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Biological Sciences

Phylogeography of Antarctic soil invertebrate fauna reveals ancient origins, repeated colonization and recent evolution

Giles M. Ross[1,2], Paul D. Rymer[1], James M. Cook[1] and Uffe N. Nielsen[1]

[1]Hawkesbury Institute for the Environment, Western Sydney University, Richmond, NSW, Australia and [2]Department of Terrestrial Ecology, Netherlands Institute of Ecology (NIOO-KNAW), Wageningen, The Netherlands

Abstract

Antarctica is populated by a diverse array of terrestrial fauna that have successfully adapted to its extreme environmental conditions. The origins and diversity of the taxa have been of continuous interest to ecologists since their discovery. Early theory considered contemporary populations as descendants of recent arrivals; however, mounting molecular evidence points to firmly established indigenous taxa far earlier than the Last Glacial Maximum, thus indicating more ancient origins. Here we present insights into Antarctica's terrestrial invertebrates by synthesizing available phylogeographic studies. Molecular dating supports ancient origins for most indigenous taxa, including Acari (up to 100 million years ago; Ma), Collembola (21–11 Ma), Nematoda (~30 Ma), Tardigrada (> 1 Ma) and Chironomidae (> 49 Ma), while Rotifera appear to be more recent colonizers (~130 Ka). Subsequent population bottlenecks and rapid speciation have occurred with limited gene transfer between Continental and Maritime Antarctica, while repeated wind- or water-borne dispersal and colonization of contiguous regions during interglacial periods shaped current distributions. Greater knowledge of Antarctica's fauna will focus conservation efforts to ensure their persistence.

Key words: Biogeography, molecular taxonomy, population genetics, soil biota

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Introduction

Antarctica's terrestrial ecosystems are home to thriving populations of soil invertebrates (Chown & Convey 2016) that inhabit the seasonally snow- and ice-free soils (Chown & Convey 2007). To date, some 550 species of Antarctic invertebrates have been described, with 170 of these being endemic to the region (Adams *et al.* 2014, Velasco-Castrillón *et al.* 2014a). Morphology-based taxonomy has advanced the study of their biodiversity and distribution (Nielsen 2019). However, confirming these patterns for all Antarctic taxa has been constrained by the region's limited accessibility (Convey 2011, Chown *et al.* 2015) and the demanding taxonomic expertise required for microinvertebrate identification. Molecular approaches are now revealing profound insights into the origin, diversity and distribution of terrestrial Antarctic invertebrates, confirming certain aspects, such as climatic bioregions (e.g. Maritime and Continental Antarctica; Pugh & Convey 2008), and a consensus has formed regarding the ancient origins and complex evolutionary history of Antarctica's invertebrate biota (Marshall & Pugh 1996, McInnes & Pugh 1998), despite early speculation of there having been recent colonization (Starý & Block 1998).

Phylogeographic analysis is a powerful tool that can generate and test theories of evolutionary timelines from sequence alignments and provide statistical rigour to the evaluation of events important to species distributions. The combination of sequencing data with biogeographical histories can detail both recent and ancient ancestries. Most phylogeographic studies focus on Northern Hemisphere taxa (Beheregaray 2008), but a growing number of studies have targeted invertebrates from the Antarctic region. Here we review published phylogeographic studies of Antarctic soil fauna within its three constituent regions, each with distinct climatic and geological histories: 1) Continental Antarctica, 2) Maritime Antarctica and 3) the sub-Antarctic islands (Fig. 1). First, we introduce the geological and climatic histories that have shaped both the region and its terrestrial fauna, before providing a brief overview of the main phylogeographic approaches. We then summarize the general patterns found within and among the regions for the dominant invertebrate groups, specifically mites (Acari), springtails (Collembola), nematodes (Nematoda), rotifers (Rotifera), tardigrades (Tardigrada) and the chironomid midges (Chironomidae). Some examples of each group include the oribatid mites *Halozetes belgicae* Michael, 1903 and *Membranoppia loxolineata* Wallwork, 1965, the springtail *Cryptopygus cisantarcticus* Willem, 1901, the nematode *Scottnema lindsayae* Timm, 1971, the rotifer *Macrotrachela jankoi* Iakovenko, 2015 and the tardigrade *Hypsibius exemplaris* Doyère, 1840 (Fig. 2). While the Protozoa are considered to be soil fauna, as a subkingdom of the Protista, they are more commonly associated with marine habitats and there

Corresponding author: Giles Ross; Email: g.ross@nioo.knaw.nl

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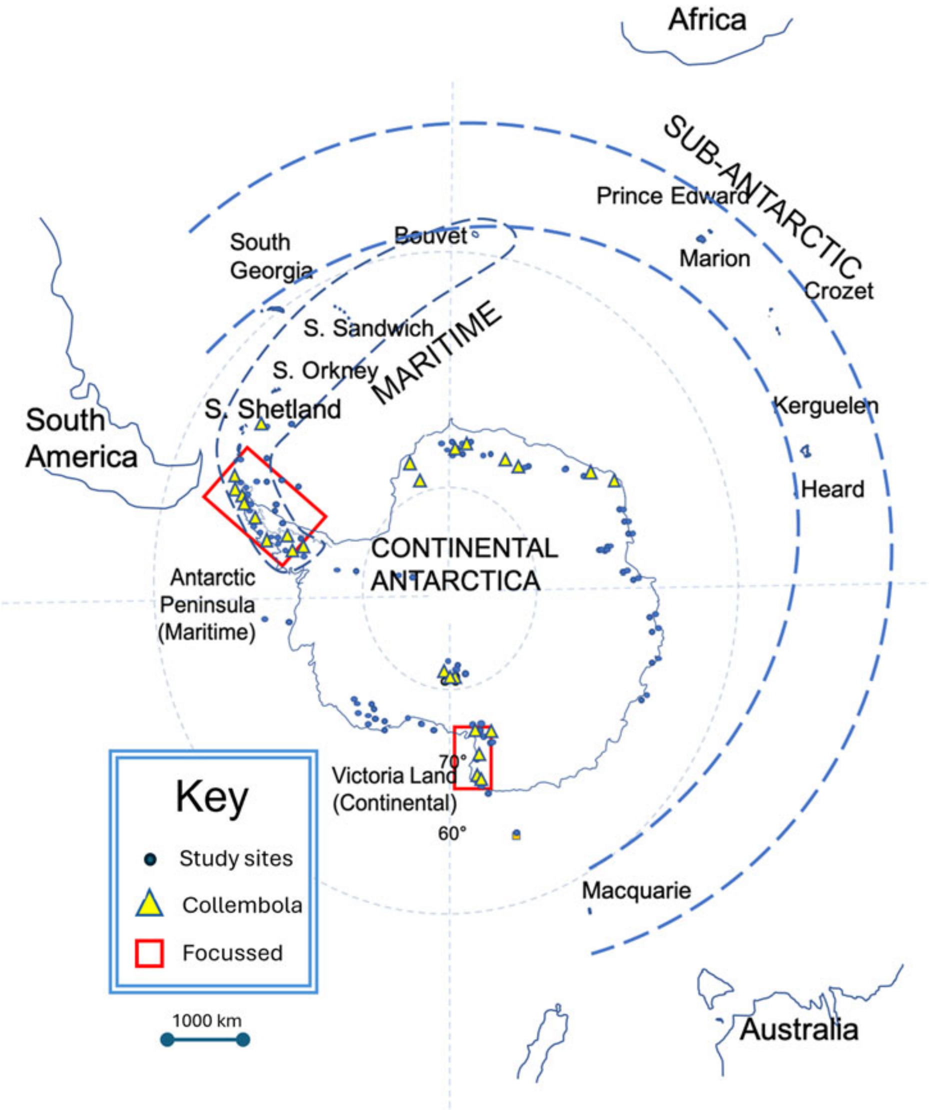

Figure 1. Map of the three Antarctic regions: continental, maritime and sub-Antarctic islands (source: Google Earth image based on Landsat and Copernicus satellite images, Maxar Technologies). Overlay of the circumpolar distributions of sequenced springtail specimens (yellow triangles) and other invertebrates (blue circles; adapted from McGaughran *et al.* 2011). Red boxes outlining Victoria Land and Graham Land are detailed in Fig. 4a,b.

are few morphological and molecular records of these in Antarctic soils (Smith 1996, Lawley *et al.* 2004, Thompson 2021). We therefore focus on other non-microbial taxa that are found predominantly in terrestrial systems. Finally, we focus on the future directions for terrestrial Antarctic invertebrate research and evaluate the capacity to monitor and protect the unique Antarctic ecosystems.

Geological history

Antarctica's current landmass and geological features have been well described (Convey *et al.* 2018), and they were historically part of the early supercontinent Rodinia that existed between 1300 and 700 million years ago (Ma; Fuck *et al.* 2008). This protocontinent underwent separation and reformed as Pangea, which itself began breaking up ~335 Ma. The rifted supercontinent of Laurasia encompassed the North American, European and Asian continents. Meanwhile, the southerly Gondwanan portion contained the Antarctic, South American, African and Australian continents (McMenamin & McMenamin 1990). As Pangea separated, Antarctica was already positioned over the South Pole (Rogers & Santosh 2004), but it then supported lush forests and a thriving dinosaur population (Rozadilla *et al.* 2015). Gondwana began to break up ~175 Ma, with Australia and South America beginning to separate 85–60 Ma, before moving swiftly northwards by 35 Ma. These final movements created the channels on either side of the Antarctic continent (Wei 2004, Hassold *et al.* 2009), allowing the establishment of the Antarctic Circumpolar Current (ACC; Siegert *et al.* 2008). This formed a profound physical barrier and affected the region's climate, limiting biotic crossings and suitable habitat (Pugh & Convey 2008).

