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Review

An Antarctic worm and its soil ecosystem: A review of an emerging research program in ecological genomics

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ABSTRACT

Relationships between the evolution of species and their ecosystems can be difficult to accurately assess due to the high number of confounding biological variables (*e.g.*, biotic interactions among community members and the resulting complex relationships between genetic pathways and organism phenotypes). Thus, progress in ecological genomics by making inferences about fundamental ecological patterns and processes is hampered by high biodiversity and subsequent complex biotic interactions. Study systems that are naturally low in biological and ecological complexity, and strongly structured by abiotic drivers, can serve as models for bridging the gap between controlled mesocosm experiments and natural ecosystems. The terrestrial ecosystems of the Antarctic dry valleys have low biodiversity and constrained ecological complexity, primarily because ecological communities are so strongly shaped by physical, rather than biological, factors. The harsh constraints of the physical environment on organismal evolution and the structure of ecological communities make this an optimal natural system for disentangling the influence of specific environmental parameters on genotype/phenotype and gene by environment interactions. This work reviews the biology, evolution, and ecology of an emerging model organism, the free-living nematode *Plectus murrayi*, in a model ecosystem, the McMurdo Dry Valleys (MDVs) of Antarctica. In the MDVs, habitat suitability, including nutrient availability, has been shown to drive organismal (nematode) life history evolution, including growth and reproduction, primarily by way of changes in the expression of developmental genes. Changes in growth rates and reproductive schedules are accomplished primarily through alterations of nuclear rRNA gene copy number. The predicted and observed responses to natural experiments have been replicated in the laboratory, providing a synthesis of field observations and experimental evolution. Studying such natural model systems as this could fill several persistent knowledge gaps in our understanding of how genetic variation, genomic architecture, and gene regulation drive the genotype-phenotype paradigm, and the consequent effects of these drivers on ecosystem structure and functioning.

1. Introduction

The field of ecological genomics aims to link changes in environmental parameters (*e.g.*, soil moisture, nutrient content, and climatic factors) with the evolution of organism phenotypes through genetic intermediaries, such as genotype and genome architecture (Rice et al., 2011). Understanding such dynamics requires identifying key environmental drivers, the organismal phenotypes associated with them, and the responses of the genetic elements coupled to those phenotypes (Pavey et al., 2012). Model organisms in low-diversity ecosystems provide an excellent *in situ* model for studying the ecological genomics of a single species relative to biotic and abiotic environments. The reduced community complexity in physically extreme environments, such as hot, dry, and cold deserts (Eshel et al., 2021), hot springs (Op den Camp et al., 2009; Sriaporn et al., 2021), abyssal zones (Gao et al., 2019), and the deep subsurface biosphere (Borgonie et al., 2011), make it possible to understand ecological and evolutionary processes in the absence of complicating variables that are inherent in more complex ecosystems. In

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addition, because model organisms can be optimally cultivated in the laboratory (with their short generation times and large population sizes) and their genetic backgrounds are well-studied, they likewise serve as highly accessible tools for revealing the complex genetic underpinnings of genotype-phenotype and gene-by-environment interactions.

Nematodes are widely distributed across all continents, including the polar regions (Bongers and Ferris, 1999; Newbold et al., 2015). To date, over 25,000 nematode species, inhabiting nearly every ecosystem on Earth, have been described (Zhang, 2013). Numerical dominance and broad geographical distribution indicate that nematodes are essential to the functioning of most ecosystems and likely the Earth's entire biosphere (Ferris, 2010; van den Hoogen et al., 2019). Due to their small size, transparent body structures and relatively short life-cycle time (*e.g.* mean of 3–4 days for *Caenorhabditis elegans*, strain N2), nematodes have been studied as model organisms in multiple scientific disciplines, including genetic engineering, medicine, and developmental biology (Andrássy, 1998; Wharton and Raymond, 2015; Markaki and Tavernarakis, 2020; Nakayama et al., 2020; Zimmermann et al., 2020). The soil nematode *Plectus murrayi* is an emerging animal model for exploring the origin and evolution of a number of stress response pathways in metazoans (Adhikari et al., 2010a) and possesses a variety of characteristics that make it a candidate model for soil ecological genomics generally.

Here, we review the biology and ecology of *P. murrayi* as a foundation for its use in exploring the molecular mechanisms underlying adaptive responses to physically dominated environmental drivers, and more broadly, evolutionary and ecological genomics. Laboratory and culturing techniques are presented in evolutionary and ecological contexts, including phylogeny, life history, population structure, and distribution ecology. Examples of how *P. murrayi* tolerates the extreme physical insults of the MDVs follow from both physiological and genetic perspectives, demonstrating how the *P. murrayi*-Antarctic soil ecosystem model is well-positioned to answer key questions in evolutionary and ecological genomics.

2. Model organism: *Plectus murrayi*

Plectus murrayi is an emerging model organism in multiple scientific disciplines, including genetic engineering, medicine, and developmental biology (Adhikari et al., 2010a; Wharton and Raymond, 2015). *P. murrayi* is a free-living limnoterrestrial nematode that plays a key ecological role in a well-studied Antarctic soil ecosystem. Its eco-evo dynamics can be compared to that of other contemporary species in the same ecosystem to better understand how natural communities, and not simply single species alone, respond to evolutionary and ecological dynamics. *P. murrayi* is an endemic Antarctic member of a globally distributed genus and thus can also be compared in a phylogenetic context to congeners to understand the genetic basis of adaptive evolution across a broad spectrum of timescales. Furthermore, it is cultivable in the laboratory, possesses a relatively short generation time (for an Antarctic invertebrate), has readily observable and measurable phenotypes, and is genomically and phenotypically comparable to other well-studied animal models, including *Caenorhabditis elegans.*

2.1. *Evolutionary genomics of P. murrayi*

Organisms evolve in response to environmental influences over long (*e.g.*, phenotype innovation) and short (*e.g.*, population structure, phenotypic plasticity, and SNPs) timescales through a variety of genetic mechanisms (*e.g.*, epigenetics, gene duplications, SNPs, mobile elements, horizontal gene transfer, and changes to genomic architecture). A robust phylogenetic framework allows for the identification of the origin and maintenance of adaptive strategies that have evolved in response to such environmental influences over different time scales (Brooks and McLennan, 1991). In turn, this information provides critical context for interpreting the ecological role of the organism in its ecosystem (Brooks et al., 1992).

Evolution over short timescales can be fast and more sensitive to interannual environmental variation as compared to evolution over periods of longer time, which is important for explaining the functional variation within and among populations that are driven by environmental changes (Thompson, 1998; Carroll et al., 2007). Due to geographic, topological, and geological legacies of the MDVs, populations are highly structured across this landscape (Jackson et al., 2022; Geyer et al., 2017; Magalhaes et al., 2012; Adams et al., 2014). Thus, studying population-level processes, including gene flow and the geographic structure of populations, provides a simple and unique way to answer fundamental questions in ecological genomics, such as how genetic variation drives and is driven by ecological interactions.

Phylogenies based on the COI gene and genome reveal that P. murrayi consists of a single lineage that was isolated from its non-Antarctic congeners at a minimum of over one million years ago (Velasco-Castrillón et al., 2014; Kagoshima et al., 2019; Xue et al., 2021). Mapping the genetic features associated with extreme-tolerant phenotypes (*e.g.*, anhydrobiosis) of *P. murrayi* provides a genetic background that can reveal the functional genes, genomic structures, or regulatory features, that have evolved in response to environmental insults. For example, it has been reported that *P. murrayi* is pre-adapted to desiccated conditions, and these adaptive responses were rapidly co-opted post-colonization (Adhikari et al., 2009).

2.2. *Life history evolution of P. murrayi*

Life history evolution and its impact on genomic architecture is a major subfield of ecological genomics. Life history research aims to provide a theoretical framework for understanding how patterns of development, growth, reproductive scheduling, and lifespan have been shaped by natural selection (Partridge and Harvey, 1988). It is particularly useful for identifying how environmental and ecological factors shape gene-by-environment phenotype/genotype interactions, including phenotypic plasticity (Flatt and Heyland, 2011; Flatt et al., 2013). Moreover, due to the ecological complexity of most natural ecosystems, it is usually difficult to determine how genes controlling life history evolution respond to the variety of selective factors in an organism's environment.

P. murrayi possess several life history traits that facilitate their persistence in dynamic dry, cold, and oligotrophic habitats in the MDV, such as a longer life cycle, parthenogenesis, and slower reproduction (de Tomasel et al., 2013). A study of growth and development in *P. murrayi* populations from Cape Hallett (coastal, northern-most part of Victoria Land) indicates that *P. murrayi* can go through multiple life cycles in a single year in the wild (Yeates et al., 2009). At harsher, higher latitudes with fewer degree days above freezing a single life cycle of *P. murrayi* could last at least two years and possibly many more (Porazinska and Wall, 2002; Simmons et al., 2009; de Tomasel et al., 2013). Whether the life cycle of *P. murrayi* is one, two, or more years, *P. murrayi* has a longer life cycle than *Plectus* nematodes outside of Antarctica (*e.g.*, *Plectus parietinus*, *Plectus velox*) (Sandhove et al., 2016). There are several possible explanations for this difference. First, *P. murrayi* growth and development is paused for a large proportion of each year while it endures adverse environmental conditions in cryptobiosis (Treonis et al., 2000; Porazinska and Wall, 2002; Kagoshima et al., 2012). Thus, an extended life cycle in *P. murrayi* could be an adaptation for surviving the long, dark, freezing Antarctic winters, during which the organisms must allocate most of their metabolic energy to stress response instead of development and reproduction. The second is that the length of its lifecycle may be a direct response to the ambient temperature in the valleys and thus appear more extended than it actually is. Metabolic rate is closely tied to ambient temperature in ectotherms and the maximum and mean annual soil temperatures in the MDV are 14.7 °C and −18.8 °C, respectively (Obryk et al., 2020). These hypotheses are easily tested under laboratory conditions; *in vitro* it takes *P. murrayi* 53 to 57 days to complete the egg-to-egg life cycle at an optimal growth temperature 15 °C (Fig. 1) (de Tomasel et al., 2013). MDV soils can reach 15 °C at 5 cm depth (Knox et al., 2016), indicating that *in vitro* and *in situ* environments are roughly comparable. *Plectus murrayi* life cycle length is still longer than non-Antarctic *Plectus* species, but it is also not truly multi-annual, suggesting that both adaptation and unique environmental conditions are strongly influencing the evolution of its life history traits.

