Polar Biology (2026) 49:79
https://doi.org/10.1007/s00300-026-03524-8

RESEARCH

Alterations of cryptogam communities over one decade of time on King George Island, Antarctica

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Received: 29 October 2025 / Revised: 8 June 2026 / Accepted: 24 June 2026 / Published online: 9 July 2026
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Abstract

Antarctica's ice-free areas are mainly colonized by cryptogamic communities, which are known to be sensitive indicators of environmental change. Despite numerous monitoring-related studies, published research on medium-term cryptogam cover changes is limited. With this study, we aimed to investigate compositional and structural changes in cryptogamic communities over a decade near the Polish Arctowski Antarctic Station. Here, a phytosociological approach was used to assess species diversity, coverage, and ecological relevance during the 2012–2013 field campaign, with results being compared to a previously published survey conducted in 2003–2004. Climatic trends were assessed to identify potential environmental drivers for the observed vegetation changes. Results revealed lower moss richness and lower ecological relevance based on coverage and frequency, particularly among cushion-forming taxa such as *Andreaea gainii* and *Syntrichia princeps*. In contrast, lichen richness increased, with species such as *Usnea aurantiacoatra* increasing in ecological importance, while *U. antarctica* declined. These species-specific trends suggest that traits such as moisture tolerance, growth form, and substrate preference influence the capacity of cryptogams to respond to changing conditions. Climatic data indicate no significant changes in temperature, relative humidity, or precipitation (2003–2013), while the long-term record showed weak trends (1990–2020). Therefore, medium-term climatic data did not support a direct attribution of the observed vegetation changes to climate variables. These findings demonstrate that successional processes and local site conditions can be associated with measurable ecological restructuring in Antarctic vegetation. By providing high-resolution floristic and ecological data, this study establishes a baseline for future monitoring, using cryptogams as indicators of environmental change.

Keywords Phytosociology · Bryophytes · Lichens · Grass · Cryptogams

Introduction

The Antarctic ecosystem is widely known as less complex and subject to limited human interference compared to tropical or temperate regions (Barnes and Peck 2008; Convey 2010; Convey et al. 2014; Convey and Peck 2019; Colesie et al. 2023). Antarctic terrestrial vegetation is characterized by a dominance of cryptogams, while the diversity of vascular plants is extremely low (Putzke and Batista Pereira 2021; Colesie et al. 2023). Cryptogams, including mosses, liverworts, lichens, and algae, do not form flowers but reproduce vegetatively or sexually via spores and are poikilohydric, meaning their water content adapts to environmental conditions (Green and Lange 1995; Büdel et al. 2024). These adaptations enable them to survive extreme environmental conditions, such as prolonged drought, freezing

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temperatures, high UV-B radiation, low nutrient availability, and fluctuations in wind patterns and precipitation (Convey and Peck 2019). In Antarctica, their physiological activity increases primarily during the austral summer season after the winter snow has melted (Longton 1988; Schroeter et al. 2011, 2021). In ice-free areas, cryptogams play essential roles in nutrient cycling, soil formation, and successional processes (Longton 1988). Lichens primarily occupy rock surfaces, forming biological rock crusts, sometimes growing on mosses, and they also cover available soil surfaces as biological soil crusts (Lindsay 1978; Putzke and Batista Pereira 2021; Weber et al. 2022). Bryophytes, in contrast, are most abundant in wet habitats where lichens are sparse or absent (Ochyra et al. 2008).

Nevertheless, climate trends have not been uniform in recent decades. Antarctica has been experiencing notable climatic variation, including warming in parts of the Antarctic Peninsula and altered precipitation regimes (Turner et al. 2009; Convey and Peck 2019; IPCC 2023). These changes were most pronounced during the second half of the twentieth century, when the Antarctic Peninsula experienced one of the strongest regional warming trends in the Southern Hemisphere, with areas of the western coast warming faster than the global average (Anisimov et al. 2007; Van Gestel et al. 2020). However, this warming trend did not continue uniformly into the early twenty-first century, when regional records showed an absence of warming since the late 1990s and a cooling trend during 1999–2014 (Turner et al. 2016). In the South Shetland Islands, part of maritime Antarctica, these climatic trends have coincided with increased precipitation variability, glacier retreat, and vegetation expansion into newly ice-free areas (Miranda et al. 2020; Putzke and Batista Pereira 2021). Climate model projections indicate that Antarctica could warm by an additional 1.5–2.5 °C before 2100 (Tewari et al. 2022; IPCC 2023; Colesie et al. 2023). These scenarios are expected to shorten the duration of seasonal snow cover and alter meltwater regimes across the region, with direct implications for soil moisture, nutrient turnover, and microhabitat stability (Turner et al. 2009; Convey and Peck 2019; IPCC 2023; Colesie et al. 2023).

Previous studies demonstrated that ecological responses to Antarctic warming include significant changes in vegetation cover across ice-free areas. In particular, the expansion of the native vascular plants *Deschampsia antarctica* Desv. and *Colobanthus quitensis* [Kunth.] Bartl. has been recorded throughout the South Shetland Islands and in ice-free zones of the Antarctic Peninsula (Putzke and Batista Pereira 2021). Rising temperatures have been shown to influence the growth and reproductive development of both species (Day et al. 2008, 2009). Moreover, field surveys have reported an increase in cover by 25 times for *Deschampsia antarctica* and by five times for *Colobanthus quitensis* on the Argentine Islands, as well as over 190% increases on Signy Island over recent decades (Fowbert and Smith 1994; Cannone et al. 2016).

As poikilohydric organisms, cryptogams are able to colonize and survive on diverse substrates, such as soil and rocks, making them valuable indicators for studying environmental conditions and the impacts of global warming (Convey et al. 2014), especially in remote areas like the Antarctic region. The relatively low ecological complexity of the Antarctic ecosystem, attributable to low biodiversity and limited human impact, makes it an attractive model system for studying responses to environmental change (Convey and Peck 2019; Colesie et al. 2023). Knowledge of the occurrence and distribution of cryptogams is essential for assessing the dynamics of terrestrial organisms in response to environmental changes, as well as investigations on nutrient cycling, ecological succession, and trophic interactions (Weber et al. 2022). In recent decades, glacial and snowfield retreats have exposed new habitats, facilitating colonization and subsequent increase in populations of Antarctic bryophytes and lichens (Putzke and Batista Pereira 2021). In contrast to that, research on the response of cryptogams to the environmental changes in extreme conditions is limited.

Cryptogam communities have shown increases in biomass, reproductive activity, and spatial coverage, including the formation of new bryophyte-dominated assemblages on recently exposed terrain (Longton 1988; Miranda et al. 2020; Putzke and Batista Pereira 2021; Colesie et al. 2023, 2025). These patterns demonstrate the ability of some Antarctic vegetation components, particularly vascular plants and bryophytes, to respond to environmental changes. Several studies have described how global climate change has influenced Antarctic cryptogam communities specifically, highlighting the roles of rising temperatures, altered precipitation regimes, and increased availability of ice-free substrate in shaping their physiological activity, phenology, and spatial distribution. However, responses differ among organism groups, and lichen responses are often slower and more species-specific than those of vascular plants or bryophytes (Longton 1988; Convey and Peck 2019; Putzke and Batista Pereira 2021; Schroeter et al. 2021; Colesie et al. 2023). However, these climate drivers threaten the stability of cryptogam populations, potentially altering their growth patterns and community structure (Convey and Peck 2019; Schroeter et al. 2021; Colesie et al. 2023). Although several studies have examined the dynamics of cryptogam populations, revealing important ecological patterns, their responses remain comparatively understudied relative to those of vascular plants.

Here, we aim to analyze the status and alteration in composition, abundance, and spatial distribution of Antarctic cryptogams and their phytosociological communities over

time. We investigate how these changes relate to climatic parameters to understand the population dynamics of bryophytes and lichens in ice-free areas of Antarctica. This integrated approach should provide insights into the ecological response of Antarctic bryophytes and lichens to medium-term environmental variation and successional processes.

Materials and methods

Study area

This study was conducted in the area surrounding the Henryk Arctowski Polish Antarctic Station (62° 9.518′ S, 58° 28.421′ W) (Pasik et al. 2017) close to the Ecology Glacier on King George Island, being part of the South Shetland Islands (Fig. 1). The glacier and its adjacent ice-free areas form part of the Antarctic Specially Protected Area 128 (ASPA No. 128), which was established to preserve and protect the local fauna and vegetation from both expected and unforeseen anthropogenic disturbances (Secretariat of the Antarctic Treaty 2024). Despite this protection, minor anthropogenic impacts, such as the presence of trace metals and polycyclic aromatic hydrocarbons (PAHs), have been reported in the vicinity of the Arctowski Station (Ribeiro et al. 2011; Szumińska et al. 2021; Potapowicz et al. 2022). The vegetation on King George Island comprises two vascular plants (*Colobanthus quitensis* and *Deschampsia antarctica*) and a wide variety of cryptogams, including macro- and microlichens, mosses, and liverworts, all of which typically colonize exposed ice-free habitats (Bednarek-Ochyra et al. 2000; Øvstedal and Smith 2001; Molina-Montenegro et al. 2013; Olech 2004).

Field sampling and data collection

Field sampling was conducted by members of the Brazilian Antarctic Program (PROANTAR) during the austral summer season 2012–2013 and compared to an earlier austral summer sampling in 2003–2004 (Victoria et al. 2009b). In the first, already published campaign, six sampling sites were selected, based on the extent and distinctiveness of vegetation cover and landscape. In the current study, the number was increased to 20 sites (S1 to S20) in the same region, including the six previously studied sites, across different land types: moraines, valleys, hills, cliffs, peaks, marine terraces, and plateaus. For direct temporal comparisons, only the same sites common to both surveys were used.

