



SOIL SCIENCE

Soils under seal carcasses with varying degrees of decomposition: oasis of nutrients and vegetation in Antarctica

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Abstract: Areas of high concentration of seal carcasses have been observed in localized areas of James Ross Island, Antarctica. Such carcasses show an unusual vegetation development, in a semi-arid area with bare soils under intense winds, high salinity and sandy texture. We investigated carcasses of seals around a lake in James Ross Island, with four different stages of decomposition, with three replicates: Seal (S01), with recently mummified carcasses; S02, with partially degraded carcasses; S03, with broken carcasses with partially degraded exposed bones, and S04, with completely broken, scattered skeletons. The vegetation showed a maximum degree of development in carcasses at stages S02 and S03, with the environment between the skin and the skeleton as the preferred place for vegetation establishment. The chemical alteration was greater with increasing carcass decomposition but reduced with the spreading and final decomposition of the bones, with anomalous values observed only in the vicinity of the carcasses. It is concluded that the presence of carcasses of seals, concentrated in wet places, even in a semi-desert climate, represent important oases of nutrients, with a combination of physical and chemical effects throughout the decomposition process that favor plant establishment and succession.

Key words: animal bones, Antarctic soils, nutrient cycling, phosphatization.

INTRODUCTION

Seal carcasses in varying degrees of mummification have been reported in the Antarctic literature since the dawn of exploration of the continent (Scott 1905, Wilson 1907). Since the earliest scientific expeditions on the continent, mummified seals and their skeletons have been numerous reported in several ice-free areas, highlighting the McMurdo Sound Dry Valleys - Victoria Land - East Antarctica (Bull 1959, Péwé et al. 1959, Balham 1960, Caughley 1960, Claridge 1961, Evteev 1962, Barwick & Balham 1967, Dort 1971, Stirling & Kooyman 1971, Mabin 1985) and the Antarctic Peninsula and

surrounding islands (Gordon & Harkness 1992, Björck et al. 1996, Nelson et al. 2008, Negrete et al. 2011, Nývlt et al. 2016). In both areas, the seal carcasses consist predominantly of crabeater seals *Lobodon carcinophaga* (Hombron & Jacquinot 1842) with a smaller number of Weddell seals *Leptonychotes weddellii* (Lesson 1826) and leopard seals *Hydrurga leptonyx* (Blainville 1820), sequentially, reflecting the predominance of crabeater seals within the Southern Ocean (Banks et al. 2010).

In McMurdo Sound, the carcasses possess ages ranging from some decades to more than 200 to 300 years old (Dort 1971). Most carcasses

are located on or near the valley floors, although specimens were also found at altitudes of up to 1200 m a.s.l., and at recorded distances of 50 to 100 km from the coast (Banks et al. 2010, Péwé et al. 1959). Although more recently studied, the seal carcasses in the Antarctic Peninsula ice-free areas have been considered very relevant in a palaeogeographical viewpoint, even surpassing the McMurdo Sound findings in terms of number of individuals recorded (Nývlt et al. 2016).

The Peninsula Ulu, located on James Ross Island – Weddell Seal Sector, presents one of the most extensive records of seal carcasses in the Antarctic Peninsula region, with 401 individual carcasses identified (Nelson et al. 2008). In general, the carcasses were found at altitudes of up to 100 m a.s.l. and surfaces with slope $< 5^\circ$, besides maximum distances of ~5 km inland. The studies of the carcasses in James Ross Island also indicated age-at-depth varying from young sexually immature (< 5 years old) to mature (> 20 years) individuals (Nývlt et al. 2016). This differs substantially from the recorded in McMurdo Sound, where the carcasses were mainly of individuals with no more than one year old (Dort 1971). The studies also showed the deaths accumulated in the last century, in agreement with findings in the near South Shetland Island (Gordon & Harkness 1992) and Seymour Island (Negrete et al. 2011). There is also a wide range in the taphonomic state of the seal carcasses, varying from fresh carcasses to isolated bones (Nývlt et al. 2016).

Zones of mammal bone accumulation represent important plant colonization and diversification hotspots in Antarctica. The deposition of these materials, subjected to decomposition and dissolution over time can contribute to the formation of soils with distinct chemical and physical characteristics (Putzke et al. 2022), which creates a favorable soil micro-environment involving especially

chemicals related to organic contents and P–Ca forms (Schaefer et al. 2004). Olech (1996) report whale bones as an important substrate for the development of an apophytic flora in Antarctica, which is related to the nutrients retained in the bone pores (Albuquerque et al. 2018). In turn, Putzke et al. (2022) reports the development of a cryptogamic vegetation under and adjacently to the skeletons because of nutrient cycling and new microclimate conditions (greater moisture). Like whale bones, decaying seal carcasses are spots of nutrients and in deficient subpolar environments such as James Ross Island constitute excellent sites for colonization by algae, cyanobacteria, lichens, and mosses (Nývlt et al. 2016).

The decaying seal carcasses also represent spots of phosphatization (Simas et al. 2007), an important pedogenic process in Antarctica associated with the incorporation of P-rich organic compounds into soil and subsequent geochemical and mineralogical transformations, which also bring about changes in soil physical and micromorphological attributes (Almeida et al. 2021, Schaefer et al. 2008, Simas et al. 2006). Although the phosphatization process is more expressed in sea bird (e.g., penguins) activities in Antarctica (Michel et al. 2006, Rodrigues et al. 2021), it also occurs in the continent from the action of mammalian species (Bedernichek et al. 2020), although without the same intensity. The influence of mammals, including alive specimens or carcasses, has scarcely been recorded on chemical and microbiological characteristics of Antarctic soils (Ramírez-Fernández et al. 2019, Zvěřina et al. 2016) and thus, need to be better clarified.

Although approaching the decaying seal carcasses of James Ross Island as representing loci of nutrients release, Nývlt et al. (2016) did not determine the magnitude of the pedogeochemical enrichment effect, which was

precisely the focus of the current study. Thus, we sought to elucidate in detail the effects of nutrient release from the mummified seals and skeletons to the adjacent soil environment, as well as the development of vegetation in these micro-oases of life in the semi-arid and nutrient deficient subpolar James Ross Island environment.

MATERIAL AND METHODS

Study area

The Ulu Peninsula is located at the northeast sector of James Ross Island on the coast of the Prince Gustav Channel (Figure 1) and represents the largest continuous deglaciated area in the islands of the Weddell Sea Sector (Daher et al. 2019). The climate of the Ulu Peninsula contributes to the desiccation and mummification of the seal carcasses from the accumulation of salinity and the strong winds blowing away the snow. The entire area of Ulu Peninsula is located on the leeward side of the northern Antarctic Peninsula, which provides a barrier to warmer air masses moving across the western coast of the peninsula. It results in a subpolar semi-arid climate with mean annual air temperature of $\sim 7^{\circ}\text{C}$ (Láska et al. 2012) and annual precipitation of 400–500 mm of water equivalent (van Lipzig et al. 2004).

Due to the cold climate, the Ulu Peninsula soils are marked by the conspicuous presence of ice-cemented permafrost, even in the lower altitudes (Daher et al. 2019). The main soil class found in the area is Turbic Cryosol (Daher et al. 2022), since the soils show general features of cryoturbation, such as irregular and broken horizons, vertical orientation of stones within the soil profile, and granular structure (Daher et al. 2019). The soils of James Ross Island are also characterized as being predominantly alkaline

with low levels of organic carbon and clay, along with higher levels of sand and silt (Vlček 2016).

