DR. ANDRÉ LUIZ CUSTÓDIO FRANCO (Orcid ID : 0000-0003-3294-6848)

Article type : Primary Research Article

Response of Antarctic soil fauna to climate-driven changes since the Last Glacial Maximum

Running title: Antarctic soil fauna post Glacial Maximum

Authors: André L.C. Franco[1], Byron J. Adams[2], Melisa A. Diaz[3a], Nathan P. Lemoine[4], Nicholas B. Dragone[5], Noah Fierer[5], W. Berry Lyons[3], Ian Hogg[6,7], Diana H. Wall[8]

List of Author's ORCID IDs:

André L.C. Franco – 0000-0003-3294-6848

Byron J. Adams - 0000-0002-7815-3352

Melisa A. Diaz – 0000-0001-6657-358X

Nathan P. Lemoine – 0000-0003-3436-7196

Nicholas B. Dragone – 0000-0002-8983-6482

Noah Fierer – 000-0002-6432-4261

W. Berry Lyons – 0000-0002-3143-7251

Ian Hogg – 0000-0002-6685-0089

Diana H. Wall – 0000-0002-9466-5235

Institutional affiliations: [1]Colorado State University, Department of Biology, Fort Collins, CO 80523

[2]Brigham Young University, Department of Biology, Evolutionary Ecology Laboratories, and Monte L. Bean Museum Provo, UT 84602

[3]The Ohio State University, School of Earth Sciences, Byrd Polar and Climate Research Center Columbus OH 43210.

[4]Marquette University, Department of Biological Sciences Milwaukee, WI 53201, and Milwaukee Public Museum Department of Zoology Milwaukee, WI 53201

[5]University of Colorado Boulder, Department of Ecology and Evolutionary Biology, and Cooperative Institute for Research in Environmental Sciences, Boulder CO 80309

[6]Polar Knowledge Canada, Canadian High Arctic Research Station, Cambridge, Bay X0B 0C0, Nunavut, Canada.

[7]School of Science, University of Waikato, Hamilton 3240, New Zealand

[8]Colorado State University, Department of Biology & School of Global Environmental Sustainability Fort Collins, CO 80523

[a]Now at Departments of Geology and Geophysics and Applied Ocean Physics and Engineering, Woods Hole Oceanographic Institution, Woods Hole, MA 02543

Contact information: Department of Biology, Colorado State University, 200 West Lake Street, 1878 Biology, Fort Collins, CO, 80523, USA. Phone: +1 970 495 4476. E-mail address: andre.franco@colostate.edu (A.L.C. Franco)

Abstract

Understanding how terrestrial biotic communities have responded to glacial recession since the Last Glacial Maximum (LGM) can inform present and future responses of biota to climate change. In Antarctica, the Transantarctic Mountains (TAM) have experienced massive environmental changes associated with glacial retreat since the LGM, yet we have few clues as to how its soil invertebrate-dominated animal communities have responded. Here, we surveyed soil invertebrate fauna from above and below proposed LGM elevations along transects located at 12 features across the Shackleton Glacier region. Our transects captured gradients of surface ages possibly up to 4.5 million years and the soils have been free from human disturbance for their entire history. Our data support the hypothesis that soils exposed during the LGM are now less suitable habitats for invertebrates than those that have been exposed by deglaciation following the LGM. Our results show that faunal abundance, community composition, and diversity were all strongly affected by climate-driven changes since the LGM. Soils more recently exposed by glacial recession (as indicated by distances from present ice surfaces) had higher faunal abundances and species richness than older exposed soils. Higher abundances of the dominant nematode *Scottnema* were found in older exposed soils, while *Eudorylaimus*, *Plectus*, tardigrades, and rotifers preferentially occurred in more recently exposed soils. Approximately 30% of the soils from which invertebrates could be extracted had only *Scottnema*, and these single-taxon communities occurred more frequently in soils exposed for longer periods of time. Our structural equation modeling of abiotic drivers highlighted soil salinity as a key mediator of *Scottnema* responses to soil exposure age. These changes in soil habitat suitability and biotic communities since the LGM indicate that Antarctic terrestrial biodiversity throughout the TAM will be highly altered by climate warming.

Keywords: biodiversity, climate change, glacial retreat, nematodes, Shackleton Glacier, soil invertebrates

1. Introduction

Predicting how polar biotic communities will respond to ongoing environmental changes requires understanding how these terrestrial ecosystems have changed since the Last Glacial Maximum (LGM), when most of the currently ice-free areas were completely glaciated (Anderson et al., 2002; Heroy & Anderson, 2005; Sugden et al., 2006). In Antarctica, the massive environmental changes associated with glacial recession since the LGM are particularly striking in the Transantarctic Mountains (TAM) region, where outlet glaciers experienced some of the largest changes in ice thickness during the LGM on the continent (Golledge, Fogwill, Mackintosh, & Buckley, 2012). Presently, atmospheric warming is accelerating faster in Antarctica than almost any other location in the world aggravated by the amelioration of the ozone hole (Bromwich et al., 2013; Kindem & Christiansen, 2001; Thompson & Solomon, 2002; Turner et al., 2007). These ongoing and projected changes in climate will promote deglaciation and impact Antarctica's terrestrial communities in ice-free areas which are dominated by soil invertebrates (Convey & Peck, 2019; Czechowski et al., 2016; Freckman & Virginia, 1998; Gooseff et al., 2017; Hogg & Wall, 2011).

The ice-free features of the Shackleton Glacier area in the TAM region, a major outlet glacier of the East Antarctic Ice Sheet (EAIS), are ideal for addressing questions about the responses of terrestrial biodiversity to glacial recession since the LGM. These ice-free features provide a relatively accessible archive of geologic legacies, as well as past and present climate variability at local to regional scales. The Shackleton Glacier has several exposed peaks of the TAM along the length of the glacier, spanning a range in elevations. Some ice-free terrestrial areas at the LGM were also ice-free through previous glacial maxima, becoming increasingly salty and challenging environment for soil organisms since at least the late quaternary (140,000 years ago), with some areas as old as 14 million years or more (Balter-Kennedy et al., 2020; Denton et al., 1989; Diaz, Corbett, et al., 2020; Pollard & DeConto, 2009). Of all the ice-free regions in the TAM, those of the Shackleton Glacier provide a repeated series of exposure ages, where ecosystem responses associated with the last interglacial have been replicated across elevational and latitudinal transects. This allows for comparisons of community structure observed at different spatial and temporal scales. These species-poor terrestrial ecosystems also allow biotic communities to be surveyed to an extent not feasible in more species-rich ecosystems. Evidence from the McMurdo Dry Valley region suggests that soil invertebrate community structure and functioning of the ice-free peaks of the TAM are correlated almost exclusively with geophysical parameters, and are probably not obscured by complex biological interactions (Parsons et al., 2004). Yet, of all the outlet glaciers of the TAM, the Shackleton Glacier region has the highest overall biodiversity recorded (Green et al., 2011). Thus, the Shackleton Glacier region is well-suited for testing hypotheses concerning the role of climate-driven changes on biotic community structure (Hogg et al., 2006).

Previous studies have suggested a correlation between soil exposure time, habitat suitability, and biotic community structure (Magalhães et al., 2012; Michalski, 2005; Ugolini & Bockheim, 2008). Typically, older ecosystems in the context of time since exposure from ice retreat support less soil biomass and lower levels of invertebrate diversity due to accumulations of atmospherically deposited salts as well as lowered water content over time (Dragone et al., 2021; Lyons et al., 2016). The connections between the composition of soil animal communities and the role that geological legacies play in shaping these communities are critical to understanding how communities respond to environmental changes (Collins et al., 2020). Our study focuses on historical patterns of deglaciation and responses of soil invertebrate communities. Global warming is accelerating the pace of deglaciation, leading to changes in habitat suitability (in terms of salinity, organic carbon content, moisture availability, pH, and nutrient availability) and community composition as soils become exposed (Andriuzzi et al., 2018; Gooseff et al., 2017). Here, we investigated whether habitat suitability, taxonomic diversity, and the composition of soil invertebrate communities (i.e., nematodes, tardigrades, and rotifers) follow predictable patterns with time since soil exposure following the LGM.