Frequency and coverage data were collected during both surveys using a modified Braun-Blanquet grid method adapted for Antarctic conditions (Braun-Blanquet 1964; Victoria and Pereira 2007; Victoria et al. 2009b). Within each cryptogamic community, a 20 m measuring tape was placed along a north-south directing transect. At five-meter

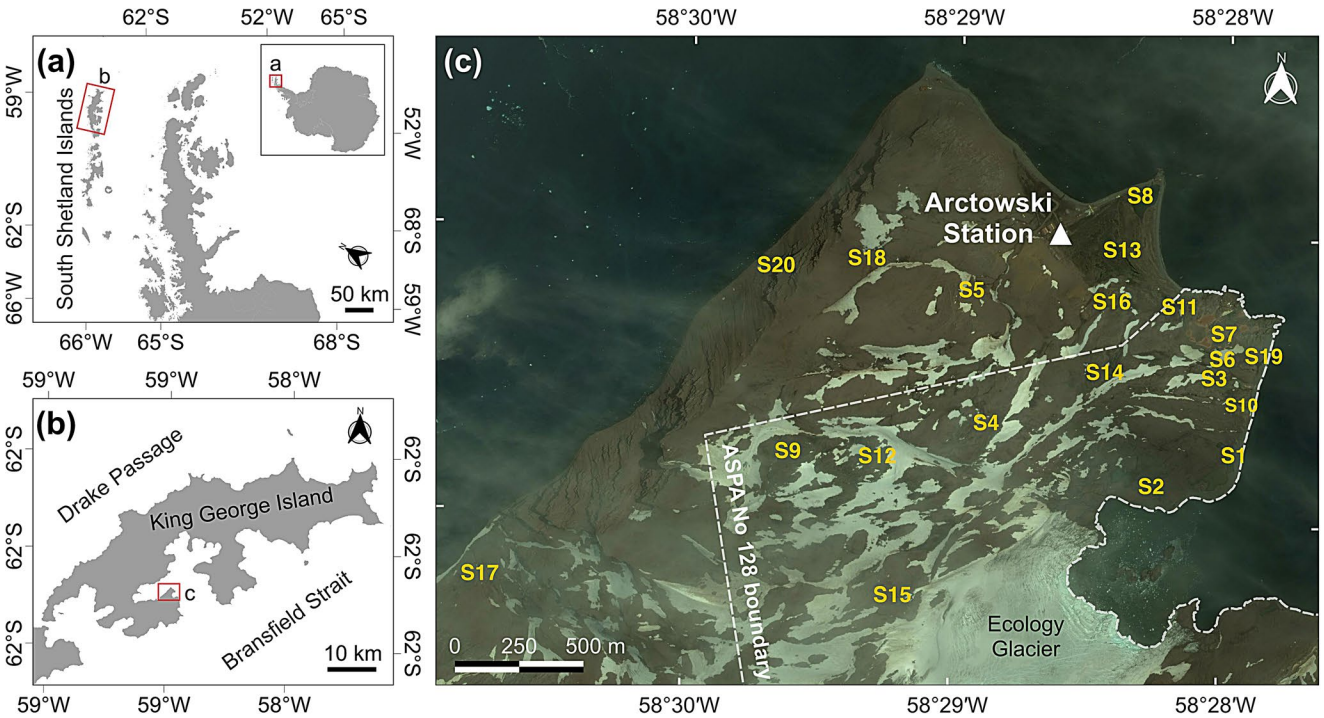


Fig. 1 Overview map of the study area located in West Antarctica (**a**), showing the South Shetland Islands (**b**), and a close-up of King George Island (**c**), the field site with sampling sites where data were collected during the austral summer season 2012–2013. The sampling sites are highlighted by yellow letters. All map elements were generated using QGIS software (version 3.34.15; https://www.QGIS.org)

intervals, a 25 × 25 cm grid, sub-divided into 100 small squares of 2.5 × 2.5 cm, was placed along the transect. The number of transects per site was determined by community size, with sampling continuing until no new species were detected across five consecutive grids. Within each grid, the frequency and coverage of each identified species was registered.

Morphological taxonomy was based on the main floras for Antarctica (Øvstedal and Smith 2001; Olech 2004; Ochyra et al. 2008), with species author citations provided by the Index Fungorum (http://www.indexfungorum.org) and Tropicos database (http://www.tropicos.org/).

Vegetation analysis

To delineate community boundaries, cryptogamic vegetation was mapped in the field using an Ashtech Promark II® DGPS (Ashtech OEM, Sunnyvale, CA, USA), and spatial coordinates were processed with the Astech Solutions® software. All data were geo-referenced to the projected coordinate system WGS84 (EPSG 3031), and maps were generated using QGIS (QGIS Development Team 2022), incorporating contour layers from the Antarctic Digital Database (Gerrish et al. 2020, 2022; Gerrish 2022).

Species ecological relevance within each community was evaluated using the Index of Ecological Importance (*IES*). This index was calculated by combining species coverage and frequency parameters. The *IES* ranges from 0 to 600, with values above 50 indicating high ecological relevance (Victoria and Pereira 2007). The *IES* calculations were performed according to Eq. (1), analogous to Victoria and Pereira (2007):

$$IES = F(1 + C) \tag{1}$$

where F is the relative frequency of the species, and C corresponds to the mean species cover. These parameters were derived as follows:

$$F = 100x/n \tag{2}$$

and

$$C = \sum (ci)/x \tag{3}$$

Here, x is the number of grids in which the species occurred, n is the total number of sampled grids, and ci represents cover class values per grid. The cover classes were based on the estimated percentage of species cover per grid, defined as follows: 0.5 (<1%), 1 (10−1%), 2 (25−10%), 3 (50−25%), 4 (75−50%), and 5 (100−75%).

Spatiotemporal change analysis

To assess changes in cryptogamic coverage over a ten-year period, we conducted a comparative analysis of frequency, coverage, and species composition, restricted to the same areas surveyed in both the 2003–2004 and 2012–2013 field campaigns. Although the second survey included 320 grids covering a wider region, the temporal comparison was limited to 184 grids from the same areas surveyed in the first campaign. Due to differing sampling efforts between our study and Victoria et al. (2009b), we applied rarefaction and extrapolation to evaluate whether both sampling efforts were sufficient to assess local diversity. This analysis utilized three metrics of species diversity: species richness, the Shannon index, and the Simpson index (Chao et al. 2014). Specifically, temporal changes were assessed at four levels.

At the species level, *IES* values were compared between two time points to identify changes in the relative importance of individual taxa. At the formation level, we compared vegetation between the two surveys using the classification scheme of Longton (1979) and Lindsay (1971), which distinguishes moss formations (e.g., carpets, turfs, cushions), lichen formations based on growth (fruticose, foliose, crustose), and phanerogamic formations. At the group level, comparisons were conducted between taxonomic groups (i.e., bryophytes and lichens), substrate types, and life forms. Life forms were defined as ecological adaptations that reflect morphology and colony structure (Oishi 2024). For bryophytes, we applied the classification according to Victoria et al. (2009a), including cushions, turfs, mats, and wefts. Similarly, lichens were categorized following Büdel and Scheidegger (2008) as crustose, foliose, squamulose, and fruticose types. Moreover, independent-samples t-tests were applied to evaluate whether mean *IES* values significantly differed across life-form categories and substrate types (e.g., soil, rocks, and pebbles) between the two surveys.

At the environmental level, we analyzed climatic trends to determine whether changes in abiotic conditions could explain changes in cryptogam communities. Meteorological data were obtained from the Henryk Arctowski Polish Antarctic Station on King George Island. The dataset included measurements of air temperature (°C), soil temperature (°C), relative humidity (%), and annual precipitation (mm), covering the time span between 2003 and 2013. Additionally, to evaluate longer-term environmental trends, we extended the analysis to the period 1990–2020 using the same variables. All data were retrieved from the Meteoblue database (http://www.meteoblue.com) to assess climatic variation within the study area. Temporal trends were assessed using linear regression models, slope coefficients, coefficients of determination (R^2), and associated p-values. Furthermore,

we used Structural Equation Modeling (SEM) to examine relationships between climatic variables and vegetation responses (Grace 2006).

All statistical analyses and plots were created in R using RStudio (R Core Team 2024) and the packages reshape2 (Wickham 2007), ggplot2 (Wickham 2016), tidyverse (Wickham et al. 2019), grid (R Core Team 2024), gridExtra (Auguie 2017), patchwork (Pedersen 2024), readxl (Wickham and Bryan 2023), lavaan (Rosseel 2012), and RColorBrewer (Neuwirth 2022).

Results

Floristic composition in 2012/13

The cryptogamic communities within the study region were characterized by a wide variety of lichens and bryophytes (Fig. S1, Online Resource 1). A total of 1163 individuals were recorded across 320 grid squares, belonging to 26 families, 37 genera, and 55 species (Table 1). Of these, 31 species were lichens, followed by 21 mosses, two phanerogams, and one terrestrial macroalga. Among the lichen families, *Parmeliaceae* was represented most with six taxa, followed by *Caliciaceae* (4), *Cladoniaceae* (3), and *Teloschistaceae* (3). In the bryophyte group, *Bryaceae* exhibited the highest representation, with five taxa, followed by *Polytrichaceae* and *Pottiaceae*, each with four taxa. In comparison, ten lichen families and four bryophyte families were represented by a single species each.

Spatial variation in species richness was also observed, as illustrated by the mapped patches of occurrence of cryptogam communities in 2012/13 (Fig. 2). Site four (S4) exhibited the highest species richness, with 24 species, while sites S3 and S5 recorded 20 and 21 species, respectively. In contrast, a lower number of species was observed at sites S2 ($n=4$) and S6, S8, S10, S15 ($n=6$) (Table S1, Online Resource 1). All identified taxa in this study had previously been cited on King George Island (Øvstedal and Smith 2001; Olech 2004; Ochyra et al. 2008).