Regarding the geology, Ulu Peninsula is composed of sedimentary rocks occupying the lowlands, overlaid by volcanic rocks which forms the structure of the high lava plateaus located in many parts of the peninsula (Smellie et al. 2008). The lowlands of Ulu Peninsula have been ice-free for most of the Holocene (Nývlt et al. 2014) and only hanging, valley and piedmont glaciers and small ice domes persist in the highlands (Davies et al. 2013). The Abernethy Flats, where the most part of the seal carcasses are found in James Ross Island, are a large flat area located on the coast of Brandy Bay and possess a surface composed of marine quaternary sediments, erosional cretaceous surfaces, braidplains, and lakes, and represent one of the lowest sectors in the Ulu Peninsula, with a maximum altitude around 20 m a.s.l (Jennings et al. 2021). In the Abernethy Flats, the highest concentration of carcasses are found around the Monolith Lake, with a density of ~ 70 individuals per square kilometer (Nývlt et al. 2016).

The flora cover of Ulu Peninsula is composed of mosses, lichens, algae, and cyanobacteria (Barták et al. 2015), although it is spatially limited due to the semiarid climate, being dependent on topography, snow accumulation and hotspots of soil nutrients. Weddell seals, Antarctic fur seals *Arctocephalus gazelle* (Peters 1875), elephant seals *Mirounga leonine* (Linnaeus 1758) and crabeater seals are occasionally present along the coast of Ulu Peninsula during the summer. However, during the winter the most common are crabeater seals (Nývlt et al. 2016), which also explains dominance of this species on the seal carcasses.

Field surveys and sampling

We investigated the soils and vegetation developed in twelve sites under the influence

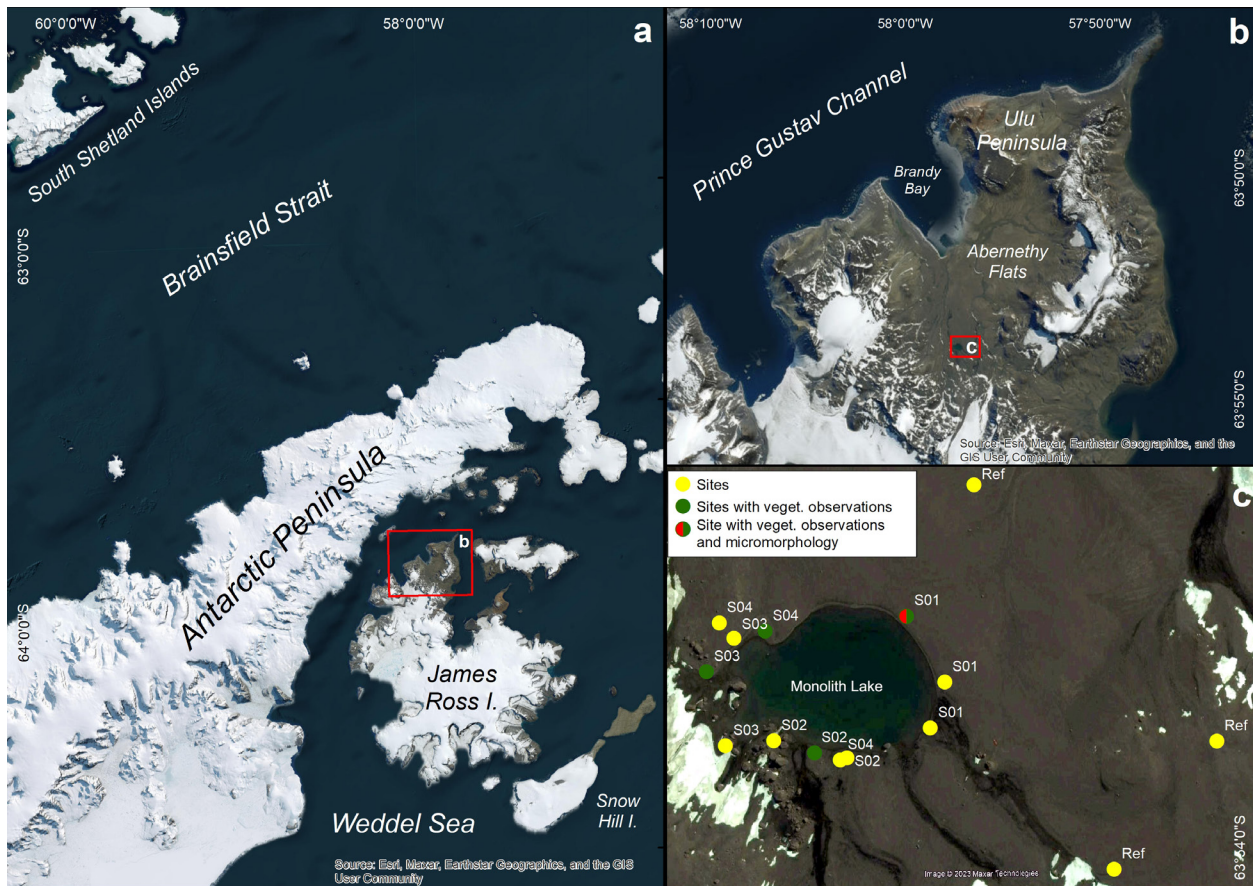


Figure 1. Location of the study area. a: location of the Ulu Peninsula, James Ross Island at the eastern coast of the Antarctic Peninsula; b: Ulu Peninsula and Abernethy Flats, highlighting the Monolith Lake location; c: Sites where the seal carcasses were investigated near the Monolith Lake.

of crabeater seal carcasses in the surroundings of the Monolith Lake, Abernethy Flats - James Ross Island. Four stages of decomposition were evaluated, being three carcasses of each decomposition type: the stage S01 represented the carcasses with a recent state of mummification and preserved skin; S02 represented the partially degraded carcass, in an initial stage of degradation of the skin; S03 was the broken carcass, with partially degraded and exposed bones, and no visible skin left on ground; and S04 is the completely broken skeleton, with the bones degraded and scattered on the ground, with a large area of redistribution (Figure 2). The fieldworks were carried out in the summer of 2016, and the soil sampling was performed

at four distances from the carcasses: below the carcasses - 0cm; adjacent to the carcasses - 5cm; 15 cm from the carcasses; and between 80-100 cm from the carcasses. Sampling was also collected in reference (Ref) sites located apart from any visible carcass, over surfaces representative of the Abernethy Flats in terms of drainage, pedregosity, and salt accumulation (Table I, Figure 1).

Vegetation survey

The vegetation sampling was conducted qualitatively through observation and collection of different species. One seal from each of four different stages of decomposition was selected for documentation of lichens and

Table I. Altitude and geographical coordinates of the sites evaluated.

Sites	Altitude (m)	Longitude	Latitude
S01.1	166	-57.951	-63.896
S01.2	164	-57.949	-63.897
S01.3	165	-57.950	-63.898
S02.1	171	-57.953	-63.898
S02.2	173	-57.955	-63.898
S02.3	176	-57.956	-63.898
S03.1	178	-57.958	-63.898
S03.2	179	-57.959	-63.897
S03.3	175	-57.958	-63.896
S04.1	176	-57.957	-63.896
S04.2	173	-57.954	-63.898
S04.1	176	-57.959	-63.896
Ref1	170	-57.948	-63.893
Ref2	175	-57.942	-63.900
Ref3	172	-57.938	-63.898

mosses present, which were identified using the relevant literature for mosses (Putzke & Pereira 2001, Ochyra et al. 2008) and lichens (Øvstedal & Lewis-Smith 2001, Olech 2004). The overall degree of development of the vegetation on each stage was evaluated.