Parthenogenesis is the dominant mode of reproduction in *P. murrayi*. Males occur very rarely and when they do occur, they are non-functional (Lahl et al., 2003; Andrássy, 2012). The lack of functional males means that there is no cost of meiosis and *P. murrayi* populations exert no energy searching for a mate during reproduction (Kito et al., 1991). This allows them to colonize novel habitats without having to find a mate (Bogart et al., 2007; Lunt, 2008; Roach et al., 2014). But the loss of sexual recombination also results in a decreased capacity to respond to environmental changes (Garcia et al., 2007; Chaudhuri et al., 2011; Cutter et al., 2019). In this trade-off, the advantages of *P. murrayi*'s reproductive strategy must outweigh any current disadvantages (Judson and Normark, 1996). This indicates that its effective environment is stable, *P. murrayi* is well-adapted to the extreme selection pressures in the MDVs (Adhikari et al., 2010a), or it has some means other than sex and recombination to generate genetic variation (Vakhrusheva et al., 2020). Future research on *P. murrayi* life history evolution could help reveal the mechanisms by which asexual animals generate and maintain sufficient genetic variation to survive in extreme and variable environments.

3. Model ecosystem: the McMurdo Dry Valleys of Antarctica

The McMurdo Dry Valleys (MDV) are located in the Antarctic bioregion of South Victoria Land (Terauds and Lee, 2016) at approximately 76°5′ to 78°5′S, 160°0′ to 164°0′E and constitute the largest ice-free terrestrial area in Antarctica (Fountain et al., 2014). These valleys are among the coldest and driest terrestrial habitats on Earth. Mean annual precipitation is <100 mm (always as snow), the yearly average air temperature is −20 °C (Priscu, 1998; Fountain et al., 1999; Doran et al., 2002; Obryk et al., 2020), and significant variation has been found in stoichiometric nutrient availability (*e.g.*, N, C, P) related to climate, soil weathering, and geography (Barrett et al., 2006; Barrett et al., 2007). The growing season for MDV biota is compressed between late November and early February (the austral summer), when soil temperatures rise above freezing; notably, soils still experience frequent freeze-thaw cycles even during this period (Freckman and Virginia, 1997; Knox et al., 2016). Between the end of March and the beginning of October (the austral winter), the region experiences total darkness. Despite these physical and climatic extremes, phylogenetically and functionally diverse microbial communities persist (Fierer et al., 2012; Thompson et al., 2020) including microfauna (tardigrades, rotifers, nematodes and microarthropods) (Adams et al., 2006). Biotic communities here are heterogeneously distributed across a landscape of mineral soils that range from arid (<1 %) to moist (>5 %, maximum ∼10 %). There are no vascular plants, and the lack of their accompanying root structure reduces the availability of water and strongly limits carbon (C) fixation, resulting in a highly simplified soil community (Wall and Virginia, 1999; Wlostowski et al., 2018). Consequently, biotic interactions are reduced in number and complexity, making abiotic factors the strongest drivers of community structure (Dunson and Travis, 1991; Caruso et al., 2019; Shaw and Wall, 2019; Thompson et al., 2021).

The MDV soil ecosystem is an optimal model system for disentangling fundamental ecological patterns and processes because it hosts a radically simplified community, naturally reducing the ecological complexity that obscures dynamic interactions in a majority of other systems. The evolution and ecology of the biota are strongly coupled to readily measured climate and physicochemical variables, such as soil chemistry, water availability, soil temperature, solar irradiance, and nutrient availability. Moreover, the environment of the MDV is extremely sensitive to climate variability, and the response of its communities to these changes can be studied comprehensively *in vivo* and in real-time. In addition, the ecosystem consists of a series of distinct landscapes with unique geological legacies, providing a series of replicated natural experiments for studying eco-evolutionary dynamics on short-term timescales (*i.e.*, hundreds to thousands of years) (Priscu, 1998).

4. *Plectus murrayi* in the MDVs

Understanding the ecology of model organisms provides the foundation for studying their ecological functions, genome evolution, and adaptive responses to biotic and abiotic interactions at the genomic level. Like free-living soil nematodes in other ecosystems, *P. murrayi* functions as a crucial link in the MDV soil microbial loop (Shaw et al., 2018), as suggested by its overwhelming abundance in the moist, productive sites where it occurs (∼500 individuals/kg soil; Adams et al., 2014; Lawson Knoepfle et al., 2009). Unlike other ecosystems, *P. murrayi* dominates a food web with highly reduced biodiversity and trophic complexity: only a single facultative predator and several other microbivores cooccur with *P. murrayi* (Shaw et al., 2018). This simplified but

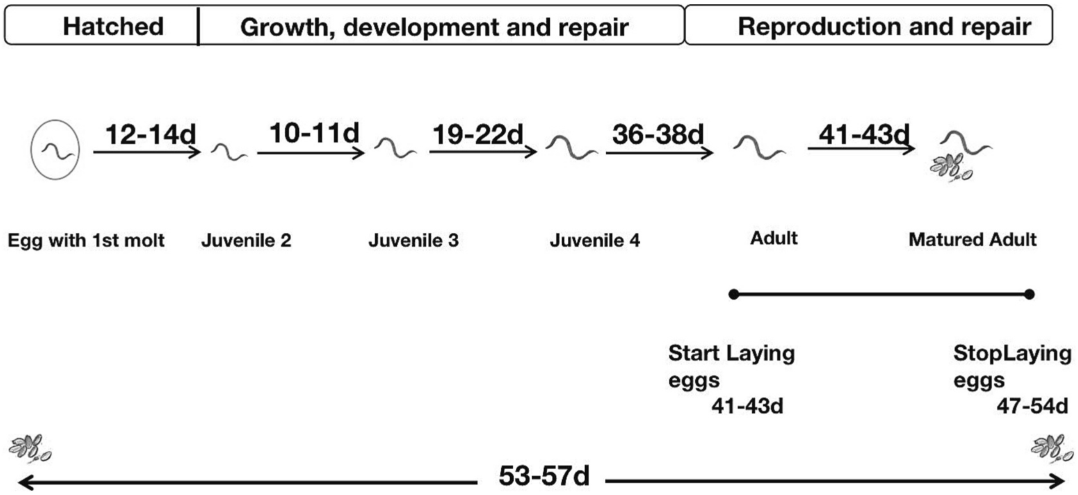

Fig. 1. The life cycle of *Plectus murrayi* at 15 °C in the laboratory, growing on agar media plates with additional sterile sand and fed on *Escherichia coli* OP-50. It takes 53 to 57 days to complete the egg-to-egg life cycle under optimal growth conditions.

still multi-faceted food web enables the study of gene to ecosystem dynamics *in situ*: changes in the physical environment induce changes in *P. murrayi* population size, behavior, and trophic interactions, which then induce further changes in the structure and functioning of the nematode's biotic community, all of which inevitably feed back and further influence the evolution of *P. murrayi*. Mapping and understanding the ecology of *P. murrayi*, its response to selective pressures from its physical environment, and the interactive pathways between *P. murrayi* and the rest of the soil community are thus helpful attributes for research programs in ecological genomics.

P. murrayi possesses a broad ecological amplitude. It can be found in semi-aquatic, aquatic, and moist soils (Yeates, 1979; Andrássy, 1998; Andrássy and Gibson, 2006; Wharton and Brown, 2012). It is more likely to occur in habitats with relatively higher soil moisture (7–10 %) (Mouratov et al., 2001), higher soil nitrogen (N) and nitrate concentration (>10 mg/kg), higher organic C (~0.41 g/kg), higher C/N ratios

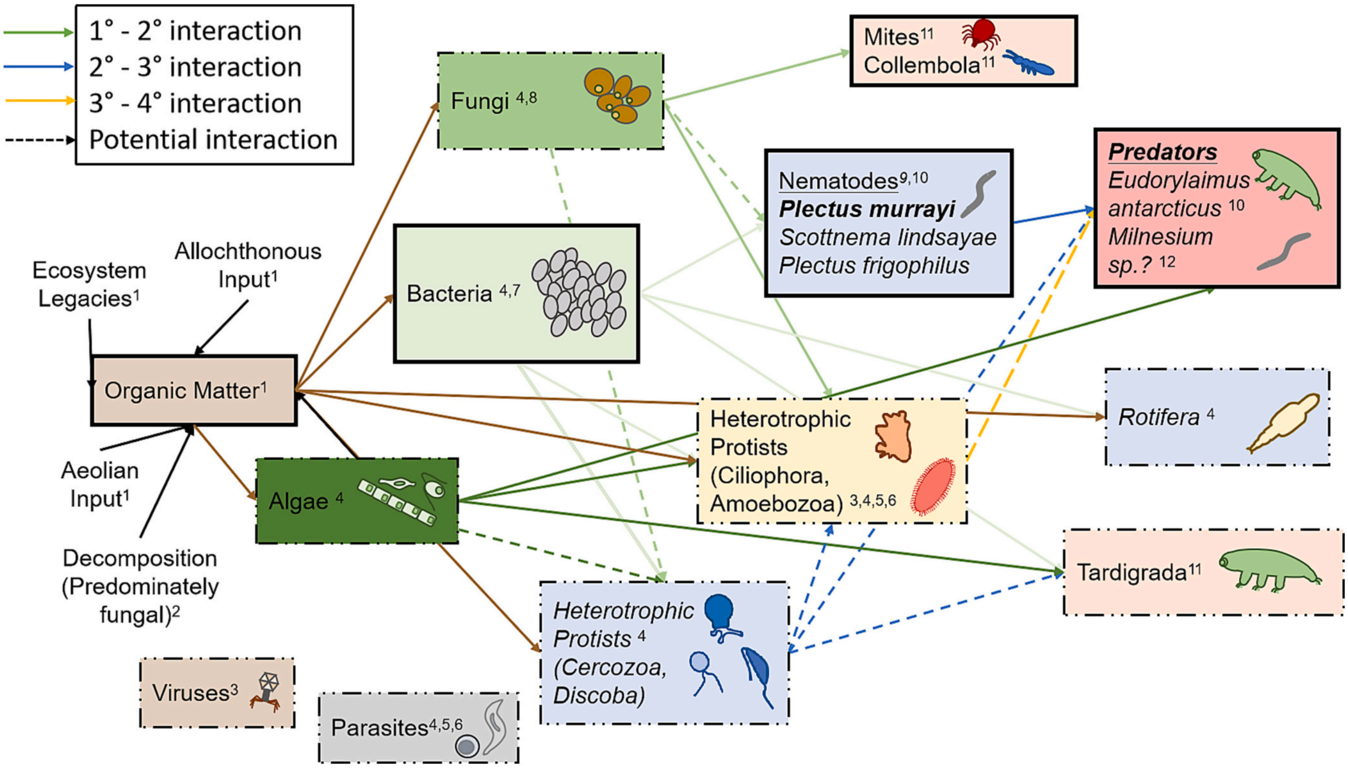

Fig. 2. Generalized food web for Antarctic Dry Valley soils. Solid arrows indicate verified relationships (see figure references); dashed arrows indicate unconfirmed but inferred relationships. Box color indicates trophic tier; arrow color indicates preceding trophic tier. Dashed boxes indicate groups that have received minimal research attention; solid boxes indicate those that have received substantial attention, relative to the whole. Light red boxes indicate known, high-tier predators/omnivores; light orange indicate possible, but unlikely, high-tier predators/omnivores. *Milnesium spp.* are pan-Antarctic and unpublished sequences suggest they may occur in or near the MDV, but there are as yet no published records. *Plectus murrayi* is bolded to emphasize its position. Organism icons included for clarity. Note how low trophic complexity (compared to more temperate soil ecosystems) facilitates a higher-resolution understanding of biotic interactions at multiple levels of ecological and evolutionary organization.

