

Report for Current Biology:

# Plants and soil microbes respond to recent warming on the Antarctic Peninsula

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**Running header:** Biological responses to rapid Antarctic warming

## Summary:

**The Antarctic Peninsula (AP) is one of the most rapidly warming regions on Earth, where annual temperatures have risen by up to 0.56°C per decade since the 1950s [1]. Terrestrial and marine**

organisms have shown changes in populations or distributions over this time [2, 3], suggesting that the ecology of the AP is changing rapidly. However, these biological records are shorter in length than the meteorological data and observed population changes cannot be securely linked to longer term trends apparent in palaeoclimate data [4]. We developed a unique time series of past moss growth and soil microbial activity from a 150-year old moss bank at the southern limit of significant plant growth based on accumulation rates, cellulose  $\delta^{13}\text{C}$  and fossil testate amoebae. We show that growth rates and microbial productivity rose rapidly since the 1960s, consistent with temperature changes [5], although recently may have stalled [2]. The recent increase in terrestrial plant growth rates and soil microbial activity are unprecedented in the last 150 years and consistent with climate change. Future changes in terrestrial biota are likely to track projected temperature increases closely and will fundamentally change the ecology and appearance of the AP.

#### Highlights:

1. Antarctic moss growth and microbial activity changes are consistent with warming
2. Isotope and testate amoeba proxies show growth increased from 1960s to 1990s
3. Biological proxies show some decrease in growth since a late 1990s maximum

## Results and Discussion:

Moss banks represent the most southerly direct record of terrestrial biological activity in Antarctica, and we have analysed peat stratigraphy and associated microbial flora to provide a terrestrial palaeoclimatic record of austral summer conditions. In 2008 we sampled a highly unusual 40 cm deep *Polytrichum strictum* (Brid.) moss bank at Lazarev Bay, Alexander Island, to the west of the Antarctic Peninsula (69°22.0'S, 71°50.7' W; Fig.1, Supplementary Figure S1), globally the southernmost formation of its kind [6]. The extraction, and subsequent analysis, of a single monolith from the moss bank was felt to be appropriate in light of the limited extent of moss growth at this exceptional and sensitive location.

### Recent climate change on the Antarctic Peninsula

Whilst there are no direct temperature records available from this part of Alexander Island, Lazarev Bay is within a region likely to have recently undergone significant recent warming (Fig. 1) [7]. The closest decadal scale instrumental meteorological records from Rothera station (Fig. 1; 67° 34'S, 68° 08'W) show that, between 1978 and 2000, a warming trend of  $+1.01 \pm 1.42^\circ\text{C decade}^{-1}$  was measured, and, further north at Vernadsky/Faraday station (Fig. 1; 65° 24'S, 64° 24'W), a significant warming trend in mean annual temperature of approx  $0.6 \pm 0.4^\circ\text{C decade}^{-1}$  was observed between 1951-2000 in one of the longest regional records [8]. To the south-east of Lazarev Bay, inland on the ice sheet, the Gomez ice core (Fig. 1; 73° 34'S, 70° 22'W, 1400 m asl) indicates substantial temperature increases of approximately  $2.7^\circ\text{C}$  over the past 50 years [5]. Along with some of the fastest rates of warming on the planet there have been significant increases in precipitation and wind speed [1]. Inferred rates of warming derived from an ice core isotope proxy from James Ross Island show that recent temperature changes are unusual, although not unprecedented, in the context of multi-millennial climate variability [4]. The recent temperature rise has been associated with changes in the physical environment of the Antarctic Peninsula and changes in the habitats of

native flora and fauna have been observed [1, 9]. Ice cover has reduced [10, 11], exposing new areas of land for the local expansion and establishment of new populations of the two native vascular plant species (*Deschampsia antarctica* and *Colobanthus quitensis*)[2] and the diverse regional cryptogamic flora. Observed changes in plant populations are generally attributed to the changing temperatures (and consequential effects on water availability) in the region, including recent evidence of slowing of rates of expansion [2]. Whilst the recent terrestrial biological changes on the AP are not in doubt, records are limited to the period since the mid-1960s and there is no longer term context against which to clearly attribute ecological change to climate variability. Here, we reconstruct moss growth rates and soil microbial activity over the last 150 years and demonstrate a clear link between the terrestrial biological record and rapid warming on the AP which has recently slowed.

### **Moss-peat formation development and characteristics**

Radiocarbon-dating of organic matter from the base of the peat core indicated the initiation of peat accumulation to have been approx. 1860 AD, and the age-depth model facilitated the translation of the depths of the transverse samples to an estimated year of growth (Fig. 2, Table S1). Microscopic examination of plant material showed that the moss bank is formed from a single species throughout (*Polytrichum strictum*) and that the physical properties of the moss bank are generally stable, with water content at 60-70% throughout the depth of the moss, decreasing slightly in the surface layers (Fig. 3c). The moss bank accumulated at around 1.25 mm yr<sup>-1</sup> throughout the late 19<sup>th</sup> and early 20<sup>th</sup> centuries and then increased growth rate from the mid-1950s to reach >5 mm yr<sup>-1</sup> by the late 1970s (Fig. 3a). The relatively stable bulk density (Fig. 3b) shows that this is not attributable to compression and rates of mass accumulation also show a similar overall pattern of change (Fig.3e). Mass accumulation rates were 0.01 g dry matter (DM) cm<sup>-2</sup> yr<sup>-1</sup> for the first 100 years of the record, rising to between 0.05 and 0.10 g DM cm<sup>-2</sup> yr<sup>-1</sup> from the

late 1950s onwards (Fig. 3e). With a carbon content of c. 40%, the initial rate of carbon accumulation ( $40 \text{ g C m}^{-2} \text{ yr}^{-1}$ ) is equivalent to that measured across 17 South American peatlands [12]. Both vertical extension and mass accumulation rates reached a maximum in the late 1970s, with a subsequent decrease in growth rate to  $3.5 \text{ mm yr}^{-1}$  (Fig. 3a) and in mass accumulation to  $0.05 \text{ g DM cm}^{-2} \text{ yr}^{-1}$  (Fig. 3e).

