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Horrocks, C. A., Newsham, K. K., Cox, F., Garnett, M. H., Robinson, C. H. and Dungait, J. A. J. 2020. Predicting climate change impacts on maritime Antarctic soils: A space-for-time substitution study. *Soil Biology and Biochemistry*. 141, p. 107682.

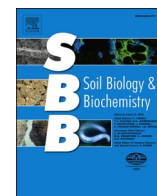
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Predicting climate change impacts on maritime Antarctic soils: a space-for-time substitution study

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ARTICLE INFO

Keywords:

Biomarkers

¹³C

¹⁴C

Climate change

¹⁵N

Sub- and maritime Antarctica

ABSTRACT

We report a space-for-time substitution study predicting the impacts of climate change on vegetated maritime Antarctic soils. Analyses of soils from under *Deschampsia antarctica* sampled from three islands along a 2200 km climatic gradient indicated that those from sub-Antarctica had higher moisture, organic matter and carbon (C) concentrations, more depleted $\delta^{13}\text{C}$ values, lower concentrations of the fungal biomarker ergosterol and higher concentrations of bacterial PLFA biomarkers and plant wax *n*-alkane biomarkers than those from maritime Antarctica. Shallow soils (2 cm depth) were wetter, and had higher concentrations of organic matter, ergosterol and bacterial PLFAs, than deeper soils (4 cm and 8 cm depths). Correlative analyses indicated that factors associated with climate change (increased soil moisture, C and organic matter concentrations, and depleted $\delta^{13}\text{C}$ contents) are likely to give rise to increases in Gram negative bacteria, and decreases in Gram positive bacteria and fungi, in maritime Antarctic soils. Bomb-¹⁴C analyses indicated that sub-Antarctic soils at all depths contained significant amounts of modern ¹⁴C (C fixed from the atmosphere post c. 1955), whereas modern ¹⁴C was restricted to depths of 2 cm and 4 cm in maritime Antarctica. The oldest C (c. 1745 years BP) was present in the southernmost soil. The higher nitrogen (N) concentrations and $\delta^{15}\text{N}$ values recorded in the southernmost soil were attributed to N inputs from bird guano. Based on these analyses, we conclude that 5–8 °C rises in air temperature, together with associated increases in precipitation, are likely to have substantial impacts on maritime Antarctic soils, but that, at the rates of climate warming predicted under moderate greenhouse gas emission scenarios, these impacts are likely to take at least a century to manifest themselves.

1. Introduction

Until the late 1990s, the maritime Antarctic was the most rapidly warming region in the Southern Hemisphere, with rises in near surface air temperatures of 0.2–0.4 °C per decade having been recorded since the 1950s (Adams et al., 2009). A recent analysis of temperature records found the warming trend in the region to have slowed at around the turn of the millennium (Turner et al., 2016), consistent with a hiatus in surface warming at the global scale (Trenberth, 2015). However, climate models forced with only moderate greenhouse gas emission scenarios predict further warming in the maritime Antarctic in the latter decades of the 21st Century, with 2–4 °C rises in surface air temperatures being forecast by 2100 (Bracegirdle et al., 2008; Bracegirdle and Stephenson,

2012). Rising air temperatures are likely to lead to increased precipitation across the region as air masses that deliver snow and occasional rain to maritime Antarctica warm and increase their capacity to retain moisture (Bromwich et al., 2014; Marshall et al., 2017).

Rising surface air temperatures are likely to have widespread effects in the maritime Antarctic, including the further recession of glaciers (Cook et al., 2005), the disintegration of ice shelves (Vaughan et al., 2003) and the expansion of vascular plant and bryophyte populations (Fowbert and Smith, 1994; Royles et al., 2012, 2013; Amesbury et al., 2017; Charman et al., 2018). However, the impacts of warming on the active layer soils overlying the 20–180 m deep permafrost that currently exists throughout ice-free areas of the maritime Antarctic (Bockheim, 1995) are more difficult to predict. This is because soil formation and

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associated processes such as plant litter decomposition are severely restricted by low temperatures and aridity in maritime Antarctica, hampering attempts to measure differences between treatments in comparative experiments. For example, in studies at Signy Island in the South Orkney Islands, weight losses of decomposing moss tissues are just 1–2% yr⁻¹, with litter decomposition being too slow to detect differences in decay rates between different moss species or years (Baker, 1972; Davis, 1986). Field experiments in maritime Antarctica using open top chambers (OTCs) have similarly shown that decomposition is too slow to detect any effects of warming on the mass loss of plant litter over 1–2 years (Bokhorst et al., 2007a). OTC experiments also indicate no effects of 1–2 °C increases in mean annual temperatures on soil bacterial community composition in the region after four years of treatment (Newsham et al., 2019), corroborating research in Icelandic geothermal habitats showing that temperature changes of c. 7–19 °C are necessary to force detectable changes to soil bacterial community composition (Radujković et al., 2018).

Determining the influence of climate change on maritime Antarctic soils, which is central to predicting how the region's terrestrial ecosystems will alter in the future (Wall et al., 2010), is hence challenging. A solution to this problem is to employ space-for-time substitutions, which were originally used to infer temporal trends by studying sites of different ages (Pickett, 1989), but which have been increasingly used to project climate-driven changes to maritime Antarctic ecosystems (e.g. Newsham et al., 2016; Dennis et al., 2019). Here, we use a 2200 km climatic gradient as a proxy to predict how vegetated maritime Antarctic soils might alter as they transition towards those of the sub-Antarctic in a warmer climate. In addition to measuring soil proximate chemistry and bulk $\delta^{13}\text{C}$, ^{14}C and ^{15}N values, we also determined the concentrations of

fungal, bacterial and plant biomarkers in soil (ergosterol, phospholipid fatty acids and *n*-alkanes, respectively). The influence on each of these parameters of soil depth, which is known to affect ^{14}C enrichment, pools of C and N and the composition of microbial communities in Antarctic soils (Royles et al., 2013; Amesbury et al., 2017; Cox et al., 2019), was also determined. In addition, because C and N inputs to soil from vegetation have a strong influence on decomposition and other soil processes (Swift et al., 1979; Lynch et al., 2018), we measured the concentrations of the two elements, C:N ratio and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values in aboveground plant biomass across the climatic gradient.

2. Materials and methods

2.1. Sampling

Soil and plant samples were collected in October and November 2011 from north-west Léonie Island (67.5984° S, 68.3561° W) in the southern maritime Antarctic, Polynesia Point on Signy Island (60.7107° S, 45.5849° W) in the northern maritime Antarctic and the Wanderer Meadows on Bird Island (54.0089° S, 38.0662° W), adjacent to South Georgia, in the sub-Antarctic (Fig. 1a). The sampling locations were chosen to reflect the substantial changes to mean air temperature (MAT) and mean annual precipitation (MAP) that occur across the sub- and maritime Antarctic, and because of their proximities (0.8–9.8 km) to British Antarctic Survey research stations. Meteorological records indicate rises in MAT of c. 8 °C between Léonie Island and Bird Island, and of c. 5 °C between Signy Island and Bird Island (Fig. 1a). Precipitation is difficult to measure in Antarctica (Turner et al., 1995), but data from several sources indicate that there is an increase in MAP of > 1000 mm