Soil properties

Soil samples were collected at the depth of 0-10 cm and were prepared with air-drying and 2 mm sieving. Then, they were submitted to granulometric and chemical analyses according to Embrapa (Teixeira et al. 2017). Particle size analysis was based on wet sieving, physical dispersion with distilled water, sedimentation, and siphoning of the <0.002 mm fraction (Ruiz 2005).

Soil pH was determined in H₂O and KCl 1 mol L⁻¹ with a soil:solution ratio of 1:2.5. Available P, K, Na, Cu, Mn, Fe and Zn were extracted with Mehlich-1 (HCl 0.05 mol L⁻¹ and H₂SO₄ 0.025 mol L⁻¹) and determined by photolorimetry

(P), flame emission (K and Na) and atomic absorption spectroscopy (micronutrients). B content was determined with hot water extractant. Exchangeable Ca²⁺, Mg²⁺ and Al³⁺ ions were extracted with KCl 1 mol L⁻¹ and determined by atomic absorption spectroscopy (Ca²⁺ and Mg²⁺) and titration (Al³⁺). The potential acidity (H+Al) was extracted with Ca(CH₃COO₂) 0.5 mol L⁻¹ solution buffered at pH 7 and determined by titration. The remaining P (Prem) was obtained with a CaCl₂ 0.01 mol L⁻¹ solution containing 60 mg L⁻¹ of P and the organic matter (OM) content was determined by titration after heating and wet oxidation in acid solution with K₂Cr₂O₇ (Yeomans & Bremner 1988).

For micromorphological analysis, 1 undisturbed soil sample and 3 bone samples were collected in Kubiena boxes from stage S01 (Figure 1). The soil sample was collected at 5 cm depth, immediately below the skeleton, whereas the fragments of bones were found dispersed in the soil. The bones were collected from the skeleton in different degrees of decomposition, with a more preserved fragment and two more degraded fragments. The samples were impregnated with resin and produced polished slides (thin sections) measuring 3 x 6 cm. For the bones, longitudinal and transverse cuts were made, totaling two thin sections for each sample. Optical microscopic investigations were performed on 7 thin sections using a Zeiss Trinocular Optical Microscope (Axiophot model) with an integrated digital camera. The precepts of Stoops (2003) and Stoops et al. (2010) were used for the micromorphological descriptions, with emphasis on bone dissolution and phosphatic features. Additionally, some features observed in a petrographic microscope were selected for micromorphological and chemical analysis using a scanning electron microscope (SEM, JEOL JSM-5510) coupled with an energy dispersive system (EDS). The microchemical analysis considered

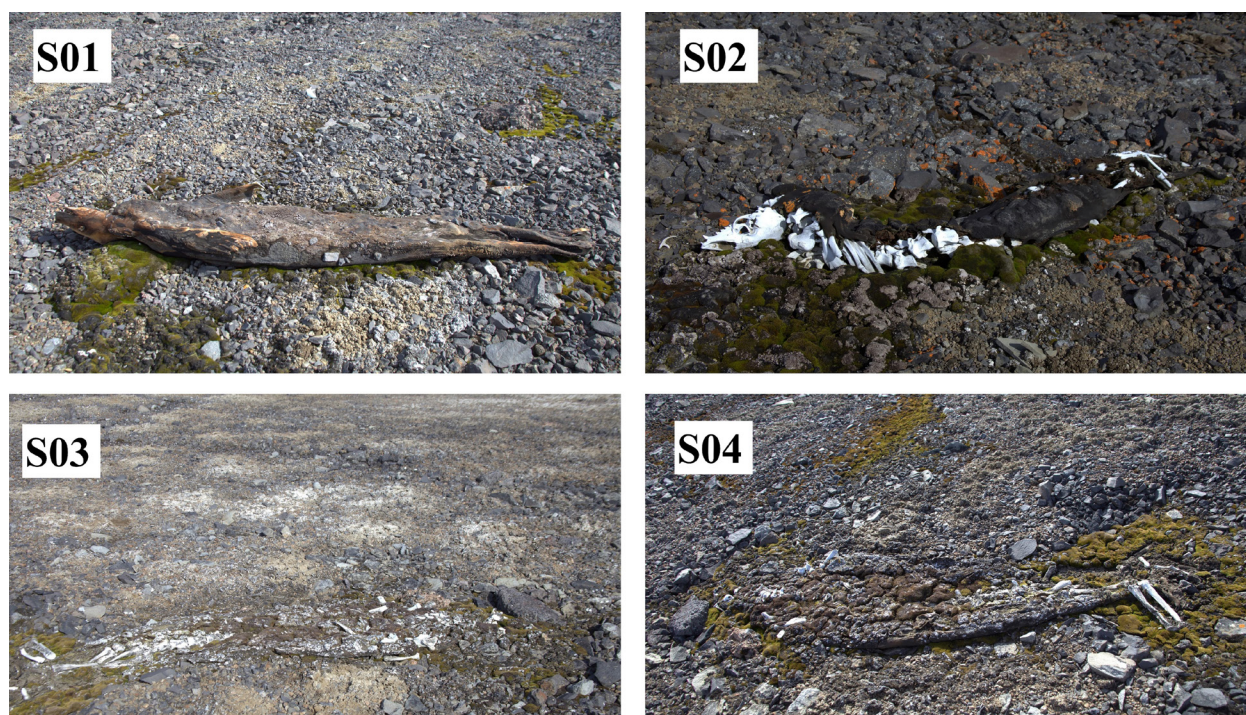


Figure 2. Different degrees of decomposition of the seal carcasses found at Ulu Peninsula, James Ross Island. S01: well-preserved mummified carcass; S02: partially degraded mummified carcass with partial skin presence and articulated skeleton; S03: disarticulated seal skeleton with bones degraded and any left skin; S04: dispersed bones representing the most advanced state of decay.

the following elements: P, Na, K, Mg, Ca, Fe, Al, Ti, S and Si.

Statistical analysis

All analyses were carried out using the R environment (R Core Team 2023). We also generated boxplot graphics using the package 'ggplot2' (Wickham et al. 2023) to display the data distribution for each decomposition stage and distance. The differences between the decomposition stages and distances were also evaluated using the non-parametric Kruskal Wallis test of the package 'stats' (R Core Team 2023) and the Dunn test of the package 'FSA' (Ogle et al. 2023) for multiple comparisons. At last, the soil properties were summarized in principal component analysis (PCA) using the package 'FactoMineR' (Husson et al. 2023)

to identify gradients of soil variation between decomposition stages and distances.

RESULTS AND DISCUSSION

Vegetation characterization

Species of mosses and lichens were identified growing on seal bones and in the surrounding areas at all stages of decomposition. In general, seven species of lichens and 5 species of mosses were quantified in all carcasses studied (Table II). The greatest richness (10 species) was found in the stage of decomposition S02, followed by S03, with eight species. The vegetation showed a maximum degree of development in carcasses at stages S02 and S03, with equivalent levels of moss and lichen species below and on top of the carcasses. The microenvironment between was the skin and the skeleton the preferred place for

Table II. Vegetation on seal carcasses at James Ross Island. The exact sites per stages of decomposition where vegetation was evaluated are depicted in Figure 1.