Past and current Antarctic climate

Since Antarctica's separation from Gondwanaland, the climate has gradually cooled, until low temperatures precipitated the southern ice cap by 44 Ma (Ehrmann & Mackensen 1992), followed by repeated cycles of glaciation and ablation occurring over the last 2 million years (2 Ma) until the Last Glacial Maximum (LGM; 22–12 thousand years ago (Ka); Davies *et al.* 2012). During this repeated glaciation, ice sheets covered most of Maritime and Continental Antarctica, reaching a depth of 7 km on the continent. This would have led to the local extinction of most of the indigenous floral and faunal species (Pugh &

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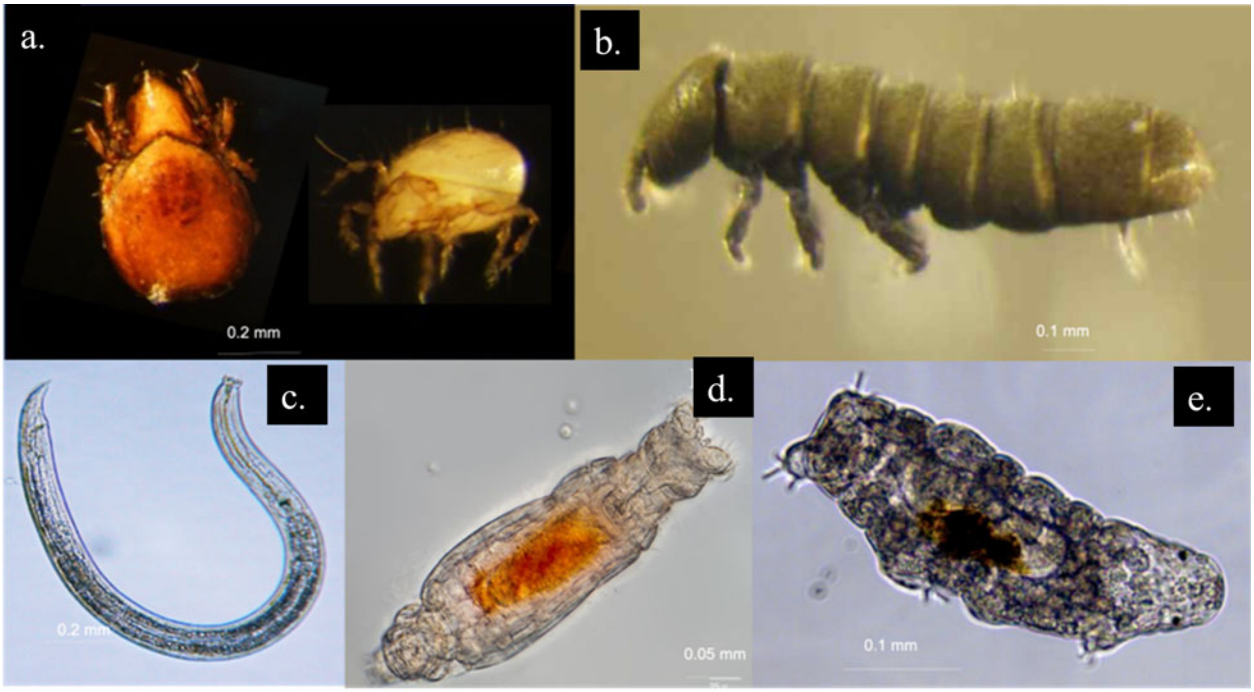

Figure 2. Photographs of the main groups of Antarctic soil fauna: **a.** oribatid mites *Halozetes antarcticus* and *Oppia loxolineata* (source: GMR), **b.** springtail *Cryptopygus cisantarcticus* (source: GMR), **c.** nematode *Scottnema Lindsayae* (source: Barcode of Life Data System (BOLD), uncredited), **d.** rotifer *Macrotrachela jankoi* (source: Iakovenko 2015; NERC Open Access Research Archive (NORA), http://nora.nerc.ac.uk/) and **e.** tardigrade *Hypsibius exemplaris* (source: Jönsson 2019).

Convey 2008). Throughout the Pleistocene (~2.5 Ma–12 Ka), at least eight glacial cycles occurred, with colder temperatures and greater snowfall advancing the ice sheets. The episodic glaciations had a pronounced 100 Ka cycle between the earlier periods (0.74–0.43 Ma; EPICA Community Members 2004), accelerating into a 40 Ka cycle in the last four glaciations starting from 430 Ka (Augustin *et al.* 2004). Interglacial periods had more favourable temperatures and greater water availability, allowing terrestrial ecosystems to thrive.

Continental Antarctic temperatures are cold and dry all year round in the high plateaus (mean annual temperature (MAT): -55°C), with milder conditions in coastal regions (MAT: -10°C; Turner *et al.* 2005, SOE 2011). Yet summer temperatures and increased solar radiation thaw soils in some regions, facilitating biological activity. In maritime areas, summer temperatures can reach 15°C but generally remain below 0°C, while rainfall is more common at lower altitudes along the Antarctic Peninsula. The maritime region is bounded by the extent of the ice shelves off the western side of the peninsula and the islands below the Antarctic Polar Front. Despite the lower latitudes, the South Shetland and Orkney islands are exposed to strong winds that keep MAT to below -4°C. The sub-Antarctic islands lie above the limit of sea ice, with MAT ~2°C and occasional rain during the summer (Turner *et al.* 2005).

Rapid deglaciation in the last century on the peninsula's west coast (Cook *et al.* 2005, 2016, Çiner *et al.* 2019) is undoubtedly linked to contemporary increases in temperatures, estimated at local rates of up to 0.56°C every decade in the latter half of the twentieth century (Turner *et al.* 2005, 2009), with additional pronounced peninsular warming since 2000 (Siegert *et al.* 2019). This has led to accelerated greening of sub-Antarctic islands, with expected increased susceptibility to invasive species (Cannone *et al.* 2022). Further local warming associated with the diminishing Antarctic ozone hole (Solomon *et al.* 2016) has been predicted to enhance glacier melt, with a 25% increase in ice-free land along the eastern Continental Antarctic coastline and peninsula predicted by 2100 (Lee *et al.* 2017). These climate scenarios are expected to expand habitable areas in the maritime and peninsular regions (Turner *et al.* 2009), with larger ranges of continental species (Barrett *et al.* 2006). These changes to vegetation and soil microhabitat may influence the distribution and diversity of native fauna (Wall & Moore 1999) or have to contend with greater colonization rates and competition, reinforcing the need for ecosystem monitoring to inform conservation efforts (Parmesan & Yohe 2003, Nielsen *et al.* 2011b).

The origins and evolution of Antarctic terrestrial fauna

Early theories regarding invertebrate origins proposed that their diversity was a result of rapid evolution following migration from surrounding oceanic islands or continental landmasses after the LGM via wave or wind dispersal (Starý & Block 1998). Pronounced glaciation during the LGM and evidence of accelerated dispersal, colonization and speciation following the LGM supported this theory (Peck *et al.* 2006). Here, the ACC can be seen to precede the majority of species radiation. This may be due to the strong physical barriers caused by the current that have limited colonization events, thereby fostering endemism. It must be noted that while dispersal and vicariance can both occur, and potentially produce similar phylogeographic patterns, detailed analyses of molecular markers are able to define the phylogenetic relatedness between species and determine the most statistically probable history based on calibrated evolutionary models. For example, high divergence among populations of endemic springtail species indicates rapid speciation *in situ* throughout the pre-Pleistocene (> 3 Ma; Knowles 2001), while

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certain indigenous mite taxa show molecular evidence of pre-Gondwanan origins (> 32 Ma; Pugh & Convey 2008). These ancient origins adhere to the idea of Gondwanan vicariance, whereby populations were split apart following the rifting of the supercontinent (Krosch *et al.* 2011). Arguments against the theory of ancient origins point to a lack of strong evidence for refugial locations (Fontaneto *et al.* 2009). However, molecular analyses support the consensus of ancient origins (Pugh & Convey 2008, Warren *et al.* 2014).

Early climate change refugees

The current consensus is that many of Antarctica's indigenous invertebrates survived through periods of glaciation *in situ*, relying on suitable refugia to endure the ice ages (Convey *et al.* 2008, 2020, Hawes 2015, Stevens & Mackintosh 2023). Despite widespread ice-sheet coverage, strong biological and phylogeographical evidence points towards the presence of habitable ice-free areas throughout the past 5 Ma (Prentice *et al.* 1993, Pugh & Convey 2008). Such refugia are thought to be associated with geothermal activity, coastal areas, the continental McMurdo Dry Valleys and high-altitude ridges, horns and arêtes, collectively named 'nunataks', that lie above the maximum glacial height (Pugh & Convey 2008, Fraser *et al.* 2014, 2018). Freshwater lakes and ponds have also been proposed as key invertebrate refugia (Wagner *et al.* 2006) before sea-level rises associated with the LGM inundated these sites with seawater (Squier *et al.* 2002, Cromer *et al.* 2006). However, not all proposed refugial sites may be habitable or ice-free given the discovery of barren, high-elevation, hypersaline sites near the continental Beardmore Glacier (Lyons *et al.* 2016) and the evidence of glaciation at potential refugial sites along the peninsula (Lau *et al.* 2020).