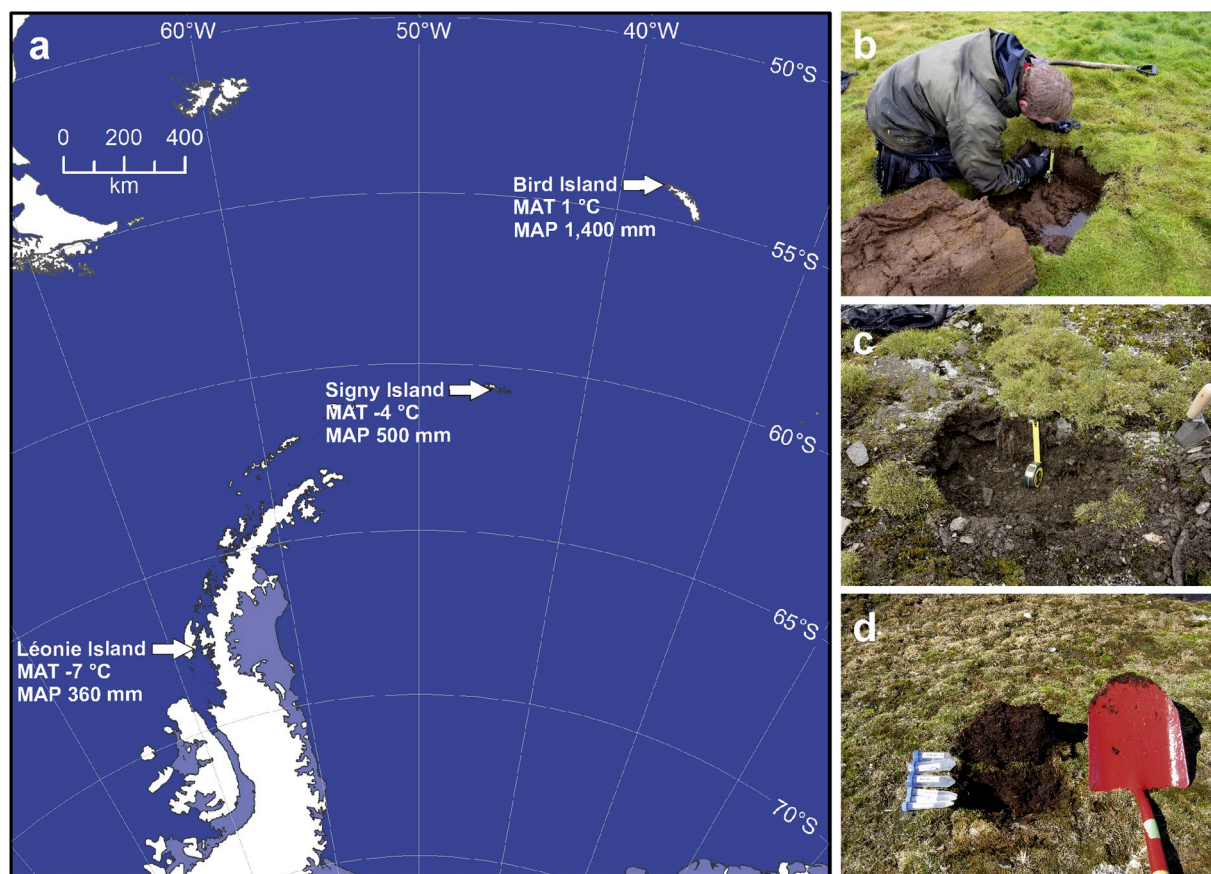


Fig. 1. (a) Map showing the locations of the sampling sites in the maritime and sub-Antarctic and images of soils sampled from under *Deschampsia antarctica* at (b) Bird Island, (c) Signy Island and (d) Léonie Island. Mean annual temperature (MAT) data are from British Antarctic Survey meteorological records (<https://www.bas.ac.uk/project/meteorology-and-ozone-monitoring/>) and the Regional Atmospheric Climate Model of Van Lipzig et al. (1999), as reported by Newsham et al. (2016). Mean annual precipitation (MAP) data are from Smith and Walton (1975), Smith (1984) and Turner et al. (2002).

between Léonie Island and Bird Island (Fig. 1a). The vast majority of the precipitation at Léonie Island falls in the form of snow, with that at Signy Island and Bird Island falling either as snow or, particularly at Bird Island, as rain (Collins et al., 1975; Smith and Walton, 1975).

At each island, three pits were dug and active layer soils overlying permafrost (present at c. 10 cm depth in some pits at all islands) were collected by inserting sterile 50 ml capacity tubes into the sides of each pit at depths of 2 cm, 4 cm and 8 cm. The pits at each island were separated by mean and maximum distances of 311 m and 1 km, respectively. In order to achieve consistency between the sampling sites, all active layer soils were collected from beneath swards of *Deschampsia antarctica* (Desv.), the dominant plant species at all of the sites sampled (Fig. 1, b–d). Also present were the higher plant species *Colobanthus quitensis*, and a range of bryophytes, including *Cephaloziella varians*, *Clasmatocolea obvoluta*, *Lophozia excisa*, *Brachythecium austrosalebrosum*, *Bryum pseudotriquetrum*, *Polytrichastrum alpinum* and *Sanionia uncinata*. Samples of aboveground plant parts of *D. antarctica* were also gathered from above each pit and air-dried. The soils were frozen at -20°C within 5 h of collection and were transported to the UK at the same temperature. After six months, approximating to the duration for which maritime Antarctic soils are frozen at depths of 2–8 cm during late autumn, winter and early spring (Chambers, 1966), the soils for the analyses described in section 2.2 were defrosted to room temperature, whilst those for the analyses in sections 2.3–2.5 were freeze dried (ModulyoD, Thermo Fisher Scientific, Waltham, MA, USA) and ground.

2.2. Soil pH, organic matter and moisture concentrations

Soil pH was measured by adding approximately the same volume of deionised water to c. 4 g (fwt) soil from each sample to generate slurries and recording pH after 10 min using a glass electrode (pH 21, Hanna Instruments, Leighton Buzzard, UK). Soil moisture was measured by heating c. 1 g of fresh soil to constant weight at 105°C for 17 h, prior to weighing. Organic matter concentrations were measured by heating the dried soil to 550°C for 4 h, also prior to weighing.

2.3. Soil C and N concentrations and ^{13}C and ^{15}N contents

Soil and plant material (c. 2.5 mg) was weighed into foil capsules and analysed for total C, total N, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ using a Carlo Erba NA1500 elemental analyser (CE Instruments, Wigan, UK) and a 20-20 isotope ratio mass spectrometer (SerCon, Crewe, UK).

2.4. Soil ^{14}C content

Soils were combusted to CO_2 either in a high-pressure combustion bomb or elemental analyser (Costech ECS4010, Italy), and were cryogenically purified and split into aliquots. One aliquot was analysed for $\delta^{13}\text{C}$ using isotope ratio mass spectrometry (IRMS; Thermo-Fisher Delta V), with results expressed relative to the Vienna PDB reference standard. A second aliquot was converted to graphite via Fe–Zn reduction and analysed for ^{14}C content by accelerator mass spectrometry. Background (^{14}C -dead) and known ^{14}C age international standards (Table S1) were processed alongside the samples in accordance with the laboratory procedures and used to verify the reliability of ^{14}C and $\delta^{13}\text{C}$ analyses. Following convention (Stuiver and Polach, 1977), ^{14}C results were normalised to a $\delta^{13}\text{C}$ of -25‰ (to account for mass-dependent fractionation) and expressed as %modern (years BP = $-8033 \times \ln [\% \text{Modern}/100]$; Stuiver and Polach, 1977) and conventional radiocarbon ages (years BP, in which 0 BP = AD 1950).