	Reference site	-> Stages of decomposition ->			
	Ref	S01	S02	S03	S04
Lichens (on skin and bones)	Not found	<i>Caloplaca</i> sp <i>Xanthoria</i> sp Microlichen 1	<i>Caloplaca</i> sp <i>Xanthoria</i> sp Microlichens 1,2,3 <i>Candelaria</i> sp <i>Candelariella</i> sp	<i>Caloplaca</i> sp <i>Xanthoria</i> sp Macrolichen 1, 2 <i>Candelariella</i> sp	<i>Xanthoria</i> sp Microlichen 1
Mosses (accounting vegetation cover windward, below the carcasses, leeward and spread laterally)	Not found	<i>Bryum</i> sp	<i>Bryum</i> sp <i>Bryum pseudotriquetrum</i> <i>Hypnum revolutum</i> <i>Schistidium</i> sp	<i>Bryum pseudotriquetrum</i> <i>Hypnum revolutum</i> <i>Brachythecium austrosalebrosum</i>	<i>Bryum pseudotriquetrum</i>

establishing the vegetation. On the other hand, fresh mummified seal carcasses (S01) and the final state of bone scattering (S04) showed a lower number of substrate colonizers, with few lichens and only one species of moss.

Lichens of the genera *Xanthoria* sp, *Caloplaca* sp, and *Candelariella* sp have also been reported by Nyvlt et al. (2016) growing on seal carcasses in James Ross Island, and their occurrence is favored by the gradual release of nutrients from the skin. *Caloplaca* sp is frequently found growing under whale bones and in Maritime Antarctica it is recognized as a pioneer in vegetation-free sites, probably because of its ideal growing conditions (Olech 2004, Albuquerque et al. 2018). The moss species *Bryum pseudotriquetrum* and *Hypnum revolutum* were also reported by Nyvlt et al. (2016) growing on seal carcasses and their adjacencies. *Bryum pseudotriquetrum* thrives in hollow sites with sand cover and exhibits vigorous growth under moist conditions (Okitu et al. 2003). Seal carcasses can provide a microenvironment that is more humid and nutrient-rich in their vicinity (Nyvlt et al. 2016). These unique characteristics within such arid surroundings can act as an environmental filter, where microsite conditions

shape and filter species with similar attributes to colonize and grow in these microhabitats (Schmitz et al. 2020a, b).

Soil chemical and physical characteristics

The seal carcass sites showed marked differences of the surface soils depending on both the degree of decomposition and the distances for the carcasses where the soil samples were collected, which can be evidenced with the Kruskal Wallis' p-values <0.05 obtained for many physical and chemical attributes (Table III). The pH H₂O values of the reference soil were distinctly higher than all others (mean of 7.3), although the great variability of the seal sites did not confer a significant difference (Figure 3). Nonetheless, the lower absolute values in all decomposition stages show effects of slight acidification promoted by the tissue's decomposition and bones dissolution, from organic (e.g., oxalic acid) (Haus et al. 2016, Lopes et al. 2022) and inorganic acids, highlighting those acids released from the nitrification. The nitrification process is the enzymatically mediated conversion of ammonium to nitrate and is considered one of the main sources of acidification during soil phosphatization

Table III. Kruskal Wallis p-value of the physical and chemical attributes for the decomposition stages (S01, S02, S03, S04) and carcasses distances (0, 5, 15, 80-100) plus the reference soils. Values < 0.05 indicate statistical significance at 5%.

Attributes	Stages	Distances
pH H ₂ O	0.053	0
pH KCl	0.069	0
P	0	0
K	0.028	0
Na	0.009	0
Ca	0.001	0
Mg	0	0
Al	0.262	0.262
H+Al	0.199	0
OM	0.03	0
P-rem	0.017	0
B	0.243	0.001
Cu	0.112	0.004
Mn	0.004	0.007
Fe	0	0
Zn	0.002	0
Clay	0.008	0
Sand	0.036	0

in Antarctica (Myrcha et al. 1985, Michel et al. 2006). Although the importance of nitrification is mainly recognized in phosphatized soils affected by birds, it is also relevant in phosphatized soils under the influence of mammals. The influence of vegetation supported by nutrient cycling is also a factor in the acidification of mammals phosphatized soils (Putzke et al. 2022).

On the other hand, the higher pH of S04 in comparison to the most samples of the others decomposition stages (Figure 3) indicates a lowering of the acidification with time due to the depletion of potentially acidifying organic compounds (with just bones left) or even the buffering from carbonates, a common process in the semi-arid environments of James Ross Island and neighbor islands (Siqueira et al. 2021).

The buffering potential of the aridity in James Ross Island can also be seen when we analyze pH according to the distance from the carcasses, with the distance 80-100 cm showing pH values almost as high as 8 (statistically similar to Ref, Figure 4). Nonetheless, the absence of pH values lower than 6 shows the acidification is not strong as in sites influenced by birds (Simas et al. 2008) or even sites influenced by colonies of mammals (Ramírez-Fernandes et al. 2019). The pH KCl showed similar values and tendency for all soils, being lower than the pH H₂O in a proportion of 0.5 to 1 unit, which indicates the dominance of negative charges, a common feature of the Antarctic soils.

The phosphatization can be well evidenced by the available P values (Rodrigues et al. 2021), with all carcasses stages showing significant increased values in comparison to the reference soils (Figure 3). In general, P contents were very low in the soil reference, slightly increased in mummified carcasses in an incipient stage of degradation (mean of 45 mg dm⁻³ at S01), and greatly increased with the progress of the degradation of the bones and skin. Maximum values occur at S03 (mean of 286 and maximum of 498 mg dm⁻³) and decrease to lower values with complete degradation and spreading of the skeleton (S04) (Figure 3). This could clearly indicate that in S03, the decomposition level on which the skeleton was reduced to many fragmented bones (thus with greater specific surface) concentrated in a high density on and in the ground, is that where the bones dissolution reaches its maximum degree, releasing with higher intensity the P present in the bone's apatite (P-Ca) (Putzke et al. 2022). As expected, the highest contents are found below the carcasses, although the very low values at 80-100 cm (Figure 4) from the carcasses indicate the lateral drainage is considerably lower than the vertical leaching, presumably due to the

