 2020
PlanetScope (Planet)	2014 to present	1 day	3 m	4 (VNIR)	Limited area coverage freely available for research projects at the time of writing.	–
Hyperspectral Satellites: Hyperion EO-1 (NASA), PRISMA (ASI), EnMAP (DLR), HypsIRI (NASA)	2000—future (EnMAP, CHIME and HypsIRI are in development at the time of writing)		20–30 m	c. 250	Varies by operator, though often free for research	Kim & Hong, 2012
Airborne imagery	N/A	Based on field plan/light conditions	1 m typical	c. 620, dependent on sensor.	Dependent on operator	Black et al., 2014
UAS Surveys	N/A	Based on field plan/light conditions	0.5–5 cm typical	c. 620 (hyperspectral), 4–9 band for multispectral sensors.	£1000–£300,000	Lucieer et al., 2010; Malenovsky et al., 2017; Turner et al., 2018; Turner, Phillips, et al., 2019; Miranda et al., 2020; Sotille et al., 2020



**FIGURE 5** Effects of trampling on moss. Here is an example from Taylor Valley, Canada glacier in continental Antarctica. Recovery rates are so slow that even after 16 years the footprint outline is still clearly visible. Photos courtesy of Prof Allan T. G. Green

### **BOX 2 Is remote sensing the future of vegetation monitoring in Antarctica?**

Monitoring vegetation in Antarctica through traditional ground sampling methods is destructive, physically intensive and limited to accessible locations. Multi-scale remote sensing platforms (UAVs to satellites) have the ability to overcome these obstacles while providing the added advantage of more frequent datasets over larger spatial scales. Advanced classification techniques applied to remotely sensed imagery (Malenovský et al., 2017; Miranda et al., 2020; Turner et al., 2018; Vieira et al., 2014) can automate the mapping process, offering the potential to completely transform the way that Antarctic vegetation is monitored in the future. Further, multivariate distribution and projection modeling of Antarctic vegetation requires large amounts of spatial and temporal data which only remote sensing is likely to efficiently provide in a critical time when rates of environmental change (Bromwich et al., 2013; Turner et al., 2014) are exceeding rates of baseline mapping. However, Antarctic vegetation is small and spatially patchy, making it a challenge to detect and discriminate using a single remote sensing platform. While freely-available optical satellite imagery (row 1–2, Table 2) has the potential for long-term monitoring over the continent, detailed and spatially explicit information (such as species identification) is constrained to sub-pixel scale by relatively coarse spatial resolution. By contrast, higher resolution satellite and UAS imagery (row 3–7, Table 2) can overcome these constraints but are limited in their scalability and ability to continuously track changes over time due to restricted access to imagery, low-altitude surveying and the general inaccessibility of Antarctica.

dataset (e.g., Casanovas et al., 2015; Fretwell et al., 2011; Hossain & Hashim, 2020; Huovinen et al., 2018; Jawak et al., 2019; Koch et al., 2008; Lucieer et al., 2010; Malenovský et al., 2017; Power et al., 2020; Sotille et al., 2020; Turner, Malenovský, et al., 2019) and investigations are predominantly focussed on maritime Antarctica. Independent of the study context, these remote sensing studies all highlight limitations of interpreting short-medium term trends on top of high intraseasonal variability, with the images used for interpretation providing only a snapshot of vegetation conditions without the context of light, temperature or water conditions, which may all be affecting the spectral characteristics of vegetation and hence its “health” in a remote sensing context.

## 5 | CONCLUSION

In this review, we have highlighted the specialized life traits that allow different groups of nonvascular and vascular vegetation to thrive in Antarctica's terrestrial ecosystems. Subsequently, we have discussed how Antarctica's vegetation is already, and will potentially in the future, respond to those changes. In maritime Antarctica, conditions might generally become milder, boosting ecosystem productivity. Vascular plants and mosses will thrive on wet soils while lakes and snow patches will bloom with algae. Alien invasions and competition will increase provoking shifts in community composition and likely result in a homogenization of the local communities. Contrasting this, in continental Antarctica, conditions will become drier and even harsher. The permafrost is predicted to retreat, further reducing water availability in this marginal habitat. As a result, the times when lichens and mosses are active are likely to become shorter and not all organisms are equipped to cope with this change. Increased evapotranspiration rates can also lead to the accumulation of salts on the ground, which can be toxic and reduce plant health further.

We have identified remote sensing as a powerful tool to detect changes in vegetation cover in Antarctica and the future will see the adoption of methodologies to derive more complex eco-physiological information. The holistic view afforded by large-scale mapping is crucial to contextualize the changes and challenges faced by vegetation in a changing Antarctica and offers a framework to observe those changes without causing additional stress on a fragile and slow-growing ecosystem.

However, any attempt to model the future vegetation change in Antarctica depends on robust and reliable baseline information, which is still sparse for most regions. Especially, research on the effects of alien and native vascular plant encroachment on nonvascular species is lacking and basically nonexistent.

The primary conclusion to be drawn from this review is that there is no universal change to be expected for Antarctica's terrestrial environments. Change is going to be drastic, and very different between maritime and continental Antarctica.

### AUTHOR CONTRIBUTIONS

**Claudia Colesie:** Conceptualization (lead); funding acquisition (equal); investigation (equal); software (equal); supervision (equal); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Charlotte V. Walshaw:** Conceptualization (equal); data curation (equal); resources (equal); writing – original draft (equal); writing – review and editing (equal). **Leopoldo G. Sancho:** Conceptualization (equal); funding acquisition (equal); project administration (equal); supervision (equal); writing – original draft (equal). **Matthew P. Davey:** Funding acquisition (equal); writing – review and editing (equal). **Andrew Gray:** Conceptualization (equal); data curation (equal); investigation (equal); project administration (equal); resources (equal); software (equal); visualization (equal); writing – original draft (equal).

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## CONFLICT OF INTEREST

The authors have declared no conflicts of interest for this article.

## DATA AVAILABILITY STATEMENT

Data sharing is not applicable to this article as no new data were created or analyzed in this study.

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