### **Biological activity derived from isotopic and testate amoeba analyses**

$\Delta^{13}\text{C}_\text{C}$ , the record of moss cellulose  $\delta^{13}\text{C}_\text{C}$  corrected for changes in the global composition of atmospheric  $\text{CO}_2$  (Supplementary Figure S2), initially shows a slow, long-term decline in  $\Delta^{13}\text{C}_\text{C}$  for the earlier part of the record, which may indicate that conditions for photosynthesis deteriorated over the early 20<sup>th</sup> century [12,13]. There was a striking increase in  $\Delta^{13}\text{C}_\text{C}$  from the 1950s onwards (Fig. 4a). In bryophytes,  $\Delta^{13}\text{C}_\text{C}$  is largely dependent upon the water status of the tissue and is also proportional to photosynthetic assimilation rate [13-15], so the measured increase in  $\Delta^{13}\text{C}_\text{C}$  is consistent with improved conditions for photosynthesis leading to increased growth rate (Fig 3a). The maximum  $\Delta^{13}\text{C}_\text{C}$  of 19.3‰ (ca.1994), which is close to the theoretical maximum  $\Delta^{13}\text{C}_\text{C}$  value, indicates that seasonal conditions for photosynthetic assimilation were near optimal at this time: water is sufficient for photosynthesis, but not in excess, which limits diffusive  $\text{CO}_2$  supply [13, 14].

We used testate amoeba population change (Fig. 4b) as an estimate of total microbial soil activity, as compared to other peat accumulation (Fig. 3a, e) and isotopic proxies (Fig. 4a). Small and abundant, the shells of testate amoebae are often well-preserved in peat sediments with morphological variation that facilitates identification of ca. 2000 described species [16]. Testate amoebae consume bacteria and fungi and thus can be considered as broadly indicative of overall microbial activity [17]. In Antarctic communities testate amoebae represent a large proportion of the biomass of terrestrial heterotroph organisms [18]. The testate amoeba assemblage was dominated by a single taxon (*Corythion dubium*, Taraneck 1881) with only a few other taxa present

(Supplementary Figure S3), thus total numbers are directly related to total microbial biomass. Testate amoeba populations were generally low ( $<1000$  tests  $\text{cm}^{-2} \text{yr}^{-1}$ ) until a rapid increase in population size from the early 1960s (Fig 4b). This suggests that testate amoebae colonised the moss bank very soon after it became established, but that conditions for population expansion remained poor for the first 100 years. Between *ca.* 1965 and *ca.* 1990, concentrations increased to between 1000 and 3000 tests  $\text{cm}^{-2} \text{yr}^{-1}$ . There was then a further increase in population in the late 1990s when the maximum value of 6000 tests  $\text{cm}^{-2} \text{yr}^{-1}$  was reached, followed by a decline to *ca.* 1800 tests  $\text{cm}^{-2} \text{yr}^{-1}$  by the early part of the twenty-first century (Fig. 4b).

The direct measurements of moss growth (Fig. 3a) and mass accumulation (Fig. 3e), as well as the proxies for photosynthesis ( $\Delta^{13}\text{C}_\text{C}$ ; Fig. 4a) and microbial activity (testate amoebae; Fig. 4b), representing indicators of austral summer growth conditions, have all tended to decline over the past two decades. This is coincident with a stabilization in the populations of *Deschampsia antarctica* and *Colobanthus quitensis* close to Faraday/Vernadsky (Fig. 1) between 1990 and 2006/7 following decades of expansion, where the rate of change in temperature has decreased since 1990, and there has been little recent change in mean annual temperature [2].

### **Biological responses to climate change**

We can conclude that the increasing temperatures recorded on the AP (Fig. 1) initially enhanced moss growth as accumulation rate (Fig 3a,e) and carbon isotope discrimination ( $\Delta^{13}\text{C}_\text{C}$ ) increased from the 1950s onwards (Fig. 4a). Despite recent temperature rises, temperatures during the summer growing season remain below the optimum for *Polytrichum* so any increase in temperature would lead to an increase in  $\text{CO}_2$  assimilation rate and carbon isotope discrimination [13]. On the South Shetland Islands the growth rates of the lichens *Rhizocarpon geographicum* and *Bellemeria* sp. appear to have increased between 1956 and 1991 [19], which has tentatively been

attributed to climate change, though without the incremental measurements that have been possible on the Lazarev Bay moss-peat, the timings of changes are more difficult to ascertain.

