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The Longest Baseline Record of Vegetation Dynamics in Antarctica Reveals Acute Sensitivity to Water Availability

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Key Points:

- The longest plant cover record in Antarctica revealed Cape Hallett, unlike sites around the Peninsula, unaffected by climate change
- Antarctic vegetation shows high plasticity, for which most of the changes can be explained by seasonal variation and water availability
- By harmonizing historic and modern monitoring methodologies we establish a sustainable biological sentinel for change in East Antarctica

Supporting Information:

Supporting Information may be found in the online version of this article.

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Abstract Against a changing climate, the development of evidence-based and progressive conservation policies depends on robust and quantitative baseline studies to resolve habitat natural variability and rate of change. Despite Antarctica's significant role in global climate regulation, climate trend estimates for continental Antarctica are ambiguous due to sparse long-term *in situ* records. Here, we present the longest, spatially explicit survey of Antarctic vegetation by harmonizing historic vegetation mapping with modern remote sensing techniques. In 1961, E. D. Rudolph established a permanent survey plot at Cape Hallett, one of the most botanically diverse areas along the Ross Sea coastline, harboring all known types of non-vascular Antarctic vegetation. Following a survey in 2004 using ground-based photography, we conducted the third survey of Rudolph's Plot in 2018 using near-ground remote sensing and methodologies closely mirroring the two historic surveys to identify long-term changes and trends. Our results revealed that the vegetation at Cape Hallett remained stable over the past six decades with no evidence of transformation related to a changing climate. Instead, the local vegetation shows strong seasonal phenology, distribution patterns that are driven by water availability, and steady perennial growth of moss. Given that East Antarctica is at the tipping point of drastic change in the near future, with biological change having been reported at certain locations, this record represents a unique and potentially the last opportunity to establish a meaningful biological sentinel that will allow us to track subtle yet impactful environmental change in terrestrial Antarctica in the 21st century.

Plain Language Summary In early 2022, record-breaking high temperatures were recorded all over Antarctica, sparking concerns about the icy continent's future. Although the effects of climate change have been observed in West Antarctica, much less observation is available for East Antarctica, where almost 90% of the Antarctic ice mass is located. It is now, that East Antarctica is at a tipping point for change, and it is now, that we need to establish progressive conservation measures. What is at stake? The vegetation in East Antarctica is distinct. Any organism that managed to survive here has highly specialized traits, and we only find lichens, mosses, cyanobacteria, and green algae. Especially the mosses are used biological sentinels because they live long and with high specificity. However, because they grow so slowly, any attempt to monitor variation in their fitness has to span decades rather than years or even seasons. This constitutes a key problem when trying to understand the natural dynamics of a functional ecosystem in East Antarctica. By applying machine learning and advanced statistics to modern aerial survey data as well as historic vegetation maps (the oldest in Antarctica, from 56 years ago), we created a unique harmonized data set and gained unique ecological insight. This allows us to establish a biological sentinel for change in East Antarctica, just before it is too late.

1. Introduction

Antarctica plays a central role in regulating global climatic and oceanographic patterns and is an integral part of global climate change discussions (Rogers et al., 2020). Warming and mass loss of outlet glaciers as described in the Sixth Assessment Report of the IPCC have been mainly observed in West Antarctica, whereas warming trends in East Antarctica have been seen as localized and inconsistent (Turner et al., 2009). Parts of East Antarctica are projected to experience greater-than-global warming in the 21st century (Meredith et al., 2019), especially in coastal areas due to relatively stronger Southern Ocean warming and effects of ozone recovery (Bracegirdle

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et al., 2020). Heatwaves are an additional concern in East Antarctica, and several high-temperature records have been documented as having a severe and long-lasting impact on local ecosystem functionality (Barrett et al., 2008; Post et al., 2019; Robinson et al., 2020). In East Antarctica, a drying trend has been observable with increased drainage from permafrost thaw (Guglielmin et al., 2014), higher potential evapotranspiration, and changes in seasonal patterns of melt (Robinson et al., 2018). Most recently in March of 2022, much of East Antarctica experienced an extreme heatwave never documented in more than 60 years of instrumented records, with Dome Concordia (more than 1,200 km from the Ross Sea coast) experiencing ambient temperatures 40°C above average and Scott Base in the Ross Sea region recording air temperatures 10°C above normal. However, there is still limited confidence in climate trend estimates for East Antarctica due to sparse *in situ* records and large interannual to interdecadal variability (Ranasinghe et al., 2021). The lack of robust long-term monitoring and knowledge of baseline variability has been highlighted as a barrier to identifying environmental trends and consequences in a warming Antarctica (Chown et al., 2012).

Ice-free areas of East Antarctica are predominantly coastal cold deserts characterized by ultraoligotrophic soils and very limited water availability. As a result, the distribution, biomass, and diversity of photosynthetic organisms and communities are very constrained (Barrett et al., 2006). Phototrophs of East Antarctica (i.e., cyanobacterial mats, terrestrial eukaryotic algae, mosses, and lichens) are poikilohydric and exclusively associated with freshwater bodies or other sparse and intermittent water sources such as glacial streams and snowbanks (Green & Broady, 2001). These organisms have a high sensitivity to abiotic climate factors such as precipitation and temperature, which is an intrinsic feature of their poikilohydric lifestyle. In contrast to vascular plants, which have evolved mechanisms to decouple their metabolic activity from the surrounding climate, the physiological state of this non-vascular vegetation reflects their immediate environmental conditions and variability (Colesie et al., 2016). Consequently, their growth rates are directly affected by the water availability regime of their habitat (Matos et al., 2015; Sancho et al., 2007) and their growth can act as an integrator of variability and change on both interannual and interdecadal scales (Bramley-Alves et al., 2014; Sancho et al., 2017, 2019). Antarctic habitats rich with poikilohydric vegetation, therefore, have the potential to serve as sentinels of subtle and episodic environmental change.

However, the detection of abnormal changes, such as those predicted to be associated with climate change scenarios, depends on knowledge of the natural variability and natural rate of change, that is, the baseline variability. Criteria for establishing a robust baseline (Gullison et al., 2015) include monitoring of climatic background trends, representative abiotic and biotic attributes and composition, logistical feasibility for repeated surveys, and a survey frequency that reflects anticipated change in the ecosystem. For Antarctic ecosystems in particular, it is important to understand the interactions between the biota and local weather variability, microclimate, and topography (Colesie et al., 2014; Convey et al., 2018; Green et al., 2011). In Antarctica, given the severe constraints on biological growth, a valid baseline must span decades rather than years or seasons. To our knowledge, only three such “long-term” monitoring sites 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 East Antarctica at Cape Hallett (Brabyn et al., 2006), which is also the only one on the Antarctic continent.

Cape Hallett (72°19'S, 170°16'E), located in Northern Victoria Land (Figures 1a and 1b), has one of the most diverse ecological communities in continental Antarctica (Green et al., 2015; Lyver et al., 2011; Sinclair et al., 2006). During a United States Antarctic Research field campaign in the austral summer of 1961/62, E. D. Rudolph (Ohio State University) visited Cape Hallett and set up a monitoring plot measuring 120 by 28 m (commonly known as Rudolph's Plot or Rudy's Plot) east of Willet Cove (Figure 1b). Rudolph comprehensively described its vegetation composition and coverage and generated the first dasytetric map of Antarctic vegetation (Rudolph, 1963), initiating the longest-running spatially explicit monitoring of Antarctic biota. The presence of Rudolph's Plot supports ongoing specially protected status for the area as part of the Antarctic Specially Protected Area (ASPA) No. 106, first created in 1966 as SPA No. 7. With Rudolph's original plot markers still in place, Rudolph's Plot is recognised as a restricted zone within the ASPA and supports fine-scale studies of spatially dependent biological processes.