[1] Adams, B., Wall, D., Virginia, R., Broos, E., Knox, M., 2014b. Ecological Biogeography of the Terrestrial Nematodes of Victoria Land, Antarctica. ZooKeys 419: 29-71. 10.3897/zookeys.419.7180.

2Shaw, E.A., Adams, B.J., Barrett, J.E., Lyons, W.B., Virginia, R.A., Wall, D.H., 2018b. 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. doi:10.1007/s00300-017-2243-8.

[3] Bamforth, S.S., Wall, D.H., Virginia, R.A., 2005. Distribution and diversity of soil protozoa in the McMurdo Dry Valleys of Antarctica. Polar Biology 28: 756-762. doi:10.1007/s00300-005-0006-4.

[4] Foissner, W., 1996. Faunistics, taxonomy and ecology of moss and soil ciliates (Protozoa, Ciliophora) from Antarctica, with description of new species, including *Pleuroplitoides smithi* gen. n., sp. n. Acta Protozoology 35: 95-123.

[5] Schwarz, A.M.J., Green, J.D., Green, T.G.A., Seppelt, R.D., 1993. Invertebrates associated with moss communities at Canada Glacier, southern Victoria Land, Antarctica. Polar Biology 13: 157-162. doi:10.1007/BF00238925.

[6] Yergeau, E., Kang, S., He, Z., Zhou, J., Kowalchuk, G.A., 2007. Functional microarray analysis of nitrogen and carbon cycling genes across an Antarctic latitudinal transect. ISME Journal 1: 163-179. doi:10.1038/ismej.2007.24.

[7] Arenz, B.E., Blanchette, R.A., 2011. Distribution and abundance of soil fungi in Antarctica at sites on the Peninsula, Ross Sea Region and McMurdo Dry Valleys. Soil Biology & Biochemistry 43: 308-315. doi:10.1016/j.soilbio.2010.10.016.

[8] Thompson, A.R., Geisen, S., Adams, B.J., 2020. Shotgun metagenomics reveal a diverse assemblage of protists in a model Antarctic soil ecosystem. Environmental Microbiology 22: 4620-4632. doi:10.1111/1462-2920.15198.

[9] Cary, S.C., McDonald, I.R., Barrett, J.E., Cowan, D.A., 2010. On the rocks: the microbiology of Antarctic Dry Valley soils. Natural Review Microbiology 8: 129-138. doi:10.1038/nrmicro2281.

[10] Adams B.J., Bardgett R.D., Ayres E., Wall D.H., Aislabie J., Bamforth S., Bargagli R., Cary C., Cavacini P., Connell L., Convey P., 2006. Diversity and distribution of Victoria Land biota. Soil Biology and Biochemistry 38(10):3003-18. doi:10.1016/j.soilbio.2006.04.030.

[11] Velasco-Castrillón A., McInnes S.J., Schultz M.B., Arróniz-Crespo M., D'Haese C.A., Gibson J.A., Adams B.J., Page T.J., Austin A.D., Cooper S.J., Stevens M.I., 2015. Mitochondrial DNA analyses reveal widespread tardigrade diversity in Antarctica. Invertebrate Systematics 29(6):578-90. doi:10.1071/IS14019.

[12] Bezuidt O.K., Lebre P.H., Pierneef R., León-Sobrino C., Adriaenssens E.M., Cowan D.A., Van de Peer Y., Makhalanyane T.P., 2020. Phages actively challenge niche communities in Antarctic soils. mSystems 5(3):e00234-20. doi:10.1128/msystems.00234-20.

(~10), and lower soil salinity (EC < 100mS cm^{-1}) than other Antarctic nematodes (Courtright et al., 2001). Thus, it is not surprising that *P. murrayi* is largely missing from the arid soils (<5 % soil moisture content) that dominate the MDV landscape (Fountain et al., 1999; Burkins et al., 2001). Instead, it is abundant in soils associated with higher amounts of liquid water, such as near ephemeral streams, ponds, snowmelt patches, and lake margins (Sohlenius et al., 1996; Powers et al., 1998; Adams et al., 2006; Adams et al., 2014; Raymond and Wharton, 2016). Thus, *P. murrayi* inhabits an extreme environment and has certainly adapted its physiology to manage those extremes, yet its micro-environment is relatively mesic, and thus the organism can be reliably compared to congeners in non-Antarctic systems.

Understanding the interaction network between competitors, the top-down activity of predators, and the bottom-up controls exhibited by prey availability for *P. murrayi* is critical for characterizing the molecular genetics of the nematode's ecological functioning. Like many nematodes, *P. murrayi* is a generalist grazer, feeding on bacteria through broad-scale suction (Heyns, 1995; Adhikari et al., 2010b), though there is likely some degree of selective feeding (Newsham et al., 2004). Other microbivores in the system include other free-living nematodes, several rotifer species, tardigrades (*e.g.*, *Acutuncus antarcticus*) and a variety of phagotrophic protists (Schwarz et al., 1993; Thompson et al., 2020), but the degree to which these compete with *Plectus* is unknown. Shaw et al. (2018) showed that although *P. murrayi*, *A. antarcticus*, and rotifers constituted a primary consumer tier, there was a distinct difference in their isotopic ratios, suggesting *A. antarcticus* and MDV rotifers have different feeding ecologies than *P. murrayi*. Additionally, tardigrades in this system are traditionally considered algivorous and rotifers bacterivorous, although there is strong evidence of trophic overlap between the two (Jaroměřska et al., 2021). Finally, due to differences in grazing behaviors, nematodes and phagotrophic protists, which feed selectively (Glucksman et al., 2010) and frequently from soil pores inaccessible to metazoans (Bamforth et al., 2005; Rønn et al., 2012), may partition prey resources such that competition between the groups is minimized (Thompson et al., 2021). *P. murrayi* co-occurs frequently with the omnivore-predator nematode *Eudorylaimus sp.*, which is the lone putative predator in the system. The predatory tardigrade *Milnesium* is pan-Antarctic but has not yet been reported in the MDV specifically (Velasco-Castrillón et al., 2015). Nematophagous Collembola (springtails) and Acari (mites) may also serve as regulators of *P. murrayi* populations, however their distribution is sporadic and limited. It is important to note that predation of *P. murrayi* by any putative predator has not been directly observed in the MDV (Fig. 2) (Freckman and Virginia, 1997; Wharton, 2003; Velasco-Castrillón et al., 2014).

4.1. *Ecological amplitude of Plectus murrayi in the MDV*

One of the overarching goals of ecological genomics is to understand the genetic mechanisms of organismal responses to environmental selection (Ungerer et al., 2008). Ecological amplitude is the adaptation range of an organism or a physiological process of an organism to changes in ecological factors, which refers to the ecological adaptability of organisms (Holling, 1973; Dajoz, 1975). Due to the extreme Antarctic environment, *P. murrayi* possesses numerous phenotypes under strong selection that provide excellent case studies for understanding the rate and mechanics of adaptive evolution. Of these selective forces, water availability is one of the most essential drivers of ecosystem structure and functioning in Antarctic ecosystems (Lee, 1999). The low average temperature in Antarctica is the primary driver of low available moisture and leads to desiccation in organisms, a process which can puncture cell membranes, damage DNA, and lead to death (Bewley, 1979; Potts, 1994; Oliver et al., 2020). To cope with the effects of desiccation *P. murrayi* employs anhydrobiosis, a type of cryptobiosis wherein both metabolism and gene expression are lowered such that cellular growth ceases and energy is only expended for minimal cellular maintenance thermal hysteresis, and anti-ice-nucleating compounds, respectively.

During anhydrobiosis, an organism evacuates over 95 % of its internal water and enters a quiescent metabolic maintenance state (Treonis et al., 2000; Weicht and Moorhead, 2004; Sandhove et al., 2016). *P. murrayi*, like other nematodes that undergo anhydrobiosis, also exhibit a coiling behavior which slows water loss by reducing the amount of exposed cuticle (Wharton et al., 2005; Demeure et al., 1979; Treonis et al., 2000). As with other Antarctic metazoans (Overhoff et al., 1993; Convey, 1997; Brown et al., 2004), it is the inactive state which likely enables *P. murrayi* to have such extended viability (de Tomasel et al., 2013). Understanding the mechanics and limits of anhydrobiosis in *P. murrayi* is thus important for understanding the organism's ecological amplitude (niche breadth) and a key factor in its evolutionary ecology.

Despite anhydrobiosis being a strategy common to many nematode, rotifer, and tardigrade lineages inhabiting hot and cold deserts around the world (Crowe and Madin, 1974; Crowe et al., 1977; Demeure et al., 1979; Treonis et al., 2000; Robert, 2003), the physiological and genetic mechanisms underlying this phenotype remain poorly known. Transcriptomics and genome assembly, both useful for identifying genes associated with specific molecular interactions that occur during anhydrobiosis, could potentially elucidate genetic pathways key to anhydrobiosis strategies (Treonis et al., 2000; Weicht and Moorhead, 2004; Goyal, 2005; Sandhove et al., 2016). To date, several of the genes responsible for synthesizing the set of core proteins involved in anhydrobiosis have been identified and include trehalose-6-phosphate synthase, aldehyde dehydrogenase, glycerol kinase, malate synthase, and heat shock proteins that enable nematodes to respond to desiccation (Treonis et al., 2000; Erkut et al., 2013; Sandhove et al., 2016). Some of these expressed gene products and co-solutes contribute to replacing structural water with a synthesized organic glass that maintains intracellular structure and function in the absence of water. Late Embryogenesis Abundant proteins (LEAs) are essential for reducing protein aggregation that occurs during desiccation and causes potential damage to cellular biological processes. Thus, LEAs are assumed to be critical for stabilizing anhydrobiosis and subsequent recovery from desiccation in nematodes. Adhikari et al. (2009, 2010c) sequenced the expressed sequence tags (EST) of *P. murrayi* exposed to different desiccation conditions and found that 28 % of differentially expressed transcripts are involved in metabolism, 19 % in environmental information processing, and 28 % in genetic information processing, in addition to many novel transcripts. Adhikari et al. (2009) induced anhydrobiosis in *P. murrayi* by lowering the relative humidity (98 % to 87 %) over 24 h at 23 °C and found that desiccation stress results in increased expression of 6-phosphate synthase, late embryogenesis abundant proteins (LEA), heat shock proteins, ubiquitin, c-type lectins, and chaperone-related proteins. Interestingly, a gene encoding an antifreeze protein was downregulated, likely because dehydration was the more pressing stressor during desiccation than freezing (Adhikari et al., 2010c; Adhikari and Adams, 2011).

