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Successional patterns along soil development gradients formed by glacier retreat in the Maritime Antarctic, King George Island

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Abstract

Background: Maritime Antarctica is severely affected by climate change and accelerating glacier retreat forming temporal gradients of soil development. Successional patterns of soil development and plant succession in the region are largely unknown, as are the feedback mechanisms between both processes. Here we identify three temporal gradients representing horizontal and vertical glacier retreat, as well as formation of raised beaches due to isostatic uplift, and describe soil formation and plant succession along them. Our hypotheses are (i) plants in Antarctica are able to modulate the two base parameters in soil development, organic C content and pH, along the temporal gradients, leading to an increase in organic carbon and soil acidity at relatively short time scales, (ii) the soil development induces succession along these gradients, and (iii) with increasing soil development, bryophytes and *Deschampsia antarctica* develop mycorrhiza in maritime Antarctica in order to foster interaction with soil.

Results: All temporal gradients showed soil development leading to differentiation of soil horizons, carbon accumulation and increasing pH with age. Photoautptroph succession occurred rapidly after glacier retreat, but occurrences of mosses and lichens interacting with soils by rhizoids or rhizines were only observed in the later stages. The community of ground dwelling mosses and lichens is the climax community of soil succession, as the Antarctic hairgrass *D. antarctica* was restricted to ornithic soils. Neither *D. antarctica* nor mosses at the best developed soils showed any sign of mycorrhization.

Conclusion: Temporal gradients formed by glacier retreat can be identified in maritime Antarctic, where soil development and plant succession of a remarkable pace can be observed, although pseudo-succession occurs by fertilization gradients caused by bird feces. Thus, the majority of ice-free surface in Antarctica is colonized by plant communities which interact with soil by litter input rather than by direct transfer of photoassimilates to soil.

Keywords: Temporal gradients, Chronosequences, Soil succession, Soil organic carbon, Ornithic, Mycorrhiza, Maritime Antarctica, King George Island

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Background

Maritime Antarctica is severely affected by climate change, leading to the acceleration of ice melting and glacier retreat in the region [1, 2]. These processes are accompanied by sea level rise, changes in ocean circulation and impacts on marine food chains [3, 4]. Glacier retreat also opens up new surfaces for terrestrial life [5], and presents an important transition from a glacial to a pedogenic geosystem. Currently, in Antarctica less than 0.35 % of the continental area is ice free and accessible for researchers studying terrestrial processes, e.g. soil scientists [6]. This ice-free area is subdivided into three distinct biogeographical zones: (i) continental, (ii) maritime and (iii) sub-Antarctic. Several research groups are focusing on Antarctic soils on the continental cold desert of the Dry Valleys, the coastal areas, and on soils from maritime Antarctic (e.g. [6, 7]). The northern part of the Antarctic Peninsula (including the associated islands) has a cold moist maritime climate that allows for different soil formation than elsewhere in Antarctica [8]. The chemical weathering is expected to be more pronounced in maritime Antarctica than in the cold deserts of the ice free areas of the continental zone, e.g. the Dry Valleys [9]. Simas et al. [10] provided important analytical and morphological data for the main soils found in the maritime Antarctic region and described the soils as being poorly developed with physical weathering and cryoturbation as the major processes in ice-free areas.

In maritime Antarctica the weathering and soil formation takes place on exposed glacial deposits. As glacier extent retreats, new development of protosoils starts at the glacier margins, while the older, formerly ice-covered areas undergo organismic succession, feeding back to soil development [11]. Therefore, glacier retreat produces temporal gradients in the landscape [12–14], which allow for a deep insight into Earth's history. Unlike glacier retreat in montane areas on temperate continents, where invasions of higher developed plants occur rapidly from nearby vegetated areas, successional gradients in Antarctica largely follow a pattern of development from cyanobacteria and eukaryotic algae towards mosses, liverworts, and lichens and without interference from higher plants. Although studies on microbiological successions in short chronosequences in proglacial areas exist [15, 16], there are few studies of vegetational succession along larger temporal gradients [17].

Recently new higher plants, such as *Colobanthus quitensis* (KunthBartl) have been recorded in maritime Antarctica [18], while others such as Antarctic hairgrass *Deschampsia antarctica* (E. Desv.) have propogated over large areas in historic times [19]. These plants may constitute new climax species of Antarctic succession, and as photoautotrophic organisms are heavily engaged in soil formation they will likely accelerate soil formation due to their different functional traits [20]. Cyanobacteria provide the first stock of soil nitrogen and help to overcome nitrogen limitations for terrestrial eukaryotic algae. As carbon stocks in soil rise, organic matter increasingly acts as an exchange matrix for other nutrients such as e.g. Mg or Ca. The establishment of lichens and mosses further add to carbon (C) stocks in soil by the addition of litter, and probably start to interact with soil by their rhizoids and rhizines. These interactions might already comprise biogenic weathering, a process where autotrophically fixed energy is used to break down primary minerals in soil, in order to gain nutrients from this source (e.g. [21]). The energy might either be acquired in a saprotrophical way by using litter as a source, or directly via a symbiotic connection to the producing plants. Such symbiotic short-cuts in energy supply are especially effective in biogenic weathering, although little is still known about the nature of the processes and the rates. Nevertheless, it can be hypothesized, that higher plants like *D. antarctica* are potentially able to generate higher biogenic weathering rates in soil, as their phototrophic activity is not limited by ambient humidity as in case of the poikilohydric lichens and mosses [22]. Furthermore, mycorrhization would enable the constant flux of photoassimilates to deeper soil layers and additionally increase biogenic weathering. Reports on mycorrhization of *D. antarctica* exist, but are contradictory [23–25].

Therefore, questions as to whether *Deschampsia* is acting as a climax species in Antarctic succession and is mycorrhized, are of crucial importance to our understanding of the future development of the Antarctic environment. In this study, as part of a larger survey on biogenic weathering and organismic succession, we have identified three temporal gradients on King George island, maritime Antarctica, which represent the three forms of temporal gradients induced by glacier retreat, lateral or vertical glacier retreat, and the formation of raised beaches due to isostatic uplift following glacier thinning and retreat, and investigated the successional patterns of plants along the temporal gradients. Finally, we determined the mycorrhizal status of the abundant plant species. Our hypotheses are (i) plants in Antarctica are able to modulate the two base parameters in soil development, organic C content and pH at relatively short time scales along the temporal gradients, leading to an increase in organic carbon and soil acidity, (ii) the soil development encourages plant succession along these gradient, and (iii) with increasing soil development, bryophytes and *D. antarctica* develop mycorrhiza in order to foster interaction with soil.

Methods

Study site

We conducted our study along three temporal gradients on the Fildes Peninsula (62°12′S, 58°58′W), King George Island and Ardley Island (62°23′S, 58°27′W), based at the Chilean research station of INACH "Prof. Julio Escudero" (Fig. 1, Table 1).

King George Island (KGI) is the largest island of the South Shetland Islands, and is separated from the northern tip of the Western Antarctic Peninsula by the Brainsfield Strait. The Fildes Peninsula itself measures approximately 7.5 × 3.5 km. KGI has a cold moist maritime climate with a mean annual temperature of −2.1 °C [26]. Temperatures on the Fildes Peninsula may reach 3 °C in the Antarctic summer between December and February, with an average of 2 °C in January/February and an average of −7 °C in winter [27]. In contrast to the extreme temperature differences of continental Antarctica, maritime Antarctica shows smaller annual temperature variations [28]. Temperature data collected during 1968 – 2003 indicate a significant warming of the Fildes Pensinsula of +0.0239 ± 0.0103 °C a^{-1} for summer and +0.0511 ± 0.0654 °C a^{-1} for winter [27]. Long-term precipitation data is lacking, but Knap et al. [29] reported 500 mm a^{-1}. The bedrock of the Fildes Peninsula is mainly basaltic with subvolcanic intrusions and pyroclastic sediments [30].