Species with high ecological relevance in 2012/13

Before comparing both surveys, we identified species with high *IES* values during 2012/13 (Table S2, Online Resource 1). At the regional scale, the grass *Deschampsia antarctica* was the most widespread, recorded at all 20 sampling sites, and often showed high *IES* values. Among bryophytes, the pleurocarpic *Sanionia uncinata*, a carpet-forming species, was the most ecologically dominant bryophyte, with an *IES* well above the relevance threshold. It was widespread and abundant across diverse habitats, particularly in wet environments such as marine terraces, moraine fields, drainage lines, and areas with fragmented rock. In these areas, *Sanionia uncinata* frequently co-occurred with *Polytrichastrum alpinum*, which also showed high ecological relevance. This turf-forming moss was commonly found in association with *Deschampsia antarctica* and *Colobanthus quitensis*. In contrast, other bryophyte species demonstrated *IES* values below the ecological relevance threshold (see Table S2, Online Resource 1).

Within the lichen group, *Usnea antarctica* was the only species with ecological relevance (*IES*=54), typically colonizing rocks and sometimes occurring on mosses. *Usnea antarctica* had the widest distribution, particularly occurring in areas near the beach and bird colonies, on rock outcrops that harbor birds, and in places where the rock is fragmented into small blocks. In comparison, *Usnea aurantiacoatra* also occurred, but with *IES* value below the relevance threshold. It was restricted to drier and higher elevation sites, where it preferentially colonized large blocks of rock. Although both species occurred on rock, these differences in elevation, substrate fragmentation, and likely moisture and nutrient regimes indicate distinct microhabitat preferences shaped by topographic and environmental gradients. This contrast within the same genus highlights the importance of species-specificity according to habitat. Beyond these species, most lichens exhibited *IES* values below the threshold (Table S2, Online Resource 1).

Changes in community composition: Sampling effort and floristic aspects

A comparative analysis of species presence across the same areas surveyed in both the 2003–2004 and 2012–2013 campaigns revealed notable changes in floristic composition. Although the same grid-method sampling strategy was employed in both campaigns, the number of sampled grids differed between the first and second surveys. Nevertheless, only the grids positioned in the same areas were used for the temporal comparison between the two periods. Based on rarefaction and extrapolation analyses, we confirmed that the sampling effort was sufficient to reliably capture the diversity of species in both study periods, as indicated by the non-significant differences between observed and expected species numbers (95% confidence interval; Fig. 3). The overall expected species richness was 48 (*CI*: 40–55) in 2003-04 and 50 (*CI*: 43–57) in 2012-13 at 400 sampling units, which indicates similar richness between the two survey periods.

Across the 2012–2013 sites selected for direct temporal comparison (S1, S2, S3, S4, S6, S7, S10, S11, S13, S14, S16, and S19), all located within the same areas surveyed in 2003–2004, a total of 48 species were recorded, compared

Table 1 List of species identified in ice-free areas of the Arctowski region, King George Island, maritime Antarctica in 2012/13. Species recorded in the same areas surveyed in both 2003–2004 and 2012–2013 are highlighted in bold

Group	Family	Taxon
Algae	*Prasiolaceae*	***Prasiola crispa*(Lightfoot) Kützing**
Bryophyta	*Amblystegiaceae*	***Sanionia uncinata*(Hedw.) Loeske**
	Andreaeaceae	***Andreaea gainii*Cardot**
		***Andreaea regularis*Müll. Hal.**
	Bartramiaceae	***Bartramia patens*Brid**
		Conostomum magellanicum Sull.
	Brachytheciaceae	***Brachythecium austrosalebrosum*(Müll. Hal.) Kindb.**
		Brachythecium glaciale Schimp.
	Bryaceae	***Bryum pallescens*Schleich. ex Schwägr.**
		***Bryum pseudotriquetrum*(Hedw.) G. Gaertn., B. Mey. & Scherb.**
		Bryum sp.
		***Pohlia cruda*(Hedw.) Lindb.**
		***Pohlia nutans*(Hedw.) Lindb.**
	Dicranaceae	***Chorisodontium aciphyllum*(Hook. f. & Wilson) Broth.**
	Polytrichaceae	***Polytrichastrum alpinum*(Hedw.) G.L. Sm.**
		***Polytrichum juniperinum*Hedw.**
		***Polytrichum piliferum*Hedw.**
		Polytrichum strictum Menzies ex Brid.
	Pottiaceae	***Hennediella heimii*(Hedw.) R.H. Zander**
		Syntrichia filaris (Müll. Hal.) R.H. Zander
		***Syntrichia princeps*(De Not.) Mitt.**
		***Syntrichia saxicola*(Cardot) R.H. Zander**
Lichens	*Caliciaceae*	*Amandinea petermannii* (Hue) Matzer, H. Mayrhofer & Scheid.
		Buellia sp. 1
		Buellia sp. 2
		Buellia sp. 3
	Cladoniaceae	*Cladonia borealis* S. Stenroos
		Cladonia glacialis Kristinsson & Ahti
		***Cladonia*sp.**
	Collemataceae	***Leptogium puberulum*Hue**
	Haematommataceae	*Haematomma erythromma* (Nyl.) Zahlbr.
	Lecanoraceae	*Rhizoplaca melanophthalma* (DC.) Leuckert & Poelt
	Ochrolechiaceae	*Ochrolechia frigida* (Sw.) Lynge
		Ochrolechia parella (L.) A. Massal.
		Ochrolechia sp.
	Pannariaceae	*Psoroma cinnamomeum* Malme
		Psoroma hypnorum (Vahl) Gray
		Psoroma sp.
	Parmeliaceae	*Cetraria aculeata* (Schreb.) Fr.
		Coelopogon epiphorellus (Nyl.) Brusse & Kärnefelt
		Parmelia saxatilis (L.) Ach.
		Pseudephebe pubescens (L.) M. Choisy
		***Usnea antarctica*Du Rietz**
		***Usnea aurantiacoatra*(Jacq.) Bory**
	Physciaceae	*Physconia muscigena* (Ach.) Poelt
	Ramalinaceae	*Ramalina flaccidissima* Bory
	Rhizocarpaceae	***Rhizocarpon geographicum*(L.) DC.**
	Sphaerophoraceae	*Sphaerophorus globosus* (Huds.) Vain.
	Teloschistaceae	***Caloplaca*sp.**
		Polycauliona regalis (Vain.) Hue
		Xanthoria elegans (Link) Th. Fr.
	Trapeliaceae	*Placopsis contortuplicata* I.M. Lamb
	Verrucariaceae	*Mastodia tessellata* (Hook. f. & Harv.) Hook. f. & Harv.
Phanerogams	*Caryophyllaceae*	***Colobanthus quitensis*(Kunth) Bartl.**
	Poaceae	***Deschampsia antarctica*E. Desv.**

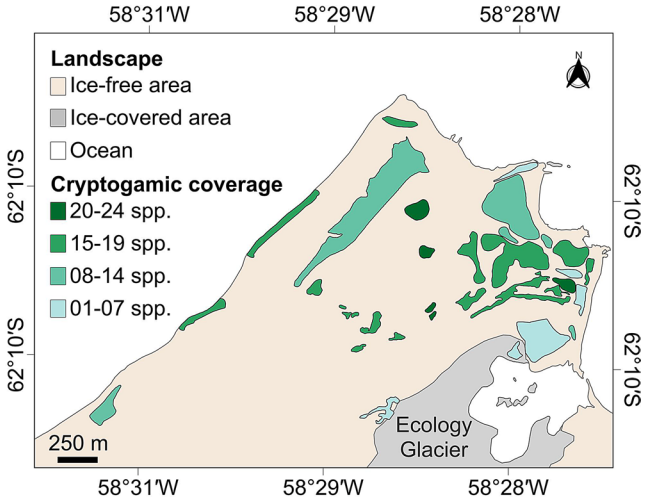


Fig. 2 Distribution map of cryptogamic communities based on field surveys (2012/13) in the Arctowski region, King George Island, maritime Antarctica. The map was plotted on an Antarctic stereographic projection (EPSG 3031) using the WGS84 datum. Green color scale illustrates species richness. All the elements were generated using QGIS software (version 3.34.15; https://qgis.org/)

to 40 species recorded in the earlier survey. The higher number of recorded taxa was mainly observed among lichens, with 27 taxa recorded in the later survey and seven in the earlier survey, whereas mosses included 18 and 28 taxa, respectively. Specifically, 13 mosses, two liverworts, and one lichen recorded in the previous campaign were not detected in the latter (Table S3, Online Resource 1). In contrast, three mosses and 22 additional lichen taxa were recorded in 2012–2013 (Table 1).

At the formation level, the comparative analysis also highlighted these alterations. In 2003–2004, the region was dominated by moss communities, including extensive moss carpet formations, frequent moss turf formations, mixed stands of moss and grass (i.e., phanerogamic formation), and moss cushion formations restricted to flooded areas and within meltwater drainage lines. By 2012–2013, turf and cushion moss dominance had declined substantially, carpets had reduced in extent, and fruticose lichen formations appeared as two small, localized patches, while crustose lichen formations were newly mapped in one restricted area near the beach. Phanerogamic formations expanded and became more fragmented across several sites (Fig. 4).