Rudolph's Plot was resurveyed in 2004 as part of the Latitudinal Gradient Project using ground-based surveying, digital photography, and processing in GIS software (Brabyn et al., 2006). A rasterised vegetation map of the plot with predetermined 1-m² grid cells was created. For each cell, the percentage cover of algae, mosses, and lichens

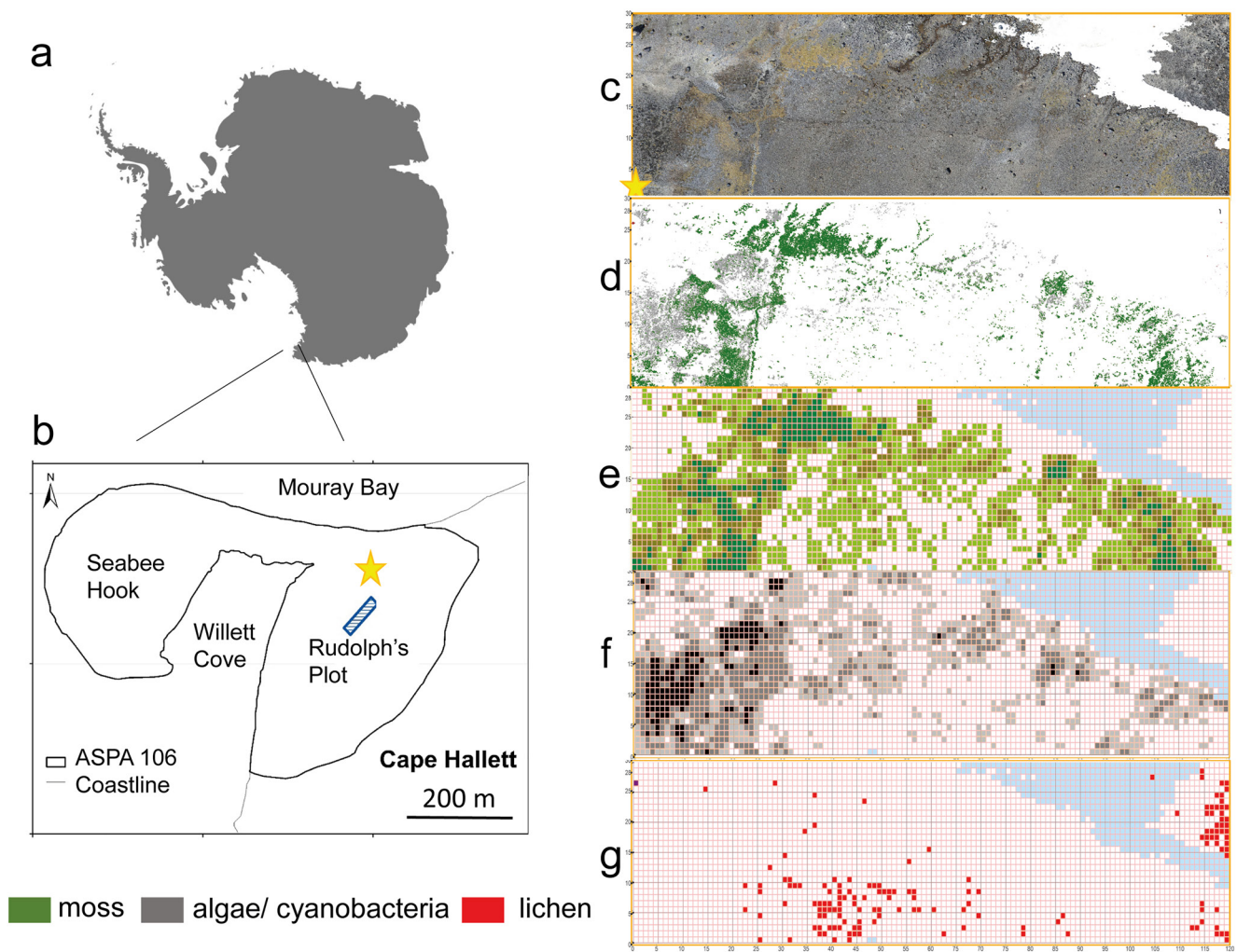


Figure 1. Survey of Rudolph's plot in 2018. (a) Cape Hallett is located along the Ross sea coastline of Northern Victoria Land in East Antarctica. (b) In 1961, E. D Rudolph established a plot for vegetation monitoring (blue quadrat) on the plain west of Willett cove, with the northwest corner ($170^{\circ}14'2.56''\text{E}$, $72^{\circ}19'11.5''\text{S}$) as the origin (star symbol). (c) In 2018, this plot was revisited, and an orthomosaic RGB image was generated. (d) A continuous map of the local vegetation indicating moss (green), eukaryotic algae/cyanobacterial (gray), and lichen (red) cover. The RGB image was georeferenced and trimmed across a 1-m² grid, and the percentage cover of each vegetation functional group (moss [e], eukaryotic algae/cyanobacteria [f], and lichen [g]) in each grid cell was calculated individually and categorized as one of four cover classes (Heavy [$>40\%$, dark color], Patchy [$10\%–40\%$, intermediate color], Scattered [less than 10% , bright color], and None [0% , white]).

were categorised following Rudolph's original scheme: Heavy ($>40\%$), Patchy ($10\%–40\%$), Scattered (less than 10%), and None (0%). The locations of the cells and control points were established relative to the plot origin (the northwestern corner) and cross-referenced with GPS coordinates. Rudolph's original map was digitised and converted to metric units using GIS software (Brabyn et al., 2006), allowing a rigorous comparison with the 2004 resurvey data. In summary, the 2004 resurvey utilised (for the time) state-of-the-art geospatial techniques and methodologies as well as automation within GIS software and built a robust foundation for future resurveys.

In this study, we conducted the third documented survey of Rudolph's Plot in 2018 using a combination of near-ground remote sensing (i.e., high-resolution RGB imagery from a remotely piloted aircraft system RPAS) and ground-based methodologies designed to enable and validate comparability with previous survey results. By harmonising methodologies across the three surveys of Rudolph's Plot and characterising its variability, we aim to answer an overarching question: can Rudolph's Plot (and potentially the wider Cape Hallett ASPA 106) serve as a useful biological sentinel capable of reflecting long-term environmental change in East Antarctica?

2. Materials and Methods

2.1. Study Site

Cape Hallett (Figure 1, 72°19′11″S, 170°13′25″E), located at the Ross Sea coast, Northern Victoria Land (Figure 1a) was visited in November 2018. Cape Hallett has one of the most diverse ecological communities in Antarctica, including 46 species of lichen, nine species of moss (Green et al., 2015), various invertebrate communities (e.g., Acari and Collembola) (Sinclair et al., 2006), and one of the largest Adélie penguin (*Pygoscelis adeliae*) colonies in the region (Lyver et al., 2011). Cape Hallett is a low-lying gravel spit of beach deposits built up by coastal currents carrying basalt material from nearby cliffs (Hofstee, Balks, et al., 2006). During summer (November–February), meltwater forms a shallow, unconfined aquifer, perched on impermeable ice cemented soil (Hofstee, Campbell, et al., 2006). Rudolph's Plot is situated on the plain, with the northwest corner (170°14′2.56″E, 72°19′11.5″S) as the origin. The southeast corner is located at 170°13′57.54″E, 72°19′14.0″S, the southwest corner at 170°13′55.52″E, 72°19′13.7″S and northeast corner at 170°14′24.36″E 72°19′11.42″S. The plot is slightly elevated in the southeast corner. Vegetation in Rudolph's plot was mainly composed of *Bryum argenteum* var. *muticum* Brid. (previously reported as *Bryum subrotundifolium*), *Prasiola crispa* (Lightfoot) Kützing, *Nostoc commune* Vaucher ex Bornet & Flahault, *Caloplaca saxicola* (Hoffm.) Nordin, and *Candelaria flava* (C.W. Dodge & Baker) Castello & Nimis.

The presence of these species in Rudolph's Plot was verified based on microscopic analysis and appropriate identification keys (Øvstedal & Smith, 2001 for lichens and Ochyra et al. (2008) for mosses).

2.2. Image Acquisition and Processing

Aerial images were obtained using a DJI Matrice 600 Pro hex-rotor RPAS equipped with a Canon EOS 5Ds camera (image size: 8,688 × 5,792 pixels, focal length: 50 mm, pixel size: 4.14 μm) on 28 November 2018 (Pan et al., 2022). The flight altitude was 30 m above ground level, and a total of 10 ground-control points were included to provide accurate geo-referencing. An orthomosaic photo and accompanying digital elevation model was generated with the acquired aerial images using Agisoft PhotoScan (now known as Metashape by Agisoft LLC, <https://www.agisoft.com/>).

