Report

Current Biology

Widespread Biological Response to Rapid Warming on the Antarctic Peninsula

Highlights

- First Peninsula-wide assessment of biological sensitivity to recent warming
- Analyze moss bank plant and microbial proxy data over 150 years and 600-km gradient
- Fundamental and widespread changes in terrestrial biosphere in response to warming
- Terrestrial ecosystems likely to alter rapidly under future warming scenarios

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In Brief

Amesbury et al. use plant and microbial material preserved in moss banks to demonstrate fundamental and widespread changes in the terrestrial biosphere of the Antarctic Peninsula in response to recent climate change. Moss growth sensitivity to climate suggests that the terrestrial biosphere and landscape will alter rapidly under future warming.

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Current Biology
Report

Widespread Biological Response to Rapid Warming on the Antarctic Peninsula

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SUMMARY

Recent climate change on the Antarctic Peninsula is well documented [1–5], with warming, alongside increases in precipitation, wind strength, and melt season length [1, 6, 7], driving environmental change [8, 9]. However, meteorological records mostly began in the 1950s, and paleoenvironmental datasets that provide a longer-term context to recent climate change are limited in number and often from single sites [7] and/or discontinuous in time [10, 11]. Here we use moss bank cores from a 600-km transect from Green Island (65.3°S) to Elephant Island (61.1°S) as paleoclimate archives sensitive to regional temperature change, moderated by water availability and surface microclimate [12, 13]. Mosses grow slowly, but cold temperatures minimize decomposition, facilitating multiproxy analysis of preserved peat [14]. Carbon isotope discrimination ($\Delta^{13}C$) in cellulose indicates the favorability of conditions for photosynthesis [15]. Testate amoebae are representative heterotrophs in peatlands [16–18], so their populations are an indicator of microbial productivity [14]. Moss growth and mass accumulation rates represent the balance between growth and decomposition [19]. Analyzing these proxies in five cores at three sites over 150 years reveals increased biological activity over the past ca. 50 years, in response to climate change. We identified significant changepoints in all sites and proxies, suggesting fundamental and widespread changes in the terrestrial biosphere. The regional sensitivity of moss growth to past temperature rises suggests that terrestrial ecosystems will alter rapidly under future warming, leading to major changes in the biology and landscape of this iconic region—an Antarctic greening to parallel well-established observations in the Arctic [20].

RESULTS

Moss Banks Are Regional Paleoclimate Archives

Moss banks are distributed sporadically along the western Antarctic Peninsula (AP) [21] from Alexander Island (69.4°S) [14] to Elephant Island (61.1°S) (Figure 1; Table S1) and northeast to Signy Island, South Orkney Islands (60.7°S) [15]. Mosses accumulate in small annual increments from new growth at the surface, and old moss growth is exceptionally well preserved [25] by year-round cold temperatures and relatively rapid incorporation into permafrost, leading to deep accumulations of moss over thousands of years. AP moss banks are often dominated by a single species (*Polytrichum strictum* or *Chorisodontium aciphyllum*) and are easily dated by radiocarbon due to their highly organic nature [13]. Relatively stable down-core bulk density and peat humification profiles (Figure S4; see also [14]) show that compaction or decomposition effects are not significant. Mass accumulation ($r^2 = 0.82$, $p = 0.013$) and growth rates ($r^2 = 0.75$, $p = 0.026$) are significantly positively related to latitude, but since latitudinal temperature variability over our study area is not significant (Figure 1; [23, 24]), these trends are likely driven by differences in the dominant moss species (Table S1). Therefore, moss bank proxies provide unique insights into the scale and rapidity of biological shifts over decadal to centennial timescales in the past and under future warming.