Calculated surface soil exposure ages across the Shackleton Glacier region are sparse, ranging from contemporary (<20,000 years) to upwards of 4,500,000 years (Diaz, Corbet, et al., 2020). In lieu of generating exposure ages for each individual sample, we use linear distance from present ice surfaces and soil nitrate (NO_3^-) concentration as proxies for time since exposure (Diaz, Corbett, et al., 2020; Diaz, Li, et al., 2020; Lyons et al., 2016). We hypothesized that soils furthest from present-day surface ice that were exposed during the LGM are less suitable habitats than those exposed through deglaciation following the LGM, having accumulated atmospherically deposited salts and depreciated available carbon (Virginia & Wall, 1999). As a result, organismal abundance and species richness in areas that were exposed during repeated glacial maxima would decrease with exposure time and distance from present ice surfaces. We also predict an inverse pattern for areas that were glaciated during the LGM, that is, abundance and biodiversity should increase with proximity to present-day ice surfaces. Failure to reject our hypothesis means that these predictable patterns of ecosystem-level responses to climate-driven environmental change can be used to improve predictions of contemporary and future soil community responses to global warming, and guide conservation efforts by identifying current hotspots and most vulnerable areas.

2. Materials and Methods

2.1 Study site and geological context

The Shackleton Glacier (~84.5 to 86.4°S; ~130 km long and ~10 km wide) is a major outlet glacier of the EAIS which drains north into the Ross Embayment (Fig. 1a,b). During glacial periods, increases in the size of the EAIS likely resulted in glacial overriding of currently exposed soils, particularly at lower elevations near the glacier terminus (Golledge et al., 2012; Talarico et al., 2012). As such, the valleys and other ice-free areas within the region have likely been modified and reworked numerous times. Exposure ages have recently been determined and range from the early Holocene to the Miocene, with the oldest ages closest to the Polar Plateau and at high elevations furthest from the glacier (Balter-Kennedy et al., 2020; Diaz, Corbett, et al., 2020).

The soils of the Shackleton Glacier contain a variety of water-soluble salts derived primarily from atmospheric deposition and chemical weathering (Claridge & Campbell, 1968; Diaz, Li, et al., 2020). The major salts are typically nitrate and sulfate salts, especially at higher elevations and further inland from the Ross Ice Shelf where total salt concentrations can exceed 80,000 $\mu g\ g^{-1}$(Diaz et al., 2021; Diaz, Li, et al., 2020). The solubilities of the salts vary, but nitrate salts are highly soluble and their occurrence at high elevation and inland locations suggests that those soils have maintained persistent arid conditions for possibly thousands of years (Claridge & Campbell, 1968; Diaz, Li, et al., 2020).

2.2 Sample collection

A total of 232 soils (0-5 cm depth) were collected from twelve ice-free areas along the Shackleton Glacier from December 2017 to January 2018. The locations include Roberts Massif, Schroeder Hill, Bennett Platform, Kitching Ridge, Mt. Augustana, Mt. Heekin, Thanksgiving Valley, Taylor Nunatak, Mt. Franke, Mt. Wasko, Nilsen Peak, and Mt. Speed (Fig. 1, panels c–n), and range from 150 to 2221 m.a.s.l. in elevation. Between 14 and 26 soil samples were collected along elevation transects (up to 2000 m in length) from each location to capture maximum variation in soil properties, geochemistry, and surface exposure age.

Each sample was collected using a clean hand trowel and stored in sterile polyethylene bags. GPS coordinates, photographs of the soil surface, elevation, and other metadata were collected at the time of soil sample collection and used to estimate the aerial distance to the Ross Ice Shelf (distance from ice shelf) and the distance to the nearest glacier (distance from glacier, including outlet glaciers, tributary glaciers, and alpine glaciers). All soils were transported to the field camp in insulated coolers, where they were frozen at -6°C and remained frozen until processing for invertebrate extractions at the McMurdo Station laboratory facilities. Finally, the samples were shipped frozen to The Ohio State University where they were prepared for subsequent geochemical analyses. The remainder of all unprocessed samples are curated in the frozen soil collection of the Monte L. Bean Life Science museum.

2.3 Soil nitrate and association to soil ages

The water-soluble nitrate and total salts data used to estimate recent versus past glaciations in this study were generated and previously reported by Diaz et al. (2021). In summary, the soils were leached at a 1:5, soil to DI water ratio for 24 hours. The leachate was filtered through a 0.4 µm Nucleopore membrane filter and analyzed for major ions on a Dionex ICS-2100 ion chromatograph, PerkinElmer Optima 8300 Inductively Coupled Plasma-Optical Emission Spectrometer (ICP-OES), and Skalar San++ Automated Wet Chemistry Analyzer (Diaz et al., 2018; Diaz, Li, et al., 2020; Diaz, Welch, et al., 2020; Welch et al., 2010). Given that soil nitrate in the TAM is derived almost entirely from atmospheric deposition (Diaz, Li, et al., 2020; Lyons et al., 2016) and is highly water-soluble, the relative concentrations of nitrate in Antarctic soils are well-correlated with estimates of maximum soil age from ^{10}Be dating and possibly represent relative atmospheric exposure age and time since last wetting (Diaz, Corbett, et al., 2020; Lyons et al., 2016).

2.4 *Soil fauna extraction, enumeration, and identification*

Nematodes, tardigrades and rotifers were extracted using a sugar centrifugation technique developed for Antarctic soils (Freckman & Virginia, 1993), and identified and enumerated via light microscopy. Mites and springtails were picked individually from each sample using a dissection microscope by mixing 50g soil with 500ml sugar solution (454g/L), and removing individual animals as they floated to the surface. However, microarthropods were depauperate such that they were not assessed in this study. Tardigrades and rotifers were identified to the phylum level, nematodes were identified to genus (*Scottnema*, *Eudorylaimus*, and *Plectus*) and as living or dead, life stage (juveniles or adults), and sex. Soil gravimetric moisture was measured by weighing 50 g subsamples before and after oven drying at 105°C for 24 h. Invertebrate abundances were assessed as the number of individual animals per kilogram of dry soil (data available in Adams et al., 2021).

2.5 *Statistical analyses*

In addition to predicting the probability that soil invertebrates occurred in the sampling plots (i.e., presence/absence), we also wanted to predict their abundance as a function of soil age in those plots where invertebrates were present. We built a zero-inflated negative binomial model to regress invertebrate abundance against geochemical and geographic explanatory variables (i.e., distance from ice shelf, distance from glacier, elevation, soil moisture, and soil nitrate concentration). The two parts of the zero-inflated model are a binary logit model to predict the zero outcome, and a count model, which in this study was a negative binomial model, to model the count process. Here, all explanatory variables were used to model abundance in the negative binomial part of the model, and the zero outcome in the logit part of the model. This model fitted the data significantly better than the null model, i.e., the intercept-only model (significant difference of log likelihoods, $P<0.0001$). Further, to test for the relationships between soil nitrate concentration and those explanatory variables from the previous analysis (count model) with stronger effects on invertebrate abundance (i.e., distance from ice shelf and distance from glacier), we generated statistical models for the nitrate concentration in our soil samples using both explanatory variables. We used linear mixed effects models with a site-level random effect term to account for possible interdependency between close soil sampling points. We built a similar model for the association between number of invertebrate taxa and distance from ice shelf. For each model, the conditional R^2 (that of the whole model, including the random effect) was calculated following Nakagawa & Schielzeth (2013).

To visualize major patterns structuring the soil invertebrate communities, we performed ordination on group composition with nonmetric multidimensional scaling (NMDS) using Bray-Curtis dissimilarity matrix of the taxonomic community structure data, on which we overlaid 'distance from ice shelf' and 'distance from glacier' data. We then tested for the effects of both explanatory variables by running nonparametric multivariate analysis of variance (npMANOVA) on the dissimilarity matrix.

Finally, we fitted structural equation models to investigate whether the effects of soil exposure age on invertebrate communities are mediated by its influences on habitat suitability or biotic interactions. We tested whether abundances of the dominant taxon *Scottnema* and of the other taxa were explained by direct effects of distance from ice shelf (A) and nitrate concentration (B), and also by indirect effects of these variables through (i) soil salinity (the total salt concentration; Ca^{2+}, Cl^-, F^-, K^+, Mg^{2+}, Na^+, NH_3, NO_3^-, PO_4^{3-}, SiO_2, SO_4^{2-}, Sr^{2+}) and (ii) through biotic interactions between the other taxa and *Scottnema*. This biotic indirect pathway was included to test for potential (negative) effects on *Scottnema*, which could arise from predation by *Eudorylaimus* (Shaw et al., 2018) or resource competition with *Plectus* (Caruso et al., 2019), whereas the salinity indirect pathway tested for soil biogeochemical controls.