Soil C mean residence times (MRTs) were calculated using a C turnover model (the Meathop Model; Harkness et al., 1986), which calculates the transient ^{14}C concentration of a C pool resulting from the incorporation of bomb- ^{14}C using:

$$A_t = \alpha A_{(t-1)} + (1-\alpha)A_i - A_{(t-1)}\lambda$$

Where A is the ^{14}C activity (content) of the soil C pool at time t , and for the preceding year ($t-1$), and A_i is the ^{14}C content of the input C (i.e. atmospheric CO_2). The model assumes steady-state, with the fraction of C exchanged annually represented as $(1-\alpha)$, and the ^{14}C decay constant ($1/\text{mean life of } ^{14}\text{C}$) represented as λ . Once the MRT curves for a range of turnover times had been generated (Fig. S1), the sample MRT was determined from the curve that most closely matched the measured soil ^{14}C content during the year of sampling. The Southern Hemisphere Zone 1–2 atmospheric ^{14}C record of Hua et al. (2013) was used for the input function (A_i).

2.5. Extraction and analyses of biomarkers

2.5.1. Ergosterol

Ergosterol was extracted according to Rousk and Bååth (2007). In brief, soil was saponified and the organic phase isolated in cyclohexane. The filtered extract was re-dissolved in methanol and passed through a PTFE syringe filter ($0.45 \mu\text{m}$, Thames Restek, Saunderton, Buckinghamshire, UK). Ergosterol was quantified using high performance liquid chromatography (HPLC; Spectra-Physics, Freemont, CA) by measuring UV absorption at 282 nm and comparing with a standard curve produced from an authentic ergosterol standard (Supelco, Bellefonte, PA, USA). A Zorbax Rx-C18 column ($3 \times 100 \text{ mm}$, $3.5 \mu\text{m}$ particle size; Crawford Scientific, Strathaven, Lanarkshire, UK), was used with a mobile phase composed of 98:2 methanol:water at a flow rate of 1 ml min^{-1} and a run time of 20 min.

2.5.2. Phospholipid fatty acids

Phospholipid fatty acid (PLFA) extraction was carried out on c. 1 g of freeze-dried soil using a modified Bligh Dyer method (Andresen et al., 2014). In brief, total lipids were extracted using excess Bligh Dyer solvent under ultrasonication. The organic phase was isolated in chloroform, and subsequently fractionated using silica gel flash column chromatography. The phospholipid fraction was obtained using a solvent series consisting of chloroform (neutral lipids), acetone (glycolipids) and methanol (phospholipids). Nonadecane in hexane was added to the phospholipid fraction as the internal standard. Fatty acids were separated from the phosphate moiety using saponification followed by acidification and converted to fatty acid methyl esters (FAMES) using dry acid methylation. The FAMES were quantified using an Agilent 6890N gas chromatograph interfaced to an Agilent 5973 Network mass spectrometer (Agilent Technologies UK Ltd., Wokingham, UK) fitted with a J&W DB225 column ($30 \text{ mm} \times 0.25 \text{ mm i.d.} \times 0.25 \mu\text{m}$; Agilent Technologies UK Ltd.) with helium as the carrier gas. The temperature programme consisted of 1 min isothermal at 80°C , followed by a ramp to 180°C at $15^{\circ}\text{C min}^{-1}$, and then to 215°C at $3^{\circ}\text{C min}^{-1}$, followed by 3 min isothermal at 215°C . Peaks were integrated using ChemStation D.01.02.16 software (Agilent Technologies UK Ltd.). FAMES were identified from the mass spectra and quantified (as $\mu\text{g g}^{-1}$ dry soil) against the peak area internal standard. The abundances of Gram positive bacteria and Gram negative bacteria were calculated by summing the concentrations of i14:0, i15:0, a15:0, i16:0, a17:0, i20:0, 10Me18:0 and 10Me17:0 (Gram positive bacteria) and 16:1 ω 7, 16:1 ω 9, cy17:0, 18:1 ω 9, 18:1 ω 7, 18:1 ω 11 and cy19:0 (Gram negative bacteria). The concentrations of all 15 PLFAs were summed to calculate the abundances of total bacteria (Zelles, 1997).

2.5.3. n-alkanes

Lipid extraction for *n*-alkane analysis was carried out according to Norris et al. (2013). In brief, total lipids were extracted from 0.25 g of freeze dried soil with 9:1 dichloromethane: methanol (v/v) under reflux for 16 h using a Soxhlet apparatus. Tetratriacontane in hexane was added as the internal standard to the solvent vessel prior to extraction. The solvent was evaporated and the total lipid extract was re-dissolved in hexane then fractionated using silica gel flash chromatography to yield the aliphatic hydrocarbons. The solvent was evaporated and the

sample re-dissolved in 100 µl hexane prior to analysis by gas chromatograph fitted with flame ionisation detection (Agilent 7890A GC; Agilent, Stockport, UK) and an HP-5 column (30 m, 0.25 µm film; Agilent, UK). The temperature programme consisted of 1 min isothermal at 40 °C, followed by a ramp to 130 °C at 20 °C min⁻¹, then to 300 °C at 4 °C min⁻¹, and then 10 min isothermal at 300 °C. The plant wax *n*-alkanes C₂₁–C₃₃ were identified using retention times and quantified against the internal standard.

2.6. Data analyses

Two way ANOVA was used to determine the main and interactive effects of island and depth on the measured parameters. One way ANOVA with Tukey's multiple range test was used to identify significant differences between means. Associations between soil physicochemical parameters likely to be associated with climate change (moisture, C and organic matter concentrations, $\delta^{13}\text{C}$ content and ^{14}C enrichment) and ergosterol concentrations, the abundances of total, Gram negative and Gram positive bacteria, and the ratio of Gram positive to Gram negative bacteria, were tested with Pearson's correlations. All analyses were carried out using MINITAB 17 software.

3. Results

3.1. Aboveground plant C and N concentrations, C:N ratio and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

Analyses of the aboveground plant parts of *Deschampsia antarctica* indicated no significant effects of island on the concentrations of tissue C or N, or on C:N ratio (all $F_{2,6} < 3.73$, $P > 0.089$). These analyses showed that aboveground *D. antarctica* tissues sampled from Bird Island were more depleted in $\delta^{13}\text{C}$ than those from Léonie Island (means \pm SEM of $-28.94 \pm 0.19\text{‰}$ and $-28.06 \pm 0.22\text{‰}$, respectively; $F_{2,6} = 6.68$, $P = 0.030$, data not shown), with the $\delta^{13}\text{C}$ values of tissues from Signy Island ($-28.15 \pm 0.15\text{‰}$) not differing from those at the other two islands. Conversely, aboveground *D. antarctica* tissues from Léonie Island were more enriched in $\delta^{15}\text{N}$ than those from Bird Island or Signy Island (means \pm SEM of $16.68 \pm 1.9\text{‰}$, $12.66 \pm 0.63\text{‰}$ and $10.82 \pm 0.60\text{‰}$, respectively; $F_{2,6} = 6.14$, $P = 0.035$, data not shown).

3.2. Soil pH values, moisture and organic matter concentrations

Mean (\pm SEM) pH values of 4.76 (± 0.07), 4.29 (± 0.20) and 4.53 (± 0.19) were recorded in the soils sampled from Bird Island, Signy Island and Léonie Island, respectively. Soil pH value did not differ between islands or different depths, and was unaffected by the island \times depth interaction (Table 1). In contrast, there were significant ($P < 0.05$) main effects of island and depth on the concentrations of moisture and organic matter in soil (Table 1), with both variables being higher in soils

Table 1

Main and interactive effects of island and depth on soil physicochemical factors, determined by two-way ANOVA^a.