Antarctic invertebrates have adapted to local conditions, allowing them to undergo desiccation (anhydrobiosis) or to enter a state of dormancy to withstand freezing (cryptobiosis). Anhydrobiosis is particularly useful for longer-term survival and is common to Antarctic springtails (Holmstrup 2018), tardigrades (Somme 1996), nematodes (Wharton & Ferns 1995, McGill *et al.* 2015), rotifers (Rebecchi *et al.* 2020) and the sub-Antarctic midge *Belgica antarctica* (Benoit *et al.* 2009). Certain groups can reduce their metabolism to almost zero, including tardigrades (Altiero *et al.* 2015), and some species of nematodes secrete anti-freezing proteins (Adhikari *et al.* 2009). Such adaptations are thought to have aided their persistence in refugia during glacial maxima.

Phylogeographic analyses

Phylogeography combines biogeographical information with phylogenetic analyses to assess patterns of speciation and colonization (Avise 2000). The approach has shown how biotic responses to climatic and ecological conditions are constrained by geological context (Graham & Fine 2008, Smith *et al.* 2014), such as the strong relationship between refugia and diversity. High-resolution distributional data for soil invertebrates supported the demarcations of Antarctic bioregions (Terauds *et al.* 2012). These partitions were informed by detailed biogeographical studies based on the morphological traits of soil invertebrates (Gressitt 1965, Wallwork 1973, Adams *et al.* 2014) and comprehensive floral records (Peat *et al.* 2007). Among the key divisions is the 'Gressitt Line', a confirmed biotic frontier separating the Antarctic Peninsula (also known as Graham Land) and Continental Antarctica (Fig. 1; Pugh & Convey 2008). This division is accompanied by substantial genetic divergence and limited overlap in species, suggesting the presence of multiple refugia on either side of the division (Chown & Convey 2007). Rigorous statistical pipelines using intra- and inter-specific differences can help us to assess theories of persistence, divergence and migration (Arbogast & Kenagy 2001). With genealogies subject to repeated colonization events at the local scale (< 1 Ma), molecular phylogenetic assessment is the best approach to resolve evolutionary histories.

Molecular taxonomy

DNA sequencing allows the measurement of genetic divergence within and among species, thereby improving phylogenetic reconstructions (Thomson *et al.* 2018). DNA barcoding is now commonly applied to identify putative species of soil fauna (Hebert *et al.* 2003). Routinely used markers are based on mitochondrial DNA (mtDNA) and nuclear DNA. Slower-evolving nuclear markers can show ancient lineages, although lower taxonomic orders may be less well resolved. However, the ability to resolve lineages is dependent upon the study taxa and genetic markers. The mtDNA cytochrome oxidase subunit I (*COI*) gene is a reliable identifier due to universal amplification and sufficient genetic variation between species but limited within-species differences (Hebert *et al.* 2003). Haplotype networks of *COI* have been used to resolve lineages of ancient populations of Collembola (Greenslade *et al.* 2011) and Lepidoptera (Hebert *et al.* 2003).

Delineation of operational taxonomic units (OTUs) is based on differences in *COI* nucleotide sequence, with values < 1% generally considered to be indicative of the same species (Hebert *et al.* 2003, Lim *et al.* 2012). An interchangeable term is the haplotype, originally used to define lineages, whereby 2–3% is the minimum difference defining a distinct species, distances > 5% indicate divergent species/genera and those > 10% indicate highly divergent lineages (Stevens *et al.* 2007, Collins *et al.* 2019). Most studies use 3% as a threshold to define invertebrate species, as has been used in rotifers (Fontaneto *et al.* 2009) and nematodes (Kumari *et al.* 2010). Comparing results across taxa with broad ranges (e.g. the springtail *Cryptopygus antarcticus*) can further test the applicability of 'rule-of-thumb' thresholds across regions. Potential effects of selecting alternative thresholds for species delineation would be shifted diversity metrics or dating of species histories or dispersal events, but doing so will have minimal influence on the interpretation of phylogeographic analyses. Similarly, cytochrome oxidase-subunit II (*COII*) is an alternative in species where *COI* is less informative (e.g. cnidarians) due to minimal genetic variation in the marker, and it has been sequenced in Antarctic springtails (Stevens *et al.* 2007, McGaughran *et al.* 2011).

An increasing number of studies use nuclear markers to support species classification, identification of ancient speciation events (Reitzel *et al.* 2013) and isolation by distance across the landscape (Teske *et al.* 2018). Such studies commonly target ribosomal DNA (rDNA) genes that encode the small 40S ribosomal subunit including *ETS*, *18S*, *ITS1*, *5.8S*, *ITS2* and *28S* tandem repeat marker genes (Hwang & Kim 1999, Adams *et al.* 2007, Evans & Paulay 2012). The thresholds for species delineation using nuclear *28S* markers histone-3 (*H3*) and *D2-D3* extension sequences have been shown to be as low as 0.1–0.5% in comparative studies (Klimov *et al.* 2019). The *18S* rRNA genes have high levels of genetic drift and are frequently used to resolve taxonomic uncertainties at the species and genus level (Guidetti *et al.* 2014), as demonstrated in nematodes (Boström *et al.* 2011), tardigrades

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(Guil *et al.* 2019) and springtails (Zhang *et al.* 2019). The *28S* rRNA markers have also yielded insights into the phylogenies of the marine Styraconyxidae tardigrades using a combination of *28S* rRNA and *COI* markers (Fujimoto *et al.* 2020), while *COI* and internal transcribed spacer 1 (*ITS1*) were sequenced to determine genetic diversity and to test theories of dispersal between Victoria Land (VL) and other Antarctic regions of *Acutuncus antarcticus* (Cesari *et al.* 2016). Additionally, *18S* rRNA and *ITS1-2* markers have revealed deep lineages in *Scottnema lindsayae* nematode populations across defined geographical areas (Adams *et al.* 2007). Other single-copy nuclear genes, such as the *H3* gene that structures the nucleosome, and commonly associated with epigenetics, have been used to assess levels of shared ancestry and phylogeographic dispersal among Antarctic mites (Mortimer *et al.* 2011), while the well-conserved Wnt signalling pathway genes have been targeted in tardigrades (Hodgson *et al.* 2010), and the wingless gene (*Wg*) has been used to identify intergeneric and interspecific mite taxonomies (Czechowski *et al.* 2012).

Molecular clocks

Molecular clocks are an essential part of estimating when divergence events occurred. The homogeneous substitution rate across the mitochondrial genome (mitogenome) simplifies their use in dating (Czechowski *et al.* 2017a,b). Secondary calibration that accounts for the uncertainty of phylogenetic-based calibration applies corrections to earlier calibrations (Kodandaramaiah 2011, Schenk 2016). This has been shown to improve the accuracy of molecular clocks (Hipsley & Müller 2014), such as that used in dating marine invertebrates (Loeza-Quintana *et al.* 2019). In the absence of verified ages for indigenous Antarctic taxa, studies commonly use molecular substitution rates derived from non-Antarctic insect phylogenies, with a consensus formed for an evolutionary rate (R) for arthropods of $R = 1.5–2.3\%\ \mathrm{Ma}^{-1}$ (Stevens & Hogg 2006, Brewer *et al.* 2012, Beet *et al.* 2016). Basing arthropod evolution on insect-based calibrations causes overestimation of dating due to the potentially faster generation times of insects (Collins *et al.* 2019).

More recently, geological events have been used to calibrate molecular clocks. These calibrations have benefitted from computational models being used to date warmer periods and ice-sheet collapses for invertebrate analyses (Strugnell *et al.* 2018, Collins *et al.* 2020). This has led to a revised rate of $R = 3.54\%\ \mathrm{Ma}^{-1}$ being used for Antarctic springtails (Papadopoulou *et al.* 2010). The differences in R between non-Antarctic and Antarctic arthropods are considered to be a result of variation in coalescence times and post-separation gene flow (Collins *et al.* 2020). Additional factors that can improve estimations of divergence times include knowledge of generation time, metabolism and mutation rates and population size. The parthenogenetic, or asexual, nature of many oribatid mites also allows molecular clocks to be used without the complication of sexual recombination (Maraun *et al.* 2003). Yet these can yield misleading ages if rates are compared with sexually reproducing taxa. Bayesian relaxed clocks can incorporate variable estimates when setting priors, yet selection bias between competing models and variable mutation rates and generation times in natural systems mean dates are still only best estimates and can only be used as guides for relative divergence times (Guidetti *et al.* 2017). Additionally, secondary calibrations of studies relying on single calibration points might compound the unreliability of using geological events in the absence of fossils (Forest 2009).

Phylogeographic studies of Antarctic soil fauna

Antarctica is an ideal location to study the biogeographical history of soil fauna due to the high proportion of endemic species and relatively limited dispersal, both within regions and from further afield. Here, a synthesis of the evidence across all phylogeographical studies is presented to form a clearer picture of general patterns of Antarctic soil faunal distribution and evolutionary patterns based on the current literature. Most studies focus on individual taxa and regions, but comparative studies that combine analyses of taxa and/or regions can more rigorously test alternative hypothesis while providing greater explanatory power. Unless specifically stated when referring to studies, all records refer to the alpha-taxonomic nomenclature as named in the cited works.