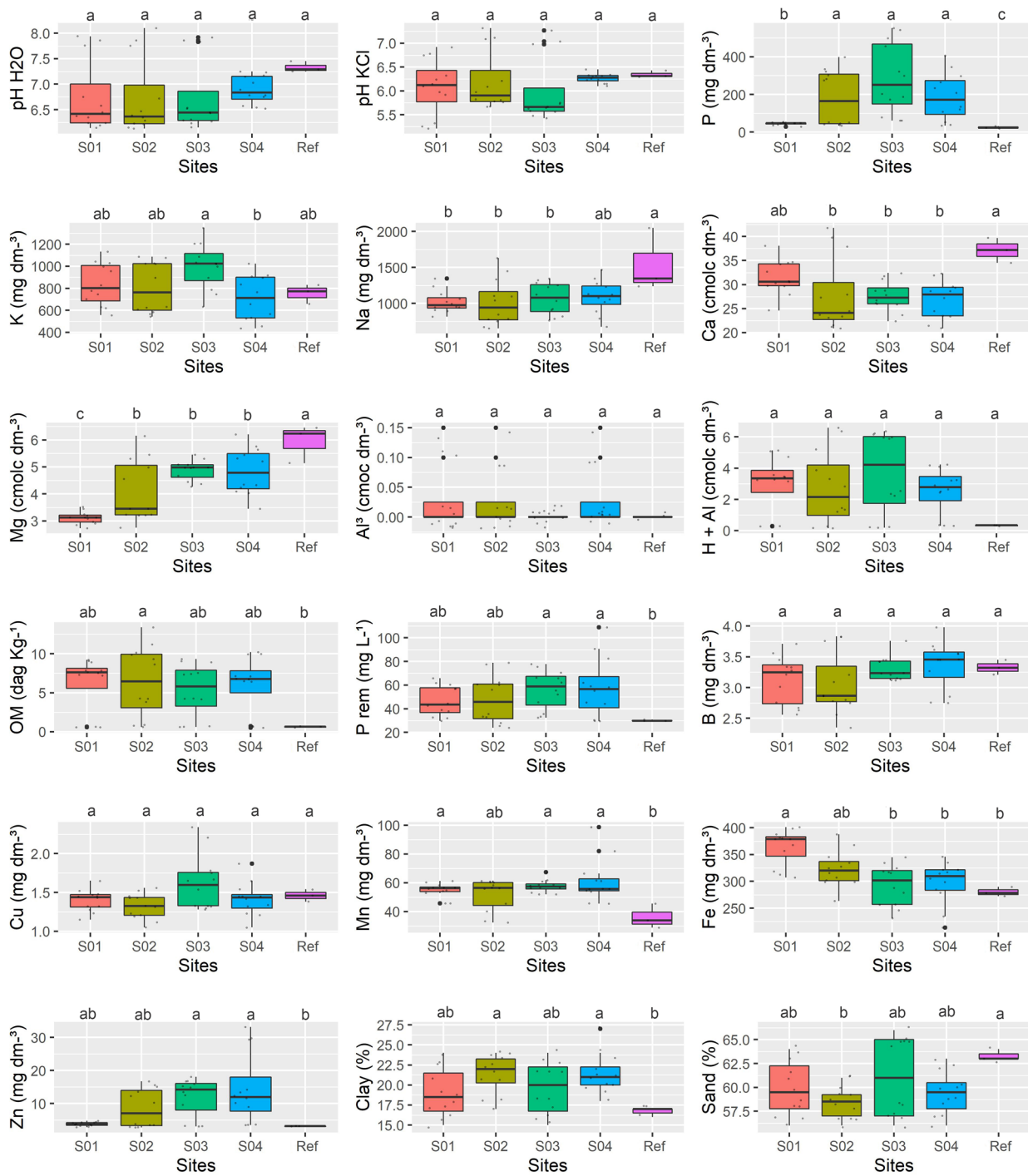


Figure 3. Boxplots of the chemical and physical soil properties according to the different seal carcasses decomposition. Letters indicate the differences obtained from the Dunn test at 5%.

negligible slope of the sites. The P-rem also presented greater values according to the proximity of the carcasses and the stages of

decomposition, with the contents at 0 and 5 cm and for S03 and S04, respectively, presenting

statistical differences for the reference soils (Figure 3, 4).

A similar pattern was also observed for K, although the background values of the reference soils are very high (above 600 mg dm^{-3} in all cases) and did not present significant differences between the reference and carcass sites (Figure 3). In general, the values show the prevailing salinity on the island, and the retention of K with the creation of microenvironments that can precipitate salts through the obstacle provided by the presence of carcasses. The contents were also greater as closer to the carcasses, reaching values of 1000 mg dm^{-3} , indicating the deposition from the seal bodies decomposition, besides the barrier effect. In the case of Na, there were no significant differences between the different carcasses, and the reference soil showed higher salinity (almost 1500 mg dm^{-3}) (Figure 3), perhaps due to the greater distance from the melting lake. The high Na and K contents in all soils are evidence of salinization as one of the most important pedogenic processes in the James Ross Island, which tends to accumulate salts in the surface soils (Daher et al. 2019). Nevertheless, the higher Na contents near the carcasses also indicate the secondary contribution of the seals in the surficial Na input (Figure 4).

The Ca^{2+} and Mg^{2+} contents showed to be lower with phosphatization and acidification, and the highest values occurred in the reference soil and in the highest distances of the carcasses' sites (Figure 4). Comparing the different levels of decomposition, The Ca^{2+} concentrations were higher in S01, of most well-preserved carcasses, indicating less leaching (although not statistically different), whereas the Mg^{2+} presented the lowest values in this site and highest in the most degraded seal (S04, with significance in the differences), indicating a possible input of this element, maybe from influence of the carcasses. Although the calcium and magnesium can also

be deposited from the bone's dissolution, the general Ca^{2+} and Mg^{2+} contents (mean of 30 and $4 \text{ cmol}_c \text{ dm}^{-3}$, respectively) seem to reflect mainly the geochemical background of the James Ross Island soils (Daher et al. 2022).

The Al^{3+} contents did not vary between soils, being always virtually null as a response for the pH values above 6. The potential acidity (H+Al) and organic matter contents increased with the phosphatization (Simas et al. 2008, Rodrigues et al. 2019), being considerably higher bellow the carcasses (mean of $5 \text{ cmol}_c \text{ dm}^{-3}$ and 10 dag dm^{-3} , respectively), whereas at 80-100 cm they are close to 0. The H+Al contents were higher at S03, following the lowest pH, whereas the organic matter was high at the sites S01 and S04). However, significant differences for the reference soils were found only close (0 and 5 cm) from the carcasses (Figure 4). Since the Al^{3+} content is negligible, we can assume the potential acidity is totally related to covalent hydrogen, which comes mainly from the strongly negatively charged surface of the organic matter. Although the data do not show a clear increase in organic matter with increasing decomposition, we can observe that seal carcasses are of utmost importance to the development of vegetation, even in the early stages of degradation (Table 2), which increases the organic matter values to extremely anomalous levels for the James Ross Island semi-arid, ahumic soils (Daher et al. 2019, Delpupo et al. 2014).

Some micronutrients, such as B and Cu, were not particularly sensitive (Figure 3). Zn content, in turn, was considerably higher and different from reference soils at 0 and 5 cm (mean of 17 mg dm^{-3}) and at the sites S04 and S03 (15 mg dm^{-3}) (Figure 3, 4), indicating that due to its close connection with bone' apatite, the Zn directly increases with the level of decomposition of the carcasses and when the bones dissolution becomes the main degradation process in