The length of the melt season has increased across the AP region since 1948 [10, 20], with earlier thawing of the growing surfaces extending the length of the growing season. Temperature is also likely to have driven increased microbial activity, as indicated by testate amoebae, probably through increased metabolic and organic matter turnover rates. Increased decay of organic matter is independently shown by the increased humification (reduced optical transmission of extracts) of the moss bank since the mid-1950s (Fig. 3d), coincident with the increased testate amoeba population growth rates.

These observations are consistent with the substantial temperature increase on the AP since the late 1950s (Fig. 1); at Vernadsky/Faraday, there has been a mean annual temperature increase of 3.8°C since 1957 [21], with smaller increases in summer temperatures ( $0.24 \pm 0.17^\circ\text{C decade}^{-1}$ ) and larger increases in winter ( $1.09 \pm 0.88^\circ\text{C decade}^{-1}$ ) [8]. Shorter records from nearby Rothera and Fossil Bluff confirm that similar trends have occurred further south, closer to the study site [22]. Critically, the  $\delta^{18}\text{O}$  record from the Gomez ice core [5] shows that the acceleration in moss growth and microbial activity tracked temperature over the last 150 years (Fig. 4c), with the recent increase in biological activity coincident with the start of 20<sup>th</sup> century warming, indicating that temperature is the most likely primary driver of plant productivity and microbial activity.

Water availability remains critical to the distribution, growth rates and activity of most terrestrial organisms across Antarctica, including mosses and soil protozoa [23]. At Vernadsky/Faraday, the proportion of precipitation falling as rain and the number of annual precipitation events have increased since the 1960s [24], both of which would increase free water availability to mosses and soil organisms. In the 1980s and 1990s precipitation at Rothera increased substantially during the summer months of December and January and also in April, whilst decreasing in winter due to the weakened Amundsen Sea low pressure zone [25]. There has also

been a significant increase in snow accumulation on the western Antarctic Peninsula as indicated in both the Gomez ice core, beginning in the 1930s and particularly clear since the 1970s [26], as has also been noted at Dyer Plateau in the central Peninsula (77° 48'S, 64° 31'W) [27]. Our data suggest that increased temperature and water availability at Lazarev Bay during the summer initially promoted moss and microbial growth, in the past fifty years. However, too much water limits moss photosynthesis [12,13] and the subsequent stalling in growth and microbial populations seen at Lazarev Bay may reflect changing seasonality and intensity of precipitation, as well as associated temperature changes.

### **Concluding remarks**

We show that the rapid increase in moss growth and microbial activity observed since the late 1950s in the moss bank record is a consequence of warming temperatures and increased summer precipitation enabling higher metabolic rates and longer growing seasons. These biological changes are unprecedented at least over the post-industrial period (since AD 1850). Thus we can attribute the direct observations of increased biological activity in the late 20<sup>th</sup> Century [28] to climate, based on direct and indirect long-term climatic baselines. The relationship between moss growth, microbial activity and climate suggests that moss banks have the potential to test the regional expression of temperature variability shown by instrumental data on the AP [7] over centennial to millennial timescales, by providing long-term records of summer growth conditions from the terrestrial western AP close to the meteorological stations. These will complement the more distant and widely dispersed ice core records from the major ice centres [4, 5, 27]. The rapid response of terrestrial systems to climate change on the AP suggests that the ecology and appearance of the AP landscape will alter rapidly in response to future changes in temperature and moisture availability during the growing season.



**Supplemental Information:** includes experimental procedures, one table (S1) and three figures (S1-S3)

## Acknowledgements

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**Figure 1. Study site location (Lazarev Bay) and regional long-term temperature trends.** Insets graphs show mean annual temperature trends as measured by instrumental records (Rothera, Faraday/Vernadsky)[22] and ice cores (Gomez)[5]. (See also Figure S1)

**Figure 2. Age-depth model for the Lazarev Bay moss bank.** Black line represents most likely year, grey shading represents the 95% confidence intervals and the blue shading represents probability distributions of each of the radiocarbon dates (See also Table S1).

**Figure 3. Physical properties and accumulation rates of the moss bank.** **a**, Growth rate determined from age depth model ( $\text{mm yr}^{-1}$ ); **b**, Bulk density ( $\text{g cm}^{-3}$ ); **c**, Water content (%); **d**, Humification (degree of decay) data measured as light transmission at 540 nm and are represented as mean  $\pm$  SEM; **e**, Peat accumulation rate determined from growth rate and bulk density ( $\text{g dry matter cm}^{-3} \text{ yr}^{-1}$ )