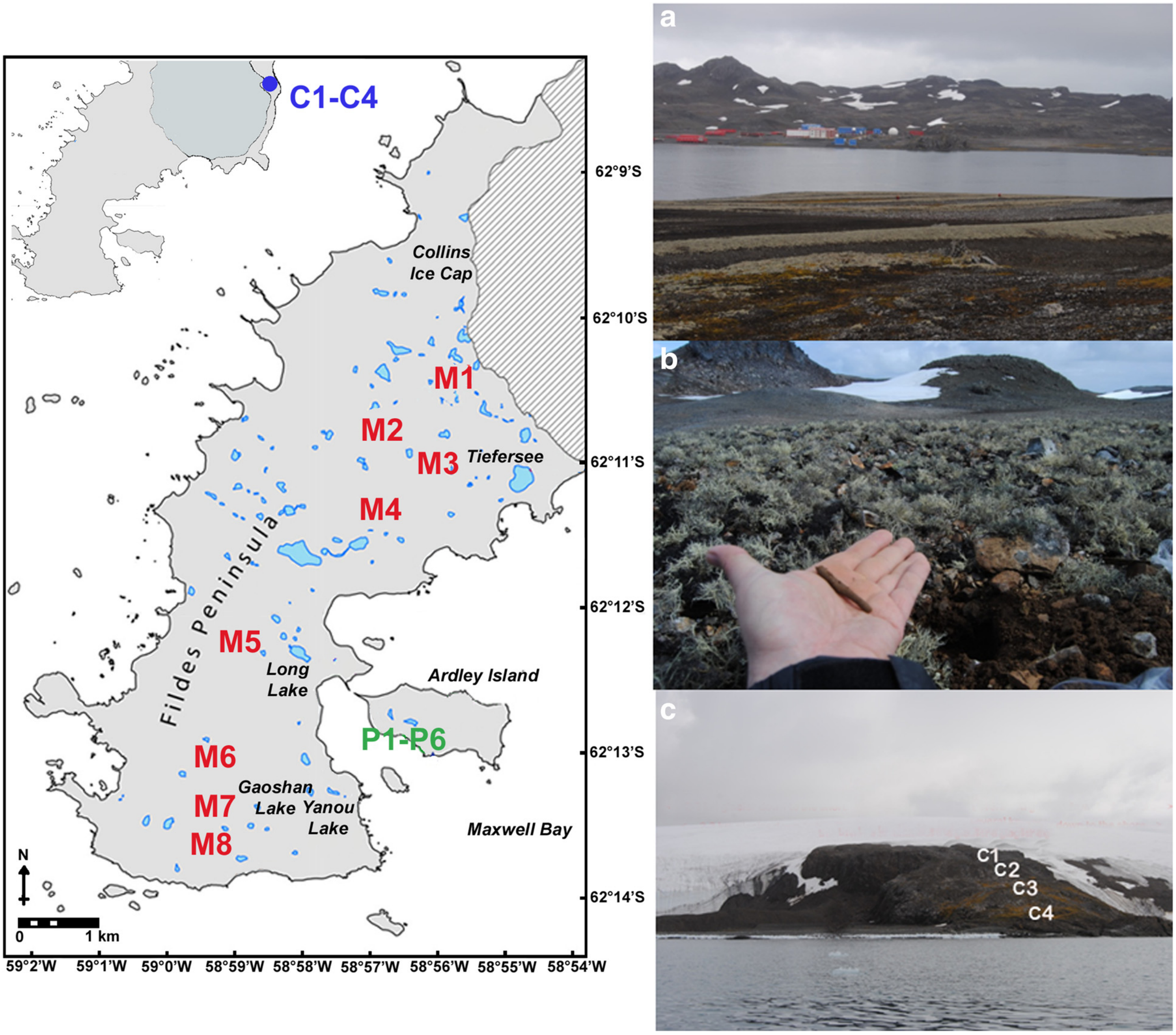

Fig. 1 *Left*: location of soil development gradients formed by glacier retreat on the Fildes Peninsula, King George Island; right: **a** Ardley Island palaeobeach sequence (P1-P6, green); **b** a typical plot at the altitudinal chronosequence 'Meseta' (M1-M8 in red), here M6, with soil having a loamy texture; the temporal gradient of 'Meseta' consists of plots of comparable altitude (~220 ma.s.l.) with almost no impact of bird feces and located as far as possible from direct sea spray, **c** temporal gradient at 'Collins' Outcrop', C1-C4 in blue. 'Collins' Outcrop' represents an altitudinal glacier retreat with *Deschampsia antarctica* .C1: Glacier till, C2: Mosses, C3: Mosses with 10 % *Deschampsia antarctica*, C4: *Deschampsia antarctica*

Table 1 Geographical position of the sampling plots along the temporal gradients

TP *Ardley*		TP *Meseta*		TP *Collins*	
plot	position	plot	position	plot	position
P1	S62°12′48.9″, W58°56′53.4″	M1	S 62°10′19.1″, W58°54′57.1″	C1	S62°10′10.0″, W58°51′27.2″
P2	S62°12′48.0″, W58°56′51.9″	M2	S 62°10′26.8″, W58°55′26.1″	C2	S62°10′10.0″, W58°51′22.9″
P3	S62°12′47.3″, W58°56′49.6″	M3	S62°13′29.8″, W58°58′53.3″	C3	S62°10′11.2″, W58°51′10.4″
P4	S62°12′46.4″, W58°56′47.5″	M4	S62°10′46.9″, W58°56′29.4″	C4	S62°10′10.8″, W58°51′05.3″
P5	S62°12′45.7″, W58°56′46.9″	M6	S62°13′03.2″, W58°58′52.6″		
P6	S62°12′44.4″, W58°56′42.9″	M7	S62°13′17.6″, W58°58′42.4″		
		M8	S62°13′31.2″, W58°58′58.0″		

Ardley island

The topography of Ardley Island is relatively low relief with the highest elevation at 65 m. Geologically the island consists mainly of Tertiary andesitic and basaltic lavas and tuffs together with raised beach terraces (Management Plan for Antarctic Specially Protected Area No. 150. 2009).

The Fildes Peninsula and adjacent smaller islands are the largest periglacial area in the South Shetland Islands. Holocene warming resulted in glacier retreat and this has been accelerated by post-glacial sea-level rise inducing hydrostatic uplift and ice retreat [28]. Isostatic uplift due to reduction of ice volume has led to the formation of chronosequences of raised beaches along the coastline. The spatial direction of glacier retreat on the Fildes Peninsula is under discussion, with rivaling concepts of lateral- (gradual retreat from the southwestern end of the Fildes Pensinula towards the present glacier frontier) and glacier thinning [31]. However, both models agree on early deglaciation at c.7200 year B.P. We identified three different temporal gradients (i) a raised beach sequence (Palaeobeaches) on Ardley Island, (ii) a temporal gradient of lateral glacier retreat on the Fildes Peninsula inland-altiplano (*Meseta*) at approximately 110 m a.s.l, and (iii) an altitudinal glacier retreat on an isolated bedrock exposure in Collins Bay from sea level to higher altitudes. The bedrock exposure is the only deglaciated outcrop in the area and is surrounded by the Collins Ice cap (Fig. 1).

(i) *Raised beach gradient (Ardley Island).* Following deglaciation on the Fildes Peninsula in the early to mid-Holocene the uplift of land led to the formation of the south-eastwards orientated palaeobeaches on Ardley Island [31]. The elevation and age of the Holocene raised shorelines are key factors in determining the time of deglaciation. Hall [32] suggests raised palaeobeaches extend to a maximum of ~22 m a.s.l. and palaeolimnological records from lakes at or above this altitude contain only freshwater diatoms [33]. The heights of the palaeobeaches on Ardley Island were surveyed and correlated to the relative sea level reconstruction provided by Watcham et al. [31].

(ii) *Lateral glacier retreat gradient ("Meseta").* The temporal gradient at *Meseta* is assumed to be little affected by sea bird feces and anthropogenic activity and was located as far as possible from direct sea spray. All plots at this sequence were established along the entire mountain crest at comparable altitudes of approximately 110 m a.s.l., similar inclination and microclimatic conditions. Watcham et al. [31] provide a chronology for deglaciation from the radiocarbon dated lake sediments along the east coast, and demonstrate an age-gradient along a lateral direction from Yanou Lake (c. 6200 year BP), over Long Lake to Tieferseelake (c. 1500 year BP). Our sample plots along the Meseta gradient correspond approximately to the chronosequence constrained by the radiocarbon dated lakes.

(iii) *Vertical retreat gradient ("Collins' Outcrop").* In Collins Bay an altitudinal temporal gradient (11–71 m a.s.l.) with 4 plots (C1 – C4) was chosen on a microclimatically exposed and SW-facing rocky promontory encircled by the Collins glacier. The temporal gradient comprises the glacier forefield (C1) on a lateral moraine formed during the Little Ice Age (~AD 1850). The lower plot C4 has been exposed since c. 7200 year BP as indicated by an adjacent series of storm beaches (own measurement). The age of the other plots could not be established. The parent material of soil development differs from till at the glacier margin to basaltic bedrock in the lower part of the chronosequence. The ice-free bedrock outcrop offers an important refugium for birds in the otherwise glaciated surrounding, with a small nesting colony of kelp gulls (*Larus dominicanus,* Lichtenstein.) at plot C4.