A Widespread Biological Response

We found significant changes in all proxies (carbon isotope discrimination, microbial productivity, moss bank vertical growth, and mass accumulation) and at all sites, reflecting increased biological activity across the length of the AP over the past ca. 50 years (Figures 2 and 3). The precise timing of these shifts varied, but the prevalent pattern of change indicates a widespread biological response to increasing temperature. We identified significant changepoints (confidence value > 0.98) in 20 of 23 time series (Figure S1), suggesting that all four proxies have undergone fundamental state changes in recent years. An alternative method for changepoint detection produced similar results with a mean difference in ages between the two methods of 13 years (Figure S2). The three $\Delta^{13}C$ time series in which changepoints were not identified (ELE3, ARD1, GRE1) still showed trends of increasing discrimination consistent with other

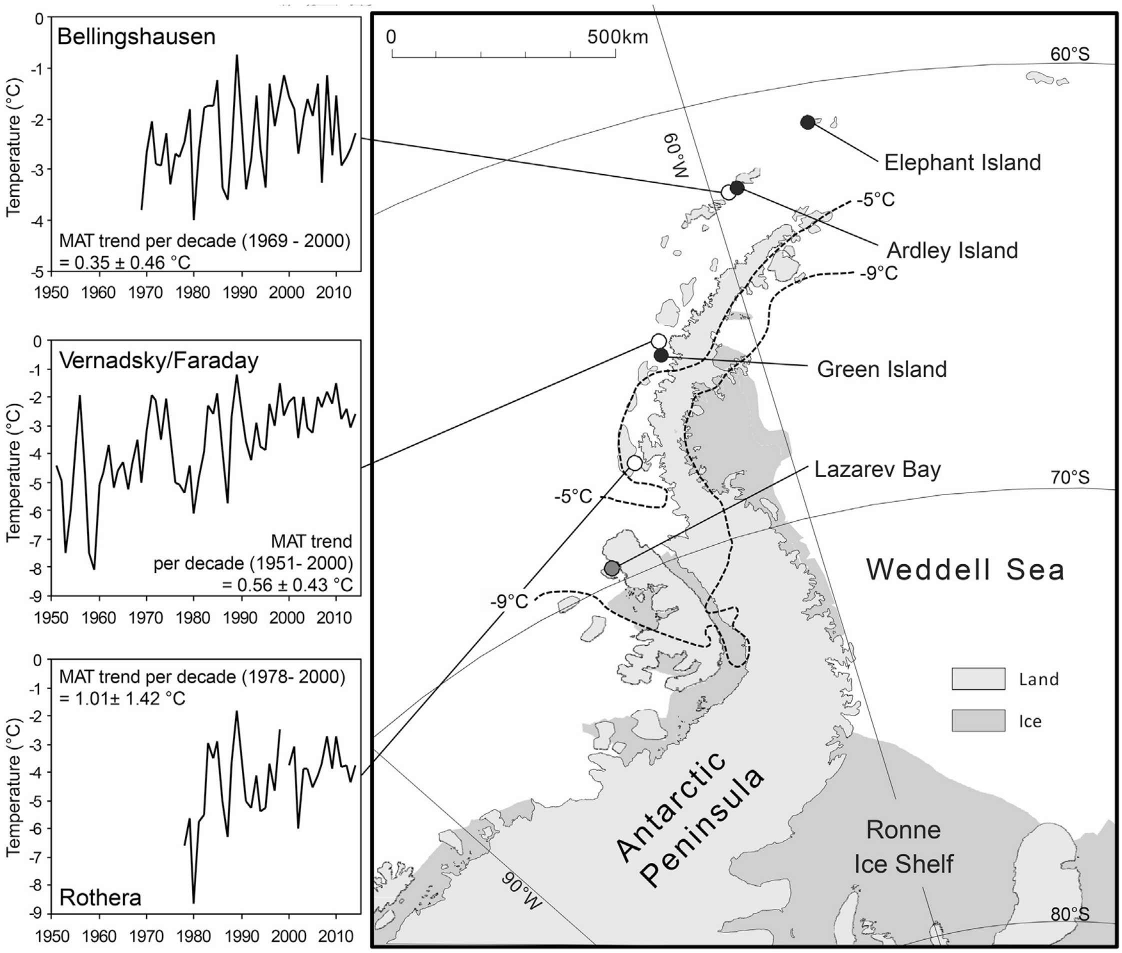


Figure 1. Regional Map of the Antarctic Peninsula Showing Moss Bank Sites and Meteorological Records of Recent Mean Annual Temperature