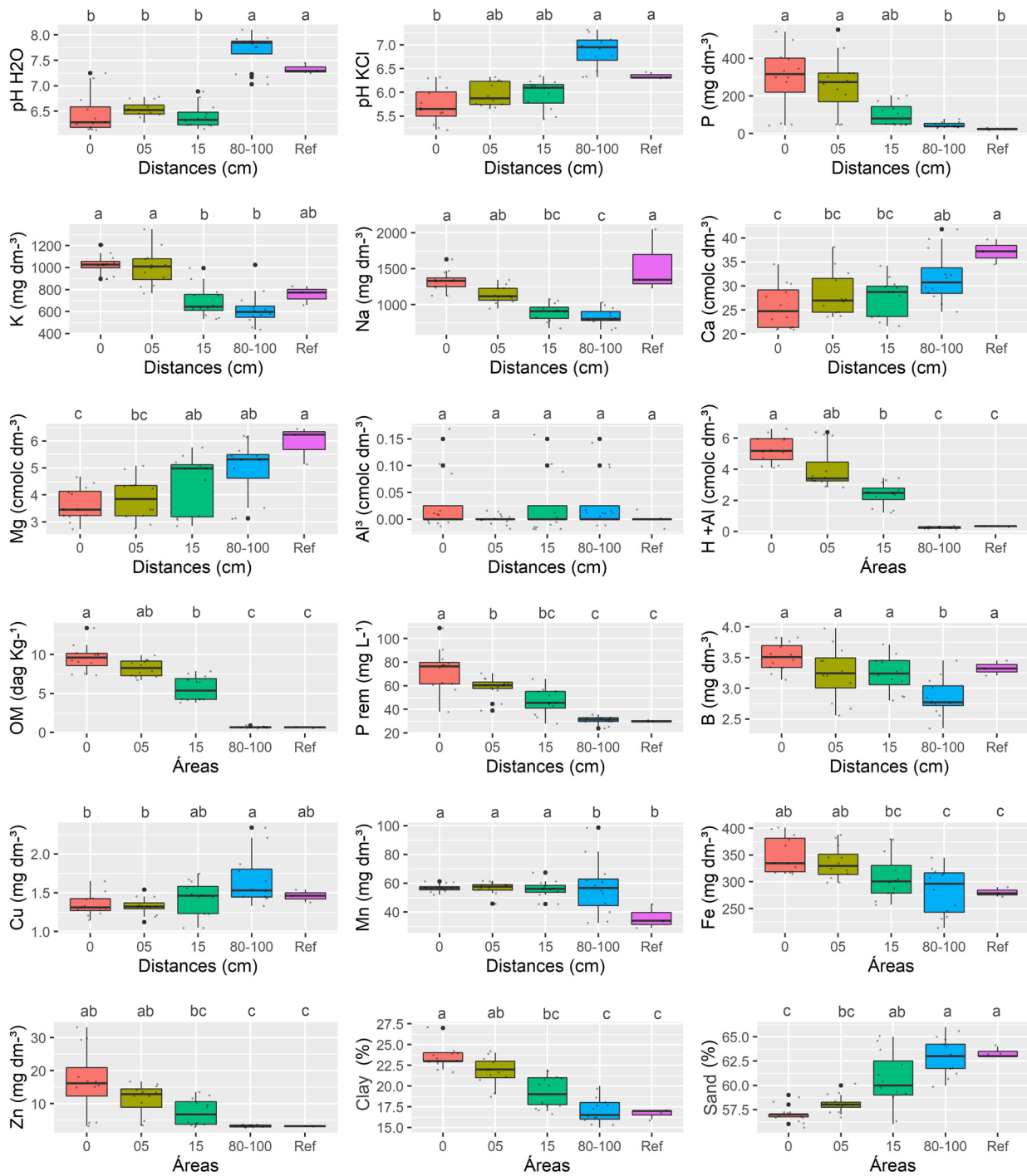


Figure 4. Boxplots of the chemical and physical soil properties according to the distances for the seal carcasses evaluated. Letters indicate the differences obtained from the Dunn test at 5%.

the phosphatized sites. The available Fe was also higher in the soils below the carcasses, indicating the influence of the phosphatization to its contents, although the highest values were

found at S01, indicating the release of Fe may be more related to the degradation of soft tissues and skin. The Mn contents are also higher in the

seals carcasses soils, but little differentiated among the sites and distances (Figure 3, 4).

Regarding the soil texture, there was an increase in clay content with phosphatization, and a concomitant reduction in sand, which is expressed at both the distances and degradation degrees, with the highest clay contents below the seal carcasses and in the S04. Although the production of clay from weathering in phosphatized soils is a common process (Pereira et al 2013a, Simas et al. 2006) it is probably that a significant part of the particles accounted as clay under the carcasses are directly associated with organic matter, since the latter was not removed during the chemical treatment before the granulometric analysis.

When analyzing the soil data through a Principal Component Analysis (PCA) biplot (Figure 5), we can see that the two main components (PC's) explained together 61.1% of the total variance, being enough to depict the strong differences between the soils according to the distances from the carcasses. So, we can affirm that the distance for the carcasses overcomes the decomposition degree effects as the most important factor for the soil differentiation in the sites evaluated. The PCA shows a strong reduction in the phosphatization process from below the carcass to the 80-100 cm distance. The 80-100 cm soil is confused with the reference soil in the graph, showing that the phosphatization does not present a high spatial expression in the sites studied.

The first component (PC1) explained 47.8% of the variance and had high positive loading of soil properties linked to the phosphatization and to the soils below the carcass, such as P, H+AL, K, Zn, Fe, OM, and clay. In turn, the PC1 presented negative loading for properties linked to the reference and 80-100 cm soils, such as sand, pH and Ca^{2+} , mainly reflecting the parent material influence in conditions of weak or none

phosphatization. The second component (PC2) explained 13.3% of the total variance and was more related to variations among the degrees of decomposition of the seal carcasses. Apart from the 80-100 cm distance, which was not sufficient to reflect the carcasses' influence, we can see a gradient within the PCA ellipses according to PC2 loading. The S01 and S02 sites presented negative loading and were more influenced by properties such Al^{3+} and Fe, which, in general, are not so significant for the characterization of phosphatization in the studied sites. On the other hand, the sites S03 and S04, which represent the greatest degree of carcasses' decomposition, had mostly positive loading and influence for the main soil properties linked to the phosphatization in the area, such as P, Zn and K. The intermediate position of H+AL, OM and clay contents suggest these properties are not so relevant to differentiate the soils according to the degradation degree.

Micromorphology

Besides the physical and chemical characteristics, the phosphatization under the influence of carcasses seals in James Ross Island is also evidenced from micromorphological features of the soils. We present the results of the comparison between the most and least preserved bone fragments (Figure 6) and the soil under the carcasses (Figure 7). Figure 6 displays an order of progressive degradation of the bones, moving from a segment with a lower rate of decomposition (a), to a higher rate of decomposition (b). It is possible to see that a whitish coloration is observed in the weakly degraded bone, with only the edges showing yellowish tones (Figure 6a). As dissolution and chemical alteration progress there is a significant increase in the orange color along the edges of the bones, indicating a process of reaction that starts at the edges and migrates

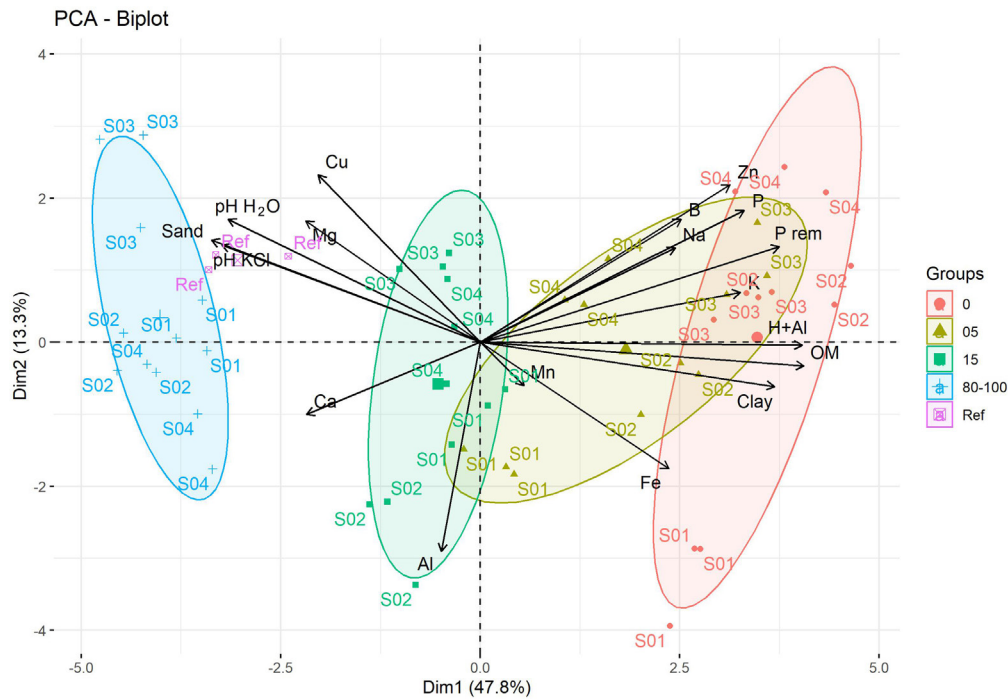


Figure 5. Principal Component Analysis of evaluated seal carcasses sites (0, 05, 15, 80-100cm and Ref) at different stages of decomposition (S01, S02, S03, S04 and Ref). For the analyses, the chemical (pH H₂O, pH KCl, P, K, Na, Mg, Al³, H+Al, OM, P rem, B, Cu, Mn, Fe, and Zn) and physical (Sand and Clay) properties were evaluated.

towards the center of the bone, intensifying the more oxidized tone (orange). The staining of the bones is related to the oxidation of the residual Fe present in the bone tissue and was also observed in other phosphatized soils of Antarctica (Rodrigues et al. 2021).