These results confirm a shift in community composition from mosses towards lichens and phanerogams, indicating a drier environment. The higher number of recorded lichen taxa was not uniform across all the sites but concentrated in particular areas, especially where fruticose and crustose taxa colonized stable rocky outcrops. Declines of mosses were most apparent at sites that had previously supported turf or cushion formations, which contracted in dominance rather than disappeared, while moss carpets persisted at

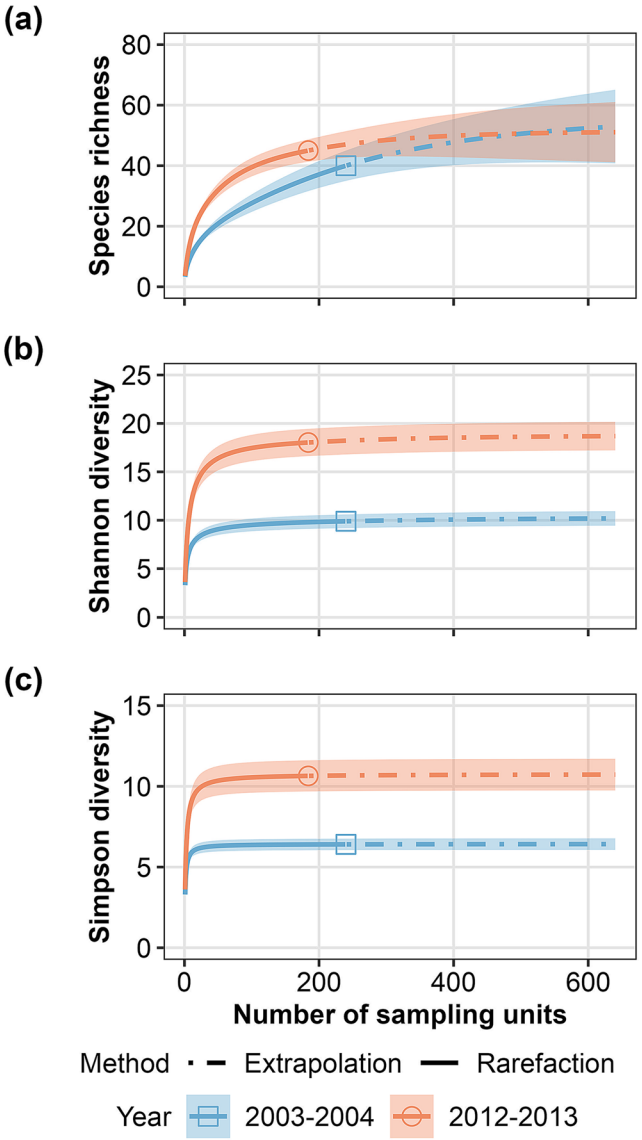


Fig. 3 Sample-size-based rarefaction (solid lines) and extrapolation curves (dotdash lines) with 95% confidence intervals (shaded area) comparing species richness (**a**), Shannon (**b**), and Simpson diversity (**c**) between 2003/04 (blue) and 2012/13 (red) sampling periods in the Arctowski region, King George Island, maritime Antarctica

specific sites and retained local importance. The overall effect was therefore a heterogeneous reorganization of community structure indicating a replacement of mosses by lichens at sites with drier environment. This transition from moss-dominated to increasingly lichen- and phanerogam-dominated formations demonstrates an ongoing ecological reorganization within the sampled sites, consistent with successional dynamics and regional environmental patterns (Turner et al. 2009; Favero-Longo et al. 2012; Cannone et al. 2016, 2021).

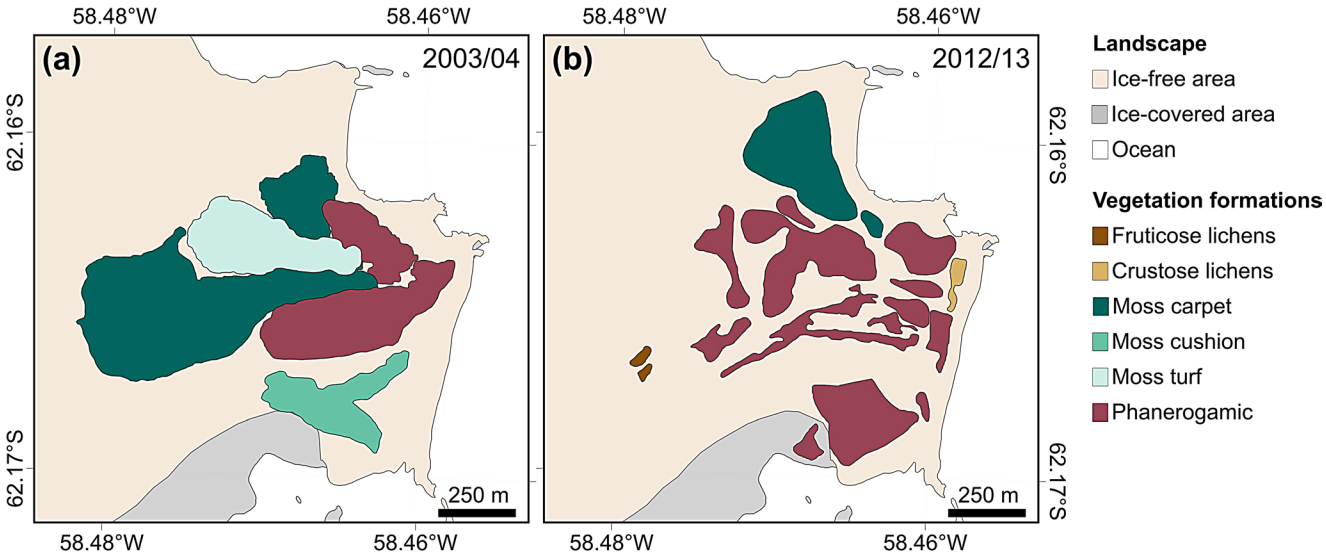


Fig. 4 Comparative changes in vegetation formations between the 2003–2004 (**a**) and 2012–2013 (**b**) surveys in the Arctowski region, King George Island. The map was plotted on an Antarctic stereographic projection (EPSG 3031) using the WGS84 datum. Formations were classified following Hu (1998) and based on phytosociological surveys. All the elements were generated using QGIS software (version 3.34.15; https://qgis.org)

Table 2 Comparison of ecological attributes of the recurrent species occurring in both studies conducted in the austral summer season of 2003–2004 and 2012–2013. *G* = number of grids in which the species was recorded; *F* = species relative frequency (%); *IES* = species index of ecological importance in the total sampling

Taxon	Group	Summer season 2003–2004			Summer season 2012–2013		
		G	F	IES	G	F	IES
Deschampsia antarctica	Phanerogam	190	79.17	245.80	150	81.52	257.07
Sanionia uncinata	Moss	177	74	215.20	106	57.61	205.43
Polytrichastrum alpinum	Moss	146	60	153.54	77	41.85	118.48
Usnea antarctica	Lichen	66	27.5	77.29	35	19.02	45.92
Bryum pseudotriquetrum	Moss	55	22.51	52.40	6	3.26	5.98
Andreaea gainii	Moss	18	7.5	24.54	8	4.35	9.24
Syntrichia princeps	Moss	21	8.75	22.96	33	17.93	44.57
Usnea aurantiacoatra	Lichen	16	6.66	15.00	12	6.52	24.46
Polytrichum juniperinum	Moss	12	5.4	10.80	3	1.63	3.53
Chorisodontium aciphyllum	Moss	2	0.83	2.03	3	1.63	5.43
Pohlia cruda	Moss	2	0.83	1.66	13	7.07	12.77
Brachythecium austrosalebrosum	Moss	1	0.83	1.66	5	2.72	6.25
Bartramia patens	Moss	6	2.5	1.62	7	3.8	7.07

Changes in community composition: Ecological aspects

Changes in ecological attributes between the two surveys were further examined by comparing the number of grids in which the species were recorded (*G*), species relative frequency (*F*), and *IES* for species recurrent in both sampling campaigns (Table 2).

The phanerogam *Deschampsia antarctica* remained the most dominant species overall, exhibiting a slight increase in *IES* from 245.80 in 2003-04 to 257.07 in 2012-13, despite a decrease in grid presence (*G*: from 190 to 150). Among the mosses, *Sanionia uncinata* consistently held high ecological relevance, although its occurrence, frequency, and *IES* values declined (*G*: 177 to 106; *F*: 74% to 57.61%; *IES*: 215.20 to 205.43). Similarly, *Polytrichastrum alpinum* showed declines across all three metrics, with a particularly marked decrease in *IES*. In contrast, *Syntrichia princeps* increased in both *G* (21 to 33) and IES (22.96 to 44.57), suggesting a broader distribution and growing ecological relevance in the recent survey. Meanwhile, *Bryum pseudotriquetrum*, once common in 2003–2004, experienced a steep decline across all metrics, indicating reduced prevalence in the later sampling. Among lichens, *Usnea antarctica* and *Usnea aurantiacoatra* were consistently present but exhibited contrasting ecological values. While *U. antarctica* decreased in both

G and *IES* (66 grids and 77.29 *IES* to 35 grids and 45.92 *IES*), *U. aurantiacoatra* showed a moderate increase in *IES* (from 15.00 to 24.46), despite presence in a lower number of grids. This difference reflects changes in cover-frequency values, not a direct estimate of population growth. Table S4 also shows different substrate associations, with *U. antarctica* recorded on rocks and pebbles, and *U. aurantiacoatra* recorded on rocks (Online Resource 1). Overall, these patterns suggest group- and species-level responses to environmental or competitive pressures, with phanerogams remaining dominant, most mosses declining, and selected lichens increasing in ecological importance over time.

Changes in community composition: Morphological aspects

In terms of group analysis, temporal differences in species cover were assessed across taxonomic groups, substrate types, and life forms (Fig. 5 and Table S4, Online Resource 1). Overall, cover values remained relatively stable for bryophytes and lichens between both surveys, and also the overall cover of cryptogams remained stable over time.