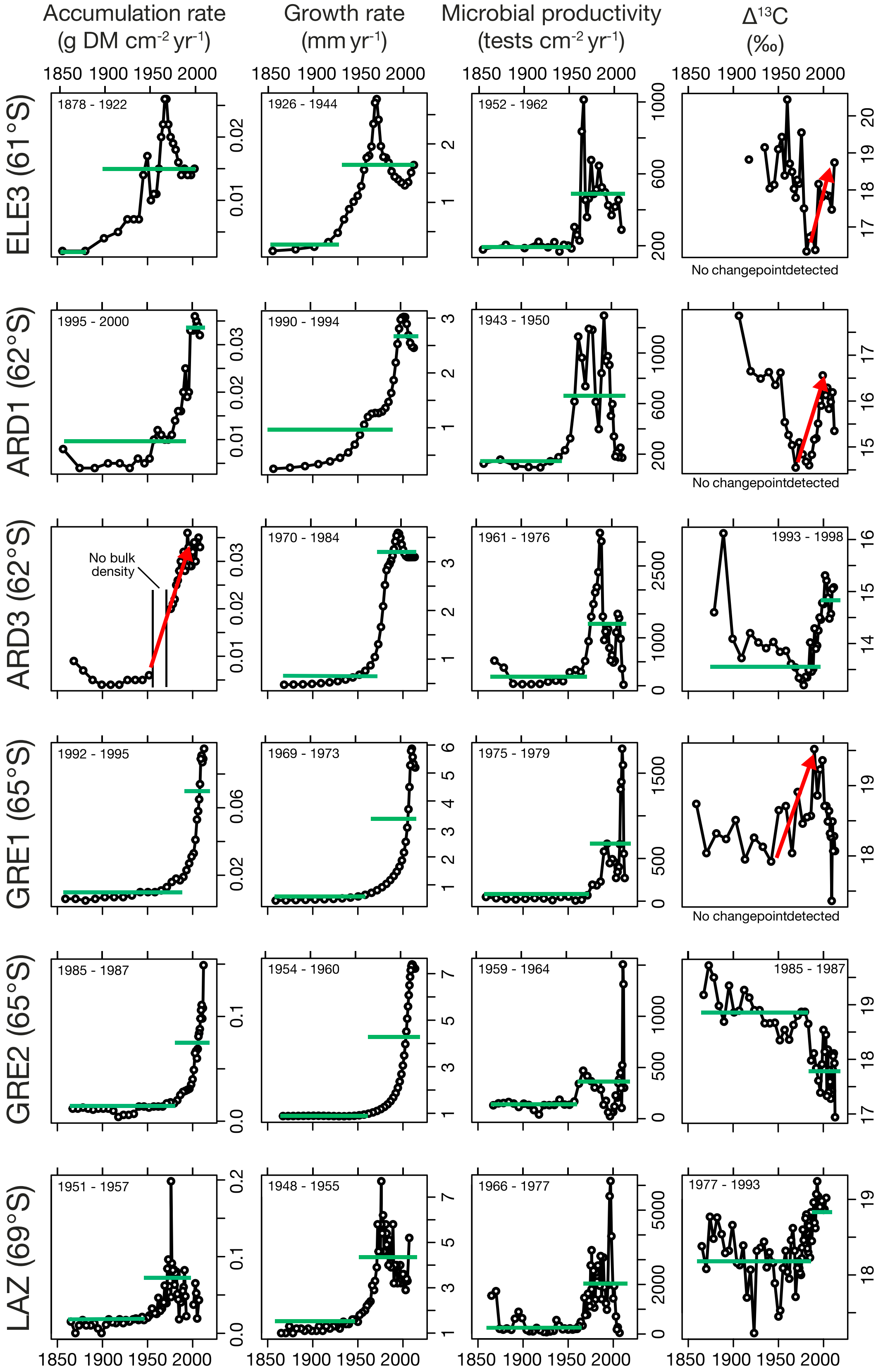
Black dots are new locations used in this analysis; gray dot is previously published [14]; white dots are meteorological records, with decadal trends [22]. Approximate position of −5°C and −9°C isotherms [23, 24] illustrates lack of significant latitudinal temperature gradients over western AP study area. See also Table S1.