Collembola

Springtails, of the arthropod subclass Collembola, were the first Antarctic invertebrates to be described (Carpenter 1902). Since their discovery, 17 continental and 25 maritime species representing 4 families having been recorded (McGaughran *et al.* 2011), with almost two-thirds of all genera being endemic (Stevens & Hogg 2003, 2006, Pugh & Convey 2008, Torricelli *et al.* 2010b). Phylogeographical work has mostly focused on springtails of continental VL (71.0–78.5°S) in eastern Antarctica and on the peninsula. Three species are present in both continental and maritime regions: *Cryptopygus antarcticus*, *Cryptopygus terranovus* Wise, 1967, and *Kaylathalia klovstadi* Carpenter, 1902. What was once considered the sole circumpolar species, *Friesea grisea* Schaffer, 1891 (initially named *Friesea antarctica* Willem, 1901), has been taxonomically reassessed, resulting in the recognition of multiple species with smaller ranges, including *Friesea propria* Greenslade and Fanciulli, 2020 and *Friesea gretae* Greenslade and Fanciulli, 2020 (Carapelli *et al.* 2020b, Stevens *et al.* 2021). *F. grisea* is now considered to be restricted to sub-Antarctic South Georgia alongside *Friesea fantaba* Greenslade, 2018. An additional three species are found in continental southern VL (sVL): *Antarcticinella monoculata* Salmon, 1965, *Cryptopygus nivicolus* Salmon, 1965, and *Gomphiocephalus hodgsoni* Carpenter, 1908 (Greenslade 2018, Collins *et al.* 2019). Taxonomic and phylogeographical studies have described local distributions and provided some insights into the ancient origins and restricted gene flow between populations arising from refugial survivors on the continent and other Antarctic regions.

Origins and refugia

Phylogeographical studies have improved theories of springtail origins, with a consensus being established of most taxa evolving from ancestors arriving on the continent ~20 Ma, prior to the formation of the ACC (Fig. 3; Stevens *et al.* 2006a, Stevens & D'Haese 2014). Several factors have promoted speciation, with several endemic species identified using molecular data, indicating more recent evolution (Table I). Intermittent dispersal events from surrounding sub-Antarctic landmasses and inland refugia may have contributed to the allopatric speciation of populations separated by glaciers and other dispersal barriers (Convey & Stevens 2007, McGaughran *et al.* 2011). Springtails show evidence of complex evolutionary histories, with certain species linked to ancient arrivals and others to more recent colonization events (Table II). The latter point to a series of post-glacial recolonization events followed by vicariant speciation. Significant divergence and a lack of shared haplotypes between continental and

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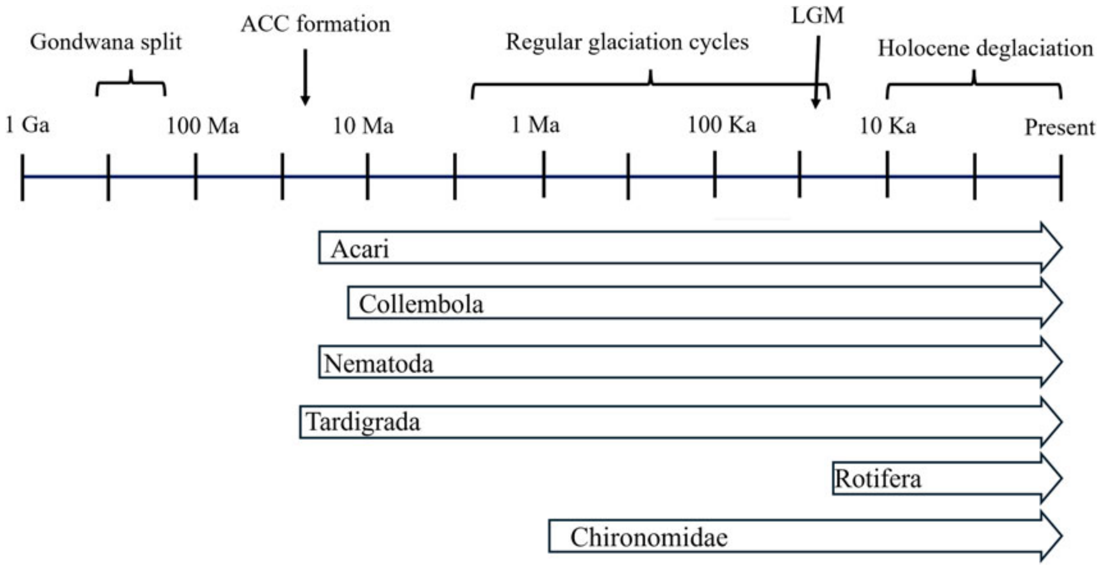

Figure 3. Graphical timeline of invertebrate groups and earliest indications of endemic Antarctic lineage. Ages are based on mean estimated origins from molecular dating studies in Continental Antarctica alongside main regional geological events over a logarithmic timeline; 1 Ga = 1000 Ma (adapted from Convey 2010). ACC = Antarctic Circumpolar Current; Ka = thousand years ago; LGM = Last Glacial Maximum; Ma = million years ago.

maritime springtail species suggest substantial dispersal barriers and long-term persistence in distinct refugia from which source populations remained separated following dispersal events (Collins *et al.* 2019, 2020). Most studies found glaciers to be major dispersal barriers, restricting gene flow (Stevens *et al.* 2006a, Bennett *et al.* 2016, Collins *et al.* 2019). This has led to the assumption of there being multiple refugia in glacial valleys throughout continental VL as the source for distinct haplotypes of *C. terranovus* (Carapelli *et al.* 2017a) and *K. klovstadi* populations (Fig. 4a; Frati *et al.* 2001).

Table I. Currently known species richness of the main invertebrate groups in continental (C), maritime (M) and sub-Antarctic (S) regions, alongside the sequenced genes for all species found within each region and estimated date of origin from cited references.

	Known species (*n*)					Estimated Antarctic arrival		
Invertebrate group	C	M	S	Total	Target genes	Ancient arrival (> 10 Ma)	Pre-LGM	Phylogeographical studies
Collembola	6	25	55	86	*COI* *COII* *18S* *28S* *16S* *ITS*	~11–21 Ma C, M	-	Beet *et al.* 2016, Bennett *et al.* 2016, Carapelli *et al.* 2017a, Collins & Hogg 2015, Collins *et al.* 2019, Fanciulli *et al.* 2001, Frati *et al.* 2001, Greenslade *et al.* 2011, Hawes *et al.* 2010, McGaughran *et al.* 2008, 2010a,c, 2011, 2019, Myburgh *et al.* 2007, Nolan *et al.* 2006, Stevens & Hogg 2003, 2006, Stevens *et al.* 2006b, 2007, Torricelli *et al.* 2010a,b
Acari	5	22	78	106	*COI* *18S* *H3*	>34 Ma C, M	-	McGaughran *et al.* 2008, Mortimer *et al.* 2011, Van Vuuren *et al.* 2018
Nematoda	33	42	12	86	*COI* *18S* *28S* *ITS*	~30 Ma C, M	-	Adams *et al.* 2014, Kagoshima *et al.* 2019, Lewis *et al.* 2009, Maslen & Convey 2006, Nkem *et al.* 2006, Velasco-Castrillón & Stevens 2014
Tardigrada	15	64	22	90	*COI* *18S* *28S* *Wg*	~40 Ma C	>1 Ma M, S	Cesari *et al.* 2016, Convey & McInnes 2005, Czechowski *et al.* 2012, Guidetti *et al.* 2014, McInnes 2010
Rotifera	20	94	81	176	*COI*	-	~130 Ka C, S	Cromer *et al.* 2006, Fontaneto *et al.* 2011, Iakovenko *et al.* 2015, Velasco-Castrillón *et al.* 2014b
Chironomidae	0	3	4	7	*COI* *28S*	-	>1 Ma S	Allegrucci *et al.* 2006, 2012

Ka = thousand years ago; LGM = Last Glacial Maximum; Ma = million years ago.

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Table II. Examples of the main Antarctic faunal types and species that have phylogenetic evidence supporting either their ancient origins or more recent dispersal in continental and maritime regions.

Invertebrate Group	Continental		Maritime	
	Ancient species (pre-LGM)	Recent dispersers (post-LGM)	Ancient species (pre-LGM)	Recent dispersers (post-LGM)
Collembola	*Friesea* spp. *Kaylathalia klovstadi* *Cryptopygus terranovus*	*Cryptopygus cisantarcticus*	*Friesea antarctica*	*Friesea grisea* *Gomphiocephalus hodgsoni*
Acari	*Maudheimia* sp. *Stereotydeus mollis*	*Halozetes fulvus* *Stereotydeus nunatakis*	*Halozetes belgicae* *Alaskozetesantarcticus*	*Halozetes. marinus* *Halozetes necrophagus*
Nematoda	*Scottnema lindsayae* *Panagrolaimus davidi* *Plectus murrayi*	*Plectus rigophilus*	*Plectus murrayi* *Plectus antarcticus*	*Eudorylaimus coniceps* *Plectus meridianus*
Rotifera	*Adineta grandis* *Philodina gregaria* *Encentrum permolle gigantheum*	*Notholca* sp. *Adineta gracilis*	*Philodena antarctica* *Brachionus bidentatus*	*Linda torulosa* *Colurella colurus*
Tardigrada	*Hypsibius antarcticus* *Milnesium tardigradum*	*Milnesium antarcticum* *Minibiotusvinciguerrae*	*Testechiniscusmeridionalis* *Adropion greveni*	*Mesobiotus aradasi* *Diphascon langhovdense*

LGM = Last Glacial Maximum.