3. Results

Across the 232 soil samples, 46% contained invertebrates. *Scottnema* was the dominant (69.7% of all individuals) and most commonly collected (41% of all samples) taxon overall, followed by *Eudorylaimus* which occurred in 18.4% of all samples. As the dominant taxon, total invertebrate abundances across the sample set mirrored patterns in *Scottnema* abundance. The log odds of invertebrate absence in our sampling plots increased by 0.048 for every additional km in distance from ice shelf ($P = 0.03$, logit model). Where invertebrates were likely present, our negative binomial regression model verified that their abundance was primarily driven by distance from ice shelf, with soils further inland and closer to the polar plateau having lower total invertebrate abundances, and also predicted zero invertebrate detection for features more than 100 km away from the ice shelf (Fig. 2A; $P = 0.02$). Similar trends were found for the associations between invertebrate abundance and distance from the nearest glacier, albeit with lower statistical support for both the count and zero-inflation components of the model ($P > 0.05$). We found no statistical support for the effects of the other explanatory variables included in the total abundance model ($P > 0.10$ for elevation, soil moisture, soil nitrate concentration, and total salt concentration), except for an increase in the odds of invertebrate absence with increasing nitrate concentrations ($P = 0.02$). However, both distance from ice shelf ($P < 0.01$, $R^2_{\text{conditional}} = 0.59$, Fig. 2B) and distance from glacier ($P < 0.01$, $R^2_{\text{conditional}} = 0.58$, Fig. 2C) were positively associated with soil nitrate concentrations, a proxy for the amount of time since the soils were last exposed to sufficient amounts of liquid water for leaching to occur (wetting age) (Lyons et al., 2016).

Soil invertebrate community composition varied with distance from the ice shelf ($F = 6.01$, $Df = 1$, $P < 0.01$, $R^2 = 0.07$) and distance from glacier ($F = 2.11$, $Df = 1$, $P = 0.04$, $R^2 = 0.02$) (Fig. 3). *Eudorylaimus* and tardigrade abundances were best correlated with shorter distances from the ice shelf (~20 km) and glacier (<200-400 m) compared to rotifers and the nematodes *Scottnema* and *Plectus* (Fig. 3). Furthermore, approximately 70% of the soils in which invertebrates were present (74 of 103 soils) had only one or two taxa, and rarely more than three taxa (Fig. 4A). One taxon, *Scottnema*, was the only taxon found in ~30% of those soils and was present in all dominant communities with two or more taxa. The number of taxa in the invertebrate communities decreased with increasing distance from ice shelf (-0.03, $P < 0.01$, $R^2 = 0.74$, Fig.

4B). Communities with two or fewer taxa and zero invertebrate counts occurred mainly in soils farther from the ice shelf compared to those soil invertebrate communities with three or more taxa (Fig. 4B).

The structural equation models fit the data adequately, as indicated by non-significant Fisher's C statistic tests ($P > 0.05$), ratio of Fisher's statistic to degrees of freedom <2, and non-significant missing pathways ($P > 0.05$). Neither distance from ice shelf nor soil nitrate concentrations had significant direct effects on the dominant taxon *Scottnema* (Fig. 5 A,B). However, soil nitrate indirectly mediated abundance of this dominant taxon through its strong and positive effect on total salt concentration in the soil, which in turn negatively affected *Scottnema* abundance (Fig. 5B). On the other hand, we found no statistical support for the relationship of soil nitrate with *Scottnema* via biotic interactions with the less abundant taxa (Fig. 5B). There were also no significant relationships between distance from ice shelf and any of the taxon abundances, although significant and negative effects of total salt concentrations on taxon abundances were evident (Fig.5B).

4. Discussion

As hypothesized, total soil faunal abundance (Fig. 2) and taxonomic composition (Figs. 3 and 4) decreased with greater surface exposure time as indicated by distances from present ice surfaces. These proxies of exposure time were in turn positively related to nitrate concentrations in the soil samples due to the accumulation of nitrate salts over time in the absence of appreciable leaching (Figs. 2B,C). Variation in soil nitrate is associated with soil age where ancient glacial tills accumulated nitrate over long periods of deposition (Bockheim, 1997; Michalski, 2005), likely because of the absence of significant leaching or denitrification. Therefore, soil wetting age and distance from ice surfaces are closely correlated and indicate that soils which were exposed during the LGM are less suitable habitats than those exposed after the LGM. Previous research in southern Victoria Land has shown that soil invertebrate communities are structured by soil properties that make habitats more or less suitable, including concentrations of nitrate and other salts, organic carbon content, moisture availability, and pH (Barrett et al., 2004; Courtright et al., 2001; Poage et al., 2008). In fact, total soil salinity is the best predictor of invertebrate distribution in the Dry Valleys (Courtright et al., 2001; Poage et al., 2008), probably because salinity integrates several important physical and geochemical processes. However, it is important to note that while we use nitrate and total salt concentrations as proxies for surface exposure age, salts can be leached from these soils even by minor wetting events. We acknowledge the limitations in inferring exposure age from salt concentration alone, though there is evidence to suggest that much of central TAM have remained hyper-arid for possibly millions of years (Claridge & Campbell, 1968; Diaz, Li, et al., 2020; Lyons et al., 2016).

At our study sites, faunal community composition, diversity, and abundances were strongly affected by climate-driven changes since the LGM. Higher abundances of the nematode *Scottnema* were found in older soils, while *Eudorylaimus* preferentially occurred in more recently exposed soils (Fig. 3), corroborating previous evidence that *Scottnema* is the more salt tolerant of the two taxa (Poage et al., 2008). In fact, approximately 30% of the soils from which invertebrates could be extracted had only *Scottnema*, and these single-taxon communities occurred more frequently in soils exposed for longer periods of time compared to communities composed of three or more taxa (Fig. 4). These results indicate that increasing exposure time since ice retreat was associated with less diverse soil invertebrate communities mainly composed of microbial grazers, while the omnivore-predator *Eudorylaimus* occurred in more diverse soil communities that were more recently exposed by deglaciation or most recently wetted. These patterns suggest that ecological processes such as colonization and community assembly happen over relatively short time periods in the context of the >4-million-year chronosequence studied here, and are limited by reduced habitat suitability in older soils.

A recent study based on stable carbon and nitrogen isotope ratios have identified the nematode *Eudorylaimus* as the sole member of a predator trophic level in soil food webs of the Dry Valleys (Shaw et al., 2018). In our study, the greater abundances of *Eudorylaimus* in more recently exposed, younger soils (Fig. 3) raises the question of whether trophic interactions and predator control over microbial grazers would mediate the effects of soil exposure age on the abundance of the dominant (and microbivore) taxon *Scottnema*. In other words, soil exposure time as indicated by distances from present ice surfaces would also affect soil communities by changing the magnitude of top-down control over the most abundant taxon. Our structural equation modeling does not suggest a significant role of this biotic interaction on the responses of *Scottnema* (Fig. 5A,B), and highlighted the abiotic drivers related to soil salinity as key mediators of *Scottnema* responses to soil exposure age (Fig. 5A,B). Although *Scottnema* is more salt tolerant than other taxa in Antarctic soils (Nkem et al., 2006), their negative relationship with soil salinity is likely due to the extremely high salt concentrations observed in some of the older soils. Total soil salinity varied in our samples from minimal to levels above the threshold for nematode survival (~2,600 $\mu g\ g^{-1}$) (Nkem et al., 2006). Salt concentration varies widely across the Shackleton Glacier region and other ice-free areas in Antarctica. For example, near the Polar Plateau at the Shackleton Glacier values greater than 80 000 $\mu g\ g^{-1}$ have been reported, whereas values as low as 10 $\mu g\ g^{-1}$ have been found at lower elevations near the outlet at the Ross Ice Shelf (Diaz et al., 2021). The endemic nematofauna vary in their tolerance to soil salt concentrations (Nkem et al., 2006). It is difficult to distinguish osmotic from freezing and desiccation stress, and these environmental insults are often considered together as forms of anhydrobiosis. Stress response mechanisms for these animals include changes in expression of heat shock proteins, aquaporins, antioxidants, carbohydrate metabolism, energy generation and the formation of organic glass (Adhikari & Adams, 2011). Poage et al. (2008) generated probabilities of nematode occurrence based on soil geochemistry at the landscape scale in the McMurdo Dry Valleys and found a strong negative relationship between soil salinity and the probability of live nematodes occurring. We infer that soil salinity is a stronger mediator of soil age effects on invertebrate communities compared to biotic interactions (Fig. 5A,B), and therefore decreased habitat suitability drives the negative responses of invertebrate abundance and community composition to post LGM deglaciation.