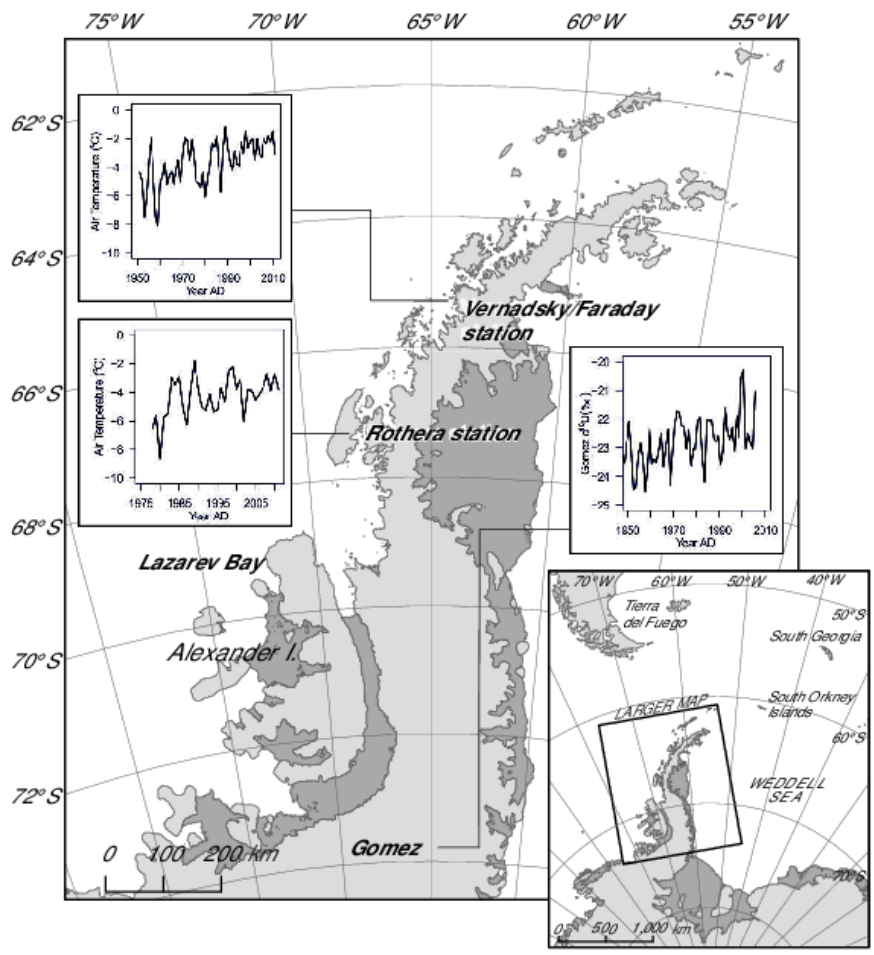
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**a**, Source-independent discrimination,  $\Delta^{13}\text{C}_c$ , determined from measured isotopic composition of cellulose ( $\delta^{13}\text{C}_c$ ) and isotopic composition of atmospheric  $\text{CO}_2$  ( $\delta^{13}\text{C}_a$ ) (See also Eq. 1 and Figure S2); **b**, Testate amoeba population concentration (tests  $\text{cm}^{-2} \text{yr}^{-1}$ ) (See also Figure S3); **c**, Temperature change as shown by  $\delta^{18}\text{O}$  from the Gomez ice core [5]. Shaded area marks period of rapid change.