The decomposition and fragmentation of bones can be observed in backscattered electron images (BSE) and punctual chemical analysis by Energy Dispersive Spectroscopy (EDS) (Figure 6). As they are dissolved, even in the arid climate conditions of James Ross, elongated residual features of biogenic apatite form (Figure 6c). A more detailed chemical analysis shows that the central portions of these features are purer in calcium phosphates, with some sulfur content, and the more degraded edges have a more diversified composition and with the Fe presence, which gives the orange color (Figure 6d). The advance of bone degradation occurs from the edges to the center and along microfractures, making it possible to perceive its internal fragmentation, with increased porosity

and formation of minute bone fragments (Figure 6e).

With the progressive comminution of the bones' fragments, related to the chemical dissolution but also the physical fractionation by ice, minute bone fragments are incorporated into the soils, modifying the composition of coarse materials of the soil groundmass (Figure 7), which was initially formed only by minerals of geological origin. The movement of these fragments from the carcasses into the soil occurs both due to the physical behavior of the surface, in the freezing and thawing cycles, and due to the melting of the snow deposited above the carcasses. This is a process highlighted by several studies in phosphatized soils influenced by birds (Almeida et al. 2021, Pereira et al. 2013b, Schaefer et al. 2008), and, according to our data, by mammals.

The minute fragments of bones immersed in the soils of James Ross Island show an advanced state of physico-chemical alteration, especially associated with decomposing organic

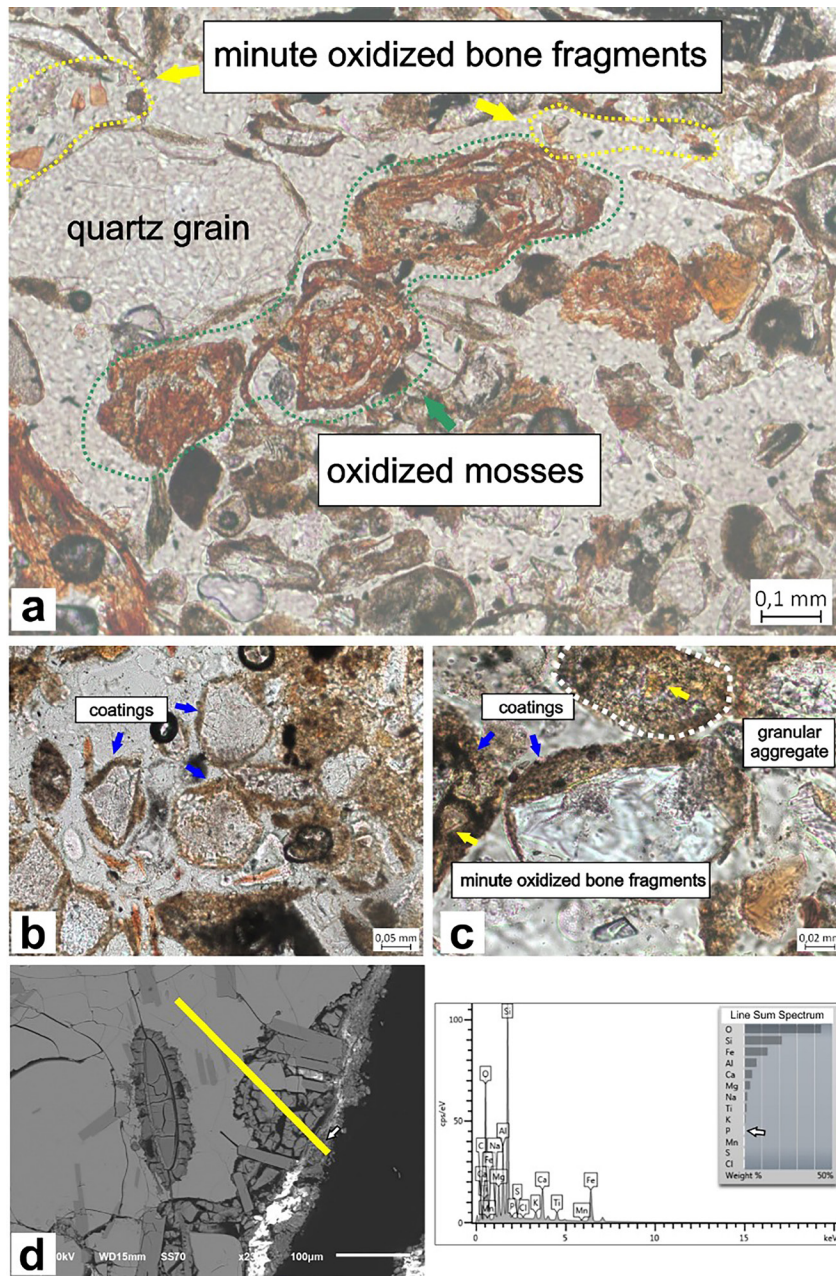


Figure 6. a) Photomicrographs in plane-polarized light (ppl) of an unaltered and slightly degraded bone fragment at the edges; b) Photomicrographs in ppl of degraded seal bone fragment, with advanced oxidation; c) Backscattered Electron Images (BSE) and punctual chemical analysis by Energy Dispersive Spectroscopy (EDS) of elongated apatite bone with high decomposition degree; d) BSE image with EDS analyses detailing the chemical composition between the edge and the center of the degraded bone fragment and e) BSE images of the formation of fragments by the decomposition of apatite bone.

matter (Figure 7a), such as fragments of mosses, capable of generating microsites of acidity that contribute the dissolution of phosphates. The dissolution of phosphates generates nutrients that allow the colonization of vegetation, and the decomposition of vegetation creates favorable conditions for this dissolution, forming a feedback system. This indicates the accentuation of the phosphatization process,

bone oxidation, and release of P into the soil from the degradation of these microscopic apatite fragments. The minute bones' fragments oxidation and dissolution are also favored by the presence of a strong porosity of the James Ross Island sandy soils, which increases the permeability that allows the percolation of fluids that accelerate the chemical reaction of the primary bone apatite.