The results presented here have potential implications for Antarctica biodiversity under present and future climate change. Antarctic terrestrial ecosystems have changed very little since the LGM, but global circulation models share a common prediction of increased climatic change in the Earth's polar ecosystems, a prediction supported by observations (Cook et al., 2005; Doran et al., 2002; Montes-Hugo et al., 2009; Post et al., 2019). By looking at how biotic communities have changed over geologic time scales since the LGM, our results add to the growing body of evidence indicating that Antarctic terrestrial biodiversity will be highly altered by present and projected climate warming (Freckman & Virginia, 1998; Gooseff et al., 2017; Hogg & Wall, 2011; Nielsen & Wall, 2013; Wall, 2007). Atmospheric warming results in increased fluxes of meltwater over soils which can produce contrasting effects on soil habitat suitability. Presuming that ecosystem primary productivity progresses at similar to higher rates as carbon demand in the newly ameliorated soils, increased soil moisture availability may improve habitability and accelerate predicted shifts in the distribution and composition of soil communities across the landscape (Andriuzzi et al., 2018), potentially shifting the drivers of community composition from abiotic (i.e. soil salinity) to biotic drivers (i.e. competition, predation). Nevertheless, increased fluxes of meltwater can also mobilize and increase transport of the highly soluble salts through the landscape (Lyons et al., 2016), potentially altering the distribution of habitable soils across the landscape. While the mode and magnitude of these contrasting changes to the soil habitat will play an important role in the responses of soil biotic communities, their combined effects can make warmed and wetted soils increasingly susceptible to invasive species with superior competitive ability over that of native ones. In the coming decades this is likely to lead to radical changes in the composition and functioning of biotic communities similar to that seen elsewhere in the Antarctic benthic marine and terrestrial ecosystems (Gutt et al., 2020; Nielsen & Wall, 2013). Furthermore, since these invertebrate communities are key contributors to soil carbon dynamics, we expect that climate-induced shifts in faunal communities will have corresponding impacts on ecosystem-level processes in terrestrial Antarctic environments (Barrett et al., 2008)

Acknowledgements

We thank Marci Shaver-Adams, Natasha Griffin, and Thomas Powers for their help with the laboratory analyses, Cecilia Milano de Tomasel for help with permits and sample shipment, and Marci Shaver-Adams and Geoff Schellens for help with sample collection and field safety support. We also thank the Crary Lab staff, pilots and technicians of PHI helicopters, and the Shackleton Glacier camp staff for supporting our field campaign. This work was supported by grants from the U.S. National Science Foundation (OPP 1341648 to D.H.W., B.A., N.F., W.L., and OPP 1637708 to B.A). Data management support was provided by the National Science Foundation for Long Term Ecological Research via grant OPP 1115245.

Data Availability Statement

Soil Samples: Soil samples are deposited and cataloged in the frozen collections of the BYU Life Museum.

Extracted Organism Vouchers: Representative tissues and individual voucher organisms (eukaryotes) are accessioned into the frozen and we collections (respectively) at Brigham Young University.

Geochemistry Data: Geochemistry data are available at USAP-DC, via accession number PRJNA699250 USAP-1341736.

Invertebrate diversity and abundance data: All data presented in this study are archived in the Environmental Data Initiative (EDI) Data Repository (Adams et al., 2021).

References

Adams, B. J., Wall, D. H., Fierer, N., Lyons, W., Hogg, I. D., Diaz, M. A., Dragone, N. B., Lemoine, N. P., Franco, A. L. C., Shaver-Adams, M., & Schellens, G. (2021). Soil invertebrate surveys from the Shackleton Glacier region of Antarctica during the 2017-2018 austral summer. *Environmental Data Initiative*. https://doi.org/10.6073/pasta/7959821e5f6f8d56d94bb6a26873b3ae

Adhikari, B. N., & Adams, B. J. (2011). Molecular analysis of desiccation survival in Antarctic nematodes. In R. N. Perry & D. A. Wharton (Eds.), *Molecular and Physiological Basis of Nematode Survival* (pp. 205–232). CABI International.

Anderson, J. B., Shipp, S. S., Lowe, A. L., Wellner, J. S., & Mosola, A. B. (2002). The Antarctic Ice Sheet during the Last Glacial Maximum and its subsequent retreat history: A review. *Quaternary Science Reviews*, *21*(1–3), 49–70. https://doi.org/10.1016/S0277-3791(01)00083-X

Andriuzzi, W. S., Adams, B. J., Barrett, J. E., Virginia, R. A., & Wall, D. H. (2018). Observed trends of soil fauna in the Antarctic Dry Valleys: early signs of shifts predicted under climate change. *Ecology*, *99*, 312–321. https://doi.org/10.1002/ecy.2090

Balter-Kennedy, A., Bromley, G., Balco, G., Thomas, H., & Jackson, M. S. (2020). A 14.5-million-year record of East Antarctic Ice Sheet fluctuations from the central Transantarctic Mountains, constrained with cosmogenic 3He, 10Be, 21Ne, and 26Al. *The Cryosphere*, *14*(8), 2647–2672. https://doi.org/10.5194/tc-14-2647-2020

Barrett, J. E., Virginia, R. A., Wall, D. H., & Adams, B. J. (2008). Decline in a dominant invertebrate species contributes to altered carbon cycling in a low-diversity soil ecosystem.

Global Change Biology, *14*(8), 1734–1744. https://doi.org/10.1111/j.1365-2486.2008.01611.x

Barrett, J. E., Virginia, R. A., Wall, D. H., Parsons, A. N., Powers, L. E., & Burkins, M. B. (2004). Variation in biogeochemistry and soil biodiversity across spatial scales in a polar desert ecosystem. *Ecology*, *85*(11), 3105–3118. https://doi.org/10.1890/03-0213

Bockheim, J. G. (1997). Properties and Classification of Cold Desert Soils from Antarctica. *Soil Science Society of America Journal*, *61*(1), 224–231. https://doi.org/10.2136/sssaj1997.03615995006100010031x

Bromwich, D. H., Nicolas, J. P., Monaghan, A. J., Lazzara, M. A., Keller, L. M., Weidner, G. A., & Wilson, A. B. (2013). Central West Antarctica among the most rapidly warming regions on Earth. *Nature Geoscience*, *6*(2), 139–145. https://doi.org/10.1038/ngeo1671

Caruso, T., Hogg, I. D., Nielsen, U. N., Bottos, E. M., Lee, C. K., Hopkins, D. W., Cary, S. C., Barrett, J. E., Green, T. G. A., Storey, B. C., Wall, D. H., & Adams, B. J. (2019). Nematodes in a polar desert reveal the relative role of biotic interactions in the coexistence of soil animals. *Communications Biology*, *2*(1), 1–9. https://doi.org/10.1038/s42003-018-0260-y

Claridge, G. G. C., & Campbell, I. B. (1968). SOILS OF THE SHACKLETON GLACIER REGION, QUEEN MAUD RANGE, ANTARCTICA. *New Zealand Journal of Science*, *11*, 171–218. https://www.coldregions.org/vufind/Record/27838/Details

Collins, G. E., Hogg, I. D., Convey, P., Sancho, L. G., Cowan, D. A., Lyons, W. B., Adams, B. J., Wall, D. H., & Green, T. G. A. (2020). Genetic diversity of soil invertebrates corroborates timing estimates for past collapses of the West Antarctic Ice Sheet. *Proceedings of the National Academy of Sciences of the United States of America*, *117*(36), 22293–22302. https://doi.org/10.1073/pnas.2007925117

Convey, P., & Peck, L. S. (2019). Antarctic environmental change and biological responses. In *Science Advances* (Vol. 5, Issue 11, p. eaaz0888). American Association for the Advancement of Science. https://doi.org/10.1126/sciadv.aaz0888

Cook, A. J., Fox, A. J., Vaughan, D. G., & Ferrigno, J. G. (2005). Retreating glacier fronts on the Antarctic Peninsula over the past half-century. *Science*, *308*(5721), 541–544.

https://doi.org/10.1126/science.1104235

Courtright, E. M., Wall, D. H., & Virginia, R. A. (2001). Determining habitat suitability for soil invertebrates in an extreme environment: The McMurdo Dry Valleys, Antarctica. *Antarctic Science*, *13*(1), 9–17. https://doi.org/10.1017/S0954102001000037

Czechowski, P., White, D., Clarke, L., McKay, A., Cooper, A., & Stevens, M. I. (2016). Age-related environmental gradients influence invertebrate distribution in the Prince Charles Mountains, East Antarctica. *Royal Society Open Science*, *3*(12), 160296. https://doi.org/10.1098/rsos.160296

Denton, G. H., Bockheim, J. G., Wilson, S. C., Leide, J. E., & Andersen, B. G. (1989). Late Quaternary ice-surface fluctuations of Beardmore Glacier, Transantarctic Mountains. *Quaternary Research*, *31*(2), 183–209. https://doi.org/10.1016/0033-5894(89)90005-7

Diaz, M. A., Adams, B. J., Welch, K. A., Welch, S. A., Opiyo, S. O., Khan, A. L., McKnight, D. M., Cary, S. C., & Lyons, W. B. (2018). Aeolian Material Transport and Its Role in Landscape Connectivity in the McMurdo Dry Valleys, Antarctica. *Journal of Geophysical Research: Earth Surface*, *123*(12), 3323–3337. https://doi.org/10.1029/2017JF004589

Diaz, M. A., Corbett, L. B., Bierman, P. R., Adams, B. J., Wall, D. H., Hogg, I. D., Fierer, N., & Lyons, W. B. (2020). Relative terrestrial exposure ages inferred from meteoric 10Be and NO3- concentrations in soils along the Shackleton Glacier, Antarctica. *Earth Surface Dynamics*, *3*, in review.