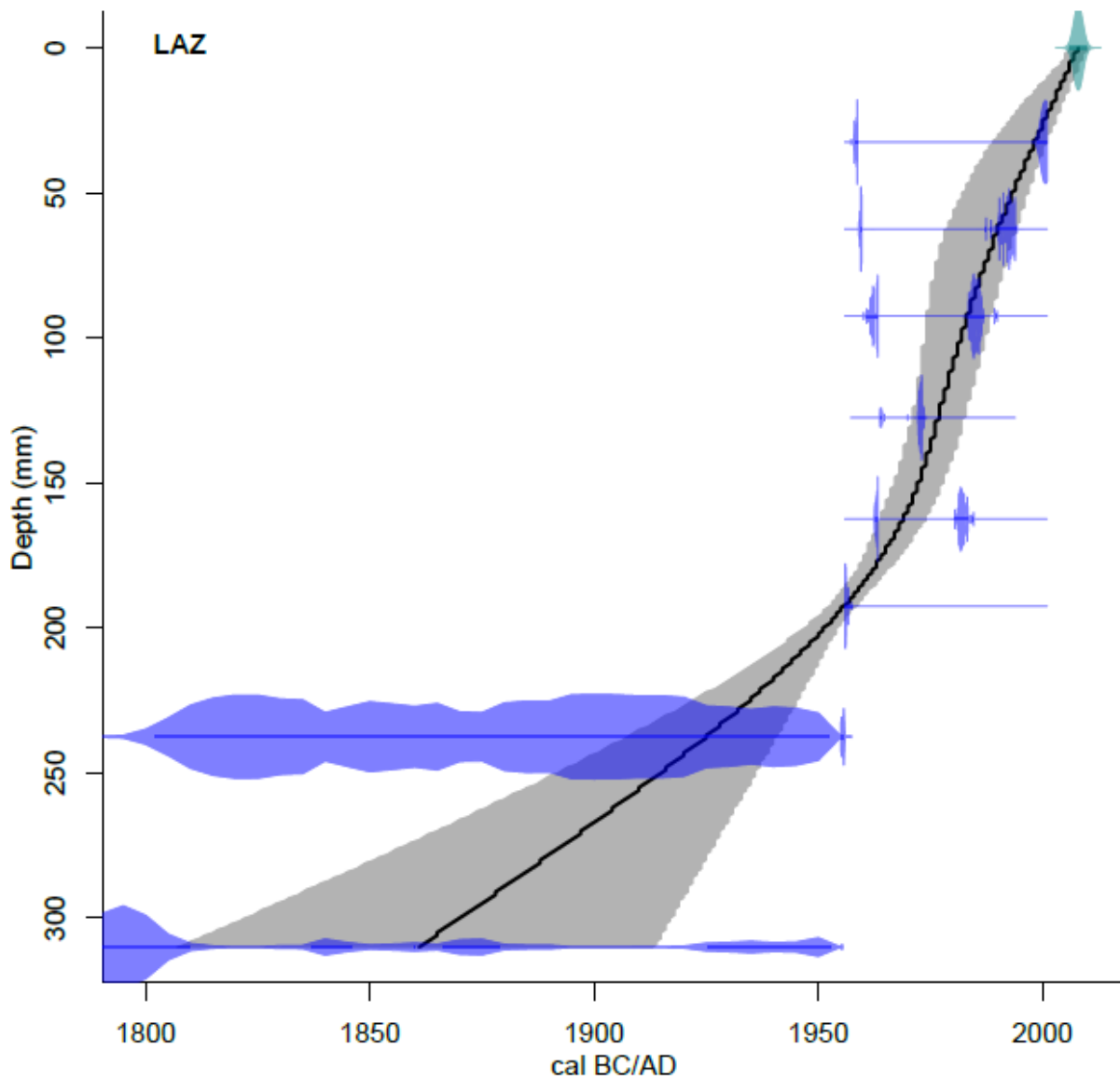
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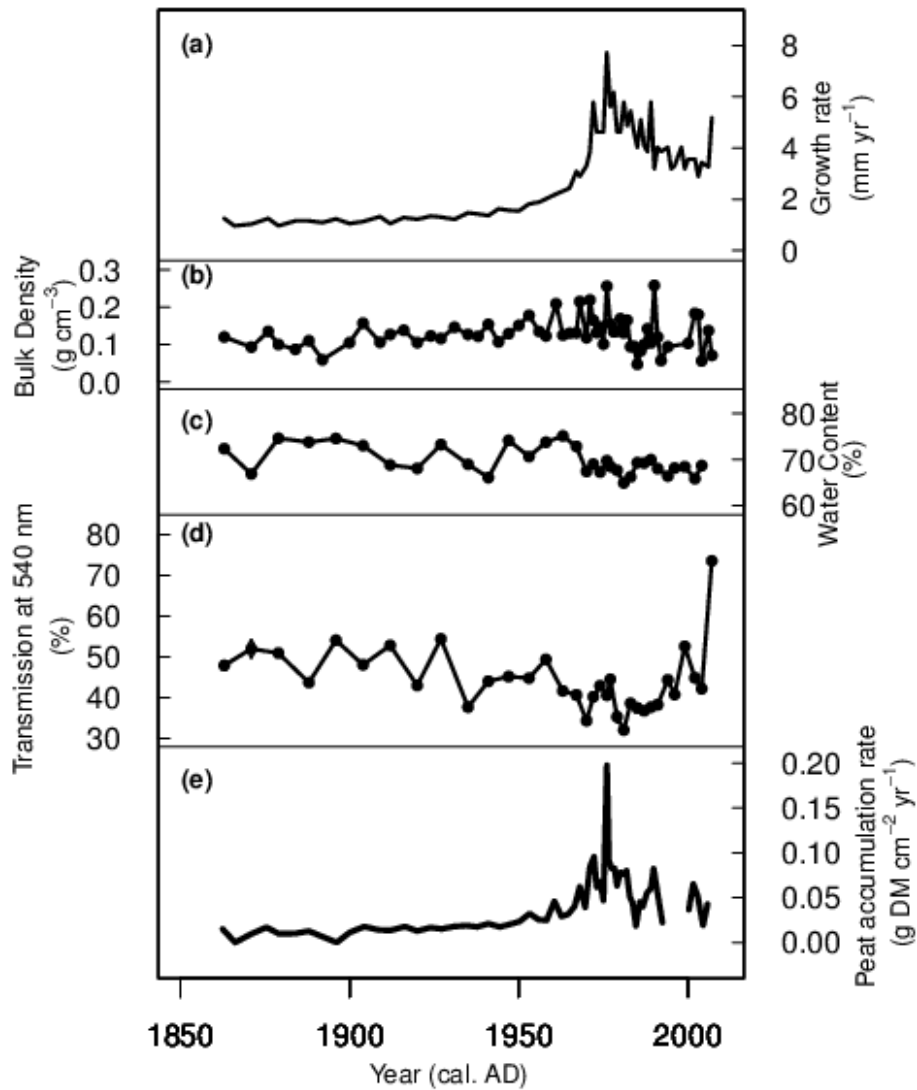
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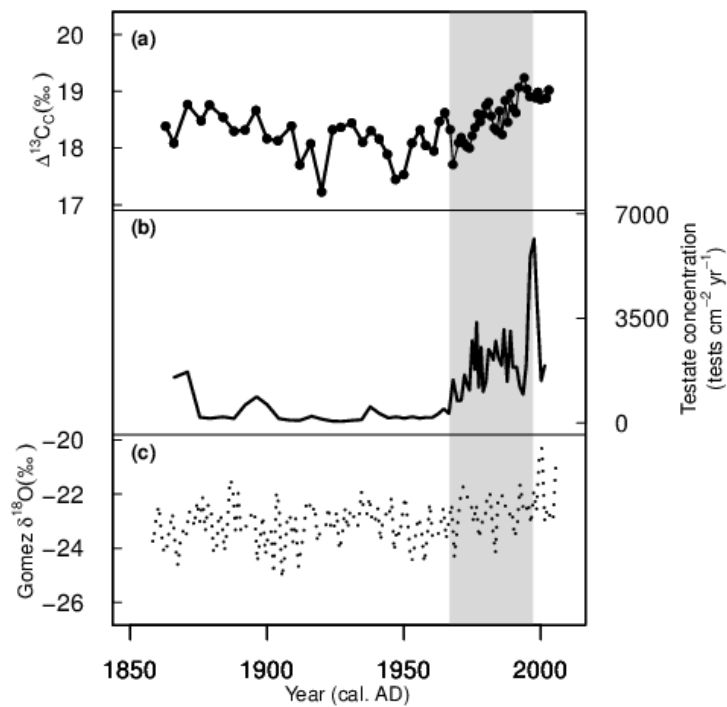
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**b**, Testate amoeba population concentration (tests  $\text{cm}^{-2} \text{yr}^{-1}$ ) (See also Figure S3); **c**, Temperature change as shown by  $\delta^{18}O$  from the Gomez ice core [5]. Shaded area marks period of rapid change.