Soil analyses

Soil sampling was performed volumetrically and stratigraphically down to bedrock. Soil classification was carried out according to *World Reference Base for Soils Resources* [34]. In the field, soil color was determined on moist soils according to Munsell colour charts and texture was assessed by finger test. Soil samples of at least 200 g were taken from all soil horizons for later analysis, dried and separated into the fine earth fraction (< 2 mm) and soil skeleton by sieving.

The pH was measured in a soil suspension (aqua bidest.) at a soil-to-water ratio of 1:2.5 using a pH-electrode. Organic carbon, total nitrogen and stable carbon isotopic composition ($\delta^{13}C$) of homogenized and ground soil samples were measured using an IsoPrime 100 IRMS coupled to an Elementar vario MICRO cube after removal of inorganic carbon by HCl vaporization. Carbon stocks were calculated with reference to soil bulk density and rock content.

Species composition analyses

Species cover was estimated at three randomly chosen 1 × 1 m areas per plot. Specimen were separated directly after collection, photographed and measured before drought. Lichens and mosses were classified according to Ochyra et al. [35] for mosses, Bednarek-Ochyra et al. [36] for liverworts and Redon [37], Olech [38] Ovstedal and Lewis Smith [39] for lichens, respectively.

Statistical analyses

In order to analyze the spatial distribution of chemical parameters we performed a hierarchical cluster analysis. Sampling sites were used as factor clusters while C/N ratios, C and N stocks (uppermost 10 cm of soil) were used to build up a distance matrix between individual observations. The cluster solutions were plotted into a dendrogramme using R 3.1.3 [40].

Determination of mycorrhizal status

Eight root samples of *D. antarctica* at C4 and five samples of a mixture of mosses were taken. The root fragments ($n = 24$) and the entire moss gametophyte ($n = 20$) were stained and observed under microscope for fungal colonization using the ink and vinegar staining technique [41]. Root fragments and gametophytes were mounted on glass slides and observed at 400× magnification by using an Olympus BH2 microscope for the percentage of root length colonization. Around 100 intersections were observed from each sample.

Results & discussion

Soil development along the temporal gradients

Ardley island

At the chronosequence of Ardley Island a gradient of soil development was already visually observable (Fig. 2). Three soil horizons, a thin O horizon followed by two AC horizons, with a total depth of 15 cm were observed at P1. The rock content in the latter horizons exceeded 60 % with increasing clast size below 10 cm depth. The fine earth fraction had a sand content of 30 %. P2 had an additional C horizon down to 20 cm with saprolite and the rock content in the two AC horizons were higher than 90 %. An increase of pH from 4 to 5.3 with increasing soil depth was measured. Interestingly, plot P3 appears to be the most developed soil with five

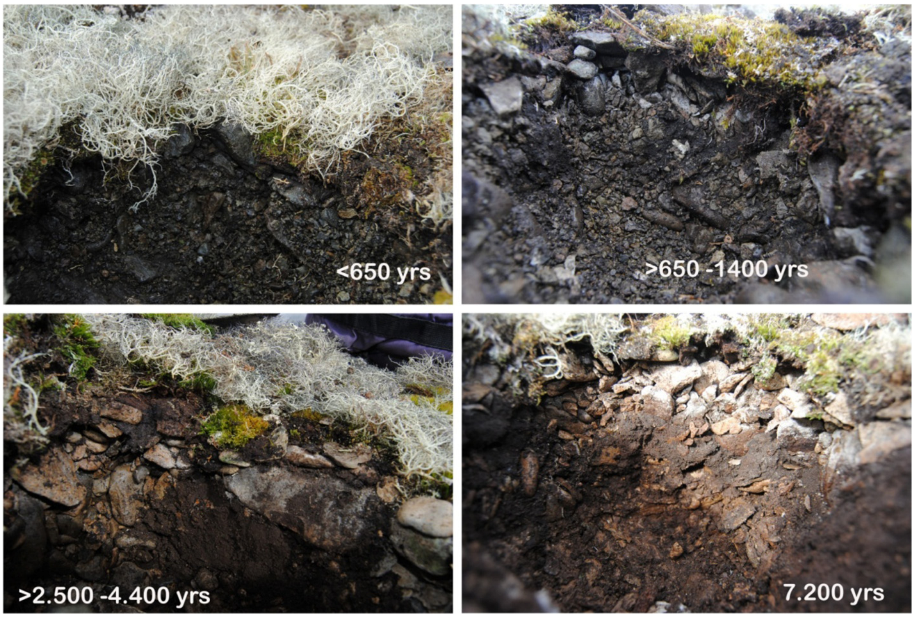

Fig. 2 Soil development along the chronosequence, Ardley Island. Upper left: P1, upper right: P2, lower left: P4, lower right: P6

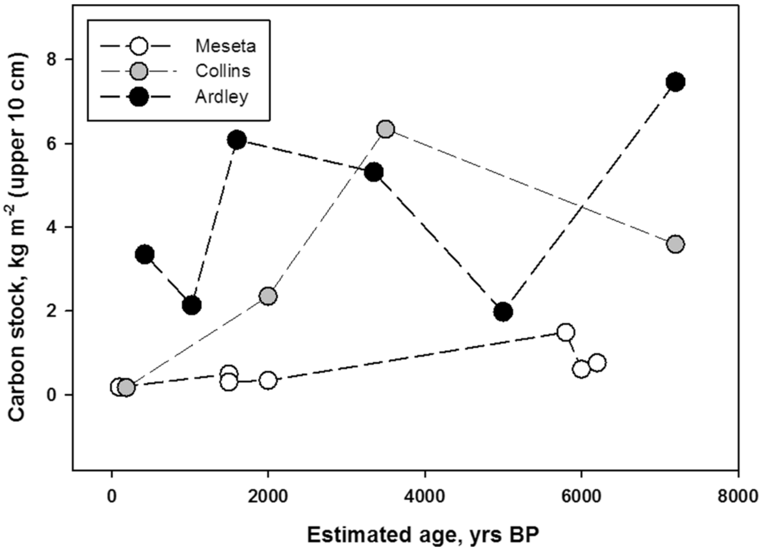

Fig. 3 Increasing carbon stocks along the temporal gradients with age of soil development on the Fildes Peninsula, maritime Antarctica

horizons: O, OC, and AC, as well as a Bw horizon, latter being a weathered layer with formation of pedogenic minerals (Fe-oxides), and a thick C horizon with 15 cm depth with initial physical weathering of the parent material. Rock content here lay between 55 and 70 %. An increase of pH from 4.5 to 5.0 (in C horizon) with depths was observed. The horizons of the plots P4 and P5 were comparable with an organic layer (O) as first horizon followed by three AC horizons, transitional zones of organic soil accumulated mineral layer mixed with consolidated bedrock. Rock content ranged between 50 and 90 % at P4 and 70 to almost 100 % at P5. At the plots P4 and P5, pH in the upper layer was around 4.5, however, at P4 pH increased to 5.1 while at P5 pH was 4.7. Soil development extended to a greater depth (20 cm) at plot P6 in comparison to P4 and P5, and the upper two AC horizons were overlain by two more organic matter-containing OC horizons. Rock content was around 30 % at OC1 and almost 90 % at OC2 and AC. Both OC1 and OC2 horizons showed a pH of 4.4. Generally, pH increased with soil depths. Carbon and nitrogen stocks increased over the temporal gradient at the temporal gradient at Ardley Island (Figs. 3 and 4), although heterogeneity seems high and to be biased by the different sizes of the parent material, which is determined by the kinetic energy forming the beaches and

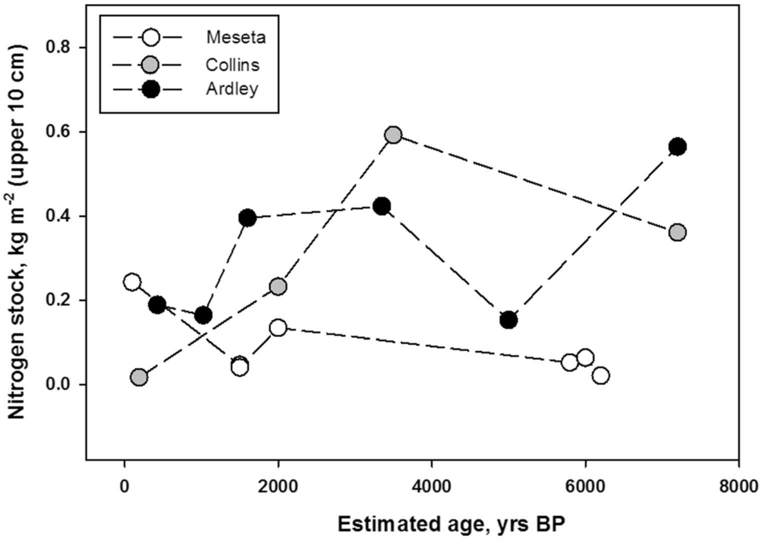

Fig. 4 Nitrogen stocks along the temporal gradients on the Fildes Peninsula, maritime Antarctica