Response	Island		Depth		Island \times depth	
	$F_{2,18}$	<i>P</i>	$F_{2,18}$	<i>P</i>	$F_{4,18}$	<i>P</i>
pH value	2.01	0.163	0.79	0.471	0.65	0.634
Moisture concentration	105.04	< 0.001	5.32	0.015	3.52	0.027
Organic matter concentration	12.64	< 0.001	3.66	0.046	0.64	0.641
C concentration	7.27	0.005	1.46	0.259	0.64	0.640
N concentration	5.56	0.013	0.38	0.692	0.06	0.992
C:N ratio	32.66	< 0.001	0.31	0.740	0.44	0.776
$\delta^{13}\text{C}$ content	18.88	< 0.001	3.24	0.063	0.97	0.446
$\delta^{15}\text{N}$ content	57.34	< 0.001	1.54	0.241	0.04	0.996

^a Analyses were based on nine values per island, derived from depths of 2 cm, 4 cm and 8 cm in each of three independent replicate pits dug at the island.

from sub-Antarctic Bird Island than in those from the two maritime Antarctic islands, and declining at increasing depth (Fig. 2a and b). There was also a significant ($P = 0.027$) interactive effect of island and depth on moisture concentration (Table 1), with more pronounced declines in moisture at greater depths on Léonie Island than at the other two islands (Fig. 2a).

3.3. Soil C and N concentrations, C:N ratio and $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values

Two way ANOVA indicated a significant ($P = 0.005$) main effect of island on total soil C concentration (Table 1), with soils from sub-Antarctic Bird Island having higher C concentrations than those from Signy Island or Léonie Island (Fig. 2c). Depth, and the interaction between island and depth, did not influence soil C concentrations (Table 1). Two way ANOVA also showed a significant ($P = 0.013$) effect of island on total soil N concentration (Table 1), with soils from Léonie Island having higher N concentrations than those from Bird or Signy islands (Fig. 2d). Depth and the island \times depth interaction had no effect on this parameter (Table 1). Soil C:N ratio also differed significantly ($P < 0.001$) between islands, with lower ratios at Léonie Island and Signy Island than at Bird Island (means \pm SEM of 9.22 ± 0.22 , 10.82 ± 0.35 and 15.72 ± 0.85 , respectively; data not shown), but with no effects of depth or the interaction between island and depth on this parameter (Table 1). The same analyses similarly showed there to be a highly significant ($P < 0.001$) main effect of island on soil $\delta^{13}\text{C}$ content (Table 1), with soils from Bird Island being ^{13}C -depleted by 2.6‰, compared with the soils from the other two islands (Fig. 2e). There was also a slight ($P = 0.063$) effect of depth on ^{13}C content (Table 1), with less depleted $\delta^{13}\text{C}$ values further down the soil profile, particularly at Signy Island, where soil from 8 cm depth was ^{13}C -enriched by 2.5‰ compared with soil from 2 cm depth (Fig. 2e). Analyses of soil $\delta^{15}\text{N}$ content also indicated highly significant ($P < 0.001$) differences between islands (Table 1), with soils from Léonie Island being ^{15}N -enriched by 5.9–6.6‰ compared with those from Bird and Signy islands (Fig. 2f). There were no effects of depth or island \times depth on soil ^{15}N values (Table 1).

3.4. Soil ^{14}C content

Radiocarbon analyses indicated that the bulk soils from Bird Island at 2 cm, 4 cm and 8 cm depths all contained bomb- ^{14}C (Table 2). Modelling of bomb- ^{14}C turnover indicated more rapid C cycling at Bird Island than at the other two islands, with estimated mean C residence times in soil ranging from 6 to 30 years across all three depths at the northernmost island (Table 2). At Signy Island, clear evidence of bomb- ^{14}C was restricted to soils at 2 cm and 4 cm depths, while the ^{14}C content of the soil at 8 cm depth ($98.80 \pm 0.45\%$ modern), the estimated age of which was 97 ± 37 years BP, was suggestive of a predominantly pre-bomb source. The soils from Léonie Island showed the greatest spans in ages. Post bomb- ^{14}C at this island was only present at 2 cm depth, with soils from 4 cm to 8 cm depths being too ^{14}C -depleted to be investigated using the bomb- ^{14}C model (Table 2). The oldest soil at Léonie Island, with a conventional radiocarbon age of c. 1745 \pm 35 years BP, was recorded at 4 cm depth, with soil at 8 cm depth having an estimated radiocarbon age of 681 \pm 37 years BP (Table 2).

3.5. Ergosterol and PLFA biomarkers

Concentrations of the fungal biomarker ergosterol differed between islands, with two way ANOVA indicating a highly significant ($P < 0.001$) reduction in its concentration in soils from Bird Island compared with those from the other two islands (Table 3; Fig. 3a). Ergosterol concentration also differed significantly ($P = 0.012$) between depths (Table 3), with higher concentrations at depths of 2 cm compared with 4 cm and 8 cm depths in the maritime Antarctic, and particularly at Léonie Island (Fig. 3a). Two way ANOVA also showed there to be a highly significant