Genetic pathways associated with freeze-tolerance (sudden and lasting) are key to resolving the ecological role of this organismal function in natural ecosystems (Raymond and Wharton, 2013; Storey and Storey, 2013). Adhikari et al. (2010c) showed that the rate of exposure to desiccation and freezing plays a vital role in the initiation of anhydrobiosis in *P. murrayi*, and presumably other nematodes (Crowe et al., 1977; Wharton, 1996; Erkut et al., 2013; Erkut and Kurzchalia, 2015). High tolerance to different rates of dehydration is likely a key survival strategy in Antarctic soils where freeze-thaw cycles occur on a regular basis, sometimes on timescales as short as several minutes (Knox et al., 2016). Previous studies showed that exposure to gradual dehydration (a decrease from 98 % to 55 % RH over 48 h) not only improves extreme desiccation survival but also promotes enhanced cold tolerance (Adhikari et al., 2010c; Wharton and Raymond, 2015). When exposed to moderate desiccation (55–50 % RH), more *P. murrayi* survived than when exposed to lethal desiccation (5–10 % RH) and freezing (− 1 °C to -4 °C), and freezing combined with 97 % RH promoted both the number of surviving nematodes at subsequent exposure to 0 % RH and −10 °C.

How anhydrobiotic ability compares between Antarctic *Plectus* and other nematodes, including non-Antarctic *Plectus*, is currently unclear but could illustrate how the Antarctic environment has influenced desiccation tolerance strategies. Other nematodes undergo anhydrobiosis, however the degree to which they do is dependent on their environment. *C. elegans* only exhibits anhydrobiosis during the non-reproducing dauer larvae stages (Wharton, 2011; Erkut et al., 2013) whereas *P. murrayi,* like other Antarctic nematodes, can enter anhydrobiosis in all its life stages (Treonis et al., 2000; Weicht and Moorhead, 2004; McGill et al., 2015; Sandhove et al., 2016). Whether ancestral *Plectus* populations in Antarctica were capable of undergoing anhydrobiosis, how effective their phenotypes were, and how rapidly the evolution of that trait, if any, occurred are questions that remain unanswered. These questions could be answered by comparing the ecological genomics of anhydrobiosis in Antarctic *Plectus* with congeners endemic to lower latitudes.

4.2. *Elemental stoichiometry and the growth rate hypothesis (GRH)*

Both field and laboratory studies of elemental stoichiometry in *P. murrayi* provide examples of its use as an effective model for testing the growth rate hypothesis (GRH) under various elemental conditions. For example, such research tests the hypothesis that cellular phosphorus (P)-content regulates the rate of organismal development as postulated by the GRH (Xue et al., 2023). The GRH (Elser et al., 2000; Elser et al., 2003; Elser et al., 2009) predicts that organismal growth rates are directly correlated with the available P in the environment. Because the growth rate of an organism is influenced by its ribosomal RNA (rRNA) synthesis rate, factors that influence rRNA production should indirectly modify growth rate. Providing additional amounts of limiting nutrients, such as P, during high rates of rRNA synthesis should therefore increase growth rate (Elser et al., 2000; Elser et al., 2003). Previous studies have shown evidence supporting the GRH in crustacean zooplankton and herbivorous insects, finding a positive association among growth rate, rRNA, and somatic P-content (Gorokhova and Kyle, 2002; Weider et al., 2004). Furthermore, lab experiments examining variation in rRNA in different organisms reveal a link between available environmental P and genetic variation at the genomic level (Perkins et al., 2004; Weider et al., 2005). Although few studies have shown this relationship in soil ecosystems due to the complexity of natural nutrient compositions, doing so is valuable for assessing adaptation under natural elemental compositions and limitations. Studying the relationship between *P. murrayi* and P-content in a simplified ecosystem like the MDV provides a natural model for exploring life history evolution under resource-limited conditions and a good example of how to integrate nutrient and energy cycles in organisms and ecosystems at the genomic level (Xue et al., 2023).

Although several studies have examined the consequences of dietary P deficiency at moderate to high levels (Acharya et al., 2004; Perkins et al., 2004), few have examined P limitation in organisms when nutrient sources are scarce. P content in soil mainly depends on its cycle. In the MDV, P content is highly limited by low biological activity and reduced apatite weathering rates (Campbell et al., 1998, 2013; Blecker et al., 2006). Meanwhile, N and C cycling in the MDV are limited by low decomposition rates, salt accumulation, and water constraints (Bockheim, 2002; Barrett et al., 2007). Different concentrations of P and N combined with lower-than-average organic C availability in MDV soils leads to a highly heterogeneous stoichiometry (Fig. 3) (Campbell et al., 1998, 2013; Bockheim, 2002; Blecker et al., 2006; Barrett et al., 2007). Consequently, the availability of these elements tends to drive the distribution of most Antarctic biota at regional and landscape scales. The biological processes are limited and slow, making the growth rate of a population more sensitive to P content. Moreover, differences in rRNA synthesis from P-limited and P-rich soils could be amplified in the extremely harsh MDV soil ecosystem (Xue et al., 2023).

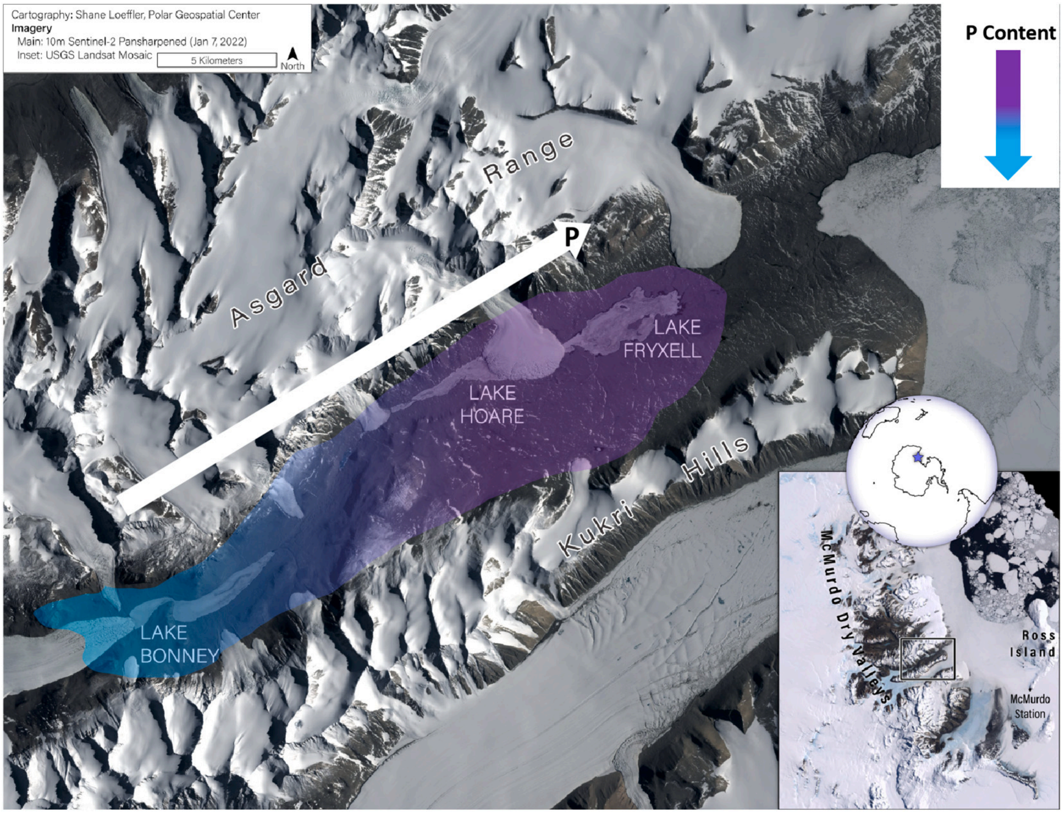

Fig. 3. Map of Taylor Valley, Antarctica. Purple indicates areas of high soil P-content; cyan indicates low soil P-content.

The amount of available soil P is higher in the Fryxell basin (Ross Sea till) than it is in the Bonney basin (Taylor II till), and the P fraction distribution in both Fryxell and Bonney basins reflects the general relationship between weathering intensity and P distribution seen in other arid ecosystems (Blecker et al., 2006; Bate et al., 2008). By comparing the effect of elemental stoichiometric constraints on growth rates of *P. murrayi* populations from different valley basins, researchers could elucidate which adaptations to specific habitats and environmental conditions may underlie differences in life history evolution. However, it remains unclear which mechanisms underlie how environmental nutrients influence rRNA evolution and the expression of related functional genes in animals from more complex ecosystems. A model species (*P. murrayi*) and simple ecosystem (MDV) approach should be helpful for understanding patterns between functional genes and environmental variation. For example, using the MDV and *P. murrayi* model study system, Xue et al. (2023) show that stoichiometric constraints drive rRNA copy number and the evolution of differential expression of genes associated with development and reproduction. The evolved changes in gene copy number produce differences in life history traits, such as longevity, fecundity, body size at maturity, and reproductive schedules. Such an approach could be extended to improve our understanding of the role of environmental stoichiometry in shaping the structure and evolution of communities more generally.

5. Ecological regime shifts and climate change

Global climate change can lead to significant environmental transformation and subsequent shifts in patterns of biodiversity that are reflected in organismal genotype-phenotype plasticity (Potvin and Tousignant, 1996; Scheiner et al., 2020). Thus, an ecosystem and its organisms that are sensitive to climate change provide a tractable model system to dissect mechanisms of adaptative responses to physical and genomic constraints.