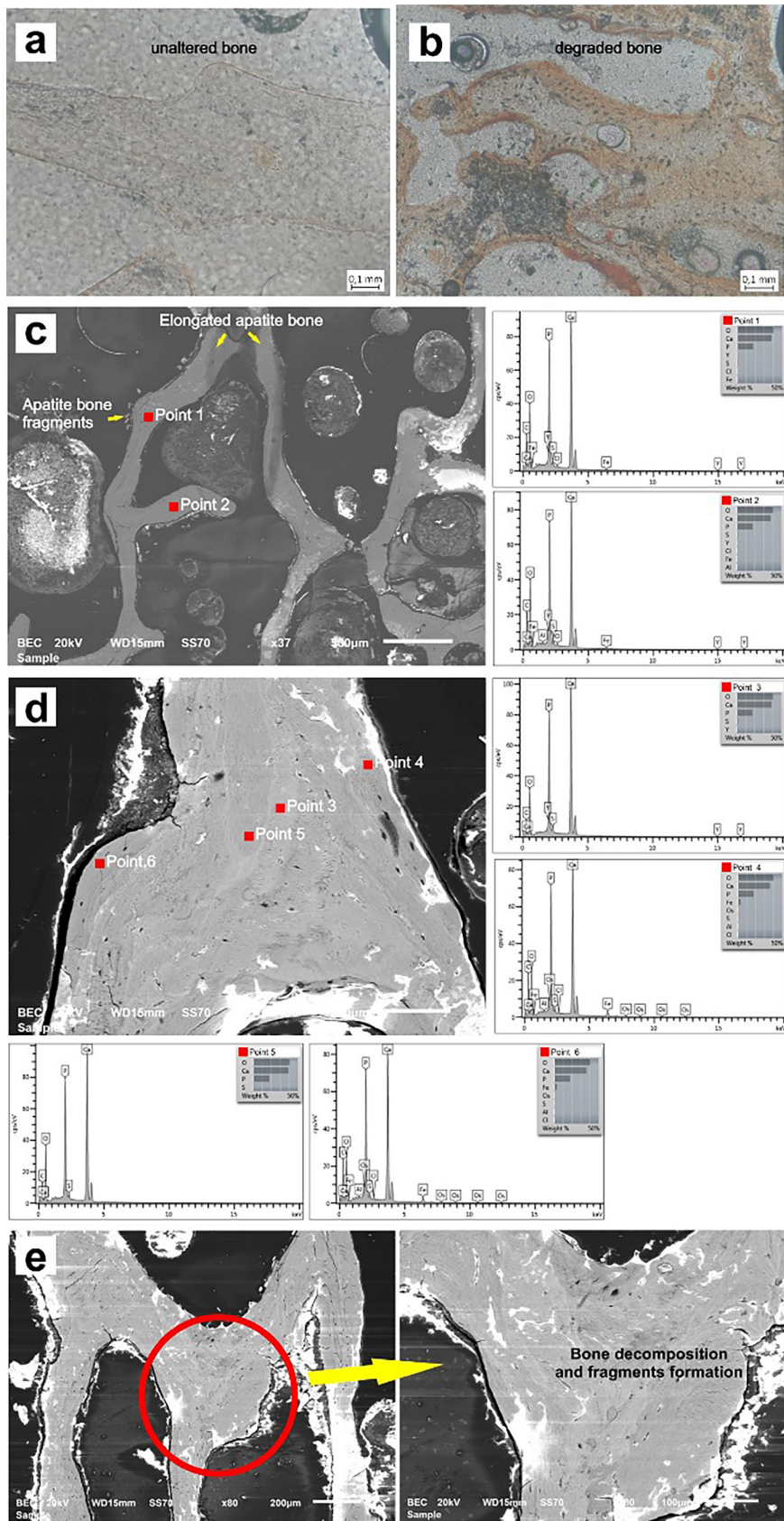


Figure 7. a) Photomicrographs in plane-polarized light (ppl) of mineral and organic materials of the groundmass of soil associated with seal carcasses, highlighting the presence of minutes fragments of oxidized bone (yellow arrows), fragments of mosses (green arrows) and quartz grains, separated from each other by a complex packing void system; b) Photomicrographs in ppl of coatings around mineral grains (blue arrows); c) Photomicrographs in ppl of coatings around mineral grains with internal fragments of oxidized bone and granular aggregate (white arrow) associated with freezing and thawing process and d) BSE image and linear chemical analysis by EDS showing the diversified chemical composition, with the presence of P on the edges of the rock fragment.

It is probable that part of the available P made by the decomposition of bone fragments is removed by the high percolation of the sandy soils in James Ross Island. However, there is evidence of the presence of phosphate in coatings around mineral grains and rock fragments (Figures 7b, 7c and 7d). Illuvial coatings and infillings are one of the most important features of phosphatization in Antarctica and can be used to interpret the degree of evolution of phosphate soils (Pereira et al. 2013b). In phosphatic soils of high development degree under influence of birds, these pedofeatures are commonly formed by Al-Fe-K phosphates (Almeida et al. 2021). In our soils, they are composed of a mixture of fine materials, mainly in the silt and clay fractions, but also with some fine sand content. They are not exclusively phosphate coatings but have phosphates in their composition.

The types of coatings observed in thin sections have been reported to be associated with freezing and thawing processes (Van Vliet-lanoë 1985, 2010, Mellor 1986, Dasog et al. 1987, Todisco & Bhiry 2008). They are features formed under conditions of ultra-desiccation, flocculation, and mechanical compaction (Van Vliet-lanoë 2010), characteristics that allow their survival in conditions of collapse of microstructures, and subsequent transformation into granular aggregates. Cryoturbation tends to fracture the caps, and rotation of the grains (frost jacking) leads to their detachment and formation of granules. In this case, phosphates are present as amorphous material embedded in the soil micromass, and as minute bone fragments (Figure 7c).

In fact, a coating of mainly phosphate composition was not observed, as in Simas et al. (2007) Schaefer et al. (2008), Pereira et al. (2013b) and Rodrigues et al. (2021) in ornithogenic soils, but that does not mean that it cannot be

present or developing. This is because the EDS sensor used does not allow the separation of the composition of very thin and small features, and more detailed techniques, such as the electronic microprobe, can favor this detailing. Even so, the low reactivity with quartz and the thin thickness suggests that the main form of phosphate present is calcium phosphate, evidencing initial degrees of pedogenesis.

CONCLUSIONS

- 1) This study described the influence of seal carcasses in the creation of nutrient-rich soil environments in a semi-arid soils from James Ross Island, Antarctica.
- 2) This enrichment is crucial for plant establishment, and vegetation showed a maximum degree of development under carcasses at intermediate stages of decomposition, with equivalent levels of moss and lichen species below and on top of the carcasses.
- 3) The environment between the skin and the skeleton is the preferred place for establishing the vegetation. The two extremes (the recent mummified seal carcasses and the final state of bone scattering) showed a lower number of substrate colonizers, with few lichens and only one species of moss.
- 4) The progressive phosphate reaction was clearly demonstrated at optical microscopy, with increasing degradation and dissolution from new to old carcasses, and soils.
- 5) The chemical analyzes of the underlying soils revealed a strong increase in the contents of P, Zn, K and OM, below and in the vicinity of the carcasses, being reduced with the distance from the carcasses.
- 6) The chemical effects were greater with increasing carcass decomposition but

reduced with the spreading and final decomposition of the bones, with anomalous values only in the vicinity of the carcasses.

- 7) The incipient stage of carcasses' decomposition, with intact skin, shows very low values of nutrient contribution to the nearby or adjacent soil.
- 8) The presence of carcasses of seals concentrated in wet places, even in a semi-arid climate, represent key oases of nutrient concentration, with a combination of physical and chemical effects throughout the decomposition process. The new environment harbors plant species, especially mosses and lichens, which are practically absent in the surrounding natural environment.

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Author contributions

CEGRS designed the study. EOS and MDP carried out the fieldwork, CEGRS and MRF execution of the research, DS and RGS interpreted the results and wrote the first version of the manuscript. JP identified the plant species. EOS and ASMI collected and prepared the soils samples. FSO and LGM processed micromorphology samples and helped the writing discussion. CEGRS supervised the research, contributed to the discussion and to the text review.