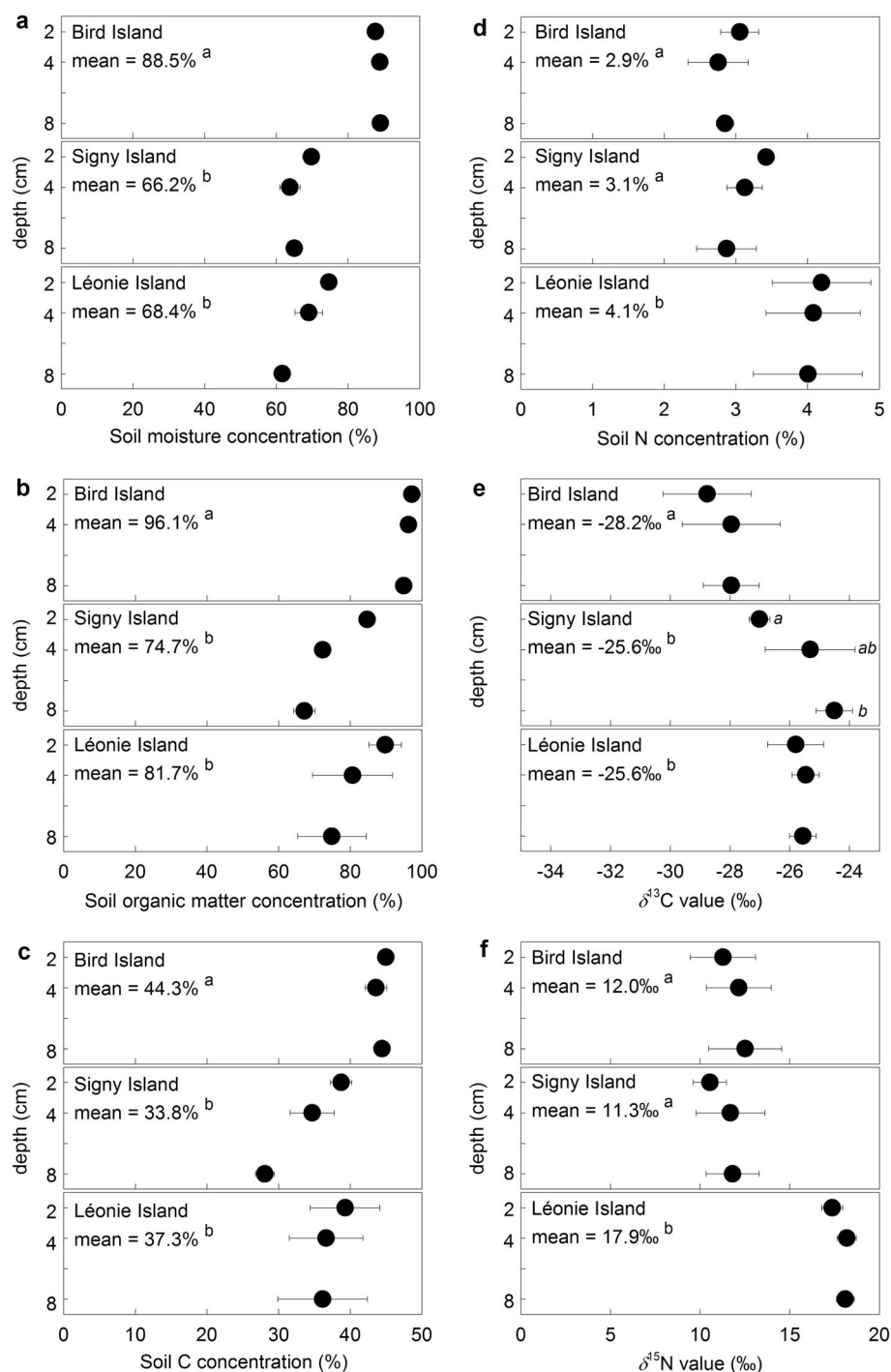


Fig. 2. Mean (a) moisture concentration, (b) organic matter concentration, (c) C concentration, (d) N concentration, (e) $\delta^{13}\text{C}$ value and (f) $\delta^{15}\text{N}$ value of soils sampled from depths of 2 cm, 4 cm and 8 cm at Bird Island, Signy Island and Léonie Island. Each value is a mean of three independent replicates and bars represent SEM. Mean values across all depths at each island are also shown, with superscripted unitalicised letters indicating significant ($P < 0.05$) differences in means between islands. Values that differ between distinct depths at Signy Island in (e) are denoted by different italicised letters.

Table 2

$\delta^{13}\text{C}$ content, ^{14}C enrichment (%Modern), conventional radiocarbon age and modelled mean residence time of C in bulk soil sampled from 2, 4 and 8 cm depths from three Antarctic islands.

Island	Depth (cm)	$\delta^{13}\text{C}_{\text{VPDB}}^*$ (‰)	^{14}C enrichment (% Modern $\pm 1\sigma$)	Conventional Radiocarbon Age (years BP $\pm 1\sigma$)	Mean Residence Time (years) ^a
Bird	2	-28.3	107.14 \pm 0.47	n/a	6 [110]
	4	-27.0	109.67 \pm 0.48	n/a	10 [75]
	8	-27.1	115.35 \pm 0.53	n/a	30
Signy	2	-27.1	109.98 \pm 0.48	n/a	10 [70]
	4	-27.2	119.36 \pm 0.55	n/a	30
	8	-24.4	98.80 \pm 0.45	97 \pm 37	375
Léonie	2	-25.8	109.47 \pm 0.48	n/a	9 [75]
	4	-25.0	80.47 \pm 0.35	1745 \pm 35	–
	8	-25.0	91.88 \pm 0.42	681 \pm 37	–

*Note that, despite separate $\delta^{13}\text{C}$ measurements being reported (Fig. 2e), these data are also shown as they were used to normalise the ^{14}C values.

^a In some cases, two MRT values are possible, reflecting the rising and falling parts of the bomb ^{14}C curve (the MRT considered least likely is given in square brackets, based on the assumption that turnover time will increase with depth). MRTs are not calculated for samples with <97% Modern because these samples show no evidence of bomb ^{14}C incorporation, and therefore the conventional radiocarbon age provides an estimate of the MRT (Bol et al., 1999). Abbreviation: n/a, not applicable.

Table 3

Main and interactive effects of island and depth on the concentrations of biomarkers in soils, determined by two-way ANOVA^a.

Response	Island		Depth		Island \times depth	
	$F_{2,18}$	P	$F_{2,18}$	P	$F_{4,18}$	P
Ergosterol concentration	15.41	< 0.001	5.67	0.012	2.49	0.080
Total bacterial PLFA concentration	16.16	< 0.001	7.06	0.006	0.11	0.978
Gram negative bacteria PLFA concentration	38.35	< 0.001	11.17	0.001	0.40	0.804
Gram positive bacteria PLFA concentration	4.17	0.033	1.55	0.239	0.03	0.998
Gram positive: Gram negative bacteria ratio	16.57	< 0.001	3.26	0.062	2.46	0.083
Total <i>n</i> -alkanes concentration	13.25	< 0.001	0.68	0.517	0.46	0.765

^a Details of analyses as in Table 1.

($P < 0.001$) effect of island on the concentrations of total bacterial PLFA biomarkers (Table 3), with concentrations of total bacterial PLFAs being higher in soils from Bird Island than in those from the two maritime Antarctic islands, and concentrations of these biomarkers in soil at Signy Island being higher than in soil at Léonie Island (Fig. 3b). There was also a significant effect ($P = 0.006$) of depth on total bacterial PLFAs (Table 3), with reductions in the concentrations of these biomarkers in deeper soils (Fig. 3b). An interactive effect of island and depth was not recorded on the concentrations of total bacterial PLFAs (Table 3). The concentrations of PLFA biomarkers for Gram negative bacteria and Gram positive bacteria also altered significantly between the three islands: there was a highly significant ($P < 0.001$) effect of island on those for Gram negative bacteria (Table 3), with higher concentrations of the biomarkers for these taxa in soil from Bird Island than those from the other two islands (Fig. 3c). There was also a significant ($P = 0.001$) effect of depth on the concentrations of Gram negative bacteria biomarkers (Table 3), with declining concentrations of PLFAs for these taxa at increasing depths (Fig. 3c). The concentrations of Gram positive bacteria biomarkers also differed between islands (Table 3), with higher concentrations in soils from Bird and Signy islands than in those from Léonie island (data not shown). A highly significant ($P < 0.001$) effect of island on the ratio of Gram positive bacteria to Gram negative bacteria

biomarkers was also recorded (Table 3), with two way ANOVA indicating that this ratio was lower at Bird Island than at the two maritime Antarctic islands (Fig. 3d). There was also a slight ($P = 0.062$) effect of depth on the ratio of Gram positive bacteria to Gram negative bacteria biomarkers (Table 3), with a tendency towards higher ratios at greater depths in the soil profile, particularly at Signy Island (Fig. 3d).

Correlative analyses between the concentrations of ergosterol and soil physicochemical parameters likely to be associated with climate change indicated a negative association with soil moisture concentration, and a positive association with soil $\delta^{13}\text{C}$ content (Table 4). They also indicated consistent positive associations between the abundances of total bacteria and Gram negative bacteria in soil and the concentrations of soil moisture, organic matter and C (Table 4). The concentrations of PLFA biomarkers for total bacteria and Gram negative bacteria were also both negatively associated with soil $\delta^{13}\text{C}$ content (Table 4). In contrast to the responses for total and Gram negative bacteria, there were relatively few associations between the abundances of Gram positive bacteria in soil and the soil physicochemical parameters, with a negative association between the abundances of these bacteria and soil $\delta^{13}\text{C}$ content (Table 4). The Gram positive: Gram negative bacteria ratio was negatively associated with concentrations of soil moisture, organic matter and C, with a positive association between the ratio and soil $\delta^{13}\text{C}$ content (Table 4). Along with the concentrations of ergosterol and bacterial PLFA biomarkers, this ratio was not associated with soil ^{14}C enrichment (Table 4).