Regarding life forms, turf-forming and mat-forming mosses exhibited similar median cover across both samplings, whereas cushion-forming mosses experienced a statistically significant decrease. Fruticose lichen cover did not change over time. Substrate-specific comparisons revealed that soil, rocks, and pebbles supported similar levels of cryptogam cover across both time periods, with no significant differences detected between them. Overall, soil remained the dominant substrate for bryophytes, while rocks and pebbles were equally preferred by fruticose lichens and cushion-forming mosses. These results suggest that although cover remained relatively stable across most ecological categories, cushion mosses may be more sensitive to environmental changes over time.

Changes in local abiotic conditions

Climate data from the Arctowski Station revealed weak trends across the period 2003–2013, with no evidence of local warming during the sampling interval (Fig. 6). Annual precipitation showed a slight but non-significant increase (slope = 0.0022, $R^2 = 0.1535$, $p = 0.23$). In contrast, other climate variables, including air temperature (slope = -0.0002, $R^2 = 0.0047$, $p \leq 0.0001$) and soil temperature (slope = -0.0002, $R^2 = 0.0085$, $p \leq 0.0001$), showed weak declining trends, while relative humidity (slope = -0.0001, $R^2 = 0.0002$, $p = 0.32$) showed no significant trend. A statistically significant decline in cushion-forming mosses, including *Andreaea gainii* and *Syntrichia princeps* ($p = 0.03$), was observed between the two surveys. This decline may reflect successional processes and local environmental variation rather than a direct response to warming during the study interval. Although a longer-term climatic dataset (1990–2020) was analyzed to assess broader environmental trends (Fig. S2, Online Resource 1), air temperature showed a weak positive trend (slope = 0.0001; $R^2 = 0.0027$; $p \leq 0.0001$), and soil temperature showed a similar trend (slope = 0.0001; $R^2 = 0.0077$; $p \leq 0.0001$). Relative humidity showed a weak but significant decline ($R^2 = 0.0004$; $p = 0.03$), whereas annual mean precipitation showed a weak positive trend that did not reach statistical significance (slope = 0.0007; $R^2 = 0.1214$; $p = 0.05$). SEM showed no significant relationships between the survey period (2003–2013) and air temperature (β = -0.28, $R^2 = 0.08$, $p = 0.41$), soil temperature (β = -0.31, $R^2 = 0.10$, $p = 0.35$), relative humidity (β = -0.06, $R^2 = 0.003$, $p = 0.86$), or precipitation ($\beta = 0.39$, $R^2 = 0.15$, $p = 0.23$). Climate-vegetation relationships were assessed using linear regressions and are shown as positive (i.e., $\beta = 1.00$; same-direction changes) or negative (i.e., β = -1.00; opposite-direction changes) associations between climatic variables and group-level vegetation responses (Fig. S3, Online Resource 1).

Discussion

This study reveals measurable changes in Antarctic cryptogamic communities, showing both compositional and structural changes over a period of one decade. The main findings include a decline in moss cover and in their ecological relevance, particularly among cushion-forming taxa such as *Andreaea gainii* and *Syntrichia princeps*, and an increased representation of lichen species, including *Usnea aurantiacoatra*. These observations align with studies on vegetation responses to climate variability and environmental changes across polar ecosystems, including declines in *Usnea antarctica* in field manipulation studies (Bokhorst et al. 2012, 2016), and reductions in *Usnea* spp. cover associated with increased persistence and extent of summer snow patches on King George Island, reflecting the absence of regional warming observed on the Antarctic Peninsula since beginning of the 21st century (Turner et al. 2016; Sancho et al. 2017; Miranda et al. 2020). Similar patterns have been reported for compositional changes in moss and lichen groups in continental Antarctica (Cannone et al. 2021) and broader trends of sustained greening and species turnover in the maritime Antarctic (Roland et al. 2024; Colesie et al. 2025; Puhovkin et al. 2025; Contreras and Zúñiga 2025).

Through species-level analysis using the *IES*, we confirmed a decline in both frequency and ecological relevance of dominant moss taxa. Among these, dominant pleurocarpous and acrocarpous species such as *Sanionia uncinata*

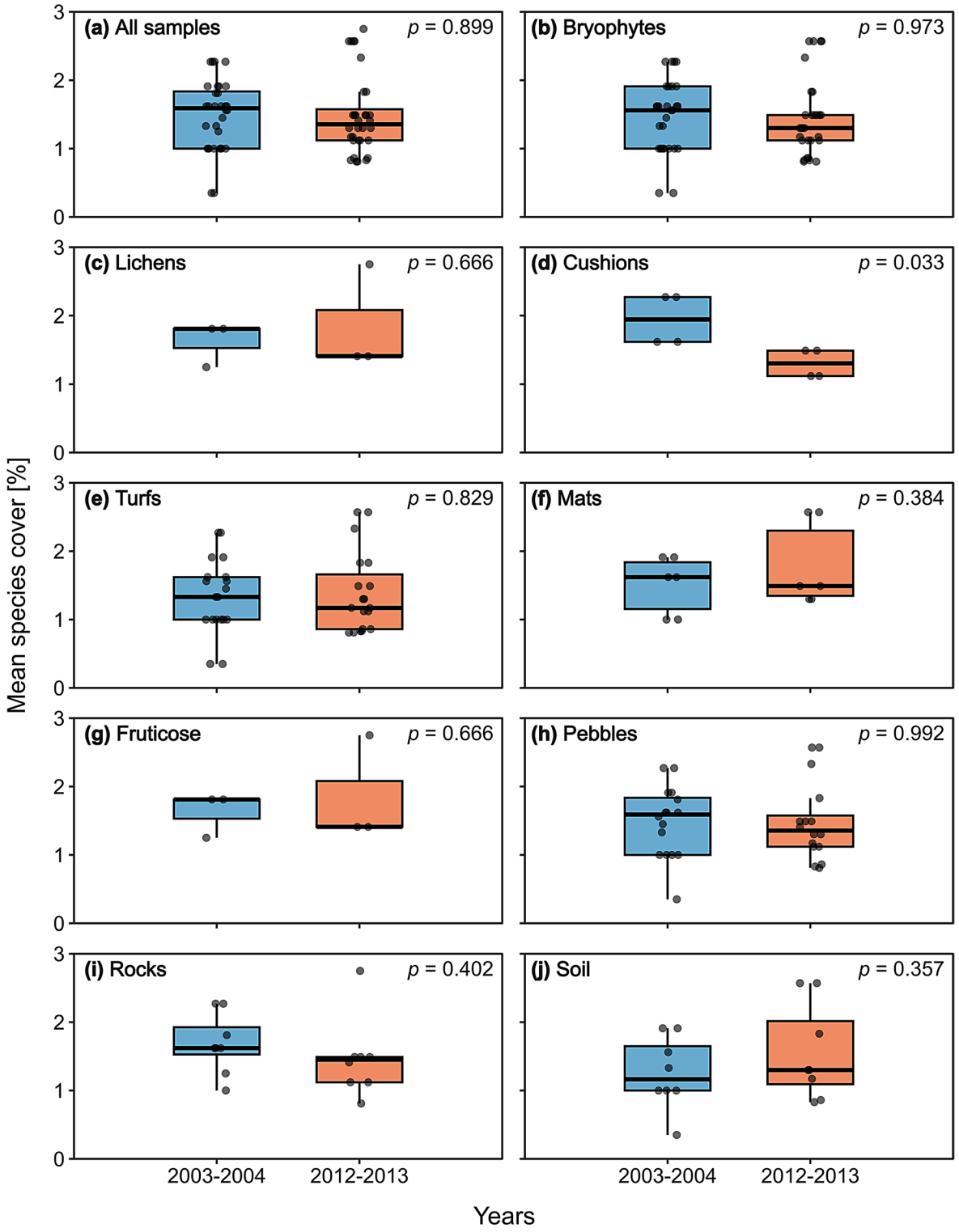


Fig. 5 Boxplots and p-values of the t-test comparing mean percent cover (%) registered during both sampling periods (2003–2004 and 2012–2013), across taxonomic groups (**a-c**), life forms (**d-g**), and substrate types (**h-j**). Bryophytes were classified into cushion, mat, and turf forms (**d-f**), whereas lichens were classified into one type (**g**)