Diaz, M. A., Gardner, C. B., Welch, S. A., Andrew Jackson, W., Adams, B. J., Wall, D. H., Hogg, I. D., Fierer, N., & Berry Lyons, W. (2021). Geochemical zones and environmental gradients for soils from the central Transantarctic Mountains, Antarctica. *Biogeosciences*, *18*(5), 1629–1644. https://doi.org/10.5194/bg-18-1629-2021

Diaz, M. A., Li, J., Michalski, G., Darrah, T. H., Adams, B. J., Wall, D. H., Hogg, I. D., Fierer, N., Welch, S. A., Gardner, C. B., & Lyons, W. B. (2020). Stable Isotopes of Nitrate, Sulfate, and Carbonate in Soils From the Transantarctic Mountains, Antarctica: A Record of Atmospheric Deposition and Chemical Weathering. *Frontiers in Earth Science*, *8*(3), 1–19. https://doi.org/10.3389/feart.2020.00341

Diaz, M. A., Welch, S. A., Sheets, J. M., Welch, K. A., Khan, A. L., Adams, B. J., McKnight, D.

M., Cary, S. C., & Lyons, W. B. (2020). Geochemistry of aeolian material from the McMurdo Dry Valleys, Antarctica: Insights into Southern Hemisphere dust sources. *Earth and Planetary Science Letters*, *547*, 116460. https://doi.org/10.1016/j.epsl.2020.116460

Doran, P. T., Priscu, J. C., Berry Lyons, W., Walsh, J. E., Fountain, A. G., McKnight, D. M., Moorhead, D. L., Virginia, R. A., Wall, D. H., Clow, G. D., Fritsen, C. H., McKay, C. P., & Parsons, A. N. (2002). Antarctic climate cooling and terrestrial ecosystem response. *Nature*, *415*(6871), 517–520. https://doi.org/10.1038/nature710

Dragone, N. B., Diaz, M. A., Hogg, I. D., Lyons, W. B., Jackson, W. A., Wall, D. H., Adams, B. J., & Fierer, N. (2021). Exploring the Boundaries of Microbial Habitability in Soil. *Journal of Geophysical Research: Biogeosciences*, *126*(6), e2020JG006052. https://doi.org/10.1029/2020JG006052

Freckman, D. W., & Virginia, R. A. (1993). Extraction of nematodes from Dry Valley Antarctic soils. *Polar Biology*, *13*(7), 483–487. https://doi.org/10.1007/BF00233139

Freckman, D. W., & Virginia, R. A. (1998). Soil Biodiversity and Community Structure in the Mcmurdo Dry Valleys, Antarctica. In J. C. Priscu (Ed.), *Ecosystem Dynamics in a Polar Desert: the Mcmurdo Dry Valleys, Antarctica* (72nd ed., pp. 323–335). American Geophysical Union (AGU). https://doi.org/10.1029/ar072p0323

Golledge, N. R., Fogwill, C. J., Mackintosh, A. N., & Buckley, K. M. (2012). Dynamics of the last glacial maximum Antarctic ice-sheet and its response to ocean forcing. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(40), 16052–16056. https://doi.org/10.1073/pnas.1205385109

Gooseff, M. N., Barrett, J. E., Adams, B. J., Doran, P. T., Fountain, A. G., Lyons, W. B., McKnight, D. M., Priscu, J. C., Sokol, E. R., Takacs-Vesbach, C., Vandegehuchte, M. L., Virginia, R. A., & Wall, D. H. (2017). Decadal ecosystem response to an anomalous melt season in a polar desert in Antarctica. *Nature Ecology and Evolution*, *1*(9), 1334–1338. https://doi.org/10.1038/s41559-017-0253-0

Green, T. G. A., Sancho, L. G., Türk, R., Seppelt, R. D., & Hogg, I. D. (2011). High diversity of lichens at 84°S, Queen Maud Mountains, suggests preglacial survival of species in the Ross Sea region, Antarctica. *Polar Biology*, *34*(8), 1211–1220. https://doi.org/10.1007/s00300-

011-0982-5

Gutt, J., Isla, E., Xavier, J. C., Adams, B. J., Ahn, I., Cheng, C. -H. C., Colesie, C., Cummings, V. J., di Prisco, G., Griffiths, H., Hawes, I., Hogg, I., McIntyre, T., Meiners, K. M., Pearce, D. A., Peck, L., Piepenburg, D., Reisinger, R. R., Saba, G. K., … Wall, D. H. (2020). Antarctic ecosystems in transition – life between stresses and opportunities. *Biological Reviews*, *19*(1), brv.12679. https://doi.org/10.1111/brv.12679

Heroy, D. C., & Anderson, J. B. (2005). Ice-sheet extent of the Antarctic Peninsula region during the Last Glacial Maximum (LGM) - Insights from glacial geomorphology. *Bulletin of the Geological Society of America*, *117*(11–12), 1497–1512. https://doi.org/10.1130/B25694.1

Hogg, I. D., Craig Cary, S., Convey, P., Newsham, K. K., O'Donnell, A. G., Adams, B. J., Aislabie, J., Frati, F., Stevens, M. I., & Wall, D. H. (2006). Biotic interactions in Antarctic terrestrial ecosystems: Are they a factor? *Soil Biology and Biochemistry*, *38*(10), 3035–3040. https://doi.org/10.1016/j.soilbio.2006.04.026

Hogg, I. D., & Wall, D. H. (2011). Global change and Antarctic terrestrial biodiversity. In *Polar Biology* (Vol. 34, Issue 11, pp. 1625–1627). Springer. https://doi.org/10.1007/s00300-011-1108-9

Kindem, I. T., & Christiansen, B. (2001). Tropospheric response to stratospheric ozone loss. *Geophysical Research Letters*, *28*(8), 1547–1550. https://doi.org/10.1029/2000GL012552

Lyons, W. B., Deuerling, K., Welch, K. A., Welch, S. A., Michalski, G., Walters, W. W., Nielsen, U., Wall, D. H., Hogg, I., & Adams, B. J. (2016). The Soil Geochemistry in the Beardmore Glacier Region, Antarctica: Implications for Terrestrial Ecosystem History. *Scientific Reports*, *6*(1), 1–8. https://doi.org/10.1038/srep26189

Magalhães, C., Stevens, M. I., Cary, S. C., Ball, B. A., Storey, B. C., Wall, D. H., Türk, R., & Ruprecht, U. (2012). At Limits of Life: Multidisciplinary Insights Reveal Environmental Constraints on Biotic Diversity in Continental Antarctica. *PLoS ONE*, *7*(9), e44578. https://doi.org/10.1371/journal.pone.0044578

Michalski, G. (2005). Isotopic composition of Antarctic Dry Valley nitrate: Implications for NO $_y$ sources and cycling in Antarctica. *Geophysical Research Letters*, *32*(13), L13817. https://doi.org/10.1029/2004GL022121

Montes-Hugo, M., Doney, S. C., Ducklow, H. W., Fraser, W., Martinson, D., Stammerjohn, S. E., & Schofield, O. (2009). Recent changes in phytoplankton communities associated with rapid regional climate change along the western Antarctic Peninsula. *Science*, *323*(5920), 1470–1473. https://doi.org/10.1126/science.1164533

Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, *4*(2), 133–142. https://doi.org/10.1111/j.2041-210x.2012.00261.x

Nielsen, U. N., & Wall, D. H. (2013). The future of soil invertebrate communities in polar regions: different climate change responses in the Arctic and Antarctic? *Ecology Letters*, *16*(3), 409–419. https://doi.org/10.1111/ele.12058

Nkem, J. N., Virginia, R. A., Barrett, J. E., Wall, D. H., & Li, G. (2006). Salt tolerance and survival thresholds for two species of Antarctic soil nematodes. *Polar Biology*, *29*(8), 643–651. https://doi.org/10.1007/s00300-005-0101-6

Parsons, A. N., Barrett, J. E., Wall, D. H., & Virginia, R. A. (2004). Soil carbon dioxide flux in antarctic dry valley ecosystems. *Ecosystems*, *7*(3), 286–295. https://doi.org/10.1007/s10021-003-0132-1