Several studies support the refugial theory and the potential for multiple source populations (Marshall & Coetzee 2000, Fanciulli *et al.* 2001, Frati *et al.* 2001, Stevens & Hogg 2006, McGaughran *et al.* 2008). Evidence from the *Friesea* genus shows potential colonization by a common ancestor > 20 Ma (Miocene/Oligocene), with subsequent local speciation occurring and no haplotype sharing between the Antarctic Peninsula and VL regions (Torricelli *et al.* 2010b, Collins *et al.* 2019), nor between the Antarctic Peninsula and South Shetland Islands (Torricelli *et al.* 2010a).

The northern VL (nVL) species *K. klovstadi* (formerly *Isotoma klovstadi* and of the *Desoria* genus) show divergences between subspecies that are geographically close to each other, further supporting multi-refugial sources (Stevens *et al.* 2006b, 2007, Stevens & D'Haese 2016). The identification of different dominant haplotypes of *K. klovstadi* between the peninsular Adelaide, Lagoon and Killingbeck islands led to theories of separate lineages, with multiple refugial populations undergoing rapid evolution throughout the Pleistocene (Fig. 4b; Hawes *et al.* 2008). These patterns of distribution following refugial dispersal have also been observed on the Antarctic continent (Carapelli *et al.* 2020a). Another study that supports the idea of multiple refugia maintaining isolated populations found lower-than-expected genetic distances between *G. hodgsoni* populations on the peninsula, indicating a scenario whereby dispersal from a singular refugial source was followed by minimal genetic admixing (McGaughran *et al.* 2010c).

Dispersal effects on broad-scale and regional distribution

Springtails are highly motile at short ranges and more infrequently disperse longer distances via wind or water-borne flotation (Hawes *et al.* 2008, McGaughran *et al.* 2010a). There is evidence of high rates of divergence among haplotypes and patchy distributions of *Friesea* spp., *C. antarcticus* subspecies and *C. cisantarcticus* populations in maritime regions and continental VL (Table III; McGaughran *et al.* 2011).

The nVL *C. cisantarcticus* was studied alongside the sVL springtail *G. hodgsoni*, with lower genetic diversity between *C. cisantarcticus* haplotypes signalling multiple dispersals from elsewhere in the continent during the Pleistocene (McGaughran *et al.* 2008). These data support an earlier study that also found minimal divergence within *C. cisantarcticus* populations (Hawes *et al.* 2010), suggesting a Pliocene divergence event ~5 Ma, with distributional patterns indicative of recent gene flow from local refugia to the continental foothills.

Evidence of refugia as sources of ancient dispersal and broad-scale distribution has also been found regarding more recent dispersal events that have contributed to complex regional distribution patterns. Accordingly, *Friesea* spp. populations were suspected of more recent dispersal than *C. terranovus* or *G. hodgsoni* populations from unidentified regional refugia. These aligned with the shorter intervals between glacial cycles and barriers to dispersal preceding the LGM (Table III; Warren *et al.* 2014, Collins *et al.* 2019). Furthermore, Collins *et al.* (2019) found much higher divergences between *C. cisantarcticus* populations than between *K. klovstadi* populations across a similar geographical range: that of an individual glacier. Yet, lower divergences between populations in an adjacent glacier were the result of greater dispersal abilities of *C. cisantarcticus* influencing distribution patterns (Stevens *et al.* 2006b, McGaughran *et al.* 2010a; Carapelli *et al.* 2017a).

A study that combined *G. hodgsoni* with two species from sVL (*C. nivicolus* and *A. monoculata*) estimated a speciation event ~4 Ma, followed by glacial isolation that promoted speciation in *G. hodgsoni* and *C. nivicolus* over *A. monoculata* populations. A period of isolation between 3 and 4 Ma matched the collapse and reformation of the West Antarctic Ice Sheet (Beet *et al.* 2016). The link between populations and access to liquid water was given as a cause for highly divergent *G. hodgsoni* populations (Collins *et al.* 2019).

Evidence from phylogeographical studies of Antarctic springtails reveals that at the broad scale interactions with climate and

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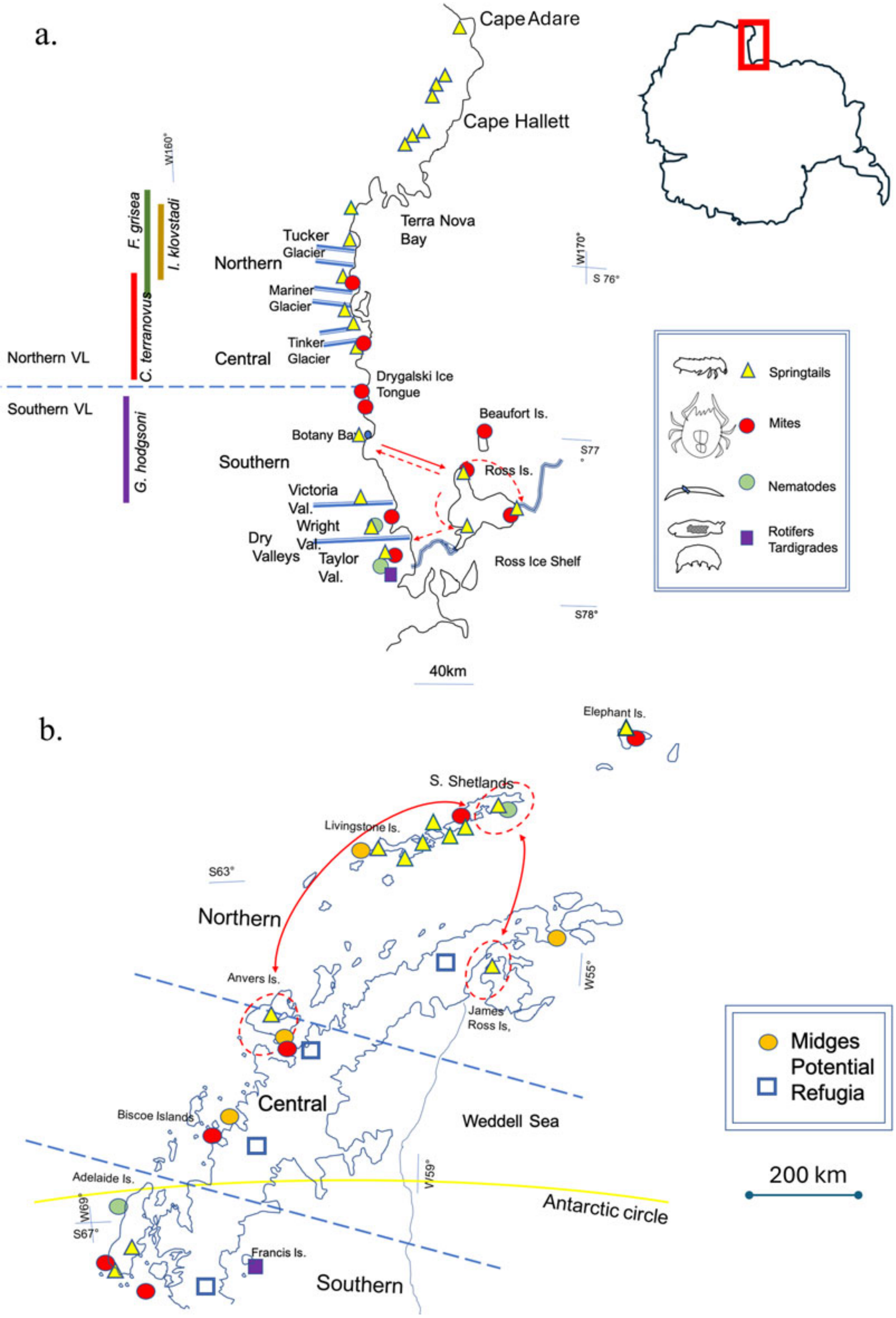

Figure 4. a. Map of Victoria Land (VL) with major glacial features and compiled results from phylogeographical studies. Springtail geographical ranges are indicated by coloured lines on the left panel from McGaughran *et al.* (2008), with theorized dispersal routes to Ross Island from Stevens & Hogg (2003) and Collins *et al.* (2019, 2020). Dashed lines demarcate biotic boundaries used to define population groups, with symbols representing genetically distinct populations of springtails (yellow triangles), mites (red circles), nematodes (green circles) and rotifers and tardigrades (purple squares; sources: Barrett *et al.* 2006, Torricelli *et al.* 2010a, McGaughran *et al.* 2011, Convey *et al.* 2014, Brunetti *et al.* 2021b). **b.** Map of the Antarctic Peninsula (Graham Land), with theorized dispersal routes between springtail populations indicated by red arrows from McGaughran *et al.* (2010a). Symbols represent genetically distinct populations of midges (orange circles) and potential refugial locations (empty squares; sources: Torricelli *et al.* 2010a, Allegrucci *et al.* 2012, Convey *et al.* 2014, Velasco-Castrillón *et al.* 2014b, Carapelli *et al.* 2017b).

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Table III. Summary of mean levels of *COI* and *COII* sequence divergence and number of haplotypes in springtail species and regions as reported in cited references.