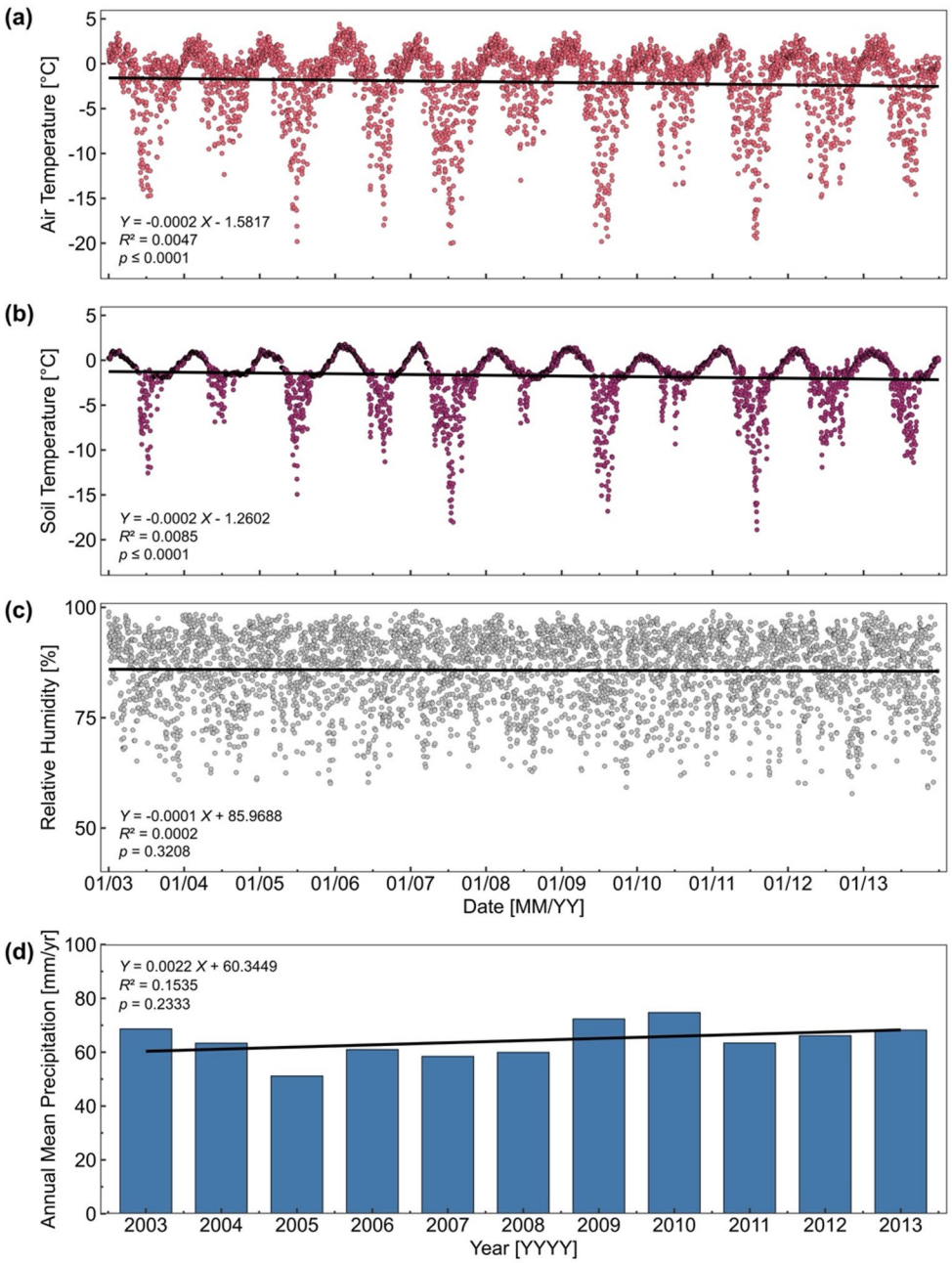


Fig. 6 Year-to-year variation in air temperature (**a**), soil temperature (**b**), relative humidity (**c**), and annual mean precipitation (**d**) recorded at the Henryk Arctowski Polish Antarctic Station on King George Island, during the period 2003–2013. Linear regression trends are shown as solid black lines. Panels (**a**-**c**) show daily observations, whereas panel (**d**) presents annual mean precipitation values

and *Polytrichastrum alpinum* exhibited substantial declines in *IES*, suggesting reduced ecological influence. This reduction was further reflected by the observed decline in moss richness across the six resampled sites. Cushion mosses, in particular, displayed a significant reduction in cover, with *Andreaea gainii* and *Syntrichia princeps* showing the highest losses. Given that cushion-forming bryophytes are physiologically adapted to conserve moisture in harsh environments, this pattern may indicate sensitivity to hydrological stressors associated with local site conditions (Victoria et al. 2009a).

Notwithstanding their known tolerance to desiccation, cushion mosses are especially susceptible to surface runoff, leaching, and freeze-thaw fluctuations (Melick and Seppelt 1992; Lovelock et al. 1995). These factors may have been influenced by local environmental variation, although the medium-term climate data cannot identify the drivers of these changes. In contrast, mat- and turf-forming mosses such as *Sanionia uncinata* maintained more stable coverage, suggesting that their horizontal growth form may confer an advantage under variable moisture conditions by improving substrate adhesion and reducing moisture loss (Melick and Seppelt 1992; Ochyra et al. 2008; Robison et al. 2023).

Hence, the observed restructuring appears to be at least partly influenced by life form-related differences in stress tolerance, although our findings provide quantitative evidence mainly for cushion mosses. Given their roles in moisture retention, soil development, and early colonization, reductions in cushion-forming mosses could reduce local water availability, thereby potentially influencing ecosystem functioning (Ochyra et al. 2008; Victoria et al. 2009a; Putzke and Batista Pereira 2021).

Conversely, lichen richness increased, supporting studies that lichen communities are expanding in Antarctic environments (Ruiz-Fernández et al. 2017). Although not all taxa responded positively, the increase in *Usnea aurantiacoatra*, alongside the declines in *Usnea antarctica* and several crustose lichens of low ecological relevance, exemplifies differentiated, species-specific responses rather than uniform group-level trends. Such differentiation is consistent with experimental field data. For instance, Bokhorst et al. (2016) reported a 71% decline in *Usnea antarctica* following passive warming on Signy Island, while crustose lichens remained stable or increased. Similarly, Bokhorst et al. (2012) found that mosses exhibited minimal response to warming, while fruticose lichens declined significantly. In a regional context, Miranda et al. (2020) observed a 10.3% reduction in *Usnea* spp. using remote sensing, linking these patterns to changes in snow cover and microhabitat availability. Taken together, these studies corroborate the present findings, suggesting that changes in cryptogam composition are not uniform but instead modulated by species-specific ecological niches, dispersal capacities, and microhabitat requirements. Moreover, variations in decline rates across studies may be due to methodological differences and the accuracy of cover estimates. Nevertheless, regardless of the method applied, ecologically relevant changes in lichen cover are evident between the two surveys, with fruticose taxa showing divergent responses, for instance, *Usnea aurantiacoatra* expanding while *Usnea antarctica* declined, and crustose forms remaining comparatively stable. This pattern indicates that functional attributes such as growth form could influence lichen development under changing Antarctic conditions.

These compositional changes may also reflect successional processes, whereby mosses act as early colonizers that stabilize substrates and regulate microclimate, gradually giving way to more competitive lichens under increasingly stable conditions. Similar pathways have been described following glacier retreat on Signy Island, where bryophytes dominate initial stages and are subsequently replaced or complemented by lichens (Favero-Longo et al. 2012). On the Barton Peninsula, Kim et al. (2016) reported a directional sequence from snow algae and crustose lichens to moss cushions and fruticose lichens, with divergence into wet moss-dominated and dry lichen-dominated stages. The present results, showing cushion moss declines and increased lichen representation, are therefore consistent with a transition along such successional trajectories. Moreover, as Schuuring et al. (2024) demonstrated in the High Arctic, dense moss layers play a key role in insulating soils, implying that their decline may also reduce microhabitat insulation capacity and facilitate the expansion of lichens in more exposed areas.

Based on these growth form patterns, the present findings align with previous studies that species-level traits, such as moisture tolerance, and substrate preference, could influence the capacity of lichens to persist or expand under changing conditions (Matos et al. 2024; Colesie et al. 2025). The replacement of the declining fruticose species *Usnea antarctica* and crustose lichens of low ecological relevance by more ecologically flexible taxa such as *Usnea aurantiacoatra* may also indicate competitive release in response to environmental filtering. Furthermore, increasing lichen richness may reflect the opening of new niches due to glacial retreat, as well as improved dispersal via abiotic and biotic vectors (Vincent 2000; Gillespie et al. 2012). As Convey and Peck (2019) discuss, lichens possess greater ecological plasticity and colonization potential under climate-driven habitat change, which may help explain their expansion.

From 2003 to 2013, air and soil temperatures showed weak declining trends, relative humidity showed no significant trend, and annual precipitation showed only a non-significant increase. Therefore, the climatic data for the study interval do not support a climate-driven interpretation of the observed vegetation changes, which likely reflect ecological restructuring associated with successional processes, site-level conditions, and species-specific responses. For cushion mosses, which rely on ambient humidity for hydration and insulation (Victoria et al. 2009a; Colesie et al. 2025), small changes in moisture availability may still affect local performance, but the available climatic data cannot directly identify this mechanism. Thus, the decline in cushion-forming mosses should be interpreted cautiously, as it may reflect local environmental variation, microhabitat conditions, and successional processes rather than a direct response to warming.

Extending the climatic record to 1990–2020 revealed only one statistically significant trend, declining relative humidity, with all other variables remaining stable. This longer-term pattern corroborates the inference that humidity, rather than temperature, may be the primary abiotic driver affecting cryptogam persistence. This is ecologically relevant because bryophytes contribute substantially to microclimatic regulation, soil structure, and water retention. Their decline could, therefore, trigger cascading impacts on

associated microbial and faunal assemblages (Lindo and Gonzalez 2010).

However, the implications of these changes extend beyond vegetation composition, since cryptogams support productivity, nutrient cycling, and biodiversity in Antarctic ice-free ecosystems by providing habitat, influencing carbon balance, and regulating surface energy exchange. A change towards lichen dominance and reduced moss biomass could therefore alter ecosystem processes at multiple levels. The observed changes in *IES* among key taxa reflect a restructuring of ecological roles, with potential consequences for biotic interactions and community assembly trajectories.

Nonetheless, this study has limitations. First, despite using standardized sampling methods across both surveys, discrepancies in the number of sampled grids may introduce biases. This was addressed using rarefaction and extrapolation methods, which confirmed sampling adequacy. Second, the absence of fine-scale microclimatic measurements limits our ability to isolate causal mechanisms linking species changes to abiotic factors. The SEM analysis was exploratory because vegetation data were available from two survey periods only. Future studies should integrate repeated vegetation surveys at shorter intervals and microhabitat sensors to assess temperature, soil moisture, and radiation at the microsite scale. Third, biotic factors such as herbivory, competition, and bird disturbance were not quantified and may also contribute to observed patterns. Fourth, vegetation formations were assessed at the growth-form level rather than as species-specific associations. Fifth, individual moss and lichen size and the exact location of each occurrence were not recorded in either survey, which limits our ability to distinguish recent establishment, growth of existing individuals, and previously undetected cover. Moreover, given the slow growth of Antarctic lichens, the higher number of taxa reported in 2012–2013 should be interpreted as additional occurrences within the newly surveyed regions, rather than as newly established taxa. Most importantly, microscale variation has a significant influence on vegetation dynamics, with functional types exhibiting distinct ecological niches (Matos et al. 2024). For instance, *Usnea antarctica* tends to dominate in lower-to-mid-elevations, whereas *Usnea aurantiacoatra* prevails on wind-exposed ridges. These findings highlight the need for predictive models that integrate microscale heterogeneity when forecasting vegetation responses to environmental change.