Poage, M. A., Barrett, J. E., Virginia, R. A., & Wall, D. H. (2008). The Influence of Soil Geochemistry on Nematode Distribution, Mcmurdo Dry Valleys, Antarctica. *Arctic, Antarctic, and Alpine Research*, *40*(1), 119–128. https://doi.org/10.1657/1523-0430(06-051)[POAGE]2.0.CO;2

Pollard, D., & DeConto, R. M. (2009). Modelling West Antarctic ice sheet growth and collapse through the past five million years. *Nature*, *458*(7236), 329–332. https://doi.org/10.1038/nature07809

Post, E., Alley, R. B., Christensen, T. R., Macias-Fauria, M., Forbes, B. C., Gooseff, M. N., Iler, A., Kerby, J. T., Laidre, K. L., Mann, M. E., Olofsson, J., Stroeve, J. C., Ulmer, F., Virginia, R. A., & Wang, M. (2019). The polar regions in a 2°C warmer world. *Science Advances*, *5*(12), eaaw9883. https://doi.org/10.1126/sciadv.aaw9883

Shaw, E. A., Adams, B. J., Barrett, J. E., Lyons, · W Berry, Virginia, R. A., & Wall, D. H. (2018). Stable C and N isotope ratios reveal soil food web structure and identify the nematode Eudorylaimus antarcticus as an omnivore-predator in Taylor Valley, Antarctica. *Polar Biology*, *41*, 1013–1018. https://doi.org/10.1007/s00300-017-2243-8

Sugden, D. E., Bentley, M. J., & Ó Cofaigh, C. (2006). Geological and geomorphological insights into Antarctic ice sheet evolution. *Philosophical Transactions of the Royal Society A: Mathematical, Physical and Engineering Sciences*, *364*(1844), 1607–1625. https://doi.org/10.1098/rsta.2006.1791

Talarico, F. M., McKay, R. M., Powell, R. D., Sandroni, S., & Naish, T. (2012). Late Cenozoic oscillations of Antarctic ice sheets revealed by provenance of basement clasts and grain detrital modes in ANDRILL core AND-1B. *Global and Planetary Change*, *96–97*, 23–40. https://doi.org/10.1016/j.gloplacha.2009.12.002

Thompson, D. W. J., & Solomon, S. (2002). Interpretation of recent Southern Hemisphere climate change. *Science*, *296*(5569), 895–899. https://doi.org/10.1126/science.1069270

Turner, J., Overland, J. E., & Walsh, J. E. (2007). An Arctic and antarctic perspective on recent climate change. *International Journal of Climatology*, *27*(3), 277–293. https://doi.org/10.1002/joc.1406

Ugolini, F. C., & Bockheim, J. G. (2008). Antarctic soils and soil formation in a changing environment: A review. *Geoderma*, *144*(1–2), 1–8. https://doi.org/10.1016/j.geoderma.2007.10.005

Wall, D. H. (2007). Global change tipping points: Above- and below-ground biotic interactions in a low diversity ecosystem. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *362*(1488), 2291–2306. https://doi.org/10.1098/rstb.2006.1950

Welch, K. A., Lyons, W. B., Whisner, C., Gardner, C. B., Gooseff, M. N., Mcknight, D. M., & Priscu, J. C. (2010). Spatial variations in the geochemistry of glacial meltwater streams in the Taylor Valley, Antarctica. *Antarctic Science*, *22*(6), 662–672. https://doi.org/10.1017/S0954102010000702

Figure Captions

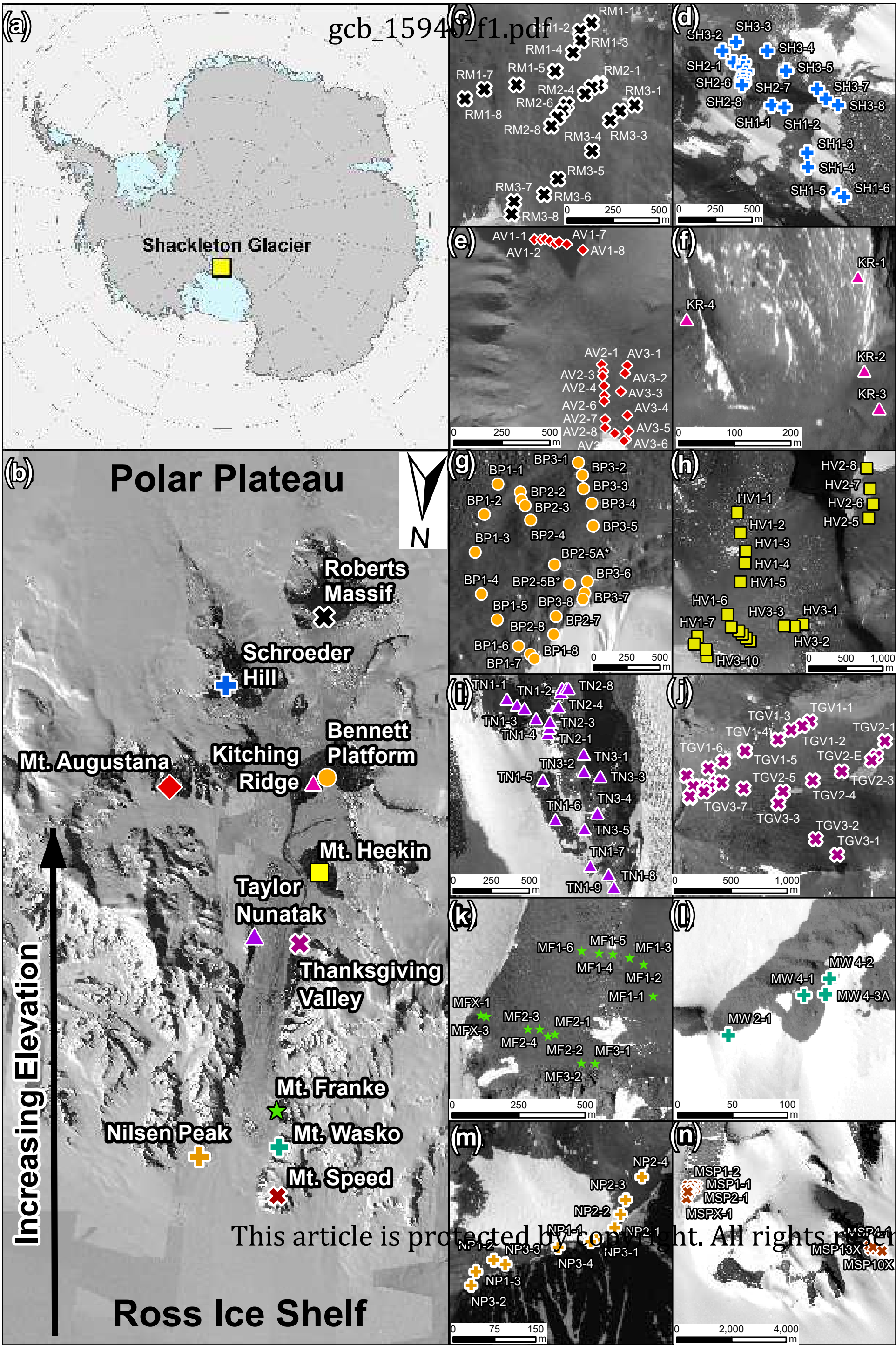
Fig. 1 (a) Map of Antarctica highlighting the Shackleton Glacier (yellow box). (b) Soil samples were collected from 12 features along the Shackleton Glacier, which flows from the Polar Plateau to the Ross Ice Shelf: (c) Roberts Massif, (d) Schroeder Hill, (e) Mt. Augustana, (f) Kitching Ridge, (g) Bennett Platform, (h) Mt. Heekin, (i) Taylor Nunatak, (j) Thanksgiving Valley, (k) Mt. Franke, (l) Mt. Wasko, (m) Nilsen Peak, and (n) Mt. Speed. The symbols represent sampling locations. All images were acquired from the Polar Geospatial Center (PGC).