Springtail species	Region	Mean *COI* inter-regional divergence (%)	Mean *COII* inter-population divergence (%)	Haplotypes (*n*)	Phylogeographical studies
Cryptopygus cisantarcticus	N	8.7 (4.3–13)	-	45	Collins *et al.* 2019
Cryptopygus terranovus	N	10.5 (6.8–14.7)	-	62	Collins *et al.* 2019, Hawes *et al.* 2010
Friesea grisea	N	6 (4.5–10.9)	-	55	Collins *et al.* 2019, Torricelli *et al.* 2010a
Kaylathalia klovstadi	N	8 (0.7–7 5)	2.25 (0.1–3.8)	69	Collins *et al.* 2019, Frati *et al.* 2001, Stevens *et al.* 2006b, 2007
Antarcticinella monoculata	S	10.7 (1.25–98.7)	-	66	Beet *et al.* 2016, Collins *et al.* 2019
Cryptopygus nivicolus	S	4.5 (1.6–5.0)	1.6 (0–1.6)	16	Beet *et al.* 2016, Collins *et al.* 2019, Stevens *et al.* 2006a
Gomphiocephalus hodgsoni	S	3.63 (1.5–7.3)	-	289	Beet *et al.* 2016, Collins *et al.* 2019, McGaughran *et al.* 2008, 2010c
Cryptopygus cisantarcticus	AP	-	4.6 (0–9.2)	19	McGaughran *et al.* 2010c
Friesea grisea	AP	-	2.7–17.2	80	Torricelli *et al.* 2010a

Note: The taxonomy of *F. grisea* has since been revised, and it is now known to represent four unique species, namely *F. grisea*, *F. antarctica*, *F. gretae* and *F. propria*.
AP = Antarctic Peninsula; N = northern; S = southern.

geography have created multilayered patterns of distribution following waves of speciation and extinction during the Pleistocene (~2.58 Ma–12 Ka), with some events separated by 100 Ka (Huybers 2006). These findings show that springtails have ancient lineages and underwent recent inter-regional dispersal (Table II), with glaciers restricting gene flow between populations and communities. It is speculated that more widespread sampling will show pockets of unaccounted speciation, confirming refugial locations in the peninsula and identifying further pan-Antarctic species.

Acari

The Acari, or mites, are the most diverse faunal group in terrestrial Antarctica (Pugh 1993). Current tallies number 105 species consisting of 5 continental, 22 maritime and 78 sub-Antarctic species, of which ~70 are endemic (Convey 2011, McGaughran *et al.* 2011). The biogeography of several mite species has been surveyed on the sub-Antarctic islands (Mortimer *et al.* 2011) and Maritime Antarctica, with limited evidence of biogeographical patterns on the continent; despite evidence of structured distributions in VL (Collins *et al.* 2023), most distributions remain unverified using molecular approaches.

Origins and refugia

First described from the *Belgica* expedition of 1897–1899 (de Man 1904), continental mites have some of the earliest links to a pre-Gondwanan lineage (Fig. 3). Several species appear to have ancient origins, including members of the oribatid mite genus *Maudheimia* Dalenius and Wilson, 1958 (> 100 Ma; Marshall & Coetzee 2000) and the prostigmatid mite genus *Stereotydeus* Berlese, 1901 mites (> 10 Ma; Stevens & Hogg 2006). While some mites have an ancient origin, it is difficult to ascribe all Antarctic taxa as having ancient lineages (Table II). Molecular analyses have shown that vicariant speciation was prevalent during interglacial periods in mites (Stevens & Hogg 2006), similar to observed patterns in springtails (McGaughran *et al.* 2008). There is evidence of local refugia with oribatid and prostigmatid mites persisting during glacial maxima, and most Antarctic mites appear to have dispersed from glacial refugia and coastal habitats (Marshall & Coetzee 2000).

Dispersal effects on broad-scale and regional distribution

Despite their ability for long-distance dispersal, the little overlap between continental and maritime populations demonstrates strong geographical barriers limiting dispersal among geographical regions (Convey *et al.* 2014). However, there is evidence of some dispersal within regions. For example, a study of eight members of the genus *Halozetes* Berlese, 1916 in Maritime Antarctica and the sub-Antarctica islands found frequent dispersal events between the sub-Antarctic islands among *H. belgicae* and populations of the mite genus *Alaskozetes* Hammer, 1955 between 6 and 10 Ma, as well as a rare case of wind- or water-borne dispersal from northern peninsular refugia to surrounding islands (Table I; Mortimer *et al.* 2011).

Restrictions to dispersal and mixing of populations, evident from a lack of shared haplotypes and gene flow, may also indicate recent colonization of the sub-Antarctic islands and continent (Mortimer *et al.* 2011, Convey *et al.* 2014). Limited ranges and high endemism have been shown in peninsular populations of *H. belgicae* and *Alaskozetes antarcticus* Michael, 1903, with further evidence of multiple refugial sources (Table II; Van Vuuren *et al.* 2018). Additionally, contemporary distribution patterns conform with the limited short-range dispersal ability of mites, linked to their low desiccation tolerance (McGaughran *et al.* 2010a). Beyond this, molecular studies on the short-range dispersal of mites are limited.

Despite thorough biogeographical investigation (Block & Starý 1996, Marshall & Coetzee 2000, Collins *et al.* 2023), knowledge on the phylogeography of Antarctic mites is limited. However,

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studies have revealed restricted distributions of several mite species (Van Vuuren *et al.* 2018), with diverse prostigmatid communities in inland oases (Lawley *et al.* 2004, Brunetti *et al.* 2021b). Phylogenetic support for their ancient lineages, combined with evidence of recent evolution linked to refugial dispersal, can be clarified through targeted sampling. This would overcome the data deficiency for these important decomposers and support arguments for their use of refugia and long-range dispersal as explanations of their diverse contemporary distribution.

Nematoda

The first terrestrial nematode to be described from Antarctica was *Plectus antarcticus* (de Man 1904), and there are now 68 recognized species, including 23 continental and 33 maritime species, with most genera endemic to Antarctica and some shared species across regions (Maslen & Convey 2006, Nielsen *et al.* 2011a, Kagoshima *et al.* 2019). However, the recorded diversity of nematodes is considered a gross underestimate (Nielsen *et al.* 2011b, Velasco-Castrillón *et al.* 2014a, Nielsen & King 2015).

Origins and refugia

Nematodes were well established throughout the Gondwanan continent, and molecular data confirm the ancient origins (> 32 Ma) of most, if not all, indigenous Antarctic taxa (Fig. 3; Maslen & Convey 2006, Adams *et al.* 2007). High levels of cryptic speciation and low levels of divergence between most nematode genera (< 5%) indicate recent speciation (Adams *et al.* 2014). This is evidenced by a combination of ancient species, such as *Scottnema lindsayae* (Maslen & Convey 2006), and those with more recent divergence, including *Panagrolaimus davidi* Timm, 1971 (Table II; Lewis *et al.* 2009). Antarctica's cyclical glaciation split some nematode species across maritime and continental regions, suggesting separate refugial origins (Andrássy 1998). Additionally, high nematode endemism on Alexander Island (> 40%) and other sites along the peninsula indicate probable long-term refugial isolation and survival in these areas (Maslen & Convey 2006).

Dispersal effects on broad-scale and regional distribution

The phylogeographical patterns of nematodes indicate their ancient origins, refugial survival and widespread contemporary distribution. Molecular studies of nematodes indicate evolutionary histories as ancient as those of the arthropods, showing them to be equally dependent on refugia for their survival. High levels of cryptic speciation within endemic taxa warrant further investigation to determine their *in situ* diversity, speciation and evolutionary processes such as convergence or stasis (Struck *et al.* 2018).

General patterns of nematode distribution are influenced at multiple scales. Minimal genetic variation in southern maritime island *S. lindsayae* populations, despite large distances between populations, could indicate a population bottleneck or gene flow with limited genetic drift of these highly adapted ancient taxa following isolation (Maslen & Convey 2006). Concerted evolution of *ITS* genes may remove intraspecific variation (Álvarez & Wendel 2003), unlike mtDNA markers (e.g. *COI*); however, the variation among species is also dependent upon the age of the lineages and differs between taxa (Evans & Paulay 2012).

Nematode *COI* sequences from the Larsemann and Vestfold hills in continental eastern Antarctica showed limited divergence among populations of *Plectus murrayi* Yeates, 1970 (< 0.5%), suggesting a high degree of connectivity. In contrast, the higher divergence rates among *Plectus frigophilus* Kiryanova, 1958 populations (8.4%) suggest cryptic speciation and taxonomic division. The contrast between *P. murrayi* and *P. frigophilus* indicates restricted gene flow in the latter species, probably because it requires more persistent bodies of water for dispersal success (Table I; Velasco-Castrillón *et al.* 2014b,c).

A more detailed understanding of these distributional ranges would improve our dating of nematode phylogenies. Constraints to robust phylogeographical modelling may be due to suspected differences in substitution rates from differences in reproductive mode and other biotic factors between species. Further investigation may reveal more widespread continental nematode species and help explain the high levels of endemism despite their ability for long-range dispersal.

Rotifera

Antarctic rotifers were among the earliest reports of terrestrial fauna from Scott's 1901–1904 *Discovery* expedition, for which an ancient origin was initially hypothesized (Murray 1910). Rotifers are semi-aquatic and generally parthenogenetic organisms capable of wind- and water-borne dispersal and anhydrobiosis. There are presently 94 recorded rotifer species, of which 66 are continental, with the remainder distributed throughout the maritime and sub-Antarctic islands (Velasco-Castrillón & Stevens 2014); however, rotifer richness and therefore endemicity are probably underestimated. Most rotifers have links to corresponding species from other Southern Hemisphere continents, while only five species are endemic to the continent (Velasco-Castrillón *et al.* 2014b), and one is shared across Maritime and Continental Antarctica (Table I; Segers 2008, Iakovenko *et al.* 2015).