Despite these limitations, this study presents a temporal dataset that shows cryptogam dynamics in response to environmental change in the maritime Antarctic. It provides a baseline for future assessments and complements existing monitoring approaches in this region. The integration of species-level analysis, functional traits (e.g., life forms), and climatic trends offers a comprehensive framework for monitoring community responses in dynamically changing environments. While the period analyzed was relatively short, the ecological signals detected highlight the sensitivity of these communities to even subtle environmental variation. However, the detection of rare or low-abundance taxa may have been constrained by grid-based sampling limitations, potentially underestimating the presence of less dominant species.

Future projections for Antarctica suggest complex scenarios of environmental change. Rintoul et al. (2018) discuss several conditions under low-emission pathways where warming remains below 2 °C, but continued ice melt may still expose new terrain. Such processes may facilitate vegetation expansion but also risk homogenizing communities or promoting invasive species. In this context, the conservation of native species, such as those listed in the present study, is necessary for the balance of the ecosystem. Understanding how these species respond to environmental changes in terms of distributions, communities, community structure, and ecological functions is essential. Such information will improve predictions of future outcomes and guide effective conservation strategies. Hence, sustained monitoring, combined with microclimatic and biotic measurements, will be crucial for disentangling interacting drivers and informing effective policy and management responses.

Conclusion

Our results indicate that measurable changes in terrestrial cryptogam communities in Antarctica can occur within less than a decade. The most significant findings include the decline of cushion-forming mosses and the increased representation of lichen species. This demonstrates that Antarctic vegetation can show measurable compositional change over one decade, although climate data do not support a direct attribution of these changes to the temperature, humidity, or precipitation trends. These results highlight that life form differences and species-specific adaptations modulate cryptogamic responses to local environmental variation. The observed restructuring, favoring lichen expansion over moss persistence, has important implications for successional pathways, biodiversity maintenance, and ecosystem function in Antarctic ice-free environments.

It has been shown that cryptogams are sensitive indicators of environmental change, and their compositional changes can likely influence terrestrial ecosystem processes such as nutrient cycling, microhabitat stability, and succession. Although field-based vegetation data can contain sampling heterogeneity, they provide direct, site-level observations that complement remote sensing and modeling approaches. This research provides valuable baseline data

on the distribution and dynamics of cryptogams in ice-free areas, allowing future studies to continue monitoring possible disturbances in the Antarctic terrestrial environment. These findings support conservation efforts and guide future studies assessing ecosystem stability in response to climate and environmental change.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-026-03524-8.

Acknowledgements The authors would like to acknowledge the Inter-Ministry Commission for Sea Resources (CIRM), the Brazilian Ministry of Science, Technology, and Innovation (MCTI), and the Ministry of Environment (MMA) for supporting this project.

Author contributions RPA, FCV, and ABP conceived the study. FCV secured funding acquisition. FCV, MPA, and ABP collected the field data. RPA conducted data analysis and structured the text with significant input from BW, ATC and CB. RPA wrote the paper with input from all authors. All authors reviewed and approved the manuscript.

Funding Open access funding provided by Graz University of Technology. This work was financially supported by the Coordination for the Improvement of Higher Education Personnel (CAPES - Finance Code 001) and the National Council for Scientific and Technological Development (CNPq - Process 407591/2018-4).

Data availability Data will be made available on request.

Declarations

Ethical approval Not applicable.

Competing interests The authors declare no competing interests.

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References

Anisimov O, Vaughan D, Callaghan T et al (2007) Polar regions (Arctic and Antarctic). In: Parry ML, Canziani OF, Palutikof JP et al (eds) Climate change 2007: Impacts, adaptation and vulnerability. Contribution of Working Group II to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change. Cambridge University Press, Cambridge, pp 653–685

Auguie B (2017) gridExtra: miscellaneous functions for grid graphics. https://doi.org/10.32614/CRAN.package.gridExtra

Barnes D, Peck L (2008) Vulnerability of Antarctic shelf biodiversity to predicted regional warming. Clim Res. https://doi.org/10.3354/cr00760

Bednarek-Ochyra H, Vána J, Lewis Smith RI (2000) The liverwort flora of Antarctica. Polish Academy of Sciences, Kraków

Bokhorst S, Bjerke JW, Tømmervik H et al (2012) Ecosystem Response to Climatic Change: The Importance of the Cold Season. Ambio. https://doi.org/10.1007/s13280-012-0310-5

Bokhorst S, Convey P, Huiskes A, Aerts R (2016) Usnea antarctica, an important Antarctic lichen, is vulnerable to aspects of regional environmental change. Polar Biol. https://doi.org/10.1007/s00300-015-1803-z

Braun-Blanquet J (1964) Pflanzensoziologie: Grundzüge der Vegetationskunde. Springer Vienna, Vienna. https://doi.org/10.1007/978-3-7091-8110-2

Büdel B, Scheidegger C (2008) Thallus morphology and anatomy. In: Nash TH (ed) Lichen Biology, 2nd edn. Cambridge University Press, Cambridge, pp 40–68. https://doi.org/10.1017/CBO9780511790478.005

Büdel B, Friedl T, Beyschlag W (eds) (2024) Biology of Algae, Lichens and Bryophytes. Springer Berlin Heidelberg, Berlin, Heidelberg. https://doi.org/10.1007/978-3-662-65712-6

Cannone N, Guglielmin M, Convey P et al (2016) Vascular plant changes in extreme environments: effects of multiple drivers. Clim Change. https://doi.org/10.1007/s10584-015-1551-7

Cannone N, Guglielmin M, Malfasi F et al (2021) Rapid soil and vegetation changes at regional scale in continental Antarctica. Geoderma. https://doi.org/10.1016/j.geoderma.2021.115017

Chao A, Gotelli NJ, Hsieh TC et al (2014) Rarefaction and extrapolation with Hill numbers: a framework for sampling and estimation in species diversity studies. Ecol Monogr. https://doi.org/10.1890/13-0133.1

Colesie C, Walshaw CV, Sancho LG et al (2023) Antarctica's vegetation in a changing climate. WIREs Clim Change. https://doi.org/10.1002/wcc.810

Colesie C, Gray AM, Walshaw CV et al (2025) Is Antarctica Greening? Glob Change Biol. https://doi.org/10.1111/gcb.70294

Contreras RA, Zúñiga GE (2025) UV-B radiation responses in Antarctic plants. Theor Exp Plant Physiol. https://doi.org/10.1007/s40626-025-00383-2

Convey P (2010) Terrestrial biodiversity in Antarctica - Recent advances and future challenges. Polar Sci. https://doi.org/10.1016/j.polar.2010.03.003

Convey P, Peck LS (2019) Antarctic environmental change and biological responses. Sci Adv. https://doi.org/10.1126/sciadv.aaz0888

Convey P, Chown SL, Clarke A et al (2014) The spatial structure of Antarctic biodiversity. Ecol Monogr. https://doi.org/10.1890/12-2216.1

R Core Team (2024) R: A Language and Environment for Statistical Computing. R foundation for statistical computing. https://www.r-project.org. Accessed 29 Oct 2025

Day TA, Ruhland CT, Xiong FS (2008) Warming increases aboveground plant biomass and C stocks in vascular-plant-dominated Antarctic tundra. Glob Change Biol. https://doi.org/10.1111/j.1365-2486.2008.01623.x

Day TA, Ruhland CT, Strauss SL et al (2009) Response of plants and the dominant microarthropod, Cryptopygus antarcticus, to warming and contrasting precipitation regimes in Antarctic tundra. Glob Change Biol. https://doi.org/10.1111/j.1365-2486.2009.01919.x

Favero-Longo SE, Worland MR, Convey P et al (2012) Primary succession of lichen and bryophyte communities following glacial recession on Signy Island, South Orkney Islands, Maritime Antarctic. Antarct Sci. https://doi.org/10.1017/S0954102012000120

Fowbert JA, Smith RIL (1994) Rapid Population Increases in Native Vascular Plants in the Argentine Islands, Antarctic Peninsula. Arct Alp Res. https://doi.org/10.2307/1551941

Gerrish L (2022) High resolution vector polygon seamask for areas south of 60S (Version 7.6). UK Polar data centre, natural environment research council, UK research, innovation. https://doi.org/10.5285/96cf916d-7aa7-464c-985e-a39692d5be83

Gerrish L, Fretwell P, Cooper P (2020). UK polar data centre natural environment research council, UK research & innovation. High resolution vector polygons of Antarctic rock outcrop (Version 7.2). https://doi.org/10.5285/e30908fb-307e-4508-b391-3ccb55da9167

Gerrish L, Fretwell P, Cooper P (2022) High resolution vector polylines of the Antarctic coastline (Version 7.6). NERC EDS UK Polar Data Centre. https://doi.org/10.5285/45174e8c-7ce8-4d87-a6f7-570db476c6c9

Gillespie RG, Baldwin BG, Waters JM et al (2012) Long-distance dispersal: a framework for hypothesis testing. Trends Ecol Evol. https://doi.org/10.1016/j.tree.2011.08.009

Grace JB (2006) Structural equation modeling and natural systems. Cambridge University Press. https://doi.org/10.1017/CBO9780511617799