sites, cores, and proxies within the past ~50 years (Figure S2). In two cases (ARD1, GRE1), there were more recent Δ^{13}C declines to lower discrimination that, combined with the higher growth rates, suggests sub-optimal growth conditions over a longer annual growing period [15]. A trend to lower discrimination was also observed in one core (GRE2) where the post-changepoint state was negative, suggesting poorer conditions for photosynthesis at this site. Summary changepoint data show that a majority of state changes occurred after 1950 (Figure 3). To investigate whether there was a significant difference before and after AD 1950 that was prevalent across the whole of the AP, we compared pre- and post-1950 states, averaged across all sites and cores (Figure 4). There was an observable difference for all proxies apart from Δ^{13}C.

DISCUSSION

Paleo-data Are Key to AP Climate Debates

The value of paleo-data in understanding Antarctic climate is highlighted by the limitations of instrumental and satellite records, which alone are not sufficient to determine whether recent trends are anthropogenically forced or remain within the range of natural climate variability [26, 27]. Ice core records indicate that warming over the past century is highly unusual in the context of natural variability over the past 2,000 years [28]. Observational records show that the physical [29–31] and ecological [9, 10] effects of “recent rapid regional” [3, 32] warming since the 1950s on the AP have been significant. However, this evidence has often been obtained from a single site [7] at a single trophic level, or is discontinuous in time [10, 11], meaning that a “baseline” ecological state has not been established and used to evaluate recent change and the likely sensitivity of future ecosystem responses [33]. In addition, the spatial heterogeneity of ecological responses to climate change makes it difficult to extrapolate from local, short-term studies of individuals and populations to an ecosystem level response to wider climatic trends [34]. Given the large interannual and decadal variability in Antarctic climate, placing recent short-term observational records in a longer-term context is important to determine and differentiate the roles of natural variability and anthropogenic forcing [35]. Our



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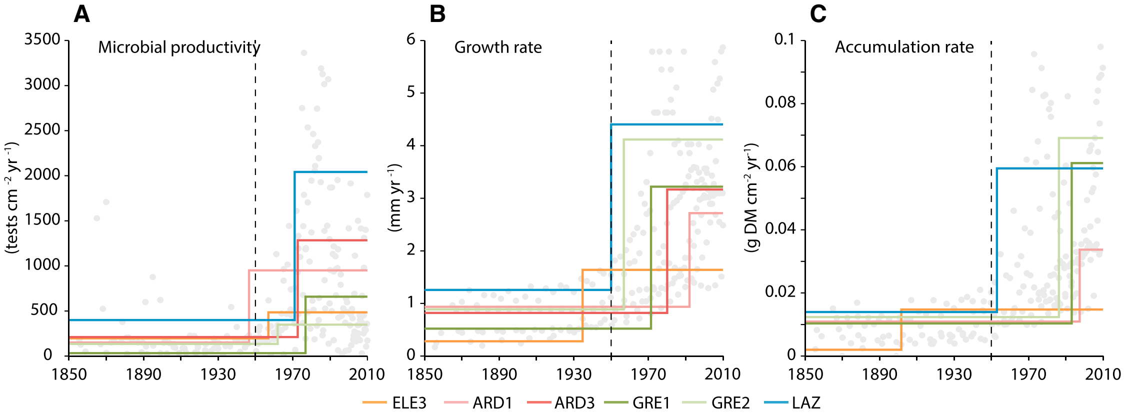

Figure 3. Summary Changepoint Data for All Proxies with the Exception of $\Delta^{13}C$

(A–C) Colored lines represent different sites, cores, and proxies; horizontal lines represent the mean values of all samples before and after the changepoint; vertical line shows timing of state change. Dashed vertical line indicates 1950. Spot data in background are individual times series from all sites, cores, and proxies. See also Table S3.

multi-proxy dataset over 150 years from moss bank cores spanning a 600-km latitudinal transect addresses these issues and enables a robust assessment of regional variability over time.