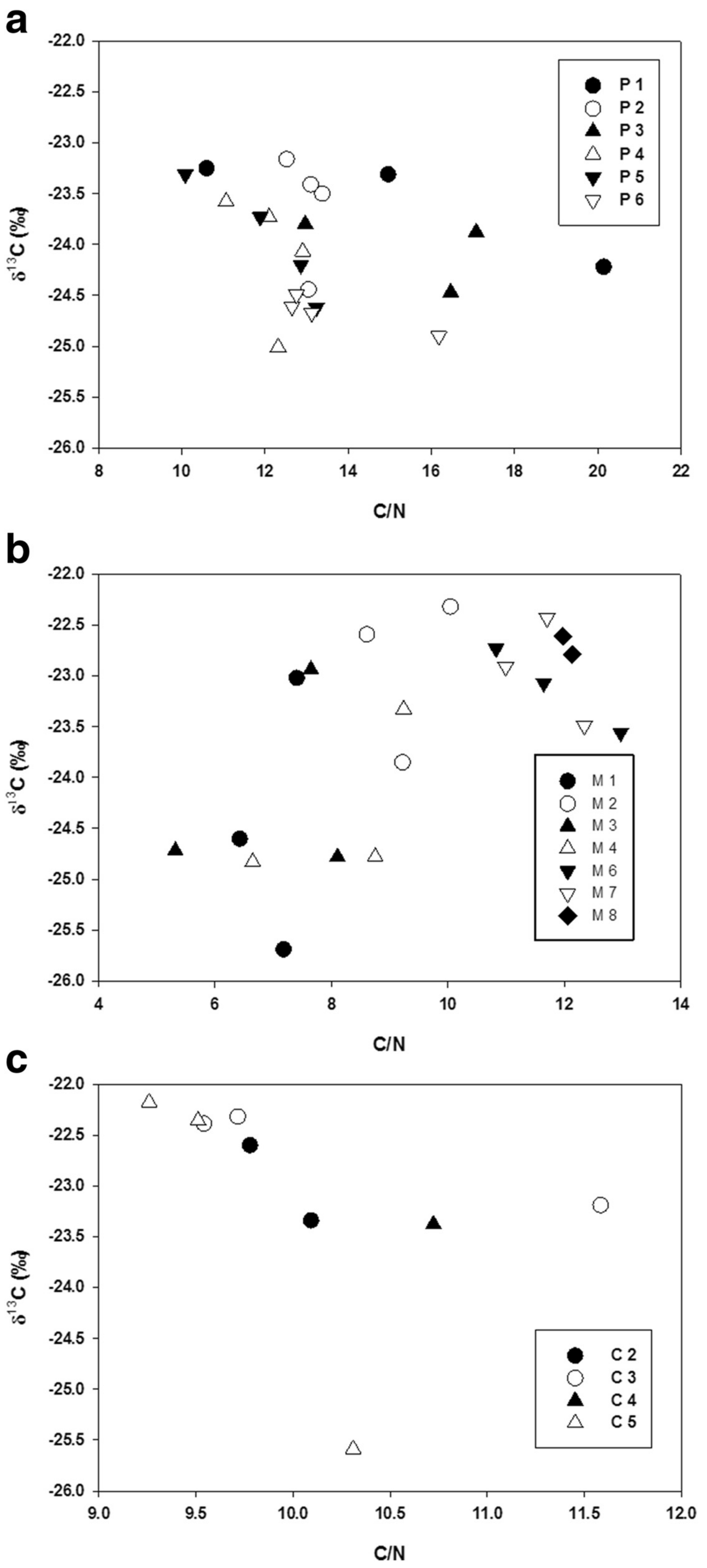

Fig. 5 Relationship between $\delta^{13}C$ and C/N ratios of soils along each temporal gradient: **a** *Ardley*, **b** *Meseta*, and **c** *Collins*

the size of the pebbles deposited. Especially at P5, larger pebbles appear to have delayed soil development.

All soil profiles at Ardley Island showed a general decrease in the C/N ratio of organic matter with increasing soil depth, indicating a preferential loss of carbon relative to nitrogen due to metabolic activities of heterotrophic soil microorganisms and preferential incorporation of nitrogen in microbial biomass (Fig. 5). Such behavior is common to most soils and have been reported also for tundra soils [42]. This relative enrichment of nitrogen is accompanied with increasing $\delta^{13}C$ ratios (Fig. 5a), which is indicative of preferential metabolization of light carbon and thus the incorporation of heavy carbon in microbial biomass during organic matter decomposition [43]. Hence, the Ardley Island soils are characterized by intensive soil organic matter decomposition processes. However, there are distinct differences within this relation along the soil chronosequence. With increasing age, the soil organic matter becomes enriched in nitrogen, and thus with increasing soil depth, the decrease in the C/N ratio is not as prominent as in the younger soils. In contrast, the ^{13}C enrichment with soil depth is similar for all soils. This reflects the ability of the ecosystem to gain and store nitrogen (Fig. 4), and the increasing $\delta^{13}C$ values due to isotopic discrimination by microorganisms along with constant C/N ratios with soil depth suggests an efficient microbial recycling of soil organic matter at the older sites [44]. The classical assumption that $\delta^{13}C$ values of a SOM increase by 1–3 ‰ with depth in temperate ecosystems agrees with the present results in cold environment (Tables 2, 3 and 4). It has been hypothesized that the mixing of new and older SOM components during decomposition result in $\delta^{13}C$ enrichments in deep and older soils. This is because: i) the microbial and fungal account for an enrichment of $\delta^{13}C$ values relative to their substrate. This enrichment is attributed to isotopic selectivity by ^{12}C molecules and metabolic discrimination and ii) the $\delta^{13}C$ ratios of atmospheric CO_2 have been decreasing because of the combustion of ^{13}C-depleted fossil fuels. Old SOM should have originated at the time when the $\delta^{13}C$ values of atmospheric CO_2 were more positive (e.g. [45]).

Meseta

Plots M1 and M2 lie in the very north of Meseta hence close to the current glacier front. At plot M1 (on

Table 2 Soil properties of the *Ardley Island* temporal gradient

Plot/Est. age [BP]	Horizon	Horizon Depth [cm]	Texture	Skeleton [%]	Color (moist)	pH	C_{org} [%]	C/N	$\delta^{13}C$ [‰]	Classification
P1/650-200	O	1–0		-			30.0	20.1	−24.22	Eutric
	AC1	0–5	S	62	10 YR 1.7/1	5.24	1.16	10.6	−23.25	Arenosol
	AC2	5–15	S	68	10 YR 2/2		6.2	15.0	−23.31	
	2C	> 15								
P2/1400-650	O	1–0		-		3.98	22.7	13.0	−24.44	Dystric
	AC1	0–5	S	94	10 YR 1.7/1	4.58	10.9	13.4	−23.50	Arenosol
	AC2	5–15	S	93	10 YR 2/2	4.98	5.33	13.1	−23.41	
	C	> 15		84		5.29	1.49	12.5	−23.16	
P3/2200-1000	O	1–0		-			28.3	16.5	−24.47	Dystric
	AC1	0–5	LS	56	10 YR 1.7/1	4.49	13.8	17.1	−23.88	Arenosol
	AC2	5–15	LS	70	10 YR 2/2	4.82	9.14	13.0	−23.80	
	C	> 15				5.03	0.99	7.7	−24.14	
P4/4400-2300	O	1–0		-			20.2	12.3	−25.01	Dystric
	AC	0–5	LS	80	10 YR 1.7/1	4.63	6.93	12.9	−24.07	Arenosol
	2 AC	5–10	LS	54	10 YR 2/2	4.81	6.67	12.1	−23.78	
	3 AC	10–15	LS	91	10 YR 2/3	5.13	4.31	11.1	−23.58	
P5/5000	O	1–0		-			18.5	13.2	−24.62	Dystric
	AC	0–7	LS	94	10 YR 2/2	4.56	8.70	12.9	−24.20	Arenosol
	2 AC	7–12	LS	71	10 YR 2/2	4.75	7.44	11.9	−23.73	
	3 AC	12–17	LS	98	10 YR 3/2		5.12	10.1	−23.31	
P6/7200	O	< 1		-	10 YR 2/2		36.8	16.2	−24.90	Dystric
	OC	0–5	Sil	30	10 YR 1.7/2	4.38	14.6	12.6	−24.61	Arenosol
	2OC	5–13	LS	88	7.5 YR 1.7/1	4.38	19.1	13.1	−24.67	
	2 AC	13–20	LS	87	10 YR 2/2		12.5	12.8	−24.49	