Segmentation and object-based image analysis was performed in eCognition (Trimble, California, USA) for two conjoint processes: image segmentation and object classification. For image segmentation, optimal parameters (i.e., scale, shape, and compactness) for multi-scale segmentation were determined through trial and error. For object classification, a Random Forest (RF) model with threshold filtering was trained and validated to create a multi-surface map of the vegetation in Rudolph's Plot. Training datasets were created for classifying non-vegetated or barren surfaces into four types (i.e., large dark boulders, surface with smaller pebbles and rocks, wet areas, and shadowed areas), and 50 polygons were identified for each type (200 in total for non-vegetated areas). Vegetated surfaces were classified into five types: moss, lichen, desiccated algae (black color), cyanobacteria (dark green-blue color), and green algae (green color), with 50 training polygons for moss, desiccated algae, and cyanobacteria and 20 training polygons for lichen and green algae due to their sparsity within Rudolph's Plot. Threshold filtering based on optical, textural, and geometric features was used to train the RF model to distinguish the nine (four non-vegetated and five vegetated) surface types. The RF model was iteratively improved by screening for objects that met specified spectral characteristics for each object type, manually identifying and removing misclassified objects, and adjusting the training parameters and thresholds for maximal classification performance. Classifications produced by the final RF model were processed to merge all non-vegetated surface types into one non-vegetated group. The moss and lichen surface types correspond to moss and lichen functional groups, and desiccated algae, cyanobacteria, and green algae surface types were merged into one that corresponds to the algae/cyanobacteria functional group to match the grouping and classification of vegetation from previous surveys.

For each group, a hit rate (the proportion of positives that are correctly identified) was calculated, and the overall accuracy (percentage of correctly labeled pixels) was also calculated. The kappa coefficient (quantitative measure of reliability for producer [RF] and user [actual] agreement to classify the same polygon, corrected for agreement by chance) was generated. The resulting multi-surface map of Rudolph's Plot was color-coded to highlight the

three vegetation functional groups and used to locate and calculate the percentage cover of each functional group individually.

2.3. Establishing Survey Comparability

To enable comparisons with the 1961 and 2004 survey results, the Lambert Conformal Conic projection from the 2004 survey was used to precisely georeference and trim the RGB image across a 1-m² grid. This approach was found useful because Rudolph's original map was already converted into this format with a spatial error of only 10 cm by Brabyn et al. (2006) and the detailed GIS shapefile, plot coordinates and grid descriptors of both the 2004 and (converted) 1961 survey were assessable. For the 2018 survey, each 1-m² grid cell in Rudolph's plot was characterized by surface type and vegetation (Pan et al., 2022). Matching the description of Brabyn et al. (2006) the physical characteristics of the surface and substrate type were identified as follows:

1. Cobble, gravel and sand (CGS) with slope less than five degrees;
2. Packed angular cobble mixed with gravel, sand (PCGS) organic matter, and scattered large boulders. The slope of this rock type surface was less than five degrees;
3. Small loose angular cobble and gravel, associated with a former penguin colony mound with a slope of 15°;
4. Large loose angular cobble (LLAC) with patchy organic skua debris and at the base of a scree slope of 22°.

To describe the vegetation in each grid cell, the classification results of the eCognition vectors were intersected and merged with the grid to obtain the area covered by vegetation. For each grid cell moss, lichen, or algae/cyanobacteria cover was extracted as one of the four cover classes (Figures 1e–1g): Heavy (>40%), Patchy (10%–40%), Scattered (less than 10%), and None (0%) as originally classified by Rudolph and also used by Brabyn et al. (2006).

To test the overall accuracy of cover classifications and ensure consistency with 2004 survey methodologies, a ground truthing approach was performed. Photographs were taken of individual cells along eight transects, running west to east across the plot at 0.5, 1.5, 15.5, 16.5, 28.5, 29.5, 116.5 and 117.5 m distance from the NW corner. Each grid cell could be identified individually with an x/y coordinate in the center and was surrounded by a rectangular frame parallel to the outer edge of the plot. A total of 174 photographs were taken and archived with Antarctica New Zealand. For each photographed grid cell, the presence of each functional group of vegetation and their cover class was assessed visually. This data set was used to evaluate the performance of the RF algorithm and eCognition cover class estimation in a confusion/error matrix for each functional group and cover class. Each row of the matrix represents the instances in the predicted class, while each column represents the instances in the actual, visually assessed class. For each cover class and functional group, the true positive rate, or sensitivity, was calculated to measure the proportion of positives that were correctly identified.

2.4. Analysis of Change

During their survey in 2004, Brabyn et al. (2006) also took photographs of 120 individual 1-m² grid cells in Rudolph's plot. These photographed cells were found during the survey in 2018 and re-photographed. Visual comparisons were made to interpret substrate stability, changes in vegetation cover and overall vegetation dynamics.

To study the change in community composition and cover over time, sample similarity scores were established for each of the 3,458 individual grid-cells in the plot. Because of the categorical nature of the vegetation cover class data and the comparisons between three individual surveys, a non-parametric test for paired nominal data (i.e., McNemar test) was used. This test describes the change in proportion for paired data and is used to analyze retrospective case-control studies. The McNemar test was performed in SPSS (IBM, version 24) to pairwise compare moss, eukaryotic algae/cyanobacteria, and lichen cover between the 1961, 2004, and 2018 datasets, independent from surface type and surface type specific (3 survey years × 3 functional groups of vegetation × 5 surface types = a total of 45 individual pairings). Some pairings could not be tested because some functional vegetation groups did not exist on certain surface types (e.g., moss on LLAC surfaces), or because the sample size was too low (Table S1 in Supporting Information S1). Total sample size for each test varied because only grid-cells that were free of snow were compared. If a grid cell was covered with snow in 1 year but not another, it was excluded from the pair-wise comparison. Where the McNemar-test output variables indicated suitable results, the kappa

Table 1
Confusion Matrix Visualizing the Performance of Modeled Vegetation Cover Classification Into Heavy (>40%), Patchy (10%–40%), Scattered (<10%), and None (0%) Cover Classes for Each Vegetation Functional Group (Moss, Eukaryotic Algae/Cyanobacteria, and Lichen)

		Actual cover class				Total	True positive rate
		Heavy	Patchy	Scattered	None		
Moss	Predicted Heavy	23	2	2	2	29	0.79
	Predicted Patchy	1	36	6	4	47	0.77
	Predicted Scattered	6	3	38		47	0.81
	Predicted None			8	43	51	0.84
	Total	30	41	54	49	174	0.80
Algae/ cyanobacteria	Predicted Heavy	14	4	1	1	20	0.70
	Predicted Patchy	8	35	17	7	67	0.52
	Predicted Scattered		3	36	2	41	0.88
	Predicted None	1	4	9	32	46	0.69
	Total	23	46	63	42	174	0.67
Lichen	Predicted Heavy						
	Predicted Patchy						
	Predicted Scattered	1	6	2		9	0.22
	Predicted None	1	13	51	100	165	0.61
	Total	2	19	53	100	174	0.58

Note. True positive identifications are indicated in green, false positives in red, and false negatives in yellow. The true positive rate shows the sensitivity for each class and the rate of correct identifications for each vegetation functional group.

test statistic was extracted as a similarity score for the pairing. To summarize this output, non-metric multidimensional scaling (NMDS) was applied, positioning the original data and their relative similarity distances in a multidimensional space. The NMDS goodness of fit is represented by a stress value and values above 0.2 are considered poor.

To compare the total cover of each functional group of vegetation between surveys, grid cells covered by snow during any of the surveys were excluded, and the overall percentage cover of heavy, patchy, and scattered vegetation was calculated for moss, eukaryotic algae and cyanobacteria, and lichen. A Pearson correlation analysis was carried out in SPSS (IBM, version 24) to compare changes in cover across the three different survey years (Table 2).