The MDVs are often referred to as a landscape on the edge of change (Fountain et al., 2014). They are the driest and coldest deserts on Earth (Fountain et al., 1999; Bockheim, 2002; Obryk et al., 2020), but unlike deserts elsewhere, there is a substantial amount of liquid water locked away as ice in the glaciers and ice sheets that are adjacent to the valleys (Priscu et al., 1998; Doran et al., 2003; Mikucki et al., 2015). Low annual temperatures maintain the many glaciers that invade the valleys from the polar plateau and surrounding peaks, but predicted future warming is likely to bring increasing amounts of liquid moisture to the region (Doran et al., 2002; Gooseff et al., 2017). Thus, in the coming decades, the MDV soil communities will likely be subject to increasing temperatures and changing moisture regimes, providing an opportunity to study a whole, simplified soil community as it responds to drastic shifts in its physical environmental drivers.

As the local climate warms, arid soils will be increasingly inundated with moisture from melting glaciers, changing precipitation regimes, and a shift towards snow melt entering the soil directly instead of sublimating away (Sylvain et al., 2014; Wlostowski et al., 2018). These changes broaden the known suitable habitat for *P. murrayi*, which dominates moist sites, but reduces the suitable habitat of *S. lindsayae* (Simmons et al., 2009; Andriuzzi et al., 2018), which currently dominates arid soil sites (Adams et al., 2014; Velasco-Castrillón et al., 2014; Caruso et al., 2019; Kagoshima et al., 2019). Thus, anthropogenic climate change may see a replacement of *S. lindsayae* with *P. murrayi* as the dominant metazoan grazer in the MDV (Simmons et al., 2009; Andriuzzi et al., 2018). Monitoring changes in the population structure and distribution of both *P. murrayi* and *S. lindsayae* could provide a tractable research program for understanding genomic underpinnings of ecological succession and subsequent impacts on the structure and functioning of the soil ecosystem as a whole.

6. Conclusion

The model organism, *P. murrayi*, in the ecologically simplified environment of the MDVs, can resolve persistent knowledge gaps in ecology by facilitating ecological genomics as a research program. Some of these knowledge gaps include identifying responses of functional genes and pathways to ecological change, understanding their ecological and evolutionary consequences, and revealing the genetic mechanisms by which organisms respond to environmental drivers at the genomic level. Such an approach makes possible the study of eco-evo dynamics over long and short timescales, potentially capturing responses from across distinct populations, and as part of dynamic systems, such as responses to dramatic ecological changes that accompany climate change. Comparing the genetic structure of lab cultured and wild organisms offers an opportunity to study and test basic ecological hypotheses at different organizational levels (individual, population, community, ecosystem; genetic, molecular, and 'omic'). Similarly, genes associated with ecological amplitude can be targeted to explore the genetic mechanisms necessary for resistant and resilient responses to environmental stress. Approaches to ecological genomics that take these mechanisms into consideration are especially effective for understanding organismal responses to environments where interference from confounding biotic and abiotic factors is greatly reduced. Similarly, approaches to ecological genomics that explore short-term and long-term responses to environmental stress, using simplified model systems, make it possible to answer fundamental questions of ecological genomics, such as the relationship between evolution and ecosystem complexity, as well as the role of elemental stoichiometry in shaping communities from more complex ecosystems. Thus, the adoption of model ecosystems and organisms could help address several persistent knowledge gaps in ecology, especially our understanding of how genetic variation, genomic architecture, and gene regulation drive the genotype-phenotype paradigm, and the consequent effects of these drivers on ecosystem structure and functioning.

Declaration of competing interest

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

Data availability

No data was used for the research described in the article.

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References

Acharya, K., Kyle, M., Elser, J., 2004. Effects of stoichiometric dietary mixing on *Daphnia* growth and reproduction. Oecologia 138, 333–340. https://doi.org/10.1007/s00442-003-1444-8.

Adams, B.J., Bardgett, R.D., Ayres, E., Wall, D.H., Aislabie, J., Bamforth, S., Bargagli, R., Cary, C., Cavacini, P., Connell, L., Convey, P., Fell, J.W., Frati, F., Hogg, I.D., Newsham, K.K., O'Donnell, A., Russell, N., Seppelt, R.D., Stevens, M.I., 2006. Diversity and distribution of Victoria Land biota. Soil Biol. Biochem. 38, 3003–3018. https://doi.org/10.1016/j.soilbio.2006.04.030.

Adams, B.J., Wall, D., Virginia, R., Broos, E., Knox, M., 2014. Ecological biogeography of the terrestrial nematodes of Victoria Land, Antarctica. Zookeys 419, 29–71. https://doi.org/10.3897/zookeys.419.7180.

Adhikari, B.N., Adams, B.J., 2011. Molecular Analyses of Desiccation Survival in Antarctic Nematodes. CABI, Wallingford, pp. 205–232. https://doi.org/10.1079/9781845936877.0205.

Adhikari, B.N., Wall, D.H., Adams, B.J., 2009. Desiccation survival in an Antarctic nematode: molecular analysis using expressed sequenced tags. BMC Genomics 10, 18. https://doi.org/10.1186/1471-2164-10-69.

Adhikari, B.N., Tomasel, C.M., Li, G., Wall, D.H., Adams, B.J., 2010a. The Antarctic nematode *Plectus murrayi*: an emerging model to study multiple stress survival. Cold Spring Harb Protoc 11, pdb–emo142.

Adhikari, B.N., Tomasel, C.M., Li, G., Wall, D.H., Adams, B.J., 2010b. Culturing the Antarctic nematode *Plectus murrayi*. Cold Spring Harbor Protocols 2010. https://doi.org/10.1101/pdb.prot5522 pdb prot5522.

Adhikari, B.N., Wall, D.H., Adams, B.J., 2010c. Effect of slow desiccation and freezing on gene transcription and stress survival of an Antarctic nematode. J. Exp. Biol. 213, 1803–1812. https://doi.org/10.1242/jeb.032268.

Andrássy, I., 1998. Nematodes in the sixth continent. J. Nematode Morphol. Syst. 1, 107–186.

Andrássy, I., 2012. On the male of the Antarctic nematode species, *Plectus murrayi* Yeates, 1970. J. Nematode Morphol. Syst. 11, 87–89 (2008).

Andrássy, I., Gibson, J.A.E., 2006. Nematodes from saline and freshwater lakes of the Vestfold Hills, East Antarctica, including the description of *Hypodontolaimus antarcticus sp.* n. Polar Biol. 30, 669–678. https://doi.org/10.1007/s00300-006-0224-4.

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.

Bamforth, S.S., Wall, D.H., Virginia, R.A., 2005. Distribution and diversity of soil protozoa in the McMurdo Dry Valleys of Antarctica. Polar Biol. 28, 756–762. https://doi.org/10.1007/s00300-005-0006-4.

Barrett, J.E., Virginia, R.A., Parsons, A.N., Wall, D.H., 2006. Soil carbon turnover in the McMurdo Dry Valleys, Antarctica. Soil Biol. Biochem. 38, 3065–3082. https://doi.org/10.1016/j.soilbio.2006.03.025.

Barrett, J., Virginia, R., Lyons, W., McKnight, D., Priscu, J., Doran, P., Fountain, A., Wall, D., Moorhead, D., 2007. Biogeochemical stoichiometry of Antarctic Dry Valley ecosystems. J. Geophys. Res. Biogeosci. 112 (G1) https://doi.org/10.1029/2005JG000141.

Bate, D.B., Barrett, J.E., Poage, M.A., Virginia, R.A., 2008. Soil phosphorus cycling in an Antarctic polar desert. Geoderma 144, 21–31. https://doi.org/10.1016/j.geoderma.2007.10.007.

Bewley, J.D., 1979. Physiological aspects of desiccation tolerance. Annu. Rev. Plant Physiol. 30, 195–238.

Blecker, S.W., Ippolito, J.A., Barrett, J.E., Wall, D.H., Virginia, R.A., Norvell, K.L., 2006. Phosphorus fractions in soils of Taylor Valley, Antarctica. Soil Sci. Soc. Am. J. 70, 806–815. https://doi.org/10.2136/sssaj2005.0333.

Bockheim, J.G., 2002. Landform and soil development in the McMurdo dry valleys, Antarctica: a regional synthesis. Arct. Antarct. Alp. Res. 34, 308–317. https://doi.org/10.1080/15230430.2002.12003499.

Bogart, J.P., Bi, K., Fu, J., Noble, D.W., Niedzwiecki, J., 2007. Unisexual salamanders (genus *Ambystoma*) present a new reproductive mode for eukaryotes. Genome 50, 119–136. https://doi.org/10.1139/G06-152.

Bongers, T., Ferris, H., 1999. Nematode community structure as a bioindicator in environmental monitoring. Trends Ecol. Evol. 14, 224–228. https://doi.org/10.1016/S0169-5347(98)01583-3.

Borgonie, G., Garcia-Moyano, A., Litthauer, D., Bert, W., Bester, A., van Heerden, E., Moller, C., Erasmus, M., Onstott, T.C., 2011. Nematoda from the terrestrial deep subsurface of South Africa. Nature 474, 79–82. https://doi.org/10.1038/nature09974.

Brooks, D.R., McLennan, D.A., 1991. Phylogeny, Ecology, and Behavior: A Research Program in Comparative Biology. University of Chicago Press, Chicago.

Brooks, D.R., Mayden, R.L., McLennan, D.A., 1992. Phylogeny and biodiversity: conserving our evolutionary legacy. Trends Ecol. Evol. 7 (2), 55–59.

Brown, I.M., Wharton, D.A., Millar, R.B., 2004. The influence of temperature on the life history of the Antarctic nematode *Panagrolaimus davidi*. Nematology 6, 883–890.

Burkins, M.B., Virginia, R.A., Wall, D.H., 2001. Organic carbon cycling in Taylor Valley, Antarctica: quantifying soil reservoirs and soil respiration. Glob. Chang. Biol. 7, 113–125. https://doi.org/10.1046/j.1365-2486.2001.00393.x.

Campbell, I.B., Claridge, G.G.C., Campbell, D.I., Balks, M.R., 1998. The soil environment of the McMurdo dry valleys, Antarctica. In: Ecosystem Dynamics in a Polar Desert: the McMurdo Dry Valleys, Antarctica, 72, pp. 297–322. https://doi.org/10.1029/AR072p0297.

Campbell, I.B., Claridge, G.G.C., Campbell, D.I., Balks, M.R., 2013. The Soil Environment of the McMurdo Dry Valleys, Antarctica. American Geophysical Union (AGU), Washington, D. C.