3.6. *n*-alkane biomarkers

There was a highly significant effect of island on the concentration of total *n*-alkanes in soils (Table 3), with higher concentrations of these biomarkers in soils from Bird Island than in those from Signy and Léonie islands (means \pm SEM of 389.1 \pm 59.0, 110.7 \pm 44.4 and 87.90 \pm 12.6, respectively; $F_{2,18} = 13.25$, $P < 0.001$; data not shown). The same pattern was recorded for the *n*-alkanes C₂₂, C₂₃, C₂₄, C₂₅, C₂₇, C₂₉, C₃₁ and C₃₃, with higher concentrations of these individual *n*-alkanes in soils sampled from Bird Island relative to those from the two maritime Antarctic islands ($F_{2,18} = 4.56$ –17.17, all $P < 0.05$; Fig. 4a–f, h–i). The exception to this pattern was the *n*-alkane C₃₀, which was lower in concentration in soils sampled from Signy Island than in those from the other two islands ($F_{2,18} = 6.53$, $P = 0.007$; Fig. 4g). There were no effects of island on the concentrations of the *n*-alkanes C₂₁, C₂₆, C₂₈ and C₃₂ (all $F_{2,18} < 3.35$, $P > 0.05$; data not shown). Depth, or the island \times depth interaction, did not affect the concentrations of total *n*-alkanes (Table 3) or of any individual *n*-alkane (all $F_{2,18} < 1.09$, $P > 0.35$ and $F_{4,18} < 0.96$, $P > 0.45$, respectively). The most abundant *n*-alkane recorded in soil was C₃₁ (mean 50.7 $\mu\text{g g}^{-1}$ soil), followed by C₂₅, C₂₉, C₃₃, C₂₃ and C₂₇ (means across all islands of 27.2, 20.8, 19.2, 17.8 and 17.2 $\mu\text{g g}^{-1}$ soil, respectively; Fig. 4). Other *n*-alkanes were present at mean

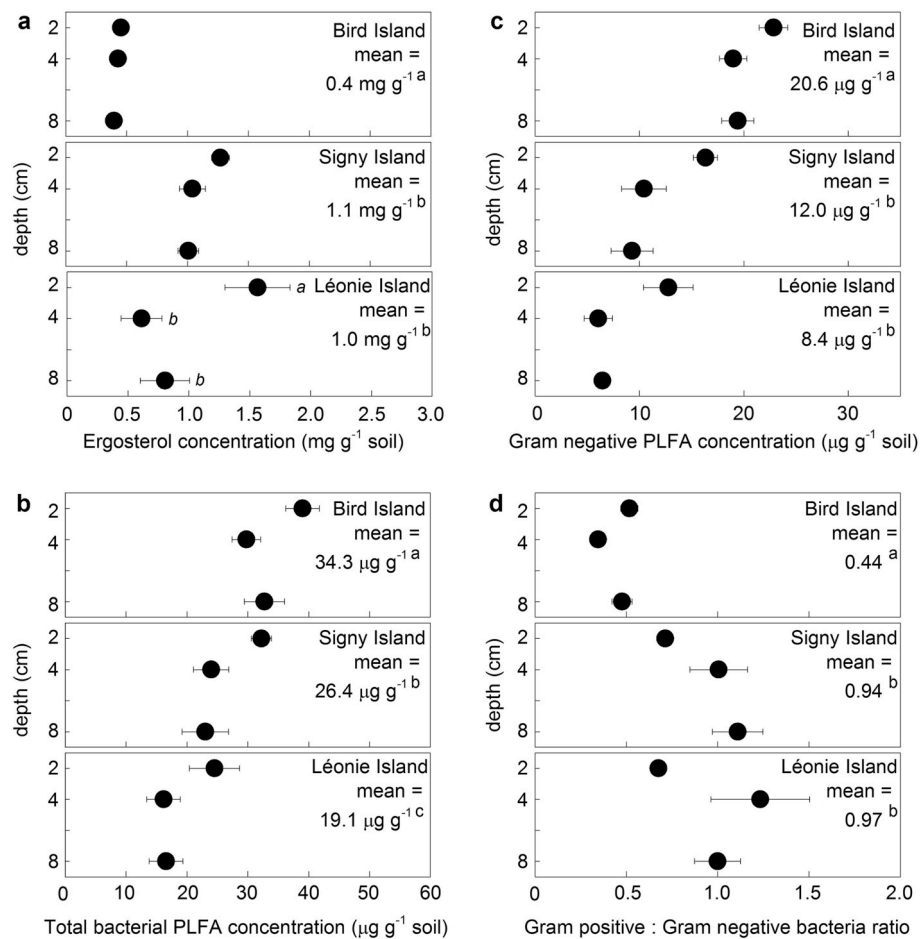


Fig. 3. Mean (a) ergosterol concentration (b) total bacterial PLFA concentration, (c) Gram negative bacterial PLFA concentration and (d) Gram positive: Gram negative bacterial ratio in soils sampled from depths of 2 cm, 4 cm and 8 cm at Bird Island, Signy Island and Léonie Island. Replication and notation as in Fig. 2. Values that differ between distinct depths at Léonie Island in (a) are denoted by different italicised letters.

Table 4

Coefficients from Pearson's correlations testing for associations between concentrations of ergosterol and bacterial PLFAs and selected soil physicochemical parameters^a. Significant coefficients are marked in bold and denoted by * $P < 0.05$ and *** $P < 0.001$.

Soil physicochemical parameter	Ergosterol concentration	Bacterial PLFA concentration			Gram positive: Gram negative bacteria ratio
		Total	Gram negative	Gram positive	
Moisture concentration	-0.451 *	0.681 ***	0.813 ***	0.281	-0.774 ***
Organic matter concentration	-0.132	0.659 ***	0.719 ***	0.318	-0.724 ***
C concentration	-0.078	0.659 ***	0.691 ***	0.308	-0.635 ***
δ ¹³ C content	0.414 *	-0.810 ***	-0.871 ***	-0.424 *	0.710 ***
¹⁴ C enrichment	0.148	0.663	0.633	0.647	-0.633

^a d.f. for all predictors were 26, except ¹⁴C enrichment, for which d.f. were eight.

concentrations of <8.4 μg g⁻¹ soil.

4. Discussion

The analyses reported here indicate substantial changes to soils sampled from across a climatic gradient through the sub- and maritime Antarctic, with those from Bird Island in sub-Antarctica having different concentrations of moisture, organic matter, total C, ¹³C and fungal, bacterial and plant biomarkers, compared with soils from Signy Island and Léonie Island in the maritime Antarctic. The concentrations of C and

N, or the C:N ratio, in aboveground plant biomass – which are key determinants of plant litter decomposition and soil development (Swift et al., 1979) – did not alter across the gradient, indicating that it is the 5–8 °C higher annual air temperature at Bird Island, combined with the island's higher precipitation, that exert substantial long-term impacts on its soils. These findings corroborate previous studies that have recorded impacts of climate on soil formation and the decomposition of plant litter, with water availability and temperature being the main factors influencing these processes at continental and regional scales (Swift et al., 1979; Meentemeyer and Berg, 1986; Berg et al., 1993).