Origins and refugia

The relatively limited genetic variation between Antarctic and non-Antarctic species points to a far more recent arrival of rotifers than other taxa (Fig. 3; Iakovenko *et al.* 2015, Cakil *et al.* 2021). A plausible scenario for this is that arrivals commenced ~130 Ka based on sedimentary evidence of *Notholca* Gosse, 1886 from the Larsemann Hills of East Antarctica (Cromer *et al.* 2006). This could be a result of their inability to survive previous ice ages due to limited cold-tolerant traits, alongside their ability for long-distance wind dispersal and the presence of multiple refugial lakes (Shain *et al.* 2016). The continental ranges of some *Adineta* Hudson and Gosse, 1886 bdelloid species extend up to 2000 km (Velasco-Castrillón *et al.* 2014c) and remain to be assessed using phylogenetic records. Antarctic bdelloid rotifers show strong patterns of increased genetic divergence with greater isolation than other non-Antarctic specimens, indicating greater periods of isolation and separation beyond what can be concluded from the molecular evidence alone (Cakil *et al.* 2021).

Dispersal effects on broad-scale and regional distribution

A thorough study of *COI* sequences from 514 rotifer specimens collected across all Antarctic regions revealed a total of 92 species, with 63 found throughout continental and maritime regions (Velasco-Castrillón *et al.* 2014a), while 7 continental species were distributed across 13 lakes (Velasco-Castrillón *et al.* 2014c). The presence of three pan-Antarctic rotifer species indicates prolonged isolation (*Adineta grandis* Murray, 1910, *Philodina antarctica* Murray, 1910 and *Philodina gregaria* Murray, 1910) but does not fully explain the high numbers of shared haplotypes with

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non-Antarctic regions (Pugh & Convey 2008). Rotifer studies of Signy Island and Tierra del Fuego in South America also indicate that rotifer diversity is highly underestimated. Sequences from 210 individuals from multiple Antarctic and non-Antarctic locations revealed 36 taxa with up to 3.6% between-species divergence for four *Adineta* species, while species divergence ranged from 0.5% to 10.3% between 55 populations (Fontaneto *et al.* 2011), clearly raising the issue of cryptic species. With a high level of cryptic speciation and undescribed species, the parthenogenetic nature of rotifers may complicate their evolutionary histories.

Regional dispersal of rotifers has been described as random and often co-occurring with tardigrades that share cold-adaptive traits (Zawierucha *et al.* 2015). Furthermore, fossil evidence of rotifers present in lakes in the eastern continental Vestfold Hills does not allow us to distinguish between the refugial or dispersal histories (Swadling *et al.* 2001). More sequence information is required to assess regional dispersal patterns in rotifers (Sohlenius & Boström 2005).

In summary, the association of rotifers with refugia may demonstrate limited dispersal ability and motility and may explain their distributions that might be linked to unknown refugia. Further analysis is required to reveal their evolutionary history and to verify the hypothesis of rapid post-LGM colonization and speciation. Targeted sampling to locate refugia in the eastern continental hills could also be used to assess their ability for long-range dispersal. Future genomic studies may reveal more information about these complex gene pools, potentially re-evaluating theories of a more ancient origin for rotifers.

Tardigrada

A total of 64 species of limno-terrestrial tardigrades, or water bears, have been recorded throughout Continental and Maritime Antarctica, with approximately half of all genera being endemic to the region (McInnes & Pugh 2007). First described in Antarctica by Richters (1904), these ‘slow-steppers’ range from 0.05 to 1.20 mm in length and are renowned for their survival ability. They tolerate the extreme cold by utilizing cryptobiosis (Wright 2001) and are capable of long-distance dispersal in a dormant state (Fontaneto 2019). Tardigrades are probably under-sampled throughout Antarctica, but the most broadly distributed continental species are *Hypsibius antarcticu* Richters, 1904 and *Milnesium tardigradum* Doyère, 1840, with no discernible species overlap between the continent and the Maritime Antarctic (Table I; Cesari *et al.* 2016).

Origins and refugia

Phylogeographical analyses of the continental *Echiniscus canadensis* Murray, 1910 using nuclear markers revealed a Gondwanan arrival with a speciation event of the ancient lineage in the Eocene (32–48 Ma; Guidetti *et al.* 2017, 2019), despite the inherent difficulties in dating tardigrade speciation (Table II). There is a lack of continental-wide surveys, but analysis of specimens from populations in Ellsworth Land in the west of the continent showed low-level genotypic endemism and divergence, implying an absence of local refugia, with subsequent Quaternary-period re-colonization by both endemic and cosmopolitan taxa (McInnes 2010). The probably ancient origin of tardigrades is supported by their well-known tolerance of harsh conditions.

Dispersal effects on broad-scale and regional distribution

Considering the relatively ancient origins of tardigrades, combined with their renowned ability for refugial survival, patterns of widespread distribution throughout Antarctic regions would be expected. A study including 343 Antarctic and non-Antarctic specimens identified 70 unique Antarctic haplotypes using *18S* rRNA, of which 25 were shared between the sub-Antarctic islands and Antarctic Peninsula and four were shared between Marion and South Georgia islands. Minimal haplotype sharing between divergent populations suggested the presence of cryptic species, as genetic divergences are comparable to those found between the distinct species *Milnesium antarcticum* Tumanov, 2006 and *M. tardigradum* (Sands *et al.* 2008).

An analysis of 126 tardigrades from two nunataks ~30 km apart in the Sør Rondane Mountains in Queen Maud Land identified 89 *COI*, 67 *18S* rRNA and 22 *Wg* haplotypes within the Macrobiotidea and Hypsibiidea families (Czechowski *et al.* 2012). More recent genetic studies using *COI* and nuclear *18S* markers of the *Mesobiotus* genus revealed deep geographical distinctions across continental populations, with potential species complexes (Short *et al.* 2022).

Unexpectedly high levels of divergence indicate strong barriers to gene flow between communities based on 42 specimens collected from the base of the Antarctic Peninsula despite their geographical proximity (McInnes 2010). As tardigrade phylogenies include high levels of cryptic speciation, a long-term presence, especially in the mountainous nunataks, has been suggested (Altmaier *et al.* 2010). More detailed phylogeographical studies of Antarctic tardigrades may shed light on the balance between long-range dispersal and refugial survival.

Chironomidae

The only known Antarctic insects are wingless species of the globally diverse Chironomidae family of the Diptera order. Two midge species of the genus *Belgica* Jacobs, 1900 are present, with *Belgica antarctica* Jacobs, 1900 endemic to Maritime Antarctica and *Belgica albipes* Seguy, 1965 endemic to the Îles Crozet sub-Antarctic islands. Earlier studies have found evidence for post-LGM vicariance between sub-Antarctic and maritime regions (Allegrucci *et al.* 2006). However, phylogenetic knowledge of the indigenous Diptera is limited. *Eretmoptera murphyi* Schaeffer 1914 that was palaeo-endemic to South Georgia was introduced to Signy Island in the 1960s (Allegrucci *et al.* 2012, Hughes *et al.* 2013).

Evidence for an ancient origin in the resident midges has been found from multiple sources. Divergence rates of *28S* rRNA sequences found a single ancestral midge as the ancestor of the three known Antarctic species, estimated to have undergone a colonization event some 49 Ma (Allegrucci *et al.* 2006). Additionally, four distinct *B. antarctica* and two *B. albipes* haplotypes are closely related to the *E. murphyi* lineages (Fig. 4b & Table I; Allegrucci *et al.* 2012). This supports an earlier study that found *B. antarctica* and *E. murphyi* distributions to result from vicariance with an ancient origin (Allegrucci *et al.* 2006).

Representatives of the *Belgica* and *Eretmoptera* Kellogg, 1900 genera show minimal gene flow between peninsular and sub-Antarctic populations, probably due to their limited long-distance dispersal ability (Convey 1992). The limited long-distance dispersal ability of the indigenous wingless chironomids reinforces vicariance as a principal driver of genetic diversity, with a wave of colonization moving south through the peninsula following the LGM (Pugh & Convey 2008). Getting a firm grasp on the genetic diversity of chironomids and other potential invasive insects should be central to conservation plans for vulnerable Antarctic ecosystems.

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Synthesis

Origins and refugia

There is increasing evidence that most of the terrestrial invertebrate fauna of Maritime and Continental Antarctica have ancient lineages, although origins differ among taxa. Strong evidence of an ancient origin in mites stems from a lack of genetic admixture between Antarctic and non-Antarctic species dating as far back as 10–100 Ma (Marshall & Coetzee 2000, Stevens & Hogg 2006). Yet this large range is indicative of the discrepancies found when estimating the origins of Antarctic taxa. The younger origins of rotifers represent an example of the difficulties of establishing an evolutionary timeline despite extensive comparison with non-Antarctic specimens (Cakil *et al.* 2021). The parthenogenetic nature of rotifers may also mask ancient lineages but can be clarified by sequencing of sister lineages. In addition to parthenogenesis, other confounding factors that can lead to discrepancies in molecular clock calculations include exogenous gene uptake, horizontal gene transfer, rapid population fluctuations, dispersal and extinction (Brown 2003, Ho & Phillips 2009). This is especially the case when dating rotifers. Further investigation of sample sets collected over larger spatial scales may suggest alternative theories on their age and arrival.