Carroll, S.P., Hendry, A.P., Reznick, D.N., Fox, C.W., 2007. Evolution on ecological time-scales. Funct. Ecol. 21 (3), 387–393. https://doi.org/10.1111/j.1365-2435.2007.01289.x.

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. Commun. Biol. 2, 63. https://doi.org/10.1038/s42003-018-0260-y.

Chaudhuri, J., Kache, V., Pires-daSilva, A., 2011. Regulation of sexual plasticity in a nematode that produces males, females, and hermaphrodites. Curr. Biol. 21, 1548–1551. https://doi.org/10.1016/j.cub.2011.08.009.

Convey, P., 1997. How are the life history strategies of Antarctic terrestrial invertebrates influenced by extreme environmental conditions? J. Therm. Biol. 22, 429–440. https://doi.org/10.1016/S0306-4565(97)00062-4.

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. Antarct. Sci. 13, 9–17. https://doi.org/10.1017/S0954102001000037.

Crowe, J.H., Madin, K.A., 1974. Anhydrobiosis in tardigrades and nematodes. Trans. Am. Microsc. Soc. 93, 513–524. https://doi.org/10.2307/3225155.

Crowe, J.H., Madin, K.A.C., Loomis, S.H., 1977. Anhydrobiosis in nematodes: metabolism during resumption of activity. J. Exp. Zool. 201, 57–64. https://doi.org/10.1002/jez.1402010107.

Cutter, A.D., Morran, L.T., Phillips, P.C., 2019. Males, outcrossing, and sexual selection in *Caenorhabditis nematodes*. Genetics 213, 27–57. https://doi.org/10.1534/genetics.119.300244.

Dajoz, R., 1975. Osnovy ekologii. Moscow. In: Ecological Amplitude. (n.d.) The Great Soviet Encyclopedia, 3rd Edition. (1970-1979).

de Tomasel, C.M., Adams, B.J., Tomasel, F.G., Wall, D.H., 2013. The life cycle of the Antarctic nematode *Plectus murrayi* under laboratory conditions. J. Nematol. 45, 39–42.

Demeure, Y., Freckman, D.W., Van Gundy, S.D., 1979. Anhydrobiotic coiling of nematodes in soil. J. Nematol. 11, 189–195.

Doran, P.T., McKay, C.P., Clow, G.D., Dana, G.L., Fountain, A.G., Nylen, T., Lyons, W.B., 2002. Valley floor climate observations from the McMurdo dry valleys, Antarctica, 1986–2000. J. Geophys. Res. Atmos. 107, 177. https://doi.org/10.1029/2001JD002045.

Doran, P.T., Fritsen, C.H., McKay, C.P., Priscu, J.C., Adams, E.E., 2003. Formation and character of an ancient 19-m ice cover and underlying trapped brine in an "ice-sealed" east Antarctic lake. Proc. Natl. Acad. Sci. 100, 26–31. https://doi.org/10.1073/pnas.222680999.

Dunson, W.A., Travis, J., 1991. The role of abiotic factors in community organization. Am. Nat. 138, 1067–1091. https://doi.org/10.1086/285270.

Elser, J.J., Sterner, R.W., Gorokhova, E., Fagan, W.F., Markow, T.A., Cotner, J.B., Harrison, J.F., Hobbie, S.E., Odell, G.M., Weider, L.W., 2000. Biological stoichiometry from genes to ecosystems. Ecol. Lett. 3, 540–550. https://doi.org/10.1111/j.1461-0248.2000.00185.x.

Elser, J., Acharya, K., Kyle, M., Cotner, J., Makino, W., Markow, T., Watts, T., Hobbie, S., Fagan, W., Schade, J., Hood, J., Sterner, R., 2003. Growth rate-stoichiometry couplings in diverse biota. Ecol. Lett. 936–943. https://doi.org/10.1046/j.1461-0248.2003.00518.x.

Elser, J.J., Andersen, T., Baron, J.S., Bergström, A.K., Jansson, M., Kyle, M., Nydick, K.R., Steger, L., Hessen, D.O., 2009. Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. Science 326, 835. https://doi.org/10.1126/science.1176199.

Erkut, C., Kurzchalia, T.V., 2015. The *C. elegans* dauer larva as a paradigm to study metabolic suppression and desiccation tolerance. Planta 242, 389–396. https://doi.org/10.1007/s00425-015-2300-x.

Erkut, C., Vasilj, A., Boland, S., Habermann, B., Shevchenko, A., Kurzchalia, T.V., 2013. Molecular strategies of the *Caenorhabditis elegans* Dauer larva to survive extreme desiccation. PLoS One 8, e82473. https://doi.org/10.1371/journal.pone.0082473.

Eshel, G., Araus, V., Undurraga, S., Soto, D.C., Moraga, C., Montecinos, A., Moyano, T., Maldonado, J., Díaz, F.P., Varala, K., 2021. Plant ecological genomics at the limits of life in the Atacama Desert. Proc. Natl. Acad. Sci. 118 (46), e2101177118 https://doi.org/10.1073/pnas.2101177118.

Ferris, H., 2010. Contribution of nematodes to the structure and function of the soil food web. J. Nematol. 42, 63–67.

Fierer, N., Leff, J.W., Adams, B.J., Nielsen, U.N., Bates, S.T., Lauber, C.L., Owens, S., Gilbert, J.A., Wall, D.H., Caporaso, J.G., 2012. Cross-biome metagenomic analyses of soil microbial communities and their functional attributes. Proc. Natl. Acad. Sci. 109, 21390–21395. https://doi.org/10.1073/pnas.1215210110.

Flatt, T., Heyland, A., 2011. Mechanisms of Life History Evolution: The Genetics and Physiology of Life History Traits and Trade-offs. Oxford university press May 12.

Flatt, T., Amdam, G.V., Kirkwood, T.B.L., Omholt, S.W., 2013. Life-history evolution and the polyphenic regulation of somatic maintenance and survival. Princeton University Press, 88, 185–218. https://doi.org/10.1086/671484.

Fountain, A.G., Lyons, W.B., Burkins, M.B., Dana, G.L., Doran, P.T., Lewis, K.J., McKnight, D.M., Moorhead, D.L., Parsons, A.N., Priscu, J.C., Wall, D.H., Wharton, R. A., Virginia, R.A., 1999. Physical controls on the Taylor Valley ecosystem, Antarctica. BioScience 49, 961–971. https://doi.org/10.1525/bisi.1999.49.12.961.

Fountain, A.G., Levy, J.S., Gooseff, M.N., Van Horn, D., 2014. The McMurdo dry valleys: a landscape on the threshold of change. Geomorphology 225, 25–35. https://doi.org/10.1016/j.geomorph.2014.03.044.

Freckman, D., Virginia, R., 1997. Low-diversity Antarctic soil nematode communities: distribution and response to disturbance. Ecology 78 (2), 363–369. https://doi.org/10.1890/0012-9658.

Gao, Z.M., Huang, J.M., Cui, G.J., Li, W.L., Li, J., Wei, Z.F., Chen, J., Xin, Y.Z., Cai, D.S., Zhang, A.Q., Wang, Y., 2019. In situ meta-omic insights into the community compositions and ecological roles of hadal microbes in the Mariana Trench. Environ. Microbiol. 21, 4092–4108. https://doi.org/10.1111/1462-2920.14759.

Garcia, L.R., LeBoeuf, B., Koo, P., 2007. Diversity in mating behavior of hermaphroditic and male–female *Caenorhabditis* nematodes. Genetics 175, 1761–1771. https://doi.org/10.1534/genetics.106.068304.

Geyer, K.M., Takacs-Vesbach, C.D., Gooseff, M.N., Barrett, J.E., 2017. Primary productivity as a control over soil microbial diversity along environmental gradients in a polar desert ecosystem. PeerJ 5, e3377. https://doi.org/10.7717/peerj.3377.

Glucksman, E., Bell, T., Griffiths, R.I., Bass, D., 2010. Closely related protist strains have different grazing impacts on natural bacterial communities. Environ. Microbiol. 12, 3105–3113. https://doi.org/10.1111/j.1462-2920.2010.02283.x.

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. Nat. Ecol. Evol. 1, 1334–1338. https://doi.org/10.1038/s41559-017-0253-0.

Gorokhova, E., Kyle, M., 2002. Analysis of nucleic acids in *Daphnia*: development of methods and ontogenetic variations in RNA-DNA content. J. Plankton Res. 24, 511–522. https://doi.org/10.1093/plankt/24.5.511.

Goyal, K., 2005. Molecular anhydrobiology: identifying molecules implicated in invertebrate anhydrobiosis. Integr. Comp. Biol. 45, 702–709. https://doi.org/10.1093/icb/45.5.702.

Heyns, J., 1995. *Plectus antarcticus* De man, 1904 from Western Dronning Maud Land, Antarctica. Nematologica 41, 1–6.

Holling, C.S., 1973. Resilience and stability of ecological systems. Annu. Rev. Ecol. Syst. 4, 1–23.

Jackson, A.C., Jorna, J., Chaston, J.M., Adams, B.J., 2022. Glacial legacies: microbial communities of Antarctic Refugia. Biology 11 (10), 1440. https://doi.org/10.3390/biology11101440.

Jaroměřska, T., Trubač, J., Zawierucha, K., 2021. Stable isotopic composition of top consumers in Arctic cryoconite holes: revealing different position in supraglacial trophic network. Biogeosciences 18, 1543–1557. https://doi.org/10.5194/bg-18-1543-2021.

Judson, O.P., Normark, B.B., 1996. Ancient asexual scandals. Trends Ecol. Evol. 11, 41–46. https://doi.org/10.1016/0169-5347(96)81040-8.

Kagoshima, H., Kito, K., Aizu, T., Shin-i, T., Kanda, H., Kobayashi, S., Toyoda, A., Fujiyama, A., Kohara, Y., Convey, P., Niki, H., 2012. Multi-decadal survival of an Antarctic nematode, *Plectus murrayi*, in a −20°C stored moss sample. Cryo Lett. 33, 280–288.

Kagoshima, H., Maslen, R., Kito, K., Imura, S., Niki, H., Convey, P., 2019. Integrated taxonomy combining morphological and molecular biological analyses of soil nematodes from maritime Antarctica. Polar Biol. 42, 877–887. https://doi.org/10.1007/s00300-019-02482-8.

Kito, K., Shishida, Y., Ohyama, Y., 1991. *Plectus antarcticus* De Man, 1094 and *P. frigophilus* Kirjanova, 1958 (Nematoda, Plectidae), with emphasis on the male, from the Soya coast, east Antarctica. Nematologica 37, 252–262. https://doi.org/10.1163/187529291X00259.