The common challenges for resurveying of historical vegetation plots are relocation error and observer bias (Kapfer et al., 2017). For our study, we carefully located boundaries of Rudolph's Plot and harmonized different survey methodologies to minimize relocation errors. Thanks to the high accuracy of Rudolph's original dasymetric map and Brabyn et al.'s (2006) careful digitization of that map into GIS layers, we were able to locate the point of origin as well as grid cell references of Rudolph's Plot. Direct comparisons of individual grid cells photographed in 2004 with corresponding ground-based photographs from 2018 also showed that individual grid cells were relocated with perfect precision (Figure 2). We, therefore, are confident that our data sets contain minimal relocation error. Observer bias typically results from differences in quantitative properties (abundance bias) and in composition (identification bias) among the samples (Scott & Hallam, 2002). By using functional types of vegetation rather than individual species, we reduced the risk for identification bias in the first place, but also our object-based interpretation of the vegetation patterns in Rudolph's Plot achieved very high accuracy levels. Abundance bias, which is not relevant for object-based analysis but a problem for grid-cell-based cover classifications, was assessed using the ground truthing approach as described above and creating a confusion matrix to visualize the performance of modeled vegetation cover classification (Table 1).

Table 2
Changes in Vegetation Cover Across the Different Surveys

	Cover (%)			Significance of change		
	1961	2004	2018	R	Covariance	P
<i>Moss</i>						
Heavy	8.87	13.04	15.23	1.00	90.99	0.05
Patchy	23.27	17.48	19.76	-0.80	-68.00	0.41
Scattered	34.87	47.62	31.13	0.06	15.94	0.96
<i>Algae/cyanobacteria</i>						
Heavy	15.98	39.20	6.85	0.00	1.99	1.00
Patchy	17.87	37.88	49.78	0.99	465.72	0.09
Scattered	21.45	18.99	16.69	-0.97	-66.93	0.17
<i>Lichen</i>						
Heavy	0.11	0.01	NA			
Patchy	4.14	2.55	0.01	-0.92	-55.68	0.26
Scattered	44.46	58.48	6.27	-0.48	-380.17	0.68

Note. Vegetation is grouped in three different functional types (moss, eukaryotic algae/cyanobacteria and lichen), each represented in three different cover classes (Heavy (>40%), Patchy (10%–40%), Scattered (less than 10%)). Percentage cover is compared between the surveys in 1961, 2004, and 2018. Significance of differences were calculated via Pearson correlations.

2.5. Analysis of the Local Weather/Regional Climate

Hourly air temperature and humidity data were available from long-term monitoring stations at Cape Hallett for the period spanning from 2004 to 2017 (2012 data missing). A second, older climate data set was available from when the US/NZ research station was still in place at Cape Hallett. This data set consisted of 3-hourly measurements of air temperature and humidity for the period spanning from 1965 to 1972.

From both datasets, November–February data were extracted, as these describe the conditions over the active growing season for the local vegetation. During the colder and drier winter months, the vegetation is dormant (Colesie et al., 2016; Schroeter et al., 2017), and any change in climate during this period is unlikely to cause any direct effect on the vegetation unless it leads to a seasonality shift (which was not observed in our data set, Figure S1 in Supporting Information S1). Mean \pm SD temperature and relative humidity, maximum, and minimum values across the years were calculated.

The temperature data were analyzed with a mixed effects model (R 4.1.0, R Core Team) because the residuals were not normally distributed with no heteroscedasticity. In the model, temperature was used as a function of year, with month and season as random effects. This set-up was determined to be the best model based on the Akaike Information Criterion (AIC). The relative humidity data were compared with a general linear model.

3. Results

3.1. The State of the Vegetation in 2018 and RF Model Evaluation

A 50.6-megapixel orthomosaic RGB image of Rudolph's Plot was obtained by orthorectifying and blending aerial photographs (Figure 1c), resulting in a spatial resolution of 0.25 cm/pixel. RGB layers were used with equal weight as input files for object-based image analysis. Through trial and error, optimal parameters (i.e., scale, shape, and compactness) for multi-scale segmentation were determined, and 274,648 spatially explicit objects were identified in the orthomosaic image for machine-learning-assisted classification using a RF model (Figure 1d). The RF model most accurately predicted non-vegetated areas with a hit rate of 99.5%, followed by algae/cyanobacteria (96.4%), mosses (94.4%), and lichens (75%). The overall accuracy of the RF model was calculated to be 98%, and the kappa coefficient for the final data set was 0.983.

15.64% of Rudolph's Plot was vegetated in 2018 (556.64 m², Figure 1d). More than half of the total vegetation was moss (305.23 m²), followed by algae/cyanobacteria (207.95 m²) and lichen (0.64 m²). Mosses, eukaryotic algae, and cyanobacteria were mainly found around the northwestern corner of Rudolph's Plot (Figure 1d) on surfaces with less than 5° slope, where the substrate was mainly composed of cobbles, gravel, and sands and along the meltwater runlets of the local snow patch. Lichens were found primarily in the slightly elevated areas along the scree in the southeast corner of Rudolph's Plot and associated with larger angular cobbles (Figure 1g, LLAC, see Section 2).

To enable comparisons with the 1961 and 2004 survey results, the Lambert Conformal Conic projection from the 2004 survey was used to precisely georeference and trim the RGB image across a 1-m² grid, generating a total of 3,458 1-m² grid cells and the percentage cover of each vegetation functional group in each grid cell was calculated individually and categorized as one of four cover classes according to Rudolph's original scheme (see Section 2, Figures 1e–1g). For moss classes, the highest level of confusion in the RF model occurred where heavy cover (>40%) was wrongly predicted as scattered (<10%) in 20% of the cases (Table 1). For eukaryotic algae/cyanobacteria, the most challenging element was the overestimation of patchy covers (10%–40%), with 27% of the scattered grid cells being incorrectly predicted as patchy (Table 1). The RF model performed poorly at predicting lichen cover, leading to severe underestimation of lichen cover in the scattered class Table (1).

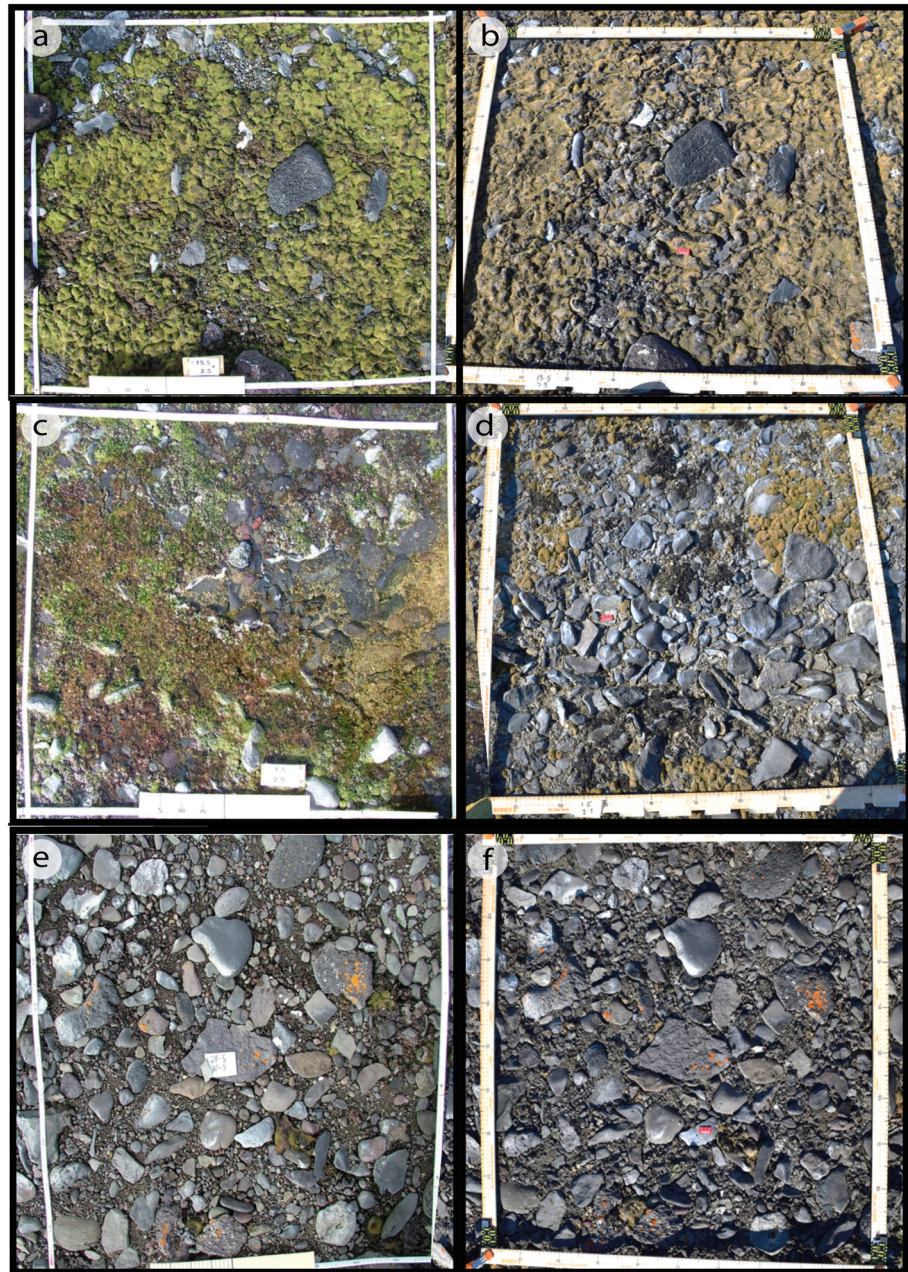


Figure 2. Qualitative comparison of individual, matching 1-m² grid cells in Rudolph's Plot. Photos were taken during the survey in 2004 (left) and 2018 (right) for mosses (a and b), eukaryotic algae and cyanobacteria (c and d), and lichens (e and f).