Certain parthenogenetic nematodes (e.g. *Panagrolaimus davidi*) are also difficult to accurately date, with estimates of origins ranging from 1.35 to 8.50 Ma depending on calculated generation times (Lewis *et al.* 2009, Schiffer *et al.* 2019). Similar ages of Antarctic nematodes (~30 Ma), tardigrades (~40 Ma) and chironomids (~49 Ma) indicate parallel evolutionary timescales. By contrast, repeated recent colonization is evident from events for Antarctic rotifers preceding the LGM (~130 Ka). Parthenogenetic reproduction in some species of oribatid mite and springtail also complicates evolutionary analyses with assumptions of consistent rates of genetic drift and background mutation, although the dominant taxa reproduce sexually.

Sub-Antarctic and maritime mite and springtail populations have some degree of shared genealogy that points to repeated mixing of ancient survivors with motile dispersers during interglacial periods and rare trans-oceanic migrations. Founder populations from maritime islands subsequently underwent varying degrees of *in situ* speciation with localized extinction events (Rogers 2007). The lack of genetic divergence and motility of mite populations along the peninsula supports a refugial ancestry (Pugh & Convey 2008). Further evidence comes from localized diversity and reinforces the narrative of multiple dispersal events.

Refugial survival has a defining role in nematode distributions, with interglacial dispersal and fast adaptation to abiotic pressures being key to the establishment of new colonies. For example, nematodes can only actively move short distances and require passive long-distance dispersal to seek out suitable habitats. Mites and springtails are susceptible to desiccation, yet their capacity for passive long-distance dispersal depended on the minimal chance of arrival on vegetated ice-free land during periods of glacial maxima (Fig. 4b; Hawes *et al.* 2008).

Contributions of dispersal to broad- and regional-scale distribution patterns

Phylogeographical studies across all main faunal types have shown a range of species distributions (Table I). Strong biotic barriers and biogeographical divisions between the continent and peninsular populations form observable divergence patterns in springtails (McGaughran *et al.* 2011, Collins *et al.* 2019), mites (Pugh 1993), nematodes (Smith 1984, Maslen & Convey 2006) and tardigrades (Cesari *et al.* 2016), although these are lacking for rotifers. At smaller scales, similar dispersal barriers were evident in multiple Antarctic regions within the continental Dry Valleys of VL (Fig. 4a; Stevens & Hogg 2003, Barrett *et al.* 2006), the Antarctic Peninsula (Fig. 4b; Chown & Convey 2007, McGaughran *et al.* 2010c) and eastern Continental Antarctica (Fig. 4a; Velasco-Castrillón *et al.* 2014c). This distribution pattern aligns with the limited motility of nematodes (Adams *et al.* 2007) and may also support a wind-borne theory of infrequent dispersal (Nkem *et al.* 2006, Ptatscheck *et al.* 2018). Localized distributions are even present in the circumpolar *Cryptopygus* springtails, giving phylogeographic support to an ancient origin for the genus (~24 Ma; Stevens *et al.* 2006a, McGaughran *et al.* 2008, 2011), with complex interactions with dispersal ability (McGaughran *et al.* 2010a). These contrast with the histories of *G. hodgsoni* and *C. cisantarcticus* that diverged > 1 Ma (Stevens & Hogg 2006, Stevens *et al.* 2006a). This may also indicate the prominence of recolonization and dispersal events in shaping distributions. Long-distance dispersal among maritime and sub-Antarctic islands is also clear from mite (Mortimer *et al.* 2011) and springtail populations (Stevens *et al.* 2006a). These dispersal events have often been linked with refugial survival and long periods of inter-glacial isolation. This is apparent from molecular evidence for mites and springtails, with further investigation being required to confirm refugial origins for the non-arthropod nematodes, rotifers and tardigrades that have generally more limited dispersal abilities.

The pre-LGM dispersal events might be masked by more frequent post-LGM dispersal events, as evidenced in springtails (Hawes *et al.* 2010, Carapelli *et al.* 2017a) and potentially occurring in mites (Van Vuuren *et al.* 2018). Recent speciation (< 20 Ka) in the prostigmatid *Stereotydeus mollis* Womersley and Strandtmann, 1963 and the sub-Antarctic oribatid *H. fulvus* mites supports a post-LGM theory of continental mite dispersal and speciation (Brunetti *et al.* 2021a). These findings align with an earlier, morphological-based study (Pugh & Convey 2008). Further comparisons of mites with *Brachionus plicatilis* Müller, 1786 showed marked similarities in divergences over similar ranges, whereby patterns of long-distance dispersal were constrained by local geography, with evidence of unsubstantiated refugia (Fontaneto *et al.* 2009).

A study of rotifers using molecular data from a defined transect within the Transantarctic Mountains found three species with limited cryptic speciation that were suggested to indicate limited starting diversity and restricted gene flow (Hodgson *et al.* 2010). Additionally, the widespread presence throughout the peninsula and sub-Antarctic islands of tardigrades is similar to those of rotifers and Southern Hemisphere nematodes (McInnes & Pugh 1998, 2007). Overcoming the data deficiency in Southern Hemisphere taxa may yet reveal more recent divergence events separating Antarctic taxa from species with shared ancestors on nearby landmasses, especially for the complex Rotifera. Sequences from regions with a Gondwanan history (e.g. South America, Sri Lanka, Australia and New Zealand) could be used to establish genetic distances and identify recent arrivals, as has been done for arachnids (Baker *et al.* 2020).

Local-scale distribution patterns

Fragmented habitats divided by glaciers and ice sheets are often associated with restricted gene flow and high levels of genetic

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differentiation, as observed in mites (Mortimer *et al.* 2011), springtails (Fanciulli *et al.* 2001, Frati *et al.* 2001, Stevens *et al.* 2007, McGaughran *et al.* 2011) and chironomids (Allegrucci *et al.* 2012). The West Antarctic Ice Sheet was shown to be a strong barrier to dispersal. Marked increases in speciation followed its collapse 5 Ma created large disparities in diversity among populations found on either side of the West Antarctic Ice Sheet (Pollard & DeConto 2009, Hawes *et al.* 2010, McGaughran *et al.* 2010b, Bennett *et al.* 2016).

At local scales, biotic distributions are influenced by both local barriers and an organism's ability for passive wind- or water-borne long-term dispersal and active local motility. This is most apparent around glaciers and other dispersal barriers, where communities often have limited gene flow despite being geographically close to each other. These speciation events are balanced by extinctions that often follow waves of dispersal and colonization, ultimately contributing to the complex gene pools that are found in mite (Marshall & Coetzee 2000, Maraun *et al.* 2003) and springtail populations (McGaughran *et al.* 2008, 2011, Collins *et al.* 2019).

Nematodes, tardigrades and rotifers tend to be more locally endemic, with limited divergence and gene flow between populations, even within the ancient members of the nematode genus *Scottnema* Timm, 1971 (Adams *et al.* 2007, Boström *et al.* 2011). Evidence of recent dispersal for mites and springtails contrasts with the less motile taxa, which tend to have a higher proportion of ancient lineages due to them being able to endure glaciation *in situ*. As such, they are associated with more cryptic speciation, as observed in persistent rotifer (Fontaneto *et al.* 2011) and tardigrade populations (Czechowski *et al.* 2012).

Future research priorities

Molecular approaches can further increase sampling depth to resolve biogeographical patterns in greater detail, pinpointing refugial locations (e.g. peninsular montane regions) and revealing population dynamics (Convey *et al.* 2014). Spatial and temporal resolutions to within 1 km around single glacier or within a glacial cycle of 10 Ka (McGaughran *et al.* 2008, Collins *et al.* 2020) can confirm repeated colonization events (Rogers 2007) and improve models of assemblage responses to ecosystem fragmentation (Struck *et al.* 2018).

The similar morphological traits and life histories of the terrestrial arthropods, mites and springtails make them ideal candidates for interspecific comparison of functions between taxa and regions (Ross *et al.* 2022). Further developments in bioinformatics and statistical software can also advance phylogeographical analyses and hypothesis testing (Beheregaray 2008, Avise *et al.* 2016). Meanwhile, comparisons with Gondwanan sister lineages can improve dating estimates. Studies have applied high-throughput sequencing, environmental DNA (eDNA) and genomic datasets to assess a range of soil biodiversity, including nematodes, rotifers and tardigrades from VL and maritime islands (Zawierucha *et al.* 2021, Czechowski *et al.* 2022) and from diverse oribatid mite assemblages in Australia (Ross *et al.* 2020). Divergences within *C. cisantarcticus*, which has low levels of cryptic speciation (relative to other Antarctic taxa) but higher mutation rates compared to other *Cryptopygus* spp., could help us to define OTU delimitation thresholds and levels of genetic drift. Detailed genomic datasets that are processed using automated learning algorithms have detailed evolutionary histories of the *Plectus* Laporte, 1840 nematodes (Xue *et al.* 2020) and sub-Antarctic springtail subspecies *C. cisantarcticus travei* Deharveng, 1981 (Monsanto *et al.* 2019).

Single-nucleotide polymorphisms (SNPs), microsatellites and diversity array technology sequencing (DArTseq) are other approaches used to extract meaningful ecological information from genomic datasets (McGaughran *et al.* 2019, Collins *et al.* 2020), while assemblage patterns have been inferred from metagenomics in mites, springtails and beetles (Arribas *et al.* 2016, 2020, 2021). It is hoped that combining molecular approaches with morphological taxonomy can highlight the importance of biodiversity to fragile ecosystems, enabling them to adapt to shifts in environmental conditions and to ensure their continued existence.

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