Green TGA, Lange OL (1995) Photosynthesis in Poikilohydric Plants: A Comparison of Lichens and Bryophytes. In: Schulze E-D, Caldwell MM (eds) Ecophysiology of Photosynthesis. Springer Berlin Heidelberg, Berlin, Heidelberg, pp 319–341. https://doi.org/10.1007/978-3-642-79354-7_16

IPCC (2023) Climate Change 2023: Synthesis report. Contribution of Working Groups I, II and III to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland. https://doi.org/10.59327/IPCC/AR6-9789291691647

Kim SC, Kim JS, Hong BR et al (2016) Assembly processes of moss and lichen community with snow melting at the coastal region of the Barton Peninsula, maritime Antarctic. J Ecol Environ. https://doi.org/10.1186/s41610-016-0008-x

Lindo Z, Gonzalez A (2010) The bryosphere: an integral and influential component of the Earth's Biosphere. Ecosystems. https://doi.org/10.1007/s10021-010-9336-3

Lindsay DC (1971) Vegetation of the South Shetland Islands. Br Antarct Surv Bull 25:59–83

Lindsay DC (1978) The role of lichens in antarctic ecosystems. Bryologist. https://doi.org/10.2307/3242188

Longton RE (1979) Vegetation ecology and classification in the Antarctic Zone. Can J Bot. https://doi.org/10.1139/b79-273

Longton RE (1988) Biology of polar bryophytes and lichens. Cambridge University Press, Cambridge

Lovelock CE, Jackson AE, Melick DR, Seppelt RD (1995) Reversible Photoinhibition in Antarctic Moss during Freezing and Thawing. Plant Physiol. https://doi.org/10.1104/pp.109.3.955

Matos P, Rocha B, Pinho P et al (2024) Microscale is key to model current and future Maritime Antarctic vegetation. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2024.174171

Melick DR, Seppelt RD (1992) Loss of soluble carbohydrates and changes in freezing point of Antarctic bryophytes after leaching and repeated freeze-thaw cycles. Antarct Sci. https://doi.org/10.1017/S0954102092000592

Miranda V, Pina P, Heleno S et al (2020) Monitoring recent changes of vegetation in Fildes Peninsula (King George Island, Antarctica) through satellite imagery guided by UAV surveys. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2019.135295

Molina-Montenegro MA, Ricote-Martínez N, Muñoz-Ramírez C et al (2013) Positive interactions between the lichen Usnea antarctica (Parmeliaceae) and the native flora in Maritime Antarctica. J Veg Sci. https://doi.org/10.1111/j.1654-1103.2012.01480.x

Neuwirth E (2022) RColorBrewer: ColorBrewer Palettes. https://doi.org/10.32614/CRAN.package.RColorBrewer

Ochyra R, Smith RIL, Bednarek-Ochyra H (2008) The illustrated moss flora of Antarctica. Cambridge University Press, Cambridge

Oishi Y (2024) Cryptogam biomass estimation using taxonomic and life form models for accurate assessment. Sci Rep. https://doi.org/10.1038/s41598-024-69851-0

Olech M (2004) Lichens of King George Island, Antarctica. Institute of Botany of The Jagiellonian University, Poland

Øvstedal DO, Smith RL (2001) Lichens of Antarctica and South Georgia: a guide to their identification and ecology. Cambridge University Press, Cambridge

Pasik M, Kowalska ME, Łapiński S et al (2017) Large-scale map and 3D modelling of the Henryk arctowski polish antarctic station. Polar Rec. https://doi.org/10.1017/S0032247417000122

Pedersen TL (2024) patchwork: the composer of plots. https://doi.org/10.32614/CRAN.package.patchwork

Potapowicz J, Szopińska M, Szumińska D et al (2022) Sources and composition of chemical pollution in Maritime Antarctica (King George Island), part 1: Sediment and water analysis for PAH sources evaluation in the vicinity of Arctowski station. Chemosphere. https://doi.org/10.1016/j.chemosphere.2021.132637

Puhovkin A, Kazantsev T, Barták M et al (2025) Development of long-term monitoring of Antarctic moss banks to recent climate changes. Polar Sci. https://doi.org/10.1016/j.polar.2025.101174

Putzke J, Batista Pereira A (2021) The Vegetation of the South Shetland Islands and the Climatic Change. IntechOpen, London. https://doi.org/10.5772/intechopen.94269

QGIS Development Team (2022) QGIS Geographic Information System. QGIS Association. https://doi.org/10.5281/zenodo.6139224

Ribeiro AP, Figueira RCL, Martins CC et al (2011) Arsenic and trace metal contents in sediment profiles from the Admiralty Bay, King George Island, Antarctica. Mar Pollut Bull. https://doi.org/10.1016/j.marpolbul.2010.10.014

Rintoul SR, Chown SL, DeConto RM et al (2018) Choosing the future of Antarctica. Nature. https://doi.org/10.1038/s41586-018-0173-4

Robison AL, Deluigi N, Rolland C et al (2023) Glacier loss and vegetation expansion alter organic and inorganic carbon dynamics in alpine streams. Biogeosciences. https://doi.org/10.5194/bg-20-2301-2023

Roland TP, Bartlett OT, Charman DJ et al (2024) Sustained greening of the Antarctic Peninsula observed from satellites. Nat Geosci. https://doi.org/10.1038/s41561-024-01564-5

Rosseel Y (2012) lavaan: An R Package for Structural Equation Modeling. J Stat Softw. https://doi.org/10.18637/jss.v048.i02

Ruiz-Fernández J, Oliva M, García-Hernández C (2017) Topographic and geomorphologic controls on the distribution of vegetation formations in Elephant Point (Livingston Island, Maritime Antarctica). Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2017.02.158

Sancho LG, Pintado A, Navarro F et al (2017) Recent Warming and Cooling in the Antarctic Peninsula Region has Rapid and Large Effects on Lichen Vegetation. Sci Rep. https://doi.org/10.1038/s41598-017-05989-4

Schroeter B, Green TGA, Pannewitz S et al (2011) Summer variability, winter dormancy: lichen activity over 3 years at Botany Bay, 77°S latitude, continental Antarctica. Polar Biol. https://doi.org/10.1007/s00300-010-0851-7

Schroeter B, Green TGA, Pintado A et al (2021) Summer activity patterns for a moss and lichen in the maritime Antarctic with respect to altitude. Polar Biol. https://doi.org/10.1007/s00300-021-02939-9

Schuuring S, Halvorsen R, Bronken Eidesen P et al (2024) High Arctic Vegetation Communities with a Thick Moss Layer Slow Active Layer Thaw. J Geophys Res Biogeosciences. https://doi.org/10.1029/2023JG007880

Secretariat of the Antarctic Treaty (2024) ASPA 128: Western shore of Admiralty Bay, King George Island, South Shetland Islands. https://www.ats.aq/devph/en/apa-database/33. Accessed 29 Oct 2025

Szumińska D, Potapowicz J, Szopińska M et al (2021) Sources and composition of chemical pollution in Maritime Antarctica (King George Island), part 2: Organic and inorganic chemicals in snow cover at the Warszawa Icefield. Sci Total Environ. https://doi.org/10.1016/j.scitotenv.2021.149054

Tewari K, Mishra SK, Salunke P, Dewan A (2022) Future projections of temperature and precipitation for Antarctica. Environ Res Lett. https://doi.org/10.1088/1748-9326/ac43e2

Turner J, Bindschadler R, Convey P et al (2009) Antarctic climate change and the environment: a contribution to the International Polar Year 2007–2008. Sci Comm Antarctic Res. https://epic.awi.de/id/eprint/21227/1/Tur2009a.pdf. Accessed 29 Oct 2025

Turner J, Lu H, White I et al (2016) Absence of 21st century warming on Antarctic Peninsula consistent with natural variability. Nature. https://doi.org/10.1038/nature18645

Van Gestel NC, Ducklow HW, Bååth E (2020) Comparing temperature sensitivity of bacterial growth in Antarctic marine water and soil. Glob Change Biol. https://doi.org/10.1111/gcb.15020

Victoria FDC, Pereira AB (2007) Index of ecological significance (IES) as a tool to phytossociological and conservation studies for moss species in Admiralty Bay area, King George Island, Antarctica. Oecologia Bras. https://doi.org/10.4257/oeco.2007.1101.06

Victoria FDC, Costa DP, Pereira AB (2009a) Life-forms of moss species in defrosting areas of King George Island, South Shetland Islands, Antarctica. Biosci J 25:151–160

Victoria FDC, Pereira AB, Costa DP (2009b) Composition and distribution of moss formations in the ice-free areas adjoining the Arctowski region, Admiralty Bay, King George Island, Antarctica. https://doi.org/10.5281/ZENODO.8014129. Iheringia Sér Botânica

Vincent WF (2000) Evolutionary origins of Antarctic microbiota: invasion, selection and endemism. Antarct Sci. https://doi.org/10.1017/S0954102000000420

Weber B, Belnap J, Büdel B et al (2022) What is a biocrust? A refined, contemporary definition for a broadening research community. Biol Rev. https://doi.org/10.1111/brv.12862

Wickham H (2007) Reshaping Data with the reshape Package. J Stat Softw. https://doi.org/10.18637/jss.v021.i12

Wickham H (2016) ggplot2: Elegant Graphics for Data Analysis, 2nd ed. 2016. Springer-Verlag New York. https://ggplot2.tidyverse.org. Accessed 29 Oct 2025

Wickham H, Bryan J (2023) readxl: read excel files. https://doi.org/10.32614/CRAN.package.readxl

Wickham H, Averick M, Bryan J et al (2019) Welcome to the Tidyverse. J Open Source Softw. https://doi.org/10.21105/joss.01686

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