Supplemental Information: Royles et al.: “Plants and soil microbes respond to recent warming on the Antarctic Peninsula”

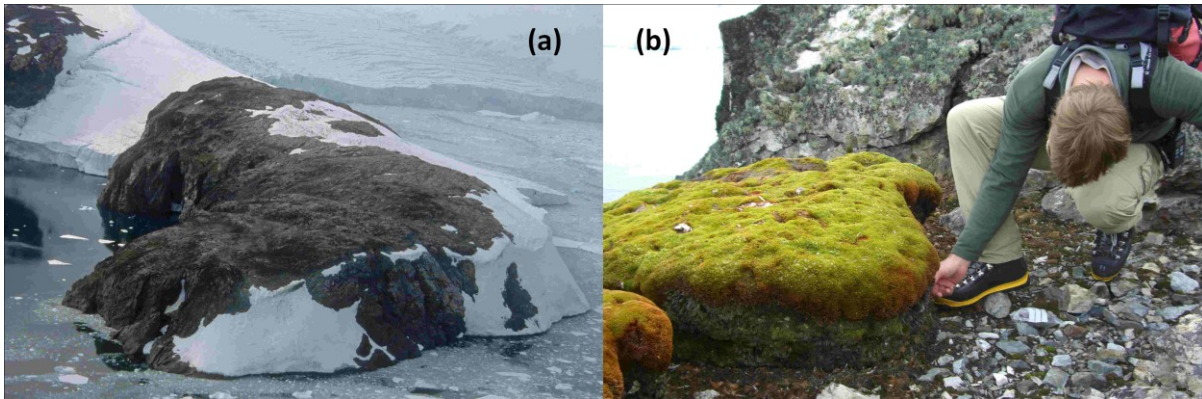


Figure S1: Sampling location photographs: a) Aerial photograph of sample location: an unnamed peninsula at Lazarev Bay on the north-west coast of Alexander Island; b) *Polytrichum strictum* moss peat formation (related to Figure 1).