Knox, M.A., Wall, D.H., Virginia, R.A., Vandegehuchte, M.L., Gil, I.S., Adams, B.J., 2016. Impact of diurnal freeze-thaw cycles on the soil nematode *Scottnema lindsayae* in Taylor Valley, Antarctica. Polar Biol. 39, 583–592. https://doi.org/10.1007/s00300-015-1809-6.

Lahl, V., Halama, C., Schierenberg, E., 2003. Comparative and experimental embryogenesis of *Plectidae* (Nematoda). Dev. Genes Evol. 213, 18–27. https://doi.org/10.1007/s00427-002-0289-1.

Lawson Knoepfle, J., Doran, P.T., Kenig, F., Lyons, W.B., Galchenko, V.F., 2009. Particulate organic and dissolved inorganic carbon stable isotopic compositions in Taylor Valley lakes, Antarctica: the effect of legacy. Hydrobiologia 632, 139–156. https://doi.org/10.1007/s10750-009-9834-5.

Lee, S., 1999. Tropical mangrove ecology: physical and biotic factors influencing ecosystem structure and function. Aust. J. Ecol. 24, 355–366. https://doi.org/10.1046/j.1442-9993.1999.00984.x.

Lunt, D.H., 2008. Genetic tests of ancient asexuality in root knot nematodes reveal recent hybrid origins. BMC Evol. Biol. 8, 1–16. https://doi.org/10.1186/1471-2148-8-194.

Magalhaes, C., Stevens, M.I., Craig, S.C., Ball, B., Storey, B.C., Diana, H.W., Türk, R., Ruprecht, U., 2012. At limits of life: multidisciplinary insights reveal environmental constraints on biotic diversity in continental Antarctica. PLoS One 7, e44578. https://doi.org/10.1371/journal.pone.0044578.

Markaki, M., Tavernarakis, N., 2020. *Caenorhabditis elegans* as a model system for human diseases. Curr. Opin. Biotechnol. 63, 118–125. https://doi.org/10.1016/j.copbio.2019.12.011.

McGill, L.M., Shannon, A.J., Pisani, D., Félix, M.A., Ramløv, H., Dix, I., Wharton, D.A., Burnell, A.M., 2015. Anhydrobiosis and freezing-tolerance: adaptations that facilitate the establishment of *Panagrolaimus* nematodes in polar habitats. PLoS One 10, e0116084. https://doi.org/10.1371/journal.pone.0116084.

Mikucki, J.A., Auken, E., Tulaczyk, S., Virginia, R., Schamper, C., Sørensen, K., Doran, P., Dugan, H., Foley, N., 2015. Deep groundwater and potential subsurface habitats beneath an Antarctic dry valley. Nat. Commun. 6, 1–9. https://doi.org/10.1038/ncomms7831.

Mouratov, S., Lahav, I., Barness, G., Steinberger, Y., 2001. Preliminary study of the soil nematode community at Machu Picchu Station, King George Island, Antarctica. Polar Biol. 24, 545–548. https://doi.org/10.1007/s003000100242.

Nakayama, K.I., Ishita, Y., Chihara, T., Okumura, M., 2020. Screening for CRISPR/Cas9-induced mutations using a co-injection marker in the nematode *Pristionchus pacificus*. Dev. Genes Evol. 230, 257–264. https://doi.org/10.1007/s00427-020-00651-y.

Newbold, T., Hudson, L.N., Hill, S.L., Contu, S., Lysenko, I., Senior, R.A., Borger, L., Bennett, D.J., Choimes, A., Collen, B., Day, J., De Palma, A., Diaz, S., Echeverria-Londono, S., Edgar, M.J., Feldman, A., Garon, M., Harrison, M.L., Alhusseini, T., Ingram, D.J., Itescu, Y., Kattge, J., Kemp, V., Kirkpatrick, L., Kleyer, M., Correia, D. L., Martin, C.D., Meiri, S., Novosolov, M., Pan, Y., Phillips, H.R., Purves, D.W., Robinson, A., Simpson, J., Tuck, S.L., Weiher, E., White, H.J., Ewers, R.M., Mace, G. M., Scharlemann, J.P., Purvis, A., 2015. Global effects of land use on local terrestrial biodiversity. Nature 520 (7545), 45–50. https://doi.org/10.1038/nature14324.

Newsham, K.K., Rolf, J., Pearce, D.A., Strachan, R.J., 2004. Differing preferences of Antarctic soil nematodes for microbial prey. Eur. J. Soil Biol. 40 (1), 1–8. https://doi.org/10.1016/j.ejsobi.2004.01.004.

Obryk, M.K., Doran, P.T., Fountain, A.G., Myers, M., McKay, C.P., 2020. Climate from the McMurdo dry valleys, Antarctica, 1986–2017: surface air temperature trends and redefined summer season. J. Geophys. Res. Atmos. 125, e2019JD032180 https://doi.org/10.1029/2019JD032180.

Oliver, M.J., Farrant, J.M., Hilhorst, H.W.M., Mundree, S., Williams, B., Bewley, J.D., 2020. Desiccation tolerance: avoiding cellular damage during drying and rehydration. Annu. Rev. Plant Biol. 71, 435–460. https://doi.org/10.1146/annurev-arplant-071219-105542.

Op den Camp, H.J.M., Islam, T., Stott, M.B., Harhangi, H.R., Hynes, A., Schouten, S., Jetten, M.S.M., Birkeland, N.K., Pol, A., Dunfield, P.F., 2009. Environmental, genomic and taxonomic perspectives on methanotrophic Verrucomicrobia. Environ. Microbiol. Rep. 1, 293–306. https://doi.org/10.1111/j.1758-2229.2009.00022.x.

Overhoff, A., Freckman, D.W., Virginia, R.A., 1993. Life cycle of the microbivorous Antarctic Dry Valley nematode *Scottnema lindsayae* (Timm 1971). Polar Biol. 13, 151–156. https://doi.org/10.1007/BF00238924.

Partridge, L., Harvey, P.H., 1988. The ecological context of life history evolution. Science 241, 1449–1455. https://doi.org/10.1126/science.241.4872.1449.

Pavey, S.A., Bernatchez, L., Aubin-Horth, N., Landry, C.R., 2012. What is needed for next-generation ecological and evolutionary genomics? Trends Ecol. Evol. 27, 673–678. https://doi.org/10.1016/j.tree.2012.07.014.

Perkins, M., Woods, H., Harrison, J., Elser, J., 2004. Dietary phosphorus affects the growth of larval *Manduca sexta*. Arch. Insect Biochem. Physiol. 55, 153–168. https://doi.org/10.1002/arch.10133.

Porazinska, D.L., Wall, D.H., 2002. Population age structure of nematodes in the Antarctic dry valleys: perspectives on time, space, and habitat suitability. Arct. Antarct. Alp. Res. 34, 159–168. https://doi.org/10.1080/15230430.2002.12003480.

Potts, M., 1994. Desiccation tolerance of prokaryotes. Microbiol. Rev. 58, 755. https://doi.org/10.1128/mr.58.4.755-805.1994.

Potvin, C., Tousignant, D., 1996. Evolutionary consequences of simulated global change: genetic adaptation or adaptive phenotypic plasticity. Oecologia 108, 683–693. https://doi.org/10.1007/BF00329043.

Powers, L.E., Ho, M.C., Freckman, D.W., Virginia, R.A., 1998. Distribution, community structure, and microhabitats of soil invertebrates along an elevational gradient in Taylor Valley, Antarctica. Arct. Alp. Res. 30, 133–141.

Priscu, J.C., 1998. Ecosystem dynamics in a Polar Desert: the McMurdo Dry Valleys, Antarctica (American Geophysical Union Antarctic Research Series. Volume 72). Ecosystem Dynamics in a Polar Desert: the McMurdo Dry Valleys, Antarctica (American Geophysical Union Antarctic Research Series. Volume 72).

Priscu, J.C., Fritsen, C.H., Adams, E.E., Giovannoni, S.J.H., Paerl, W., McKay, C.P., Doran, P.T., Gordon, D.A., Lanoil, B.D., Pinckney, J.L., 1998. Perennial Antarctic Lake ice: an oasis for life in a Polar Desert. Science 280, 2095–2098. https://doi.org/10.1126/science.280.5372.2095.

Raymond, M.R., Wharton, D.A., 2013. The ability of the Antarctic nematode *Panagrolaimus davidi* to survive intracellular freezing is dependent upon nutritional status. J. Comp. Physiol. B Biochem. Syst. Environ. Physiol. 183, 181–188. https://doi.org/10.1007/s00360-012-0697-0.

Raymond, M.R., Wharton, D.A., 2016. The ability to survive intracellular freezing in nematodes is related to the pattern and distribution of ice formed. J. Exp. Biol. 219, 2060. https://doi.org/10.1242/jeb.137190.

Rice, A.M., Rudh, A., Ellegren, H., Qvarnström, A., 2011. A guide to the genomics of ecological speciation in natural animal populations. Ecol. Lett. 14, 9–18. https://doi.org/10.1111/j.1461-0248.2010.01546.x.

Roach, K.C., Feretzaki, M., Sun, S., Heitman, J., 2014. Unisexual reproduction. Adv. Genet. 85, 255–305. https://doi.org/10.1101/cshperspect.a019281.

Robert, M., 2003. Adaptations of nematodes to environmental extremes. Fla. Entomol. 86, 138–142. https://doi.org/10.1653/0015-4040(2003)086.

Rønn, R., Vestergård, M., Ekelund, F., 2012. Interactions between bacteria, protozoa and nematodes in soil. Acta Protozool. 51, 223–235. https://doi.org/10.4467/16890027AP.12.018.0764.

Sandhove, J., Spann, N., Ristau, K., 2016. The anhydrobiotic potential of the terrestrial nematodes *Plectus parietinus and Plectus velox*. J. Exp. Zool. A Ecol. Genet. Physiol. 325, 434–440. https://doi.org/10.1002/jez.2028.

Scheiner, S.M., Barfield, M., Holt, R.D., 2020. The genetics of phenotypic plasticity. XVII. Response to climate change. Evol. Applic. 13, 388–399. https://doi.org/10.1111/eva.12876.

Schwarz, A.M.J., Green, J.D., Green, T.G.A., Seppelt, R.D., 1993. Invertebrates associated with moss communities at Canada Glacier, southern Victoria Land, Antarctica. Polar Biol. 13, 157–162. https://doi.org/10.1007/BF00238925.

Shaw, E.A., Wall, D.H., 2019. Biotic interactions in experimental Antarctic soil microcosms vary with abiotic stress. Soil Syst. 3, 57. https://doi.org/10.3390/soilsystems3030057.