Drivers of Rapid Change

Our data indicate a widespread biological response to recent rapid warming on the AP. The extent of the site network and multi-proxy approach show that spatial and temporal variability, across multiple trophic levels, is small in relation to overall trends (Figure 2) such that we can have confidence in the overall widespread nature of the observed biological response to recent warming. However, the detailed patterns of change in individual proxies, particularly in $\Delta^{13}C$, allow further analysis of the response to microclimatic and microtopographic conditions specific to each moss bank location [12].

Abrupt shifts in microbial population change, growth, and mass accumulation rates were found in all cores, with significant differences between pre- and post-changepoint states (Figure 2). This suggests not only that moss banks have responded to gradual warming [22] (Figure 1) but also that rapid changes can occur across thresholds, which may not be temperature driven (for example, moisture availability during the growing season). Water availability is a key control on the growth rates and activity of Antarctic terrestrial organisms [36], including mosses and soil protozoa [14]. Free water availability is likely to have increased over the AP since the 1950s in concert with trends in temperature, precipitation, and growing season length [1, 6] but is governed by spatially heterogeneous precipitation trends and site-specific (micro)topography to a greater extent than temperature. Moisture availability may also increase in the future as a result of poleward contraction of westerly winds and increased meridional circulation [4, 37].

$\Delta^{13}C$ data support the hypothesis that the moisture status during periods of net photosynthetic assimilation has been spatially and temporally variable, with differences in $\Delta^{13}C$ both between and within sites. Measured $\Delta^{13}C$ values indicate the optimality of conditions for photosynthesis, integrated over the growing period [13, 15]. High $\Delta^{13}C$ values are associated with minimal diffusion limitation for CO_2 at the tissue surface and therefore drier conditions [38]. Wind conditions, evaporation, and surface microtopography as well as temperature and precipitation all affect leaf level surface moisture. Long, damp seasons can result in high growth rates but low $\Delta^{13}C$ values, while warm, dry periods can result in an instantaneously high $\Delta^{13}C$ before desiccation ends assimilation and little biomass is preserved. In general, $\Delta^{13}C$ increased between the 1970s and 2000, in concert with rising temperatures and likely improving conditions for photosynthesis, prior to a recent decline. Reduced $\Delta^{13}C$ since around 2000 coincides with the cessation of warming [4] and, potentially, reduced evaporation. The two Green Island cores, taken from within 100 m, show contrasting patterns, with GRE1 following the general trend of a non-significant increase in $\Delta^{13}C$ preceding a recent decline, whereas GRE2 shows a significant drop in $\Delta^{13}C$ around 1965. As precipitation, temperature, and wind are similar between the two core sites, a more local control is likely. For example, changes in microtopography at GRE2 may have resulted in surface water pooling where mosses were still able to photosynthesize and grow, but CO_2 diffusion and therefore $\Delta^{13}C$ were reduced.

The strong response of moss growth and microbial populations to increasing temperature, coupled with the $\Delta^{13}C$ results, suggest that these systems are driven primarily by temperature, strongly modified by more localized changes in water availability at both regional and local scales. Increasing temperature has

Figure 2. Time Series of Proxies for Moss Productivity and Soil Microbial Activity alongside Moss Growth and Mass Accumulation Rates for All Sites and Cores

Green lines represent the mean values of samples before and after each identified changepoint. All changepoints are significant at a confidence value >0.98. Years shown for changepoint occurrence represent the min–max range of the modeled date of the first sample in the new state. Red arrows show direction of primary recent trend in time series where significant changepoints were not identified. For ARD3, changepoint analysis was not possible due to a break in the record (see Table S4). Note differing y axis scales. See also Figure S2 and Table S3.