Table 3 Soil properties along the *Meseta* temporal gradient

Plot/Est. age [BP]	Horizon	Horizon Depth [cm]	Texture	Skeleton [%]	Color (moist)	pH	C_{org} [%]	C/N	$\delta^{13}C$ [‰]	Classification
M1/100	C1	0–1	LS	52	10 YR 2/3	7.0	0.11	7.2	−25.69	Eutric
	C2	1–10	LS	12	10 YR 3/3	6.9	0.26	7.4	−23.02	Arenosol
	C3	> 10	LS		10 YR 3/3	6.78	0.10	6.4	−24.60	(Ochric)
M2/1500	AC1	0–2	LS	17	10 YR 3/2	5.38	0.82	9.2	−23.85	Skeletic
	AC2	2–11	SL	28	10 YR 3/3	5.85	0.58	8.6	−22.59	Eutric
	AC3	> 11	SiL	69	10 YR 4/4	6.27	0.64	10.0	−22.32	Regosol
M3/1500	AC1	0–1	LS	55	10 YR 2/3	5.81	0.35	8.1	−24.78	Eutric
	AC2	1–3	LS	9.3	10 YR 2/3	5.81	0.33	7.3	−24.72	Regosol
	BC	4–12	SiL		10 YR 2/3	6.27	0.45	7.7	−22.94	(Ochric)
M4/2000	AC1	0–1	S	51	10 YR 2/3	5.5	0.32	8.8	−24.78	Skeletic
	AC2	1–4	LS	40	10 YR 2/3	5.53	0.31	7.7	−24.83	Eutroc
	BC	4–12	SiL		7.5 YR 2/3	6.16	0.57	9.2	−23.33	Regosol
M6/5800	A	0–1	SiL	50	10 YR 2/3	4.46	3.55	13.0	−23.56	Dystric
	AB1	1–7	SiL	28	10 YR 2/3	4.96	2.01	11.7	−23.07	Regosol
	AB2	7–20	L		10 YR 2/3	5.23	1.78	10.8	−22.73	
	C	> 20								
M7/6000	A	0–3	LS	88	10 YR 2/3	5.32	1.18	12.3	−23.49	Skeletic
	2AB	3–12	SiL	39	10 YR 3/3	5.91	0.94	11.7	−22.43	Eutric
	3 AC	> 20	SL	76	7.5 YR 3/4	6.71	0.51	11.0	−22.91	Regosol
M8/6200	A	0–2	LS	54	10 YR 2/2	5.62	0.98	12.1	−22.79	Eutric
	AB	2–10	SL	23	7.5 YR 2/3	6.1	0.75	12.0	−22.61	Regosol
	C	> 10								

youngest moraine sediment), three C horizons could be differentiated (Table 3); no signs of organic matter accumulation on the surface were visible. Soil skeleton content was 52 % in the uppermost C horizon and declined to 12 % in C2. The pH ranged 7.0 – 6.8. Plot M2 lies ~100 m from the glacier front, and showed a more developed AiC horizon of 2 cm depth followed by two C horizons. Rock content increased between the horizons with depths from 17 to 69 %. Despite the proximity of M1 and M2, the pH decreased at M2 to values between 5.4 in AiC to 6.3 in C2. M3 comprises an AiC1 horizon (skeleton of 55 % with loose boulders) followed by an AiC2 horizon with 9 % coarse material. Below a transitional layer of subsoil and unconsolidated parent material (BC) was found to a depth of 12 cm. Interestingly the OC concentration increased with soil depth. The pH ranged between 5.8 and 6.3. Plot M4 showed similar horizons and SOC stocks as M3, with

Table 4 Soil properties of the *Collins' Outcrop* temporal gradient

Plot/Est. age [BP]	Horizon	Horizon Depth [cm]	Texture	Skeleton [%]	Color (moist)	pH	C_{org} [%]	C/N	$\delta^{13}C$ [‰]	Classification
C1/< 200	CA	0–1	LS	-	10 YR 2/3	6.42	0.47	9.8	−22.60	Skeletic
	C1	1–8	LS	65	10 YR 3/3	6.42	0.28	10.1	−23.34	EutricRegosol
	C2	> 8	LS	48	10 YR 3/3	7.13	0.20	11.1	−22.13	(Ochric)
C2/2000	A	0–1	SL	-	10 YR 2/2	4.58	8.90	11.6	−23.19	Skeletic
	AC1	1–6	SL	14	10 YR 2/3	4.70	2.09	9.5	−22.39	Dystric
	AC2	6–12	LS	36	10 YR 2/3	5.07	1.94	9.7	−22.32	Regosol
C3/3500	A	0–6	SL	18	10 YR 2/2	4.76	13.8	10.7	−23.38	DystricLepto-
	R	> 6								sol (Stagnic)
C4/7200	O	0–3		2.3		5.58	20.7	10.3	−25.59	Eutric
	A	3–11	SL	50	10 YR 2/3	5.29	3.84	9.3	−22.18	Regosol
	AB	11–16	SiL	30	10 YR 3/1	5.62	4.31	9.5	−22.36	(Ornithic)

the M3 soil being more developed although younger than M4. The pH was slightly lower than an M3 ranging between 5.5 and 6.2. Rock content lay between 40 and 50 %. At Plot M6, four horizons were identified: the mineral topsoil (A) with 50 % soil skeleton and a pH of 4.5, a transitional layer of accumulated mineral topsoil and subsoil mixed with carbonate-containing bedrock (AB) with 28 % of coarse material and a pH of 5.0, a B horizon with a pH of 6.7 and a C horizon. Plot M7 comprises an AC horizonas the topmost layer with gravel overlay and organic material in the mineral topsoil followed by a brown and loamy B horizon and by a C horizon of unspecific depth. The rock content ranged between 88 % at AC, 39 % at B and 77 % at the C horizons respectively. The pH increased from 5.3 in the upper layer to 6.7 in the C horizon. The soil at M8 was shallow with a small A horizon with 54 % coarse material followed by a AB horizon with 23 % rocks, an illuviation-zone and a C horizon starting from 10 cm depth. Between the AB and B horizon an increase of pH from 5.6 to 6.1 was observed. Carbon stocks increased consistently over the temporal gradient on the Meseta (Fig. 3). Carbon stocks were much lower in comparison to the other temporal gradients, pointing towards a lower productivity at the Meseta plots due to colder and drier microclimatic conditions. Unlike the lower temporal gradients at Ardley Island and Collins' Outcrop, the Meseta receives a prolonged snow cover, shortening the growth season substantially (field observations in 2012, 2013, 2014).

The C/N ratios of the Meseta soils can be clustered into two groups (Table 3, Fig. 5). The younger soils had C/N ratios of about 5–10, which is typical for microorganisms. This clearly reflects the soil organic matter source, i.e., primarily cyanobacteria and eukaryotic algae. In contrast, the older sites showed higher C/N ratios, indicating an increasing contribution of lichens and mosses to the soil organic matter formation. Over all the Meseta sites, the relationship between the $\delta^{13}C$ values and C/N ratios is opposite to that observed for the Ardley Island soils. This can be most likely explained by the different $\delta^{13}C$ values of the organic matter input, i.e., the different phototrophic organisms. Young profile M1 to M4 show depleted $\delta^{13}C$ and low C/N ratio compared with more developed soils profile (M5-M8) with more enriched ^{13}C by the same reasons formerly given. When considering individual soil profiles, the pattern in the older Meseta sites are similar to the Ardley Island soils. Hence, with soil profile development decomposition processes of soil organic matter by soil microorganisms also leads to a differentiation in the soil organic matter composition. However, no such trend is visible in the younger soils.