3.2. How the Vegetation has Changed Since 1961

Direct photographic comparisons of matching grid cells between the 2004 and 2018 surveys showed stable location, position, and cover for mosses (e.g., Figures 2a vs 2b). For eukaryotic algae and cyanobacteria, in 2004 (Figure 2c), thalli covered larger areas than they did in 2018 (Figure 2d). Individual lichen thalli photographed in 2004 were identified in photographs from 2018 with little observable difference (e.g., Figures 2e vs. 2f).

As a general pattern, in all surveys across the years, most vegetation in Rudolph's Plot occurred on the flat areas around the northwestern corner (Figures 3a–3c). When compared on a grid-cell basis, with all three functional types of vegetation and all different cover classes included, there were no intuitively obvious change across the

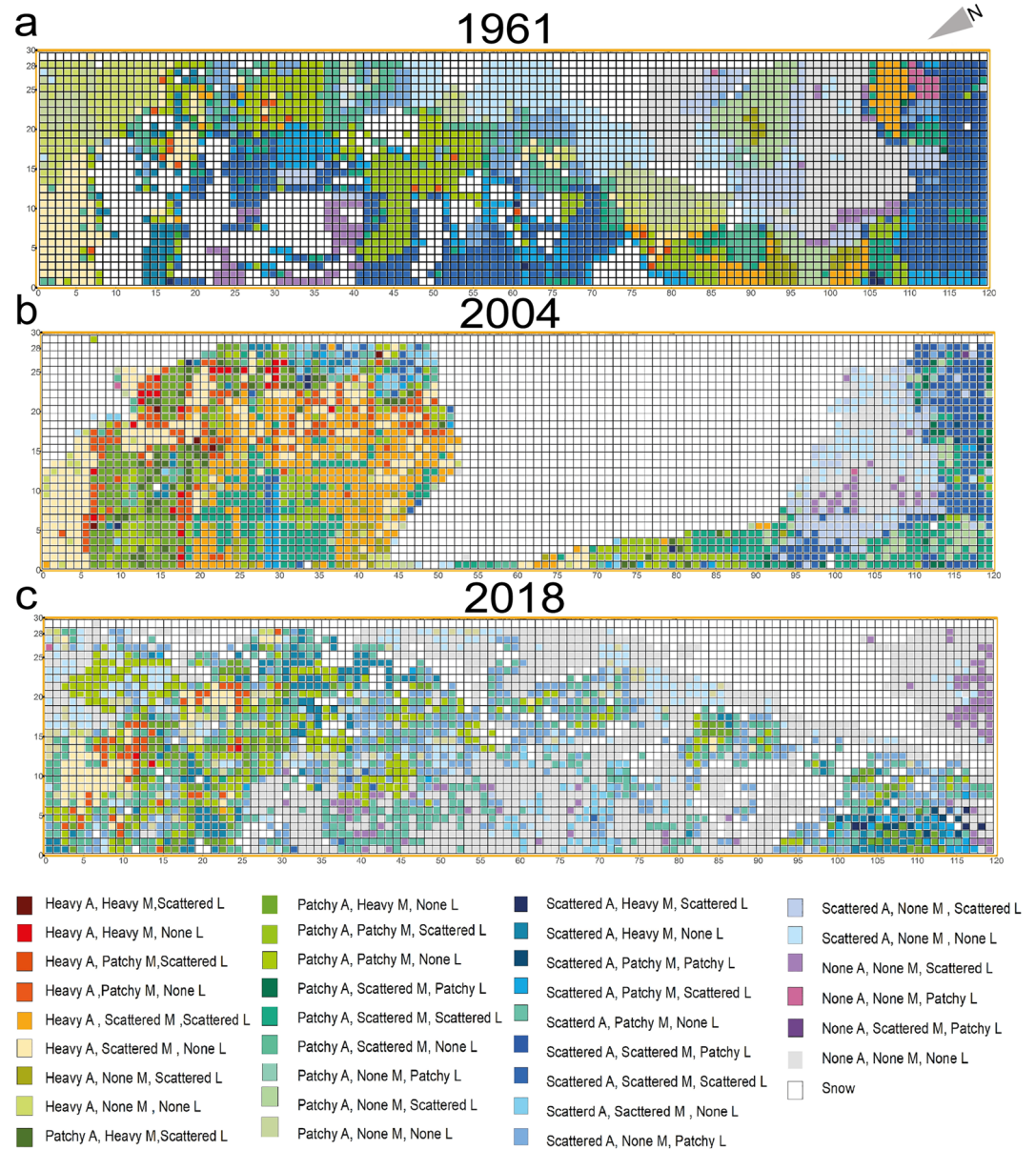


Figure 3. How Rudolph's Plot has changed in the past five decades. Composite grid-cell based maps of the vegetation in Rudolph's Plot in (a) 1961, (b) 2004 and (c) 2018. The coloration of the figure legend is coded for the four different cover classes (Heavy (>40%), Patchy (10%–40%), scattered (less than 10%), and None (0%) and the presence of mosses (M), eukaryotic algae and cyanobacteria (A) and lichens (L).

three surveys. The extent of the snowpack was much larger in 2004 than in 1961 and 2018, and there is a remarkable similarity in snowpack extent and location between the 1961 and 2018 surveys.

Overall, the distribution and cover of the vegetation was most similar between Rudolph's original survey and the survey in 2018 and most dissimilar between the 1961 and 2004 surveys (Figures 4a and 4b). This pattern was independent of the surface substrate type for mosses (Figure 4a), and the same for eukaryotic algae and cyanobacteria (Figure 4b).

The only statistically significant change across all three surveys was an increase in heavy moss cover (Table 2). The Pearson correlation coefficient for this relationship was 1, indicating that the number of heavily moss-covered grid cells doubled over the past 57 years. The increase in grid cells with dense moss cover was primarily on surfaces packed with angular cobbles mixed with gravel, sand, organic matter, and scattered large boulders (PCGS) and

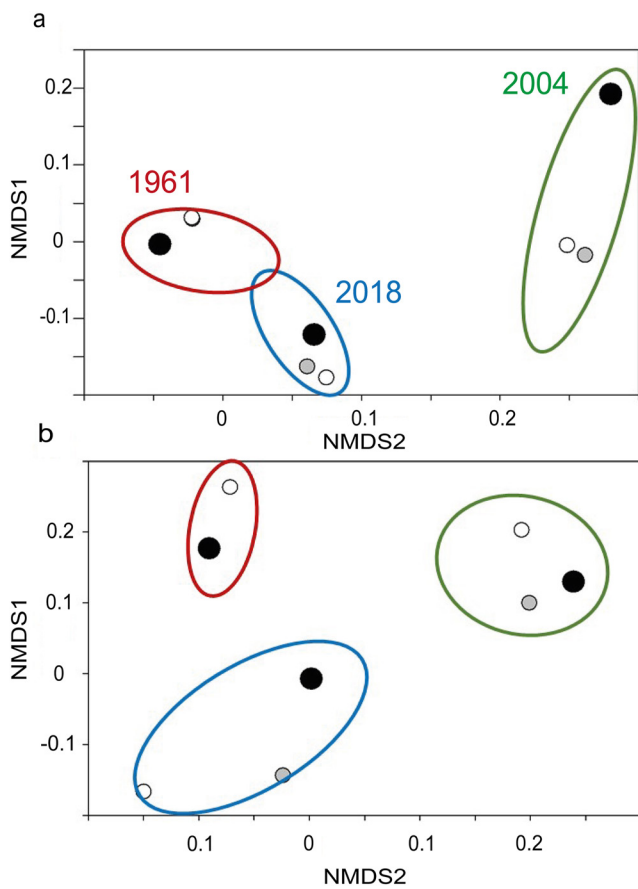


Figure 4. To test similarities between the surveys, McNemar kappa similarity scores were plotted on a non-metric multidimensional scale (NMDS) for (a) mosses and (b) eukaryotic algae/cyanobacteria in Rudolph's Plot. Black dots represent vegetation independent of substrate type, gray dots represent vegetation on cobble, gravel, and sand (CGS) substrates, and white dots represent vegetation on packed angular cobble mixed with gravel, sand (PCGS) substrates.

mostly in the southwest corner of the plot (Figure 5). For all other functional types of vegetation and cover classes, change was insignificant.