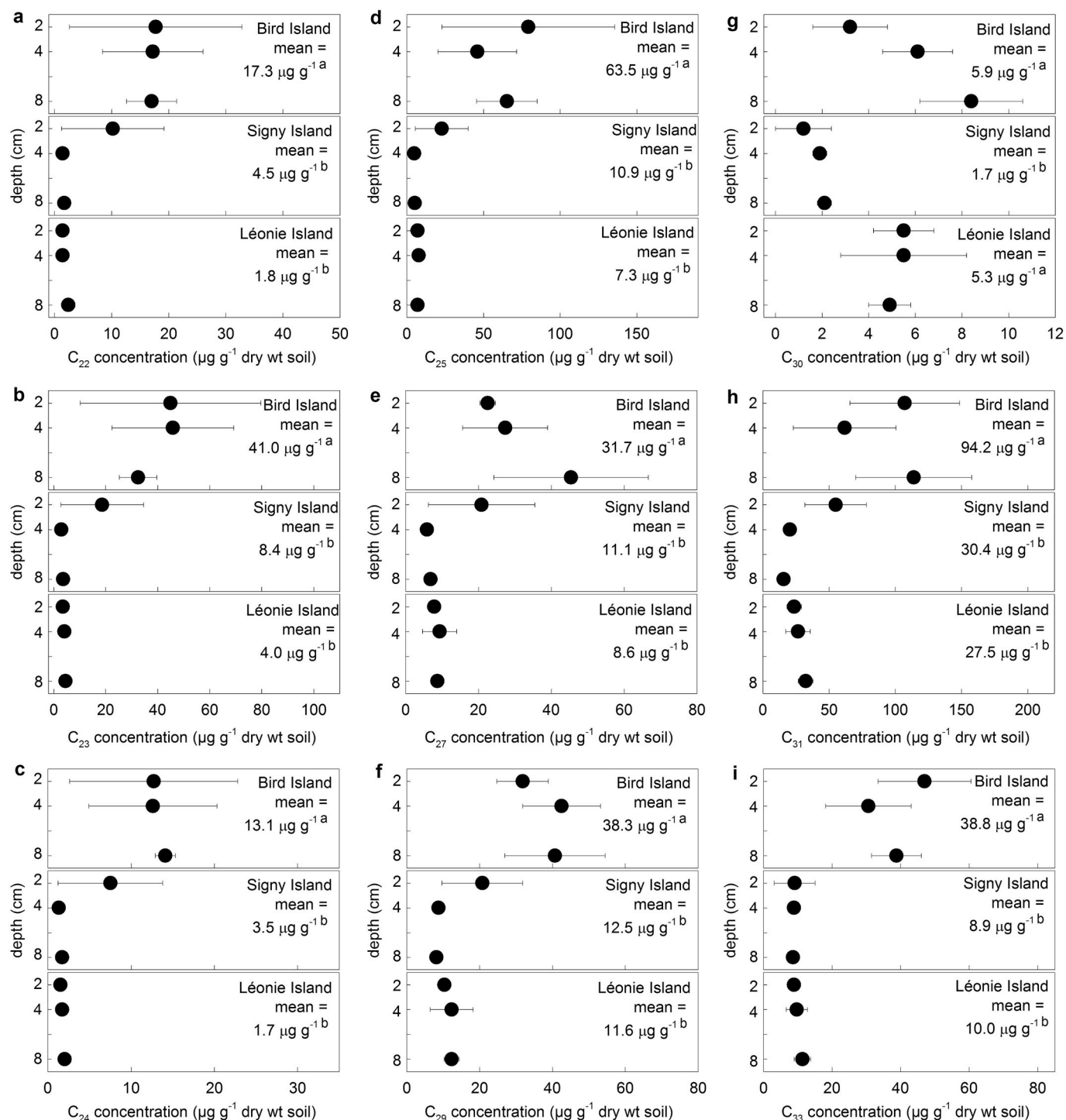


Fig. 4. Mean concentrations of the *n*-alkanes C₂₂–C₂₅, C₂₇, C₂₉–C₃₁ and C₃₃ in soils sampled from depths of 2 cm, 4 cm and 8 cm at Bird Island, Signy Island and Léonie Island. Replication and notation as in Fig. 2. Note that there were no differences between depths for the concentrations of any *n*-alkane.

The ¹⁴C analyses here identified long-term effects of the warmer and wetter environment at Bird Island on the turnover of soil C. The soils sampled from this island at 2 cm, 4 cm and 8 cm depths all contained bomb-¹⁴C, unambiguously indicating that all, or a substantial component, of the C in these soils was fixed from the atmosphere after the mid 1950s. In contrast, and in agreement with previous studies showing that the estimated age of C in maritime Antarctic moss banks increases with depth (Royles et al., 2013; Amesbury et al., 2017), modern ¹⁴C was restricted to depths of 2 cm and 4 cm at the two maritime Antarctic islands, with C at 8 cm in these soils all originating from before c. 1955.

¹⁴C modelling also indicated slower C turnover at Signy Island compared with Bird Island, particularly for the deepest soils. The oldest C, aged to c. 1745 years BP, was present in the soil sampled from Léonie Island, corroborating previous studies showing the presence of millennium-age C in maritime Antarctic and sub- or High Arctic soils (Björck et al., 1991; Royles et al., 2012; Hartley et al., 2012; Charman et al., 2018; Vaughn and Torn, 2019), and the recent finding that a saprotrophic fungus present in maritime Antarctic soil respire C to the atmosphere that is up to c. 1200 years BP in age (Newsham et al., 2018). However, the soil containing this millennium-aged C was sampled from a depth of 4 cm,

and not 8 cm, suggesting a disturbance event at Léonie Island, possibly associated with the thawing of permafrost or cryoturbation (Ernakovich et al., 2015).

In contrast to the frequent differences between islands in the majority of the parameters measured here, depth in the soil profile had relatively few effects on the soils studied, with, as recorded in Antarctic, Arctic and temperate soils, moisture, organic matter and microbial biomarker concentrations being higher in shallower soils (Schmidt and Böhler, 2002; Elberling et al., 2006; Baldrian et al., 2012). However, in agreement with the more depleted $\delta^{13}\text{C}$ contents of aboveground plant biomass and soils recorded at Bird Island than at the maritime Antarctic islands, reflecting the higher water availability and more favourable conditions for photosynthesis in sub-Antarctica (Farquhar et al., 1989), there was also a slight ($P = 0.063$) effect of depth on ^{13}C , with more enriched ^{13}C contents in deeper soils. While we cannot rule out the influence of other factors in explaining this trend, such as the isotopic fractionation of ^{13}C during decomposition (Schweizer et al., 1999), it is probable that changes to the $\delta^{13}\text{C}$ signature of the atmosphere since the 1850s are responsible for the more depleted $\delta^{13}\text{C}$ signatures of shallower soils. As coal and oil are of organic origin and are thus depleted in $\delta^{13}\text{C}$, since the Industrial Revolution, the $\delta^{13}\text{C}$ signature of atmospheric CO_2 has declined by 1.5–1.7‰ (Francey et al., 1999; McCarroll and Loader, 2004). This has led to a corresponding decline in the $\delta^{13}\text{C}$ contents of plant tissues (Leavitt and Lara, 1994), including those of maritime Antarctic mosses, the cellulose of which has shown a decline in $\delta^{13}\text{C}$ from −24.4‰ to −26.5‰ over the previous 150 years (Royles et al., 2013). In the soils from Signy Island at a depth of 2 cm, which ^{14}C analyses indicated were formed from plant material originating since the mid 1950s, C was ^{13}C -depleted by 2.5‰ relative to the soil C sampled from 8 cm depth, which was aged to 97 ± 37 years, suggesting that this lower $\delta^{13}\text{C}$ signal arises from changes to the ^{13}C content of atmospheric CO_2 . We also cannot discount the possibility that the more depleted ^{13}C contents of soils from Bird Island, which were all formed post-1955, may have been in part owing to the declining $\delta^{13}\text{C}$ signature of atmospheric CO_2 during the previous century. At present, however, it is unclear why the $\delta^{13}\text{C}$ contents of soils from distinct depths at Léonie Island did not differ, but, as discussed above for the ^{14}C signatures, it is possible that these soils may have become mixed as a result of physical disturbance.