Collins' Outcrop

At plot C1 (Table 4) young soils were lacking an organic horizon. Instead, the topsoil was a mix of an initial Ai horizon and weathered parent material (AiC) of just 1 cm depth, followed by two horizons of unconsolidated bedrock (C1 and C2). Rock content in mineral

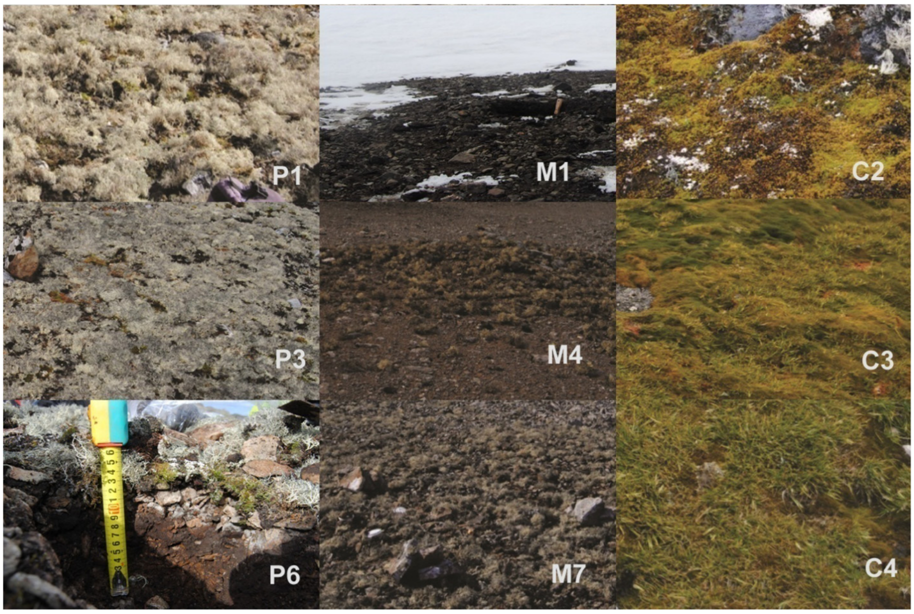

Fig. 6 Vegetation observed along the three temporal gradients on the Fildes Peninsula, maritime Antarctica. *Left*: *Ardley Island*, *middle*: *Meseta*, *right*: *Collins' Outcrop*

soil horizons ranged between 14 and 65 %. C1 is a very young plot on glacier till with a pH of 6.4 in the upper layer, presumably this pH on till represents the starting point on the temporal gradients - leading to pH 7 in deeper horizons. The glacier till found at C1 indicates that this plot has a different parent material compared to the other plots at Collins' outcrop which are formed of solid basaltic bedrock. At C2, an incipient organic horizon was identified followed by a transitional AB horizon and a mix of subsoil and unconsolidated weathered parent material (BC). Rock content increased with increasing soil depth up to around 37 % in the BC horizon. A large increase in acidification was also observed compared to C1, indicating that possibly parent material at C2 (along with the other plots down the slope from C2) differ from C1. Also the biological activity of mosses growing at this plot might have contributed to acidification. C2 may also reflect particular conditions for soil development as the basaltic rocks are forming a small bowls that collect water. At C3 a peat horizon (A) with anoxic and acidic (pH 4.7) conditions was found with already 6 cm of depth underlain by solid bedrock (R). The first horizon at C4, the most developed soil at Collins' Outcrop, was a transitional horizon of soil accumulated mineral material with high organic content (O), followed by a mineral layer (A) and a mix of mineral and unconsolidated parent material (BC). Coarse particle content ranged between 2 and 50 % and pH ranged between 5.2 and 5.6. Carbon stocks increased over time along the temporal gradient at Collins' Outcrop (Fig. 3), with a comparable high carbon stock at C3 due to the waterlogged conditions, leading to the formation of a peat horizon.

At Collins' Outcrop, the development of $\delta^{13}C$ values and C/N ratios along the succession followed a similar trend as at Ardley Island (Fig. 5). The O horizon of C4 (under *D. antarctica*) provided a $\delta^{13}C$ ratio, typical for C3 grasses. Interestingly the C/N ratio is relatively narrow for an O horizon and this likely reflects the input of bird feces [46].

When comparing the pH between the temporal gradients, soils at Ardley Island are generally more acidic (pH range from 4 to 5.3) than at the Meseta (4.5–7), while Collins' Outcrop shows the widest range of pH from 4.6 to 7.1 depending on the plot. There was a decreasing pH with increasing soil age observed (Tables 2, 3 and 4). Thus, pH decreases with larger contributions of the vegetation to the soil development process. Increasing carbon stocks over all temporal gradients reflect the estimated age gradients in the observed accumulation of organic carbon over time.

Successional patterns along the temporal gradients

Ardley Island

Plot P1 lies 4 m a.s.l. on the second raised beach (this is the first beach) and is the closest plot to the sea (Fig. 1). Vegetation cover was around 95 % (Fig. 6) with two to three layers of the lichen *Usnea sp.* (top), a black moss (middle) and encrusted lichens (bottom, Table 5). *Usnea fasciata* covered with 80 % the greatest part of the plot. The rest of the vegetation consisted of the green cushion-moss *Chorisodontium sp.* (Dicranaceae), the yellow-green bryophyte *Sanionia uncinata* (Scorpidiaceae), the black moss *Andreaea sp., Cladonia borealis* (Cladoniaceae), *Himantormia lugubris* (Parmeliaceae) and various other encrusted lichens. Vegetation density at P2 (5 m a.s.l.) was 95 % with around 70 %, with *Usnea fasciata* as the dominating species. Further vegetation consisted of *Chorisodontium sp.* (20 %), *Andreaea sp.*, *Himantormia lugubris* and

Table 5 Successional patterns and total vegetation cover [%] along the temporal gradient of Ardley Island, Fildes Peninsula, Antarctica

Plot	Vegetation cover [%]	Lichens	Bryophytes
P1	*95*	*Usnea fasciata* *Pseudephebe pubescens* *Ochrolechia frigida* *Cladonia borealis* *Stereocaulon alpinum* *Himantormia lugubris* *Cornicularia aculeata* *Pseudephebe pubescens* *Rhizocarpon geographicum*	*Sanionia uncinata* *Chorisodontium sp.* *Polytrichum piliferum* *Andreaea sp.*
P2	*95*	*Himantormia lugubris* *Stereocaulon sp.1* *Cornicularia aculeata* *Usnea fasciata* *Cladonia borealis* *Placopsis contortuplicata* *Stereocaulon alpinum* *Pseudephebe pubescens* *Lecania brialmotii* *Ochrolechia frigida* *Rhizocarpon geographicum*	*Chorisodontium sp.* *Sanionia uncinata* *Polytrichum piliferum* *Chorisodontium sp.* *Andreaea sp.*
P3	*100*	*Usnea fasciata* *Himantormia lugubris* *Cladonia metacorallifera* *Stereocaulon alpinum* *Cladonia borealis* *Pseudephebe pubescens* *Ochrolechia frigida* *Cornicularia aculeata* *Stereocaulon alpinum*	*Chorisodontium sp.* *Polytrichum piliferum* *Andreaea sp.* *Sanionia uncinata*
P4	*100*	*Usnea fasciata* *Himantormia lugubris* *Rhizocarpon geographicum* *Cornicularia aculeata* *Placopsis contortuplicata*	*Chorisodontium sp.* *Polytrichum piliferum* *Andreaea sp.* *Sanionia uncinata*
P5	*100*	*Usnea fasciata* *Himantormia lugubris* *Cornicularia aculeata* *Placopsis contortuplicata*	*Chorisodontium sp.* *Polytrichum piliferum* *Andreaea sp.* *Polytrichum piliferum*
P6	*100*	*Usnea fasciata* *Cornicularia aculeata* *Stereocaulon alpinum* *Himantormia lugubris* *Placopsis contortuplicata*	*Chorisodontium sp.* *Polytrichum piliferum* *Andreaea sp.* *Sanionia uncinata*

Species identification according to Godoy et al. [53]

the orange, ramified lichen *Cornicularia aculeata* as well as other encrusted lichens (Table 5). Plot P3 lies 8 m a.s.l and is comparable to P2, except that *Usnea fasciata* dominates with 90 % of the total 100 % vegetation cover. Plot P4 (16 m a.s.l.) differs from P3 in a way that dissimilarly sized stones with a clear difference in size was observable from 1 to 10 cm. The plots P5 (16 m a.s.l.) and P6 (17 m a.s.l.) were comparable regarding vegetation composition to the other plots on Ardley Island, although soil development, especially the enrichment of organic matter, is more advanced. This points towards little connection between the lichen and moss communities and the soil. Although the formation of beach terraces on Ardley Island is well dated with an age range of 200 year BP to 7500 year BP, a pronounced succession of vegetation was not observed.