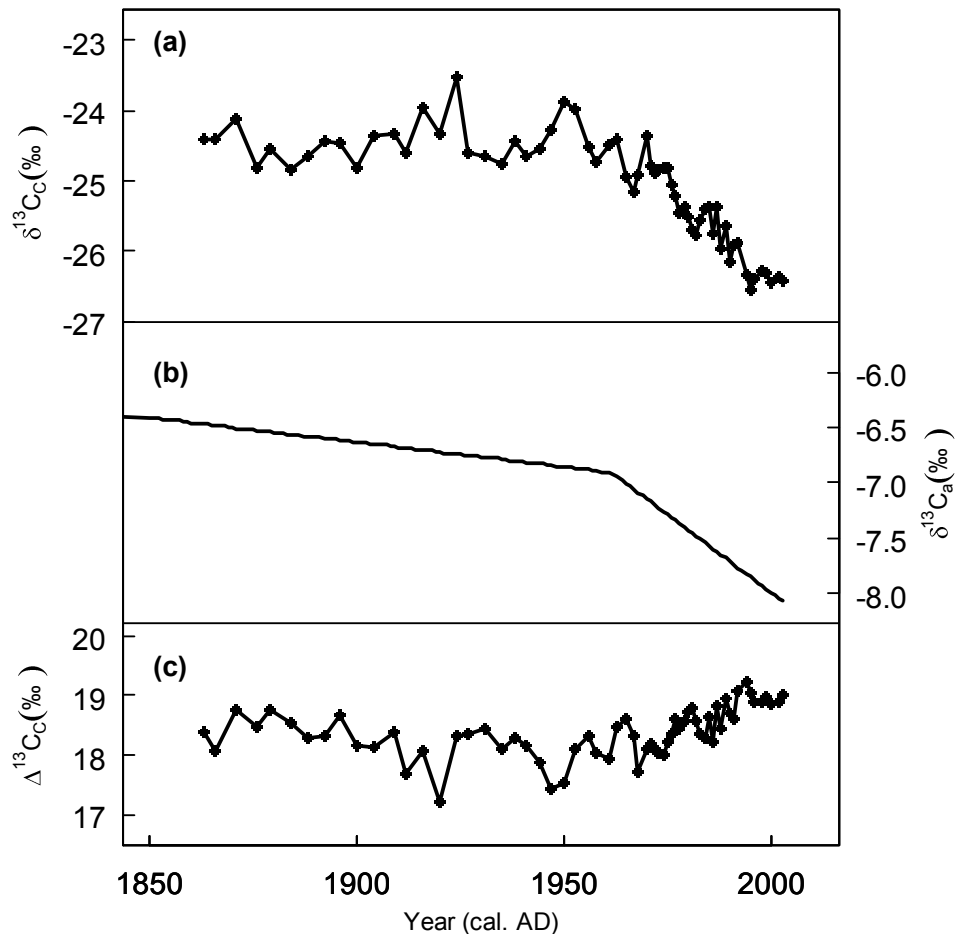
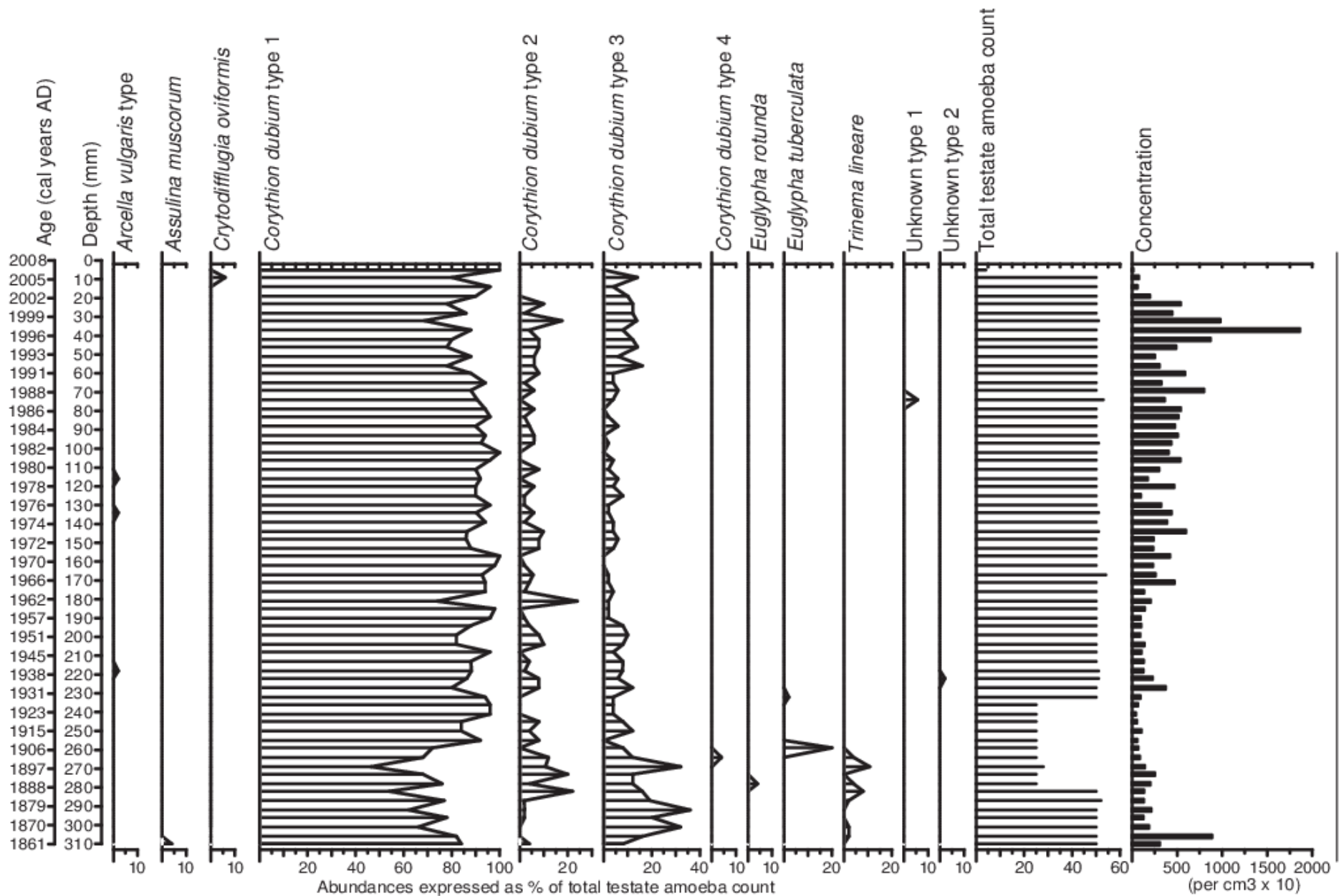


Figure S2. Carbon isotope composition of cellulose: a) Measured carbon isotope composition of cellulose ( $\delta^{13}C_C$ ) of subsamples from Lazarev Bay moss-peat core plotted over time; b) Carbon isotope composition of the atmosphere ( $\delta^{13}C_a$ ) [26]; c) Source-independent discrimination ( $\Delta^{13}C_C$ ; measured  $\delta^{13}C_C$  corrected for variation in  $\delta^{13}C_a$ ; see Eq. 1 in Experimental Procedures, related to Figure 4a).



**Figure S3. Testate amoeba diagram for Lazarev Bay.** Species composition expressed as % of the total count, total number of tests counted and test concentrations. 'Best' age estimate reported from CLAM age-depth model output (see experimental procedures for details). *Corythion dubium* is sub-divided by size fraction; T1 length 30-35 $\mu$ m, width 20-25 $\mu$ m T2 length 30-35  $\mu$ m, width 25-30  $\mu$ m T3 length 35-45  $\mu$ m, width 25-35  $\mu$ m T4 length >45  $\mu$ m, width 25-35  $\mu$ m (related to Figure 4b).