The main environmental variables that will alter as the climate of maritime Antarctica changes are surface air temperature and water availability, with increases in the latter being associated with more frequent snowmelt and rainfall events (Bromwich et al., 2014; Marshall et al., 2017). In the soils of the region, these changes are likely to lead to deeper active layers, with associated positive effects on soil and plant community development (Guglielmin et al., 2008; Biskaborn et al., 2019), soil moisture concentrations (Fisher et al., 2016) and pools of C and organic matter as aboveground plant productivity increases (Fowbert and Smith, 1994; Royles et al., 2012, 2013; Amesbury et al., 2017; Charman et al., 2018). The correlative analyses here indicate that substantial increases in soil moisture, with associated depletion of soil $\delta^{13}\text{C}$ contents, will lead to declines in fungal biomass, as the habitat for the fungi that inhabit these usually arid soils, such as *Pseudogymnoascus*, the most frequent fungal taxon in maritime Antarctic soils (Newsham et al., 2016), becomes less favourable. These analyses also suggest that the relative abundances of Gram positive bacteria, such as members of the Actinobacteria, which have thick cell walls composed of peptidoglycan, enabling their survival in arid soils at low temperatures (Schimel et al., 2007), will also decline in wetter, ^{13}C -depleted maritime Antarctic soils containing more organic matter. This observation is in accordance with a previous study showing reductions in the ratio of Gram positive to Gram negative bacteria in soils from Signy Island (60 °S) compared with those from south-eastern Alexander Island (72 °S) in the more arid southern maritime Antarctic (Dennis et al., 2013). In contrast, the analyses here suggest that Gram negative bacteria are likely to become more abundant in maritime Antarctic soils as they transition towards those of sub-Antarctica. Notably, members of the *Betaproteobacteria* and

Bacteroidetes, such as the *Comamonadaceae* and *Chitinophagaceae*, which are more frequent in warmer maritime Antarctic habitats (Dennis et al., 2019) and in nutrient-amended Arctic soils (Koyama et al., 2014), are likely to become more abundant in maritime Antarctic soils, enhancing decomposition rates and C efflux (Fierer et al., 2007).

Analyses of *n*-alkanes, lipids which are derived from plant epicuticular waxes that are resistant to degradation, enable changes to plant community composition to be determined as ecosystems develop (Norris et al., 2013). The predominant pattern recorded here for these biomarkers was of higher concentrations in soils from Bird Island compared with those from the two maritime Antarctic islands, reflecting the more productive plant community at the sub-Antarctic island, and, as found elsewhere (Eglington and Hamilton, 1967), a predominance of odd number-chained *n*-alkanes in soils. As anticipated for soils dominated by *Deschampsia antarctica*, we also found an abundance of the *n*-alkanes C_{31} and C_{29} , which are biomarkers for monocotyledonous plant species (Maffei, 1996). The shorter-chain alkane C_{25} , which is typically found in bryophyte tissues (Baas et al., 2000), was also found to be more abundant in soil at Bird Island, possibly reflecting an increased biomass of lower plants at this location. However, despite these changes to the concentrations of *n*-alkane biomarkers in soils from along the climatic transect, our analyses showed that their concentrations did not alter with depth through the soil profile. This observation suggests that, despite rising surface air temperatures in the maritime and sub-Antarctic between the 1950s and late 1990s (Adams et al., 2009; Turner et al., 2016), plant community composition in the region has not altered appreciably. It contrasts with observations from the Arctic, in which shrubs have become more frequent in warmer habitats over the last half century (Myers-Smith et al., 2011) – possibly associated with the capacity of this plant form to retain new C inputs belowground (Lynch et al., 2018) – and with those from Eastern Antarctica, where moss community composition has changed rapidly since the turn of the millennium owing to increased aridity (Robinson et al., 2018).

Although the analyses here indicated consistent differences in C pools and the majority of biomarkers between the soils at sub-Antarctic Bird Island and the two maritime Antarctic Islands, soils at Léonie Island had the lowest C:N ratios, and also had 0.7–1.2% higher N concentrations than those sampled from Bird Island and Signy Island. These differences most probably arose from higher N inputs from guano at Léonie Island. In a previous study, Bokhorst et al. (2007b) reported that N inputs to soil at Anchorage Island (a member of the Léonie Islands group) are an order of magnitude higher than at Signy Island, with the majority of the N arising from guano of south polar skuas (*Catharacta maccormicki*), a bird species that is also frequent at the sites on Léonie Island studied here. Soils and plant material in the Léonie Islands group are also highly ^{15}N -enriched, with mean soil and bryophyte $\delta^{15}\text{N}$ values of 14.0‰ and 8.5–15.8‰, respectively (Bokhorst et al., 2007b), compared with the $\delta^{15}\text{N}$ values of 17.9‰ and 16.7‰ recorded here for soil and aboveground *D. antarctica* tissues, respectively. The highly ^{15}N -enriched soil and plant material at these islands can be ascribed to higher inputs of guano from *C. maccormicki*, emphasising the importance of marine vertebrates in transferring N from the sea to the land in the maritime Antarctic (Bokhorst et al., 2019).

5. Conclusions

We conclude that further climate warming in maritime Antarctica, with associated increases in snowmelt and precipitation (Adams et al., 2009; Bromwich et al., 2014; Medley and Thomas, 2019), is likely to have a substantial influence on the vegetated soils of the region. Specifically, the analyses here indicate that rising air temperatures and water availability will enhance C and soil organic matter concentrations, deplete soil $\delta^{13}\text{C}$ contents, accelerate decomposition rates and decrease mean C residence times, increase the abundances of *n*-alkanes and alter soil microbial communities by favouring Gram negative bacteria over Gram positive bacteria and fungi. However, in accordance with previous

studies, which concluded that substantial warming (4–8 °C) will be required before organic matter decomposition is affected in maritime Antarctic soils (Bokhorst et al., 2007a), the present data show that the majority of the observed effects occur between soils from islands that differ in mean annual air temperatures by 5–8 °C. Although changes to the soils of maritime Antarctica will be accelerated by unrestricted emissions of greenhouse gases to the atmosphere (e.g., representative concentration pathway [RCP] 8.5; IPCC, 2014), at the rates of climate warming predicted to occur under moderate greenhouse gas emission scenarios (0.2–0.4 °C per decade; Bracegirdle et al., 2008; Bracegirdle and Stephenson, 2012), significant alterations to these soils will take at least a century to manifest themselves in the natural environment. Irrespective of the rate at which these changes occur, given the central importance of soil processes and microbial communities to ecosystem development (Wall et al., 2010), they are nevertheless likely to have substantial impacts on maritime Antarctic terrestrial habitats.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

This research was funded by an Antarctic Funding Initiative grant and associated awards from the UK Natural Environment Research Council (grant numbers NE/H014098/1, NE/H014772/1 and NE/H01408X/1) and a NERC Radiocarbon Facility NRCF010001 allocation (1690.0313). The British Antarctic Survey's Logistics Group and the officers and ship's company of the RRS James Clark Ross provided transport to and from sampling sites. Mick Mackey, Andy Wood, Mike Dunn, Ash Cordingley, Ian Rudkin, Ana Bertoldi, Steph Stenna and Stacey Adlard helped to collect samples. Laura Gerrish drew the map shown in Fig. 1. Anonymous reviewers supplied helpful comments. Our much-valued colleague, the late Jiri Vána of Charles University in Prague, helped to identify liverworts. All are gratefully acknowledged.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.soilbio.2019.107682>.

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