Shaw, E.A., Adams, B.J., Barrett, J.E., Lyons, W.B., 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 Biol. 41, 1013–1018. https://doi.org/10.1007/s00300-017-2243-8.

Simmons, B.L., Wall, D.H., Adams, B.J., Ayres, E., Barrett, J.E., Virginia, R.A., 2009. Long-term experimental warming reduces soil nematode populations in the McMurdo Dry Valleys, Antarctica. Soil Biol. Biochem. 41, 2052–2060. https://doi.org/10.1016/j.soilbio.2009.07.009.

Sohlenius, B., Boström, S., Hirschfelder, A., 1996. Distribution patterns of microfauna (nematodes, rotifers and tardigrades) on nunataks in Dronning Maud Land, East Antarctica. Polar Biol. 16, 191–200. https://doi.org/10.1007/BF02329207.

Sriaporn, C., Campbell, K.A., Van Kranendonk, M.J., Handley, K.M., 2021. Genomic adaptations enabling Acidithiobacillus distribution across wide-ranging hot spring temperatures and pHs. Microbiome 9, 135. https://doi.org/10.1186/s40168-021-01090-1.

Storey, K.B., Storey, J.M., 2013. Molecular biology of freezing tolerance. Compr. Physiol. 3, 1283–1308. https://doi.org/10.1002/cphy.c130007.

Sylvain, Z.A., Wall, D.H., Cherwin, K.L., Peters, D.P., Reichmann, L.G., Sala, O.E., 2014. Soil animal responses to moisture availability are largely scale, not ecosystem dependent: insight from a cross-site study. Glob. Chang. Biol. 20, 2631–2643. https://doi.org/10.1111/gcb.12522.

Terauds, A., Lee, J.R., 2016. Antarctic biogeography revisited-updating the Antarctic conservation biogeographic regions. Divers. Distrib. 22, 836–840. https://doi.org/10.1111/ddi.12453.

Thompson, J.N., 1998. Rapid evolution as an ecological process. Trends Ecol. Evol. 13, 329–332. https://doi.org/10.1016/S0169-5347(98)01378-0.

Thompson, A.R., Geisen, S., Adams, B.J., 2020. Shotgun metagenomics reveal a diverse assemblage of protists in a model Antarctic soil ecosystem. Environ. Microbiol. 22, 4620–4632. https://doi.org/10.1111/1462-2920.15198.

Thompson, A.R., Roth-Monzón, A.J., Aanderud, Z.T., Adams, B.J., 2021. Phagotrophic protists and their associates: evidence for preferential grazing in an abiotically driven soil ecosystem. Microorganisms 9, 1555. https://doi.org/10.3390/microorganisms9081555.

Treonis, A.M., Wall, D.H., Virginia, R.A., 2000. The use of anhydrobiosis by soil nematodes in the Antarctic dry valleys. Funct. Ecol. 14, 460–467. https://www.jstor.org/stable/2656539.

Ungerer, M.C., Johnson, L.C., Herman, M.A., 2008. Ecological genomics: understanding gene and genome function in the natural environment. Heredity 100, 178–183. https://doi.org/10.1038/sj.hdy.6800992.

Vakhrusheva, O.A., Mnatsakanova, E.A., Galimov, Y.R., Neretina, T.V., Gerasimov, E.S., Naumenko, S.A., Ozerova, S.G., Zalevsky, A.O., Yushenova, I.A., Rodriguez, F., 2020. Genomic signatures of recombination in a natural population of the bdelloid rotifer *Adineta vaga*. Nat. Commun. 11, 1–17. https://doi.org/10.1038/s41467-020-19614-y.

van den Hoogen, J., Geisen, S., Routh, D., Ferris, H., Traunspurger, W., Wardle, D.A., de Goede, R.G.M., Adams, B.J., Ahmad, W., Andriuzzi, W.S., Bardgett, R.D., Bonkowski, M., Campos-Herrera, R., Cares, J.E., Caruso, T., de Brito Caixeta, L., Chen, X., Costa, S.R., Creamer, R., da Cunha, Mauro, Castro, J., Dam, M., Djigal, D., Escuer, M., Griffiths, B.S., Gutierrez, C., Hohberg, K., Kalinkina, D., Kardol, P., Kergunteuil, A., Korthals, G., Krashevska, V., Kudrin, A.A., Li, Q., Liang, W., Magilton, M., Marais, M., Martin, J.A.R., Matveeva, E., Mayad, E.H., Mulder, C., Mullin, P., Neilson, R., Nguyen, T.A.D., Nielsen, U.N., Okada, H., Rius, J.E.P., Pan, K., Peneva, V., Pellissier, L., Pereira, Carlos, da Silva, J., Pitteloud, C., Powers, T.O., Powers, K., Quist, C.W., Rasmann, S., Moreno, S.S., Scheu, S., Setala, H., Sushchuk, A., Tiunov, A.V., Trap, J., van der Putten, W., Vestergard, M., Villenave, C., Waeyenberge, L., Wall, D.H., Wilschut, R., Wright, D.G., Yang, J.I., Crowther, T.W., 2019. Soil nematode abundance and functional group composition at a global scale. Nature 572, 194–198. https://doi.org/10.1038/s41586-019-1418-6.

Velasco-Castrillón, A., Schultz, M.B., Colombo, F., Gibson, J.A.E., Davies, K.A., Austin, A.D., Stevens, M.I., 2014. Distribution and diversity of soil microfauna from East Antarctica: assessing the link between biotic and abiotic factors. PLoS One 9, e87529. https://doi.org/10.1371/journal.pone.0087529.

Velasco-Castrillón, A., McInnes, S.J., Schultz, M.B., Arróniz-Crespo, M., D'Haese, C.A., Gibson, J.A., Adams, B.J., Page, T.J., Austin, A.D., Cooper, S.J., Stevens, M.I., 2015. Mitochondrial DNA analyses reveal widespread tardigrade diversity in Antarctica. Invertebr. Syst. 29, 578–590. https://doi.org/10.1071/IS14019.

Wall, D., Virginia, R., 1999. Controls on soil biodiversity: insights from extreme environments. Appl. Soil Ecol. 113 (2), 137–150. https://doi.org/10.1016/S0929-1393(99)00029-3.

Weicht, T.R., Moorhead, D.L., 2004. The impact of anhydrobiosis on the persistence of *Scottnema lindsayae* (Nematoda): a modeling analysis of population stability thresholds. Polar Biol. 27, 507–512. https://doi.org/10.1007/s00300-004-0621-5.

Weider, L., Glenn, K., Kyle, M., Elser, J., 2004. Associations among ribosomal (r)DNA intergenic spacer length, growth rate, and C:N:P stoichiometry in the genus *Daphnia*. Limnol. Oceanogr. 49, 1417–1423. https://doi.org/10.4319/lo.2004.49.4_part_2.1417.

Weider, L., Elser, J., Crease, T., Mateos, M., Cotner, J., Markow, T., 2005. The functional significance of ribosomal (r)DNA variation: impacts on the evolutionary ecology of organisms. Annu. Rev. Ecol. Evol. Syst. 36, 219–242. https://doi.org/10.1146/annurev.ecolsys.36.102003.152620.

Wharton, D., 1996. Water loss and morphological changes during desiccation of the anhydrobiotic nematode *Ditylenchus dipsaci*. J. Exp. Biol. 199, 1085–1093. https://doi.org/10.1242/jeb.199.5.1085.

Wharton, D.A., 2003. The environmental physiology of Antarctic terrestrial nematodes: a review. J. Comp. Physiol. B. 173, 621–628. https://doi.org/10.1007/s00360-003-0378-0.

Wharton, D.A., 2011. Anhydrobiosis: the model worm as a model? Curr. Biol. 21, R578–R579.

Wharton, D.A., Brown, I.M., 2012. A survey of terrestrial nematodes from the McMurdo Sound region, Antarctica. N. Z. J. Zool. 16, 467–470. https://doi.org/10.1080/03014223.1989.10422914.

Wharton, D.A., Raymond, M.R., 2015. Cold tolerance of the Antarctic nematodes *Plectus murrayi* and *Scottnema lindsayae*. J. Comp. Physiol. B. 185, 281–289. https://doi.org/10.1007/s00360-014-0884-2.

Wharton, D.A., Downes, M.F., Goodall, G., Marshall, C.J., 2005. Freezing and cryoprotective dehydration in an Antarctic nematode (*Panagrolaimus davidi*) visualised using a freeze substitution technique. Cryobiology 50, 21–28. https://doi.org/10.1016/j.cryobiol.2004.09.004.

Wlostowski, A.N., Gooseff, M.N., Adams, B.J., 2018. Soil moisture controls the thermal habitat of active layer soils in the McMurdo dry valleys, Antarctica. J. Geophys. Res. Biogeosci. 123, 46–59. https://doi.org/10.1002/2017JG004018.

Xue, X., Suvorov, A., Fujimoto, S., Dilman, A.R., Adams, B.J., 2021. Genome analysis of *Plectus murrayi*, a nematode from continental Antarctica. G3 Genes|Genomes|Genetics 11, jkaa045. https://doi.org/10.1093/g3journal/jkaa045.

Xue, X., Adhikari, B.N., Ball, B.A., Barrett, J.E., Miao, J., Perkes, A., Martin, M., Simmons, B.L., Wall, D.H., Adams, B.J., 2023. Ecological stoichiometry drives the evolution of soil nematode life history traits. Soil Biol. Biochem. 177, 108891 https://doi.org/10.1016/j.soilbio.2022.108891.

Yeates, G.W., 1979. Terrestrial nematodes from the Bunger Hills and Gaussberg, Antarctica. N. Z. J. Zool. 6, 641–643. https://doi.org/10.1080/03014223.1979.10428408.

Yeates, G.W., Scott, M.B., Chown, S.L., Sinclair, B.J., 2009. Changes in soil nematode populations indicate an annual life cycle at Cape Hallett, Antarctica. Pedobiologia 52, 375–386. https://doi.org/10.1016/j.pedobi.2009.01.001.

Zhang, Z.Q., 2013. Animal biodiversity: an update of classification and diversity in 2013. Zootaxa 3703, 5–11. https://doi.org/10.11646/zootaxa.3703.1.3.

Zimmermann, J., Obeng, N., Yang, W., Pees, B., Petersen, C., Waschina, S., Kissoyan, K. A., Aidley, J., Hoeppner, M.P., Bunk, B., Spröer, C., Leippe, M., Dierking, K., Kaleta, C., Schulenburg, H., 2020. The functional repertoire contained within the native microbiota of the model nematode *Caenorhabditis elegans*. ISME J. 14, 26–38. https://doi.org/10.1038/s41396-019-0504-y.