Identifier	Sample Depth (mm)	Measured Radiocarbon Age	<sup>13</sup> C/ <sup>12</sup> C Ratio (‰)	Conventional Radiocarbon Age
Beta - 324877	0-5 (Surface)	107.0 ± 0.4 pMC	-27.2	107.5 ± 0.4 pMC
Beta - 271294 *	30-35	108.2 ± 0.5 pMC	-27.9	108.8 ± 0.5 pMC
Beta - 284152 *	60-65	114.1 ± 0.4 pMC	-26.8	114.5 ± 0.4 pMC
Beta - 284153 *	90-95	121.1 ± 0.5 pMC	-26.5	121.4 ± 0.5 pMC
Beta - 271295 *	125-130	145.9 ± 0.6 pMC	-26.5	146.3 ± 0.6 pMC
Beta - 284154 *	160-165	125.3 ± 0.5 pMC	-26.1	125.6 ± 0.5 pMC
Beta - 284155 *	190-195	100.2 ± 0.5 pMC	-24.4	100.1 ± 0.5 pMC
Beta - 271296 *	235-240	120±40 <sup>14</sup> C y BP	-26.2	100±40 <sup>14</sup> C y BP
Beta - 324876	305-310 (Basal)	240 ± 30 <sup>14</sup> C y BP	-26.4	220 ± 30 <sup>14</sup> C y BP

**Table S1. Radiocarbon dates for Lazarev Bay moss bank** (related to Figure 2) \*denotes date previously reported by Convey et al [6].

### Experimental Procedures:

**Monolith collection.** An un-named low-lying peninsula in Lazarev Bay on the north-west coast of Alexander Island (69° 22.0'S, 71° 50.7'W) was visited as part of a terrestrial biological survey in 2008 [1]. Several banks of *Polytrichum strictum* approx 1 m in diameter and 0.4 m in depth were identified. One moss-peat monolith with a surface area of approximately 15 cm x 15 cm and a maximum depth of 31 cm was removed and stored at -20°C.

**Radiocarbon dating and age depth model.** Radiocarbon dating was carried out on nine moss fragment samples (Table S1;[1]). The age-depth model was developed in R version 2.14.0 using the package CLAM [2]. Dates were calibrated using the Southern Hemisphere curve SHCal04 [3]. The surface date confirmed a modern age, but the contemporary age of the undisturbed, green moss bank surface at the time of coring (2008) was used to constrain the top of the model, as using the pMC value resulted in an age reversal due to the age falling beyond the limit of the calibration curve. A smoothed spline model was fitted

(100,000 iterations) and the smoothing level was set to the minimum value (0.4) at which no age reversals occurred in the majority of the age-depth model iterations. Confidence ranges were set at  $2\sigma$  (95%) and all other settings were default values. There were no discontinuities in accumulation apparent from visual inspection of the monolith or in either the radiocarbon date sequence (Figure 1; Table S1)).

**Sub-sampling and analysis.** Half the monolith was sliced into 4-5 mm thickness samples using a band saw. The age-depth model was used to assign an age to all sample depths so that each sample has an estimated age span and central age.

Bulk density was determined by removing a  $125 \text{ mm}^3$  cube from the frozen sample, precisely measured using callipers. This was weighed and then dried to a constant mass at  $70^\circ\text{C}$ . To check moss species composition,  $1 \text{ cm}^3$  of dry material from each sample was boiled gently in 5% KOH (aq.), washed with distilled water, filtered and transferred to a petri dish and examined at 10x – 30x under a stereoscopic binocular microscope.

The degree of humification of the peat core subsamples was assessed following standard protocols [4] as percentage transmission of 540 nm light by three successive aliquots of diluted filtrate measured using a Biowave WPA S2100 Diode Array Spectrophotometer (Biochrom, Cambridge, UK).

Testate amoebae were prepared using standard techniques [5] and counts were completed on the 300-15  $\mu\text{m}$  fraction. Concentrations were estimated from the addition of an exotic spore tablet.

Cellulose was extracted from samples of 0.2 g dry mass following the protocol of Loader [6]. For  $\delta^{13}\text{C}$  analysis, 1 mg samples of dry  $\alpha$ -cellulose were transferred into individual tin capsules and measured at the NERC Isotope Geosciences Laboratory (British Geological Survey) by combustion in a furnace (Carlo Erba NA1500 (Series 1) (now Thermo Fisher Scientific, Waltham, MA, USA)) connected on-line to a dual-inlet isotope ratio mass spectrometer (VG Triple Trap and Optima (now IsoPrime, Cheadle-Hulme, UK)). Carbon isotope ratios of samples ( $^{13}\text{C}/^{12}\text{C}$ ) were referenced to the VPDB scale using a within-run laboratory standard calibrated against NBS-19 and NBS-22. Replicate analyses of well-mixed

samples indicated a precision of  $\pm <0.1\%$  (1SD). Measured  $\delta^{13}\text{C}_c$  values were corrected for the variation in atmospheric  $\text{CO}_2$  composition using the established isotopic composition of atmospheric  $\text{CO}_2$  ( $\delta^{13}\text{C}_a$ ) for each year of growth [7]:

$$\Delta = \frac{\delta^{13}\text{C}_a - \delta^{13}\text{C}_c}{1 + \delta^{13}\text{C}_c} \text{ [Eq. 1]}$$

where  $\Delta$  represents the discrimination by the plant.

## Supplementary References

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