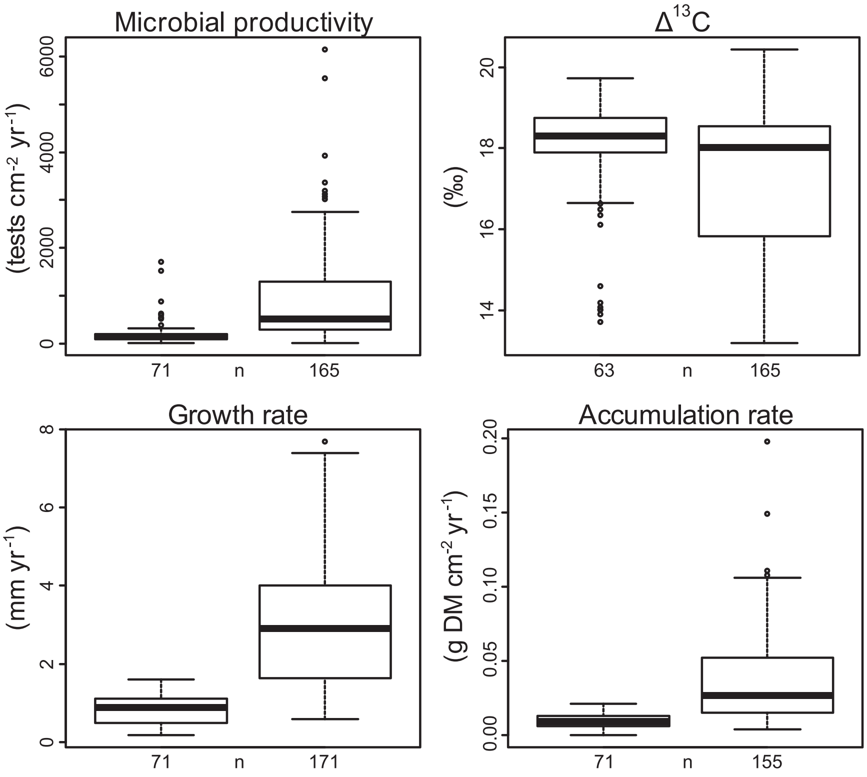

Figure 4. Pre- and Post-1950 Boxplots for All Proxies

In each panel, the left-hand boxplot is pre-1950, and the right-hand boxplot is post-1950. Data are averaged across all sites and cores. See also Figure S1.

likely driven a longer growing season and a greater number of days in the year where air temperature at the moss surface exceeds 0°C for at least part of the day. The largest increases in recorded temperature have occurred during the winter, spring, and autumn periods [35], which suggests that changing temperature has had the greatest impact on biological productivity during the shoulder periods of the growing season. Thus, while longer periods of growth have resulted in overall higher growth rates and increased microbial productivity, the changes in $\Delta^{13}C$ suggest that growing conditions at any point in time may actually have been worse, likely due to sub-optimal moisture availability. There is some suggestion (Figure 2) that very recent growth rates of moss and microbial populations may have been slower, and this could be the result of lack of moisture or a reversal in the direction of temperature change in some parts of the year [4].

Future Terrestrial Biological Change

There is no doubt that biological responses to temperature variation on the AP have been rapid and that large shifts in the ranges and growth rates of mosses and microbial communities can be expected if recent rates of temperature change increase, as predicted, even recognizing the current reversal of warming in this region [1, 4], and associated environmental changes such as glacier retreat [31] continue. Biological activity measured as moss growth or mass accumulation rates has increased 4- to 5-fold between pre- and post-changepoint states (Figure 3; Table S3), suggesting that mosses are highly sensitive to change.

The past sensitivity of moss growth and mass accumulation rates to temperature rise (see STAR Methods) was used to provide a first-order estimate of likely responses to future warming. Regionally averaged sensitivity was estimated by calculating rates of change for moss growth and mass accumulation at all sites from 1950 to 2012 and combining these with decadal temperature trends for the AP derived from reanalysis data [35]. This suggested that moss growth rates have increased by 3.2 mm $^{\circ}C^{-1}$ (range 1.8–13.4 mm $^{\circ}C^{-1}$) and mass accumulation rates by 0.05 g DM $cm^{-2}\,^{\circ}C^{-1}$ (range 0.03–0.2 g DM $cm^{-2}\,^{\circ}C^{-1}$) compared to baseline (i.e., pre-changepoint) mean rates of 0.78 mm $year^{-1}$ and 0.009 g DM cm^{-2} $year^{-1}$, respectively (Table S4). Although these estimates are variable between and within sites and constrained by chronological precision, they suggest that moss bank growth and accumulation will be highly sensitive to future temperature change.