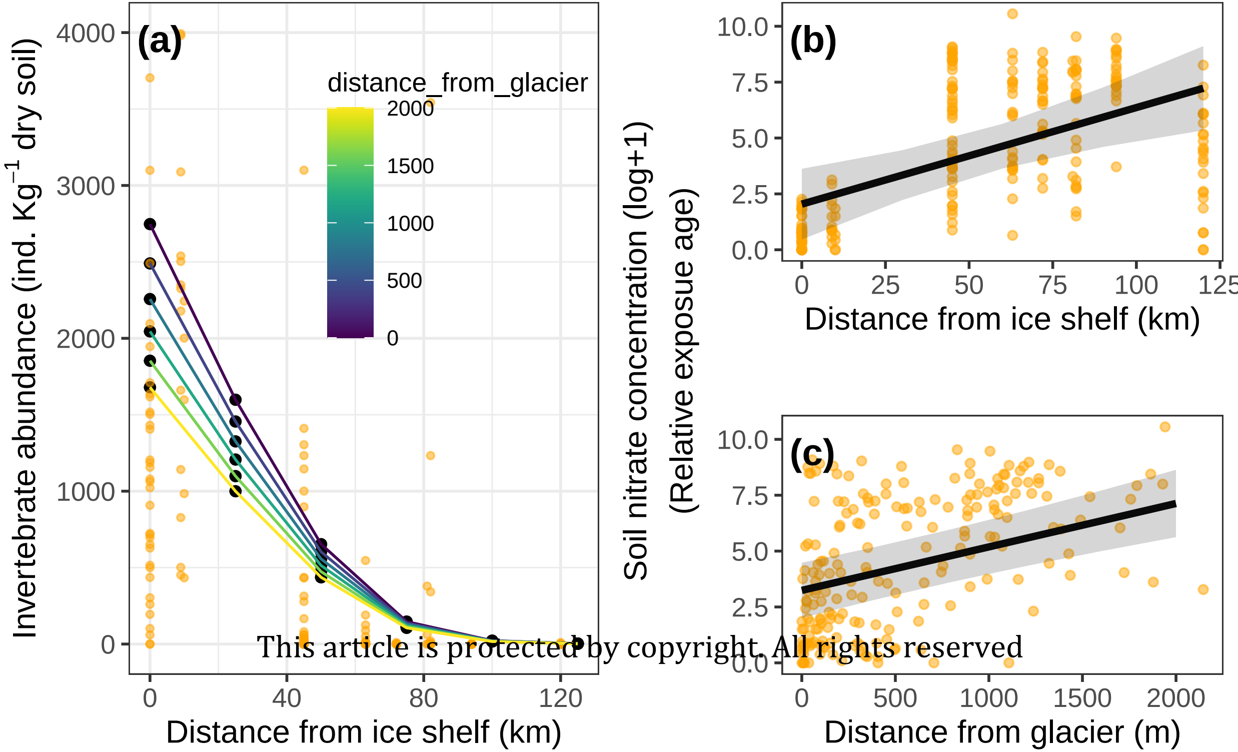
Fig. 2 Fitted relationships of total soil fauna abundance (A; negative binomial model) and soil nitrate concentrations as a proxy for relative soil exposure age (B and C; linear mixed effects models) with distance from ice shelf and distance from glacier. Orange points represent raw data points.

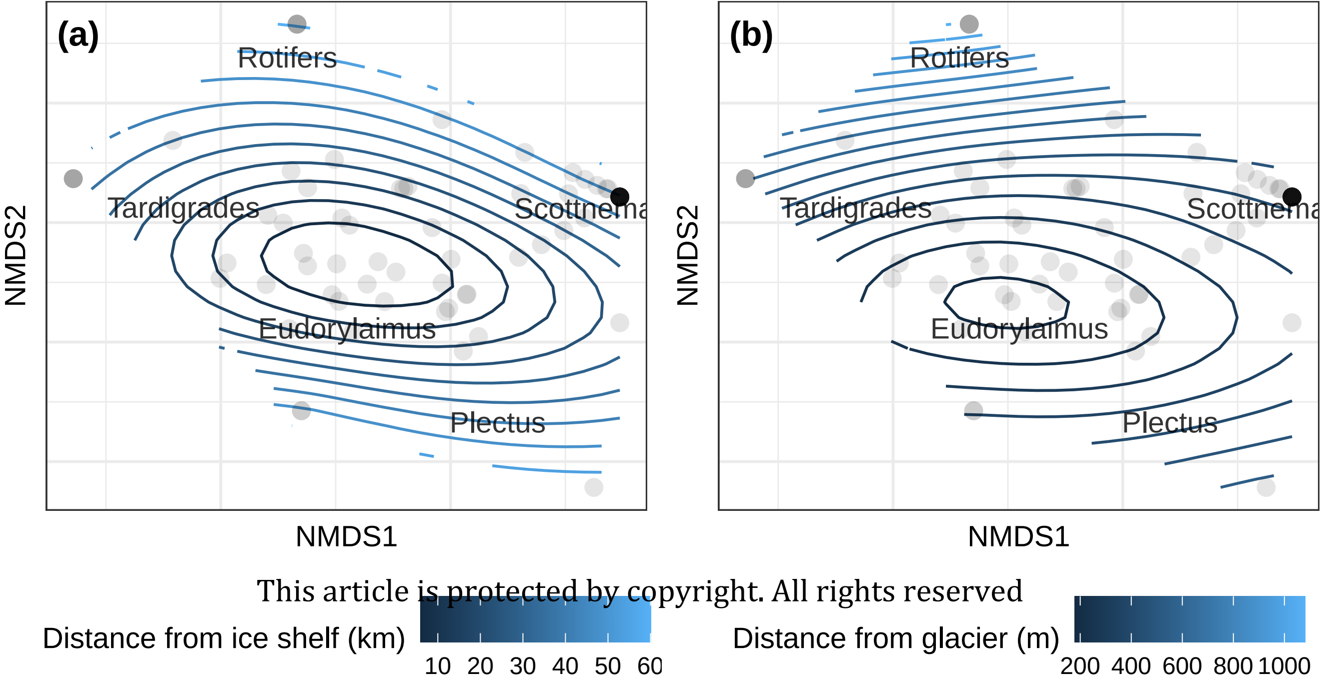
Fig. 3 Soil fauna community composition across site gradients of distance from ice shelf (A) and distance from glacier (B). Nonmetric multidimensional scaling plots (Bray–Curtis). Color-coded contour lines indicate gradients of distance from ice shelf (A) and glacier (B). Taxon names are arrayed close to samples (dark points) where each taxon was relatively more abundant.

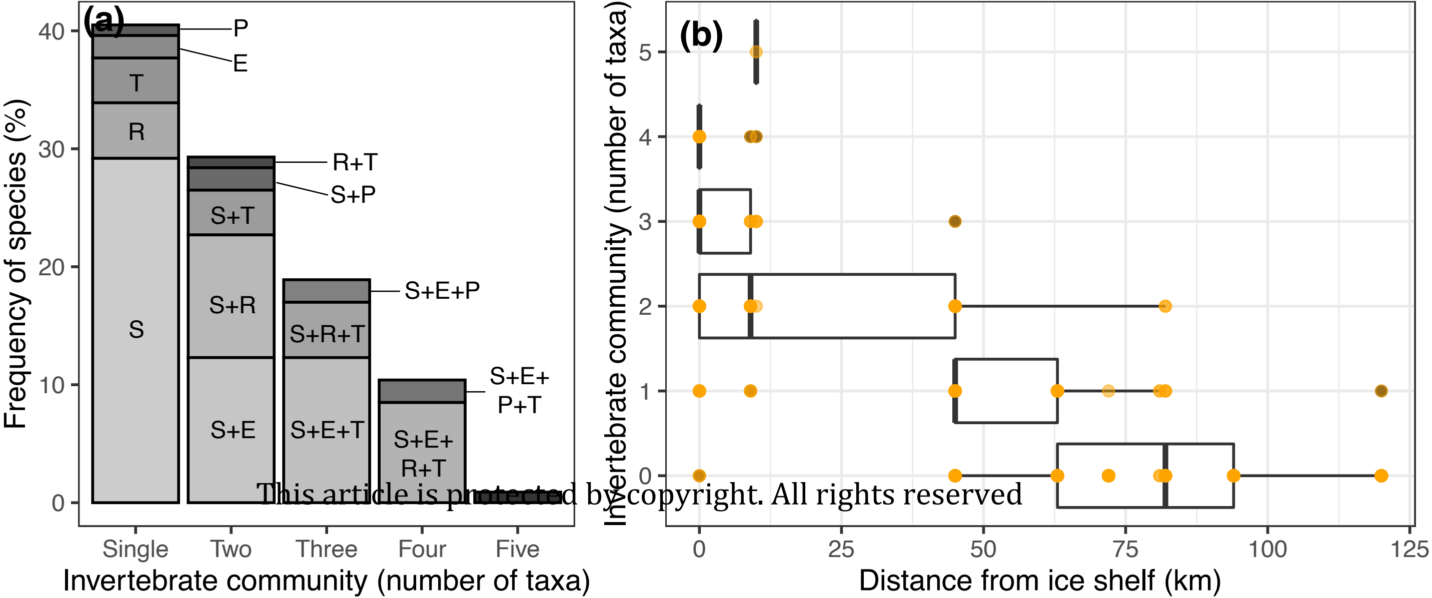
Fig. 4 The composition of soil invertebrate communities in the Shackleton Glacier region, Antarctica. (A) Frequency of soil communities having one, two, three, four or five taxa as percentage of samples in which each taxon occurred, alone or in combination ($n = 103$ samples with one or more taxon). Letters denotate the following taxa: nematodes of the genera *Eudorylaimus* (E), *Plectus* (P), and *Scottnema* (S), besides Rotifers (R) and Tardigrades (T). (B) Number of taxa in the soil communities as a function of distance from ice shelf and plotted as median values (thick lines in the boxes) and interquartile ranges. Orange points represent raw data points.