3.3. Observed Climate Trends at Cape Hallett Since 1965

There has also been no detectable change in summer air temperature at Cape Hallett since 1965 when instrumented measurements started (Figure 6a). Generally, air temperatures rose from early- or mid-November and reached above freezing by December. However, even during December and January, the air temperature rarely exceeded freezing (Figure S1 in Supporting Information S1). The mean summer (November to February) air temperature from 1965 to 2018 was $-4.83 \pm 1.68^\circ\text{C}$, with a minimum temperature of -27.22°C and a maximum temperature of 5.97°C .

In contrast, relative humidity was generally much more variable than air temperature across typical summer seasons. The mean summer relative humidity was 66.74% (minimum of 3.81% and maximum of 100%), and it appears to have increased significantly since 1965 (Figure 6b, p -value $< 2 \times 10^{-16}$, year coefficient = 0.331, $R^2 = 0.0869$).

4. Discussion

4.1. The Current Ecological Understanding of the Vegetation at Cape Hallett

Liquid water availability is the primary driver of terrestrial biodiversity and processes in Antarctica, in particular in continental Antarctica (Convey et al., 2014; Green et al., 2011). Similar to other terrestrial habitats along the Victoria Land coast (Colesie et al., 2014; Green et al., 2011), water availability also appears to be the limiting factor on vegetation growth patterns and phenology in Rudolph's Plot. The biogeography here is primarily driven by surface water coming from the ice cap at the top of the adjacent scree and, to a lesser extent, from melting snow on the plain and the local snow patch (Figures 1c and 1d). The vegetation is first hydrated by the melting of snow in mid-December (Rudolph, field notes) when, with increasing day length and radiation, the local snow patches start melting. The flows can become substantial as temperatures rise in January (Schroeter et al., 2017) and continue into late February (Green, field notes).

Mosses reactivate their physiological activity in the presence of liquid water (Schlensog et al., 2004), and, due to their growth form in dense cushions and relatively solid attachment to the substrate, they remain active for prolonged periods throughout the season (Schlensog et al., 2013). Antarctic mosses are known to elongate between 1 and 5 mm per year (Selkirk & Skotnicki, 2007), and, in Rudolph's Plot, their growth is detectable across several years (Figure 5). Areas with dense moss cover have doubled since 1961, mainly on PCGS surfaces. These surfaces are flat but elevated above the main outwash area, making them less susceptible to ephemeral flooding. Here, the mosses' denser growth in cushions allows both water storage amongst the shoots and for upward transport of water from the soil; therefore, albeit growing slower, the mosses can outcompete eukaryotic algae and cyanobacterial mats for space. *B. argenteum* var. *muticum* is the dominant moss species at Cape Hallett and in Rudolph's Plot (Green et al., 2015), and this species, in particular, has previously been described as a strong and competitive coloniser (Amesbury et al., 2017; Green et al., 2015; Raudenbush et al., 2018; Schwarz et al., 1992; Seppelt et al., 2010). Large changes in water-flow channels are known to follow extremely high flow rates in the Dry Valleys (Nielsen et al., 2012). A typical pattern of vegetation change in the Ross Sea region (particularly evident in the McMurdo Dry Valleys) is driven by changes in surface water flow coupled with low precipitation and very arid air. Occasionally, a high level of melt leads to surface water flow over larger-than-normal areas. Whilst this encourages moss growth during the high-flow years, the expanded moss colonies subsequently experience a severe lack of moisture during normal low-flow years. During typical dry summer months, evaporation

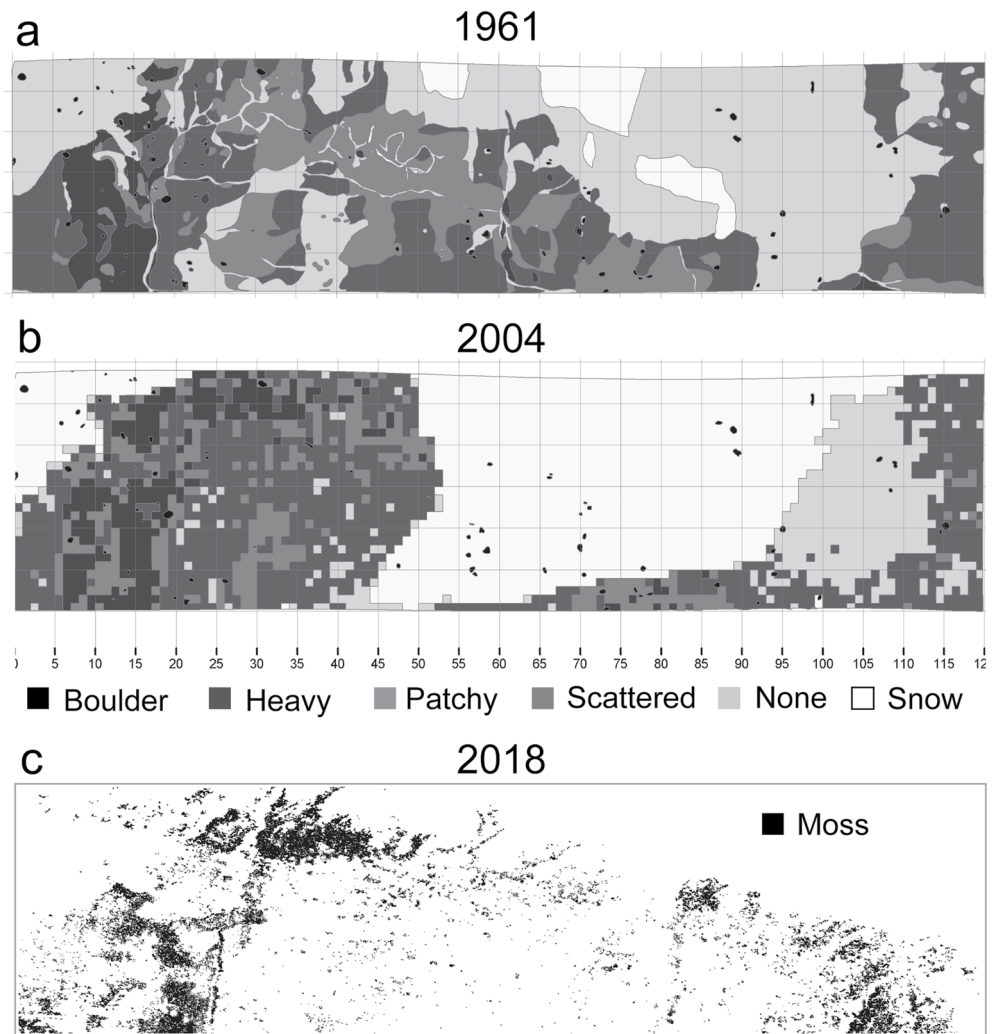


Figure 5. Changes in moss cover and survey resolution in Rudolph's Plot. (a) The original dasymetric map as hand drawn by Rudolph in 1961, distinguishing 5 different color-coded cover classes for mosses. (b) The grid-cell based map as developed by Brabyn et al. (2006), also distinguishing between five different color-coded cover classes for mosses. (c) The Random Forest (RF) model-based map of mosses in Rudolph's Plot, showing continuous cover throughout the plot.

of surface moisture leads to salination of top soils by salts carried from deeper soils. This natural phenomenon leads to the formation of moribund mosses which are typically yellow and unhealthy in colour.