Meseta

Plot M1 located 97 m a.s.l. is the closest plot to the glacier front. Vegetation was not observed and soil consisted of pure glacial silt from the glacier. Plot M2 (32 m a.s.l.) is ~100 m from the glacier snout and the vegetation cover comprises approximately 80 % *U. fasciata*, 15 % of *Himantormia lugubris*, 10 % a black cushion-moss and 5 % of *Sanionia uncinata* (Table 6). Plot M3 (113 m a.s.l.) has a low and dispersed vegetation cover of 20 %. The lichen *U. fasciata* is the most abundant species and covers half of the plot followed by a black moss, unidentified pink lichen and other encrusted lichens which were not further identified, as they were connected to a larger boulder and had no soil habitat. At Plot M4 (109 m a.s.l.) *U. fasciata* dominated with 30 % of the vegetation, which had a total cover of 40 % (Table 6). Another species was *H. lugubris*, a cushion-producing black moss. One of the three plots in the southern Meseta is M6 (113 m a.s.l.). The total vegetation cover (80 %) comprises *U. fasciata* (60 %) as the dominant species. The rest of the vegetation is represented by *Polytrichum piliferum*, *Andreaea sp.*, *H. lugubris*, and *Polytrichum sp.* Vegetation at M7 (105 m a.s.l.) shows a similar vegetation composition as plot M6. The most southern plot is M8 (109 m a.s.l.). Vegetation covers only 40 % of the plot with the same species as plot M6, but here *U. fasciata* makes up 50 % of the total vegetation cover (Table 6).

Table 6 Successional patterns and total vegetation cover [%] along the temporal gradient of the Meseta, Fildes Peninsula, Antarctica

Plot	Vegetation cover [%]	Lichens	Bryophytes
M1	*0*	–	–
M2	*100*	*Usnea fasciata* *Himantormia lugubris* *Placopsis contortuplicata*	*Sanionia uncinata*
M3	*20*	*Usnea fasciata* *Psora sp. 1* *Placopsis contortuplicata* *Lecanora sp.1*	*Andreaea sp.*
M4	*40*	*Usnea fasciata* *Himantormia lugubris* *Placopsis contortuplicata*	*Sanionia uncinata* *Andreaea sp.* *Polytrichum piliferum*
M6	*80*	*Usnea fasciata* *Himantormia lugubris* *Placopsis contortuplicata* *Ochrolechia frigida*	*Polytrichum piliferum* *Andreaea sp.* *Chorisodontium sp.* *Polytrichum sp.* *Sanionia uncinata*
M7	*80*	*Usnea fasciata* *Himantormia lugubris* *Placopsis contortuplicata* *Ochrolechia frigida*	*Polytrichum piliferum* *Andreaea sp.* *Chorisodontium sp.*
M8	*40*	*Usnea fasciata* *Ochrolechia frigida* *Rhizocarpon geographicum* *Himantormia lugubris* *Placopsis contortuplicata*	*Polytrichum piliferum* *Sanionia uncinata* *Andreaea sp.*

In total, Meseta shows little successional patterns in vegetation. *Usnea fasciata* is the dominant species at all plots growing in association with *H. lugubris,* while *Polytrichum sp.* appears only at the older plots along the temporal gradient. The initial succession from bare proglacial areas to the first dense lichen vegetation is abrupt and was found to be mainly triggered by the appearance of firm ground for root anchorage, either by the absence of cryoturbation or larger rocks armouring the soil surface. Therefore, it may be unlikely that lichens or mosses interact with soil formation (except for litter deposition).

Mosses were only found to grow into soil at the oldest plots (M6-8). On younger plots the occasional occurring mosses were found adrift on cryturbated areas, suggesting aeolian nutrient supply.

Table 7 Successional patterns and total vegetation cover [%] along the temporal gradient of the Collins' outcrop, Fildes Peninsula, Antarctica

Plot	Vegetation cover [%]	Lichens	Bryophytes
C1	*0*	-	-
C2	*100*	*Cladonia boralis*	*Sanionia uncinata* *Polytrichum piliferum* *Chorisodontium sp.* *Bryum sp.*
C3	*100*	*Usnea fasciata* *Usnea antarctica* *Ochrolechia frigida* *Cladonia metacorallifera* *Rinodina cf. turfacea*	*Warnstorfia sp.* *Bryum amblyodon* *Sanionia uncinata* *Andreaea sp.* *Polytrichum piliferum* *Deschampsia antarctica* * *Chorisodontium sp.*
C4	*100*	*Xanthoria elegans*	*Deschampsia antarctica* * *Bryum amblyodon*

* vascular plant

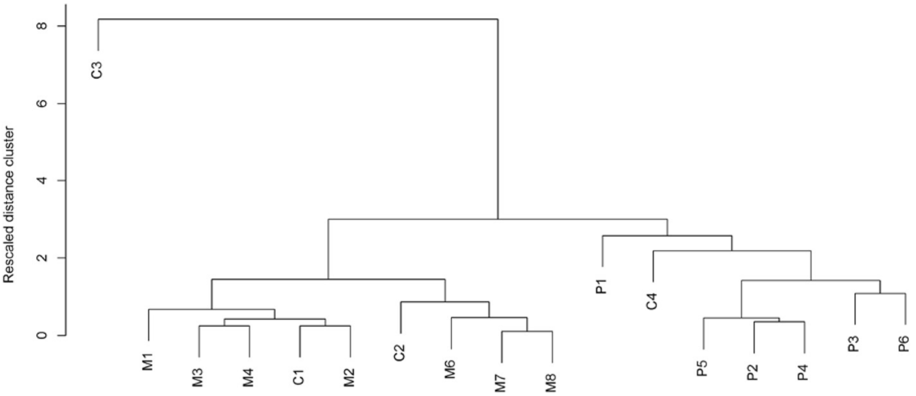

Fig. 7 Results of cluster analysis of all plots under investigation based on carbon and nitrogen stocks and C/N ratios in the first 10 cm of soil

Collins' Outcrop

Plot C1 is the highest plot at 71 m a.s.l. situated on a very young moraine ~ 15–20 m from the glacier front. Plants were not found. Plot C2 (64 m a.s.l.) is located ~120 m from the moraine and shows, according to its already differentiated soil development, a dense vegetation cover of 100 % consisting of mosses and lichens (Table 7). In this plot, the lichen *Usnea fasciata* and the cushion moss *Bryum sp.* were the most abundant species with 40 % coverage each. *U. fasciata* was colonizing stones and small rocky outcrops, as seen along the other temporal gradients. In plot C3 (26 m a.s.l.) vegetation cover added up to 100 % with 80 % of the compact green moss *Bryum amblyodon* (Bryaceae) which had rhizoids well connected to the peat soil underneath, 10 % Antarctic hairgrass (*D. antarctica*) and 5 % black moss (Table 7). The percentage of rocks covered with *Usnea sp.* and other encrusted lichens averaged 5 %. Other species with small coverage were the cup lichen *Cladonia metacorallifera* (Cladoniaceae) and the haircap moss *Polytrichum piliferum* (Polytrichaceae) (Table 7). Plot C4 (11 m a.s.l.) lies on a moderate slope with a dense vegetation cover of 100 %. The hairgrass *D. antarctica* and *Bryum amblyodon* were the most abundant species with 40 % coverage each. Rocks colonized by the red pigmented elegant sunburst lichen *Xanthoria elegans* (Teloschistaceae) were ~ 5 % of the vegetation cover.

Although patterns at Collins' Outcrops suggest succession, it became clearly apparent that this succession was more the result of a sea-to-land gradient of bird feces than of mutual processes between plant succession and soil development. At C4, and to a lesser extent on plot C3, kelp gulls (*Larus dominicanus*) likely interfered

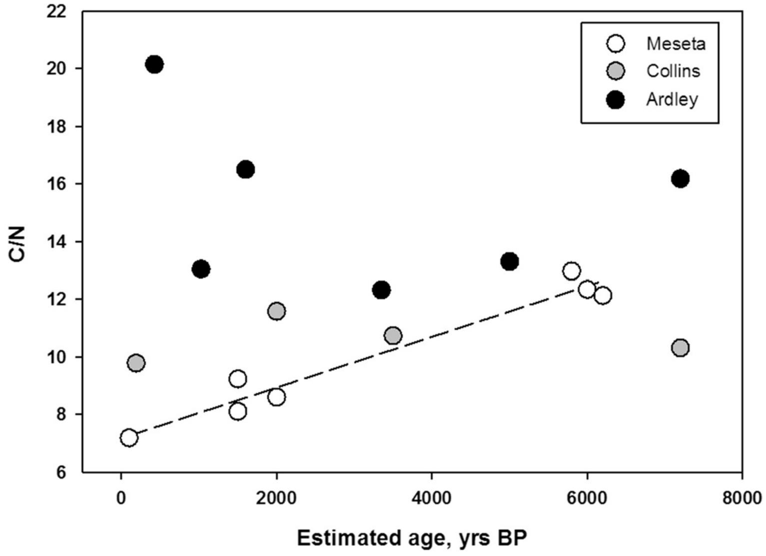

Fig. 8 Age-driven changes of C/N ratios of the temporal gradients

strongly with soil development, as a considerable part of the soil skeleton consisted of shells and, less frequently, feathers. Bird droppings were as well visible on the vegetation, aiding substantially to its nutrition (e.g. [47, 48]). This bird-induced pseudo-succession was visible all around the Fildes Pensinsula, as we were not able to find any *Deschampsia* stands not directly linked to nutrient enrichment by bird colonies. Similar results were obtained by e.g. Barcikowski et al. [49] or Zwolicki et al. [50].