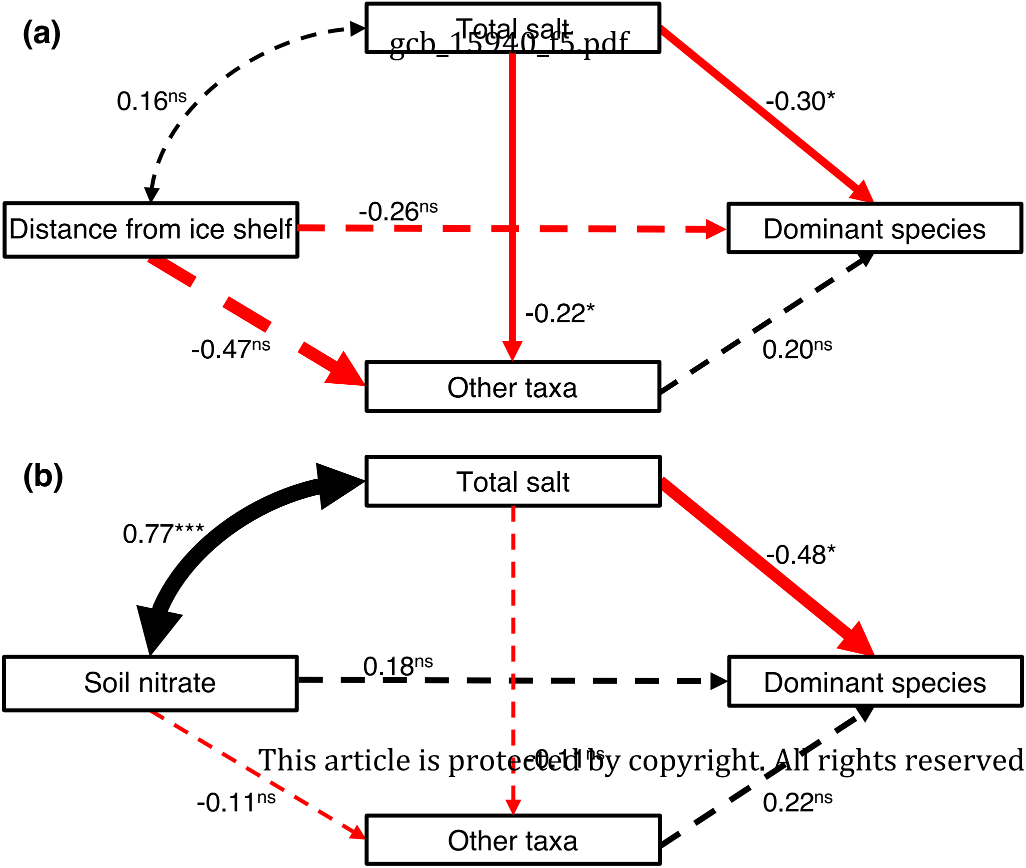
Fig. 5 Structural equation models for dominant and less common soil invertebrate species abundance as affected by direct and indirect (via abiotic and biotic paths) effects of (a) distance from ice shelf and (b) soil nitrate concentrations. Numbers next to each pathway indicate standardized coefficients, marked by asterisks if significant (**$P < 0.001$, ***$P < 0.0001$). Arrows are scaled to thickness based on coefficient to show the strength of each effect.


(a)
Shackleton Glacier
(b)
Polar Plateau
N
Roberts Massif
Schroeder Hill
Mt. Augustana
Kitching Ridge
Bennett Platform
Mt. Heekin
Taylor Nunatak
Thanksgiving Valley
Mt. Franke
Nilsen Peak
Mt. Wasko
Mt. Speed
Increasing Elevation
Ross Ice Shelf
(c)
RM1-1
RM1-2
RM1-3
RM1-4
RM1-5
RM1-7
RM1-8
RM2-1
RM2-4
RM2-6
RM2-8
RM3-1
RM3-3
RM3-4
RM3-5
RM3-6
RM3-7
RM3-8
0 250 500 m
(d)
SH3-2
SH3-3
SH3-4
SH3-5
SH2-1
SH2-6
SH2-7
SH3-7
SH3-8
SH2-8
SH1-1
SH1-2
SH1-3
SH1-4
SH1-5
SH1-6
0 250 500 m
(e)
AV1-1
AV1-7
AV1-2
AV1-8
AV2-1
AV3-1
AV2-3
AV3-2
AV2-4
AV3-3
AV2-6
AV3-4
AV2-7
AV2-8
AV3-5
AV3-6
0 250 500 m
(f)
KR-1
KR-4
KR-2
KR-3
0 100 200 m
(g)
BP3-1
BP1-1
BP3-2
BP2-2
BP3-3
BP1-2
BP2-3
BP3-4
BP3-5
BP1-3
BP2-4
BP2-5A*
BP1-4
BP2-5B*
BP3-6
BP1-5
BP3-8
BP3-7
BP2-8
BP2-7
BP1-6
BP1-8
BP1-7
0 250 500 m
(h)
HV2-8
HV2-7
HV1-1
HV2-6
HV2-5
HV1-2
HV1-3
HV1-4
HV1-5
HV1-6
HV3-3
HV3-1
HV1-7
HV3-2
HV3-10
0 500 1,000 m
(i)
TN1-1
TN1-2
TN2-8
TN2-4
TN1-3
TN2-3
TN1-4
TN2-1
TN3-1
TN3-2
TN1-5
TN3-3
TN3-4
TN1-6
TN3-5
TN1-7
TN1-8
TN1-9
0 250 500 m
(j)
TGV1-1
TGV1-3
TGV1-4
TGV2-1
TGV1-2
TGV1-6
TGV1-5
TGV2-E
TGV2-5
TGV2-3
TGV2-4
TGV3-7
TGV3-3
TGV3-2
TGV3-1
0 500 1,000 m
(k)
MF1-5
MF1-6
MF1-3
MF1-4
MF1-2
MF1-1
MFX-1
MF2-3
MF2-1
MFX-3
MF2-4
MF2-2
MF3-1
MF3-2
0 250 500 m
(l)
MW4-2
MW4-1
MW4-3A
MW2-1
0 50 100 m
(m)
NP2-4
NP2-3
NP2-2
NP1-1
NP2-1
NP1-2
NP3-3
NP3-1
NP3-4
NP1-3
NP3-2
0 75 150 m
(n)
MSP1-2
MSP1-1
MSP2-1
MSPX-1
MSP4-1
MSP13X
MSP10X
0 2,000 4,000 m


(a)
Invertebrate abundance (ind. Kg^{-1} dry soil)
4000
3000
2000
1000
0
distance_from_glacier
2000
1500
1000
500
0
0
40
80
120
Distance from ice shelf (km)
Soil nitrate concentration (log+1)
(Relative exposue age)
(b)
10.0
7.5
5.0
2.5
0.0
0
25
50
75
100
125
Distance from ice shelf (km)
(c)
10.0
7.5
5.0
2.5
0.0
0
500
1000
1500
2000
Distance from glacier (m)


(a)
Rotifers
Tardigrades
Scottnema
Eudorylaimus
Plectus
NMDS2
NMDS1
(b)
Rotifers
Tardigrades
Scottnema
Eudorylaimus
Plectus
NMDS2
NMDS1
Distance from ice shelf (km)
10 20 30 40 50 60
Distance from glacier (m)
200 400 600 800 1000


(a)
Frequency of species (%)
0
10
20
30
40
P
E
T
R
S
R+T
S+P
S+T
S+R
S+E
S+E+P
S+R+T
S+E+T
S+E+
P+T
S+E+
R+T
Single
Two
Three
Four
Five
Invertebrate community (number of taxa)
(b)
Invertebrate community (number of taxa)
0
1
2
3
4
5
0
25
50
75
100
125
Distance from ice shelf (km)


(a)
Total salt
Distance from ice shelf
Dominant species
Other taxa
0.16ns
-0.30*
-0.26ns
-0.22*
-0.47ns
0.20ns
(b)
Total salt
Soil nitrate
Dominant species
Other taxa
0.77***
-0.48*
0.18ns
-0.11ns
-0.11ns
0.22ns