Unlike the mosses' continuous growth, eukaryotic algae and cyanobacterial mats bloom within the short summer season (Barták et al., 2016; Cavicchioli, 2015). Their blooming is associated with a relatively rapid growth rate when rewetted (Møller et al., 2014) by the first meltwater flooding the plain in January. The total duration of the activity might then be as short as a few hours (Hawes et al., 1992) before water evaporates and the colony once again becomes an inactive crust, manifested in changes in pigmentation intensity and visibility (McKnight et al., 1999, Figures 2c and 2d). The dry thalli are exposed to significant ecological losses by senescence, wind export, and burial in the soil (Møller et al., 2014).

The lichens in Rudolph's Plot are mainly uncoupled from these ephemeral processes. Their habitat is elevated from the surface on larger rocks and boulders, and they are more likely to be reactivated by direct snowfall or fog (Colesie et al., 2016). Given the scarcity of these events, lichen activity periods are short, and the growth rates are among the slowest described on the planet (Sancho et al., 2007).

To capture and reflect the baseline for natural variability at Rudolph's Plot, the results from our analysis on the three distinct vegetation types must be interpreted collectively. Based on their high levels of physiological

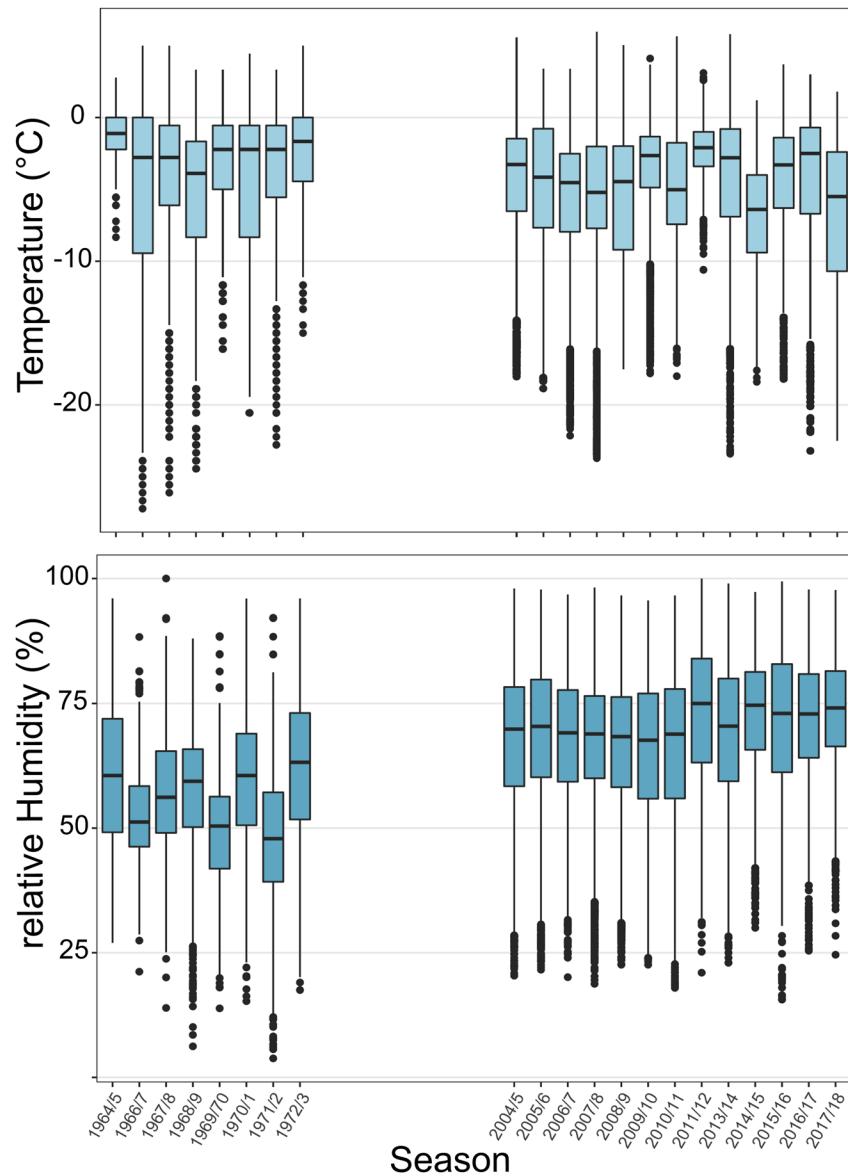


Figure 6. Regional summer climate at Cape Hallett since 1964. Seasonal (November–February) data for (a) temperature and (b) relative humidity are shown as box-whisker plots. Based on the Akaike Information Criterion (AIC), a general mixed model showed that there were no significant interannual changes in air temperature since 1965 (year coefficient = -0.026 , standard error = 0.0106 , marginal $R^2 = 0.00287$), and the null model without year as a fixed effect was marginally significant (p -value = 0.0538).

plasticity (Pannowitz et al., 2005), mosses allow for valuable insights into relevant environmental drivers, such as water availability across several years. Eukaryotic algae and cyanobacterial mats are ideal predictors for seasonal variations and indicate the current state of snowmelt (ephemeral flooding) during a specific surveying period. Lichens as the slowest growing organisms add value to the understanding of the ecological complexity by inhabiting another niche and act as habitat stress indicators (Colesie, Green, Haferkamp, & Buedel, 2014).

4.2. Insights From and Comparisons With Historic Surveys

The findings from previous surveys of Rudolph's Plot corroborate the descriptions of vegetation dynamics and phenology above. In his diary, Rudolph noted that his vegetation survey and mapping were conducted in November 1961 and that he was interrupted by heavy winds and cold weather, forcing him to wait inside the Hallett

Station for several days in between surveying. Brabyn's survey, in contrast, was completed near the end of austral summer in January 2004, and it was noted in the resulting publication that the overall vegetation cover on the plot was more extensive, mainly because of an increase in algal cover (Brabyn et al., 2006). Our survey in 2018 was similar to Rudolph's 1961 effort in that both surveys were conducted in late November, and the findings from 2018 were indeed more similar to those from 1961 than to those from 2004 (Figures 3a and 3c). In January 2004, a large area of Rudolph's Plot was covered in snow (Figure 3b), and much of the plain was flooded by melt-water (Figures 2a, 2c, and 2e). In November of 1961 and 2018, the extent of the local snowpack was relatively constrained, and the vegetation in the plot was mostly desiccated (Figures 2b, 2d, and 2f). Consequently, it is reasonable to interpret the most likely factor separating the different surveys along the NMDS2 axis (Figures 4a and 4b) as seasonality and water availability.

4.3. A Baseline for Natural Variability and Rate of Change in East Antarctica?

Assuming that the datasets described in this study so far constitute an understanding of the ecology and natural variability of the local vegetation, an obvious question is whether the assemblage of vegetation can act as a biological sentinel of future change. We argue that Rudolph's Plot (and more broadly the Cape Hallett ASPA 106) have four features that conform with good-practice guidelines for long-term biodiversity-inclusive impact assessment (Gullison et al., 2015).

The first argument for a robust baseline is knowledge of climatic background trends. We have established the absence of regional warming at Cape Hallett and found a remarkably stable climate since 1965 (Figure 6). This finding is in line with several other studies that have described that regional warming is non-existent in continental Antarctica until now (Convey et al., 2009; Doran et al., 2002; Turner et al., 2014, 2020). Consequently, we can argue that any variation in vegetation composition and cover that we report here can be seen as a result of natural dynamics rather than climatically forced change and that the natural variability and rate of change that we present can act as a useful baseline. We also acknowledge that the vegetation at Cape Hallett can act as an integrator of local microclimatic variables other than temperature, such as transient surface moisture, which are difficult to measure using automatic weather stations.