Development of the temporal gradients in comparison

Taking the C/N ratios and age along all temporal gradients as a measure of soil development, it becomes apparent that plots which start their development from glacier till are under a similar regime of early C and nitrogen accumulation (Fig. 7). Figure 8 shows decreasing C/N ratios along age for Ardley and Collins, however, young Meseta-plots (M1), as well as plot C1 from the outcrop at Collins form a cluster, while older plots at Meseta (M4-M7) and Collins (C2) are similar to each other as well. The functional factor behind is the change of primary production from photoautotrophic microorganisms towards denser lichen covers, latter contributing to C accumulation by litter. A different development of soil was observed at the raised beaches and the lower plots at the Collins' Outcrop forming an independent cluster, indicating a higher interaction of photoautotrophic plants with the solum, presumably also altered by the close proximity to the sea and occasional input of bird

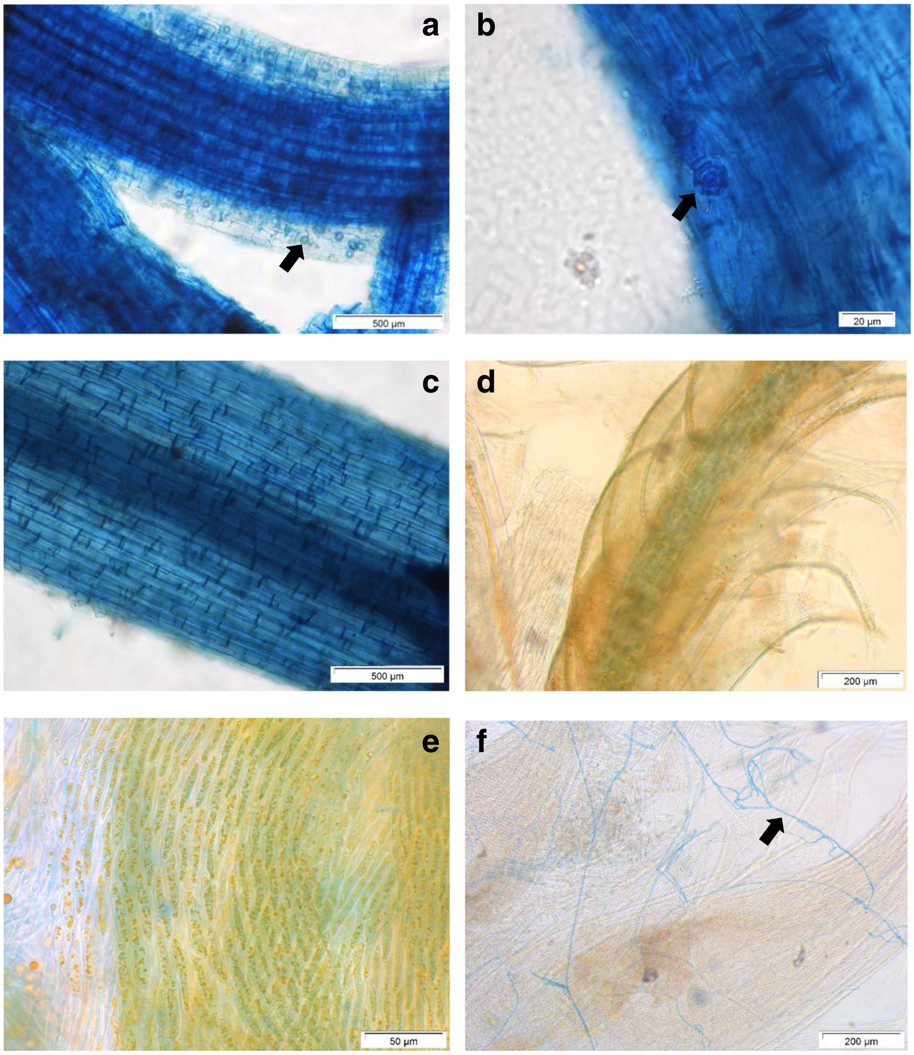

Fig. 9 Ink-vinegar stained roots and rhizoids. **a-b** Detail from a *D. antarctica* root fragment at P4 with the presence of *Olpidium* spp. resting spores (arrow). **c** Detail from a *D. antarctica* root fragment at C4 with no sign of endosymbionts. **d-e** Gametophyte from mosses growing at Collins' Outcrop (C2, C3) with no signs of endosymbionts. **e-f** Fungal structures in the rhizoidosphere without penetration (arrow) (C2, C3). Mycorrhiza was absent at all samples

feces. The waterlogged conditions at C3, clearly a condition not fostering the incorporation of C3 in temporal gradients which otherwise developed under oxic conditions, leads to a high distance to the other plots in the cluster analysis (Fig. 7).

Mycorrhizal status of mosses and hairgrass

We could not observe any fungal endosymbionts at the investigated plots, neither at moss rhizoids or roots of *Deschampsia antarctica* (Fig. 9). There was also no traces of dark septate fungi reported by Newsham et al. [24] to occur in polar regions. We only found different resting spores of *Olpidium spp.* Our results contrast also to the findings of Upson et al. [25], who found occasional arbuscules at roots of *D. antarctica*. The contrasting results seem to be best explained by a longitudinal temperature gradient. *Deschampsia antarctica* is able to develop mycorrhiza [23] and was found regularly mycorrhized in montane sites in Patagonia and further southwards to the South Georgian Islands [25]. The limited distribution of *D. antarctica* to ornithic soils or at least to heavily fertilized soils suggests, that soil development along temporal gradients does not provide sufficient nutrients for its establishment. This is reinforced by our observation that small colonies (1–3 cm diameter) can occur quite arbitrarily around isolated bird droppings, occasionally even on young soils and then typically in close vicinity to small and isolated rocks on hilltops which are used by Skuas (*Stercorarius maccormicki* Saund.) as look-out points, but were found to die back after 1 or 2 years. As excess of nutrients is known to inhibit mycorrhization (e.g. [51]), the question remains whether *D. antarctica* on ornithosols does not develop mycorrhiza for this reason, or simply has no access to inocculum of Glomerymycotan spores. The latter scenario is supported by a study of Torres-Mellado et al. [52], who found along a transect of 35 plots at the South Shetland islands, Paradise Bay, and Marguerit Bay no signs of mycorrhization of *D.antarctica* or *Colobanthus quitense*, or their spores in the soil.

Conclusion

Along three temporal gradients formed by glacier retreat along the Fildes Pensinsula and nearby Ardley Island, South Shetland Islands, in maritime Antarctica, we found gradients of soil development, which resulted in increased differentiation of soil horizons, increased stocks of organic carbon, and an increase in soil pH. The C/N ratio and stable isotope $\delta^{13}C$ patterns were similar to those developed in temperate and boreal soils. The SOM with low C/N ratio was more enriched with ^{13}C. The hypotheses of enrichment in $\delta^{13}C$ values in deep soil due to microbial discrimination and mixing soil surface materials depleted in ^{13}C to deeper soil horizons enriched with ^{13}C due to cryoturbation by repeated freezing and thawing were supported in the present study. Successional patterns of vegetation were scarce and restricted to lichens and mosses. Only in the later stages of the temporal gradient we did find lichen and moss species connected to the soil, while earlier successional stages were restricted to lichen and moss habiting rock fragments not influenced by cryoturbation. This suggests an interference with soil production processes mainly by litter additions to soil. The conditions encouraging *D. antarctica* growth were found not to have resulted from soil succession but from bird feces enrichment, leading to a pseudo-succession in vegetation where fertilization gradients around bird colonies occur. Neither *D. antarctica* nor soil-dwelling mosses were found to be mycorrhized, nor was *D. antarctica* found to be able to survive on climax stands due to soil succession. Although the soils under *D. antarctica* appear as the most developed soils in Antarctica in terms of carbon content, they have to be treated as decoupled soil environments in terms of temporal gradients of soil succession.

Competing interests

The authors declare that they have no competing interests.

Authors' contributions

JB designed the experiment, carried out part of soil sampling and successional analyses and drafted the manuscript. RG, RM, GG, OS, DB, and RMcC participated in the design of the study and helped to draft the manuscript. RG, GG, OS, DB, RMcC performed the field work between 2012–14 and identified the temporal gradients. DB and MA did the C/N and ^{13}C analyses, and AA investigated the mycorrhizal status of the climax vegetation (all helped to draft the manuscript). All authors read and approved the final manuscript.

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