The sensitivity of this response is moderated by moisture availability, but our spatially consistent records covering the last 150 years suggest that the effect of temperature is dominant. Projections of future temperature increases for the AP are subject to very large uncertainties [1], but our data on increased moss growth and increased microbial populations, combined with increased fungal diversity [39] and vascular plant distribution [11], all indicate that terrestrial plant communities and soils will undergo substantial alteration even with only modest further increases in temperature. These changes, combined with increased ice-free land areas from glacier retreat [31], will drive large-scale alteration to the biological functioning, appearance, and landscape of the AP over the rest of the 21st century and beyond. While the biogeographical isolation and low vascular plant species diversity [40] of Antarctica mean we must think differently about the two polar regions, a greening of the fringes of the Antarctic may already be underway, similar to the well-documented and extensive greening of the Arctic [20].

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

- KEY RESOURCES TABLE
- CONTACT FOR REAGENT AND RESOURCE SHARING
- METHOD DETAILS
  - ○ Moss Bank Core Collection and Sampling
  - ○ Chronology
  - ○ Carbon Stable Isotopes
  - ○ Testate Amoeba Analysis

- ○ Climate Data
- QUANTIFICATION AND STATISTICAL ANALYSIS
- DATA AND SOFTWARE AVAILABILITY

SUPPLEMENTAL INFORMATION

Supplemental Information includes four figures and four tables and can be found with this article online at http://dx.doi.org/10.1016/j.cub.2017.04.034.

AUTHOR CONTRIBUTIONS

D.J.C., D.A.H., P.C., and H.G. conceived the research project and secured funding. Fieldwork was completed by M.J.A., D.J.C., D.A.H., P.C., and J.R. Laboratory work was completed by M.J.A., T.P.R., and J.R. Data analyses were completed by M.J.A., J.R., and T.P.R. M.J.A. and D.J.C. wrote the manuscript with assistance from T.P.R. All authors provided editorial advice and contributed to revisions.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Proxy indices for carbon isotopes, microbial productivity, mass accumulation, and moss growth rates, with associated ages.	This paper	Searchable at https://data.bas.ac.uk/
Software and Algorithms		
“Changepoint” R package	Authored by Rebecca Killick, Lancaster University, UK	https://cran.r-project.org/web/packages/changepoint/index.html

CONTACT FOR REAGENT AND RESOURCE SHARING

Further information and requests for resources should be directed to and will be fulfilled by the Lead Contact, Matthew Amesbury (m.j.amesbury@exeter.ac.uk).

METHOD DETAILS

Moss Bank Core Collection and Sampling

Cores were collected in January 2012 (Elephant Island and Ardley Island) and January 2013 (Green Island) (related to Table S1). Sites were selected to access the deepest and oldest records available, while ensuring as complete spatial coverage of the AP as possible given the sporadic locations in which moss banks grow. Cores were carefully cut and removed by hand from non-permafrost near-surface sediments and stored at −20°C. Frozen core sections were sub-sampled at 5 mm resolution using a microtome slicer [41]. All information on the Lazarev Bay site has been previously published [14] and data are included here to extend the spatial transect.

Chronology

Age-depth models (Figure S3) were developed from conventional and post-bomb ^{14}C and alpha-spectrometry ^{210}Pb. All ^{14}C dates were measured on pure moss fragments. Raw ^{14}C dates and ^{210}Pb ages derived from a constant rate of supply model [42] were entered into the R package ‘clam’ [43] to develop smooth spline models using the minimum smoothing value (lower values resulting in more flexible models) at which age reversals did not occur in the majority of model iterations. All other settings were default. Moss growth rates were calculated automatically during the age-depth modeling process and therefore reflect the smoothing inherent in the age-depth model. Mass accumulation rates (g DM cm^{-2} year^{-1}) were calculated using the depth, modeled ages and bulk density values for consecutive samples; bulk density (g cm^{-3}) was calculated by freeze drying samples of known volume (for bulk density data, see Figure S4). In one core (ARD3) it was not possible to derive a complete bulk density profile due to an air pocket within the core, resulting in a discontinuous record of mass accumulation rates. Details of all ^{14}C and ^{210}Pb dates are given in Table S2. For summary proxy data, rate of change and sensitivity data for mass accumulation rate and moss growth rate, see Tables S3 and S4.