The second criterion for a robust baseline is the presence of representable biotic attributes and composition to enable the extrapolation of observed trends. The ASPA No. 106, Cape Hallett, is already recognised as one of the most diverse sites in continental Antarctica, including representative vegetation, invertebrates, and birds. The species we found in Rudolph's Plot are described to have wide distribution ranges across continental Antarctica (Colesie et al., 2014) and beyond (Cavacini, 2001; Zaccara et al., 2020). Therefore, quantitative measures of abundance, distribution, and other measures of viability and/or function, on these species could be used to support impact assessment for other terrestrial habitats across Antarctica. An important argument in this context is also the spatial representativeness of Cape Hallett. Not only is the site close to the coast, which makes it representative of most perpetually ice-free sites on the continent, it also lies north of most other ASPAs and other sites of interest along the Ross Sea coastline. Meredith et al. (2019) describe future warming across the continent will start in the north, accelerated by warmer ocean currents, very similar to what is currently observed along the Antarctic Peninsula (Convey, 2006), placing Cape Hallett right at the frontline of any potential change in the future.

The third important feature of a robust baseline is the logistic feasibility for repeated surveys. Cape Hallett's past reflects continuous research interest. Currently, the site is a hub for continuous monitoring of the local penguin colonies from multiple national Antarctic programmes (United States, New Zealand, Republic of Korea) representing an ideal vantage point for more continuous, more frequent surveys. The Antarctic Near-shore and Terrestrial Observation System (ANTOS) Expert Group of the Scientific Committee on Antarctic Research has identified Cape Hallett as a promising site for a future ANTOS installation to enable consistent and systematic monitoring of terrestrial biota and biologically relevant environmental attributes. Our study further highlights the value and suitability of ASPA No. 106, Cape Hallett as a potential ANTOS site. Our new standardised methodology and the use of near-ground remote sensing techniques drastically reduced the logistical requirements and physical impact to the survey area while allowing highly reproducible data collection. This framework is highly flexible and thus enables data harmonization with previous survey results while simultaneously providing baseline information whose resolution is not constrained by arbitrary delineations of spatial resolution and cover class designations.

Finally, for a site to serve as a biological sentinel, the survey frequency must reflect the overall biological responsiveness of the ecosystem. Until now, the lack of robust long-term monitoring has limited our understanding of the biological responsiveness of Antarctic terrestrial ecosystems, where a valid baseline must span decades rather than years or seasons. While a few such studies exist for some locations in maritime Antarctica (Cannone et al., 2016, 2017, 2022; Fowbert & Smith, 1994; Parnikoza et al., 2009), the baseline variability for Cape Hallett as the only long-term monitoring site in East Antarctica had not been characterized until this study; our findings therefore provide a foundation for establishing Rudolph's Plot as the first comprehensive biological sentinel site on the Antarctic continent. We note that, although long-term monitoring has long been recognised as fundamental for understanding the ecology and functioning of Antarctica's terrestrial systems (Bentley et al., 2021), appropriate research funding and logistical support is still scarce, resulting in only sporadic and opportunistic resurveying campaigns in the past.

In summary, the wealth of historic climate and biology data, and trajectories of regional climate change projections collectively make a convincing and evidence-based case that Rudolph's Plot (and possibly the entire Cape Hallett ASPA) can serve as an accessible, useful, scientifically robust, and unique biological sentinel for subtle and episodic changes beyond natural variability for East Antarctica.

4.4. What Are the Implications for Future Vegetation Dynamics

The strong relationship between the local water regime and vegetation dynamics has been shown for ecosystem functioning in East Antarctica before (Cannone et al., 2021; Convey et al., 2014; Robinson et al., 2018). However, our study represents the first spatially explicit long-term study to describe these effects as a natural phenomenon rather than being related to climate change. Therefore, our study represents a unique and potentially last opportunity to establish an ecologically meaningful biological sentinel site at a time when the region is projected to experience greater-than-global warming in the 21st century (Meredith et al., 2019).

For Cape Hallett, having understood that the vegetation feeds directly from the melting dynamics of the local snowpack, we can reasonably argue that if that snowpack disappears and cannot be replenished during the winter, the stable vegetation dynamics as described here can quickly be put at peril (Convey, 2006; Convey & Peck, 2019; Convey & Smith, 2005). This will have wider implications for ecosystem functioning and resilience, especially with the direct relationships between the vegetation and their diverse and dependent invertebrate fauna (Raymond et al., 2013; Sinclair et al., 2006).

Another potential scenario for Cape Hallett includes the recolonization of large penguin colonies from locations north, such as Cape Adare, driven by rising sea levels (Cimino et al., 2016). Higher nutrient inputs from marine vertebrates will most likely cause significant change for the local vegetation (Crittenden et al., 2015) and invertebrates (Bokhorst & Convey, 2016; Bokhorst et al., 2019).

The establishment of Cape Hallett as a biological sentinel of change in continental Antarctica also has implications for future environmental management. Our synthesis of site-specific information indicates that conservation approaches have been reliable, and we cannot report any immediate impact from human intervention at the site. The success of the applied site management measures allows for comparisons with other approaches and can be used to test the relative effectiveness of the wider biodiversity conservation approaches in Antarctica's terrestrial realm.

4.5. Technological Advances for Future Surveys

In addition to providing a robust baseline for detecting future change, our study also represents a technological step-change for future vegetation monitoring at Rudolph's Plot (Figure 5). The use of near-ground remote sensing techniques drastically reduced the logistical requirements and physical impact to the survey area while allowing highly reproducible data collection that will benefit from ongoing improvements in digital photography. The ease with which orthomosaic photographs can be obtained for Rudolph's Plot also means that multiple surveys can be conducted within an austral summer to capture intra-annual variations and changes following unusual warming events.

Our study also established a framework for quantitatively analyzing survey results using object-based image analysis and demonstrated the usefulness of machine learning in reducing the resource requirements for data

analysis. Importantly, our framework captured all major vegetated and non-vegetated surface types in Rudolph's Plot, which will allow us to better understand the relationship between vegetation growth and physical attributes of the underlying substrates. This framework is highly flexible and thus enables data harmonization with previous survey results while simultaneously providing baseline information whose resolution is not constrained by arbitrary delineations of spatial resolution and cover class designations.

4.6. The Next Step

Although warming trends have been most notable in parts of West Antarctica and the Antarctic Peninsula, East Antarctica is projected to experience greater-than-average warming by the end of this century (Meredith et al., 2019). However, there is a widely acknowledged lack of observation and poor understanding of natural variability for East Antarctica, resulting in low confidence in trend estimates (Ranasinghe et al., 2021). We present evidence that work at Rudolph's Plot since the 1960s has yielded unique insight to the baseline variability and rate of change, and we created and validated a framework that will enable rapid yet quantitative re-surveys of Rudolph's Plot. However, our study shows that the vegetation in Antarctica is driven by the local water regime and availability. Therefore, in the future, detailed modeling of surface melt generation should be coupled with climate change projections in order to evaluate the risks. This model could be applicable to other, similar sites around the continent as well.

A second step to improve our understanding of the vegetation dynamics has to be the improvement of taxa specific detection. Lichens were very difficult to detect with the methodologies used in our survey. This was most likely caused by the low spectral reflectance described for lichens in dry habitats in particular (Barták et al., 2018). However, accuracy might be improved in the future with the use of matched filtering techniques for the detection of lichens (Casanovas et al., 2015), ultra-high resolution multi-sensor observations (Lucieir et al., 2012), or hyperspectral image analysis (Jawak et al., 2019; Levy et al., 2020).

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5. Conclusions

This study provides a coherent and statistically robust comparison of historic survey results and represents the longest record of spatially explicit vegetation monitoring in Antarctica. The surveys together provide a vivid picture of the local vegetation assemblage composed of mosses, eukaryotic algae, cyanobacterial mats, and lichens. This vegetation has remained stable with little to no change in cover and distribution over at least the past five decades. The only significant change was an increase in dense (>40%) moss cover, which has doubled since 1961. In the absence of documented regional climate change trends, our findings can be interpreted as a reflection of the natural variability and rate of change for the vegetation at Cape Hallett and allow us to propose this site as a sentinel of future environmental change in East Antarctica.

Data Availability Statement

Images and data are publicly available via the Edinburgh Data Share Information Service here: <https://doi.org/10.7488/ds/3417>. The code utilised for this research is provided via Zenodo here: <https://zenodo.org/badge/latestdoi/373148737>. Supporting Information S1 data tables and figures are also available here: <https://doi.org/10.7488/ds/3476>.

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