Carbon Stable Isotopes

Cellulose was extracted from moss samples using a standard protocol [44]. For δ^{13}C analysis, 1 mg samples of freeze-dried α-cellulose were transferred to tin capsules and measured at the NERC Isotope Geoscience Laboratory (British Geological Survey) by combustion in a furnace connected on-line to a dual inlet isotope ratio mass spectrometer. Isotope ratios (^{13}C/^{12}C) were referenced to the VPDB scale using within-run standards. Raw δ^{13}C values were converted to carbon isotopic discrimination (Δ^{13}C) by reference to age depth models and records of atmospheric ^{13}C in Antarctica [45]. Moss bank Δ^{13}C represents a proxy for photosynthetic assimilation rate [14, 15], with high discrimination values reflecting optimal hydration and photosynthetic conditions [13, 15]. For summary proxy data, see Table S3.

Testate Amoeba Analysis

Testate amoebae were used as a proxy for microbial productivity [14]. Samples were prepared according to standard methodologies [46], with the size fraction between 300 and 15 μm retained for microscopic analysis. Volumetric concentration values (tests cm^{-3}) were calculated by the addition of an exotic spore marker, with concentration per unit surface area over time (tests cm^{-2} year^{-1}) calculated with reference to the depths, modeled ages and volumetric concentration values of consecutive samples. Minimum counts of 25 individuals were accepted for statistical analysis due to extremely low concentration in some samples. For summary proxy data, see Table S3.

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Climate Data

AP climate station temperature data (Figure 1) were downloaded from the SCAR (Scientific Committee on Antarctic Research) READER (REference Antarctic Data for Environmental Research) database (https://legacy.bas.ac.uk/met/READER/data.html).

QUANTIFICATION AND STATISTICAL ANALYSIS

Changepoint analysis was carried out on all profiles at each site with the exclusion of ARD3 accumulation rate (see Chronology methods). We used the R package 'changepoint' [47] with the cpt.meanvar function to examine concurrent changes in the mean and variance of each time series. We used default settings, which included the 'At Most One Change' method to focus the analysis on the primary changepoint in each time series. Changepoint analysis was carried out on time series data only; ages assigned to changepoints were the min – max ranges of individual samples from the relevant age-depth model. Cumulative sum control chart (CUSUM) profiles for change detection were calculated manually by plotting the cumulative sum of the differences between individual values and the time series mean against time (Figure S1). Slope directions indicate if data are trending away from or toward the mean value, with change in direction indicating sudden shifts in the mean state.

For the sensitivity analysis, we used only growth and mass accumulation rate data as they demonstrate a more direct response to long-term temperature trends, whereas microbial productivity and $\Delta^{13}C$ can be more influenced by site-specific microclimate and microtopography [12]. To assess the sensitivity of these growth parameters to temperature, we calculated decadal rates of change (i.e., change in proxy divided by change in time) from 1950 – 2012 and applied these to a DJF temperature trend from reanalysis data [35], using the temperature trend error to provide a range of possible sensitivity values. Temperature sensitivity estimates are considered to be conservative as 1) they include any recent downturn in proxy values and 2) the DJF trend will be lower than the genuine growing season trend to which moss bank proxies respond, which would include part of the SON and MAM periods, when trends are higher [35].

DATA AND SOFTWARE AVAILABILITY

All software required to perform the analyses described in the 'Quantification and statistical analysis' section is freely available to download for the open source R program. Raw proxy data is archived at the UK Natural Environment Research Council Polar Data Centre, available via the Discovery Metadata System (https://data.bas.ac.uk/).