

On the terrestrial and freshwater invertebrate diversity of the High Arctic archipelago of Svalbard: a revised species inventory and synopsis of the community composition

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Abstract

Arctic terrestrial invertebrate biodiversity is generally poorly known, but the archipelago of Svalbard has one of the most up-to-date inventories of its terrestrial and freshwater faunas of any Arctic region, offering a baseline for long term monitoring of invertebrate communities in space and time. Since the most recent review of the Svalbard invertebrate fauna was produced in 2014, knowledge of this fauna has developed and this inventory is here critically revised and updated. Our aims are (1) to critically review the inventory based on current taxonomic knowledge, (2) publish the complete species inventory, including cross-referencing to the relevant publications, in an open access data archive (GBIF), and (3) highlight the particular advantages that working in Svalbard may bring for scientists working on terrestrial, freshwater, and cryospheric environments. The inventory contains a total 1091 valid species names or interim names. A gap analysis in the Barcode of Life Data Systems reveals that 50% of the species currently documented from Svalbard lack COI (Cytochrome c oxidase subunit 1) barcode reference sequences in this database. Gaps in our knowledge of the Svalbard fauna and how these may be resolved are discussed.

Key words: biodiversity, micrometazoans, polar, microarthropod, insect, community

1. Introduction

The invertebrate fauna of the Arctic is generally poorly documented with the exception of some specific locations, for example Zackenberg and Disko Island in Greenland (Böcher et al. 2015; Gillespie et al. 2020; Disko Island 2024; Zackenberg 2024) or the Canadian High Arctic Research Station in Cambridge Bay (Nowosad et al. 2020; Jorna et al. 2023). Nonetheless, for many regions of the Arctic few species inventories exist, while those that do are often incomplete (Lento et al. 2019; Aronsson et al. 2021) or have not recently been revised. The physical environment, remote locations and consequent challenging logistics, short history of both classical taxonomic and modern molecular phylogenetic studies and lack of availability of appropriate expertise combine to make these studies particularly challenging. Yet, key for understanding the ecology of a region, and how this ecology functions and responds to the physical environment, is clear understanding of the species biodiversity present. Detailed taxonomic inventories together with ecological knowledge help to comprehend the role of species in the community, responses to environmental and anthropogenic changes and, finally, conservation priorities. Moreover, without such baseline data it is impossible to project how these ecosystems will react to environmental change.

One Arctic region for which a relatively recent and thorough inventory of the terrestrial and freshwater invertebrate fauna is available is the High Arctic archipelago of Svalbard (Coulson et al. 2014a). This inventory was collated from existing publications and has been widely used in biodiversity estimates and comparisons with other regions (Gillespie et al. 2020; Aronsson et al. 2021). However, although summary information from the inventory has been drawn upon in various studies and reports, the complete species-level inventory and corresponding source literature have not been widely available, while a number of specialist taxonomic updates and revisions applying to the Arctic invertebrate fauna have become available in the last decade. We address this here by comprehensively updating the inventory of Coulson et al. (2014a), describing developments in knowledge and archiving the inventory in the open data Global Biodiversity Information Facility database (GBIF) (Coulson et al. 2024). Downloaded search results are provided with their own DOI (Digital Object Identifier) and can be readily cited.

Records of invertebrate studies in Svalbard commenced around 1869 and, to date, over 700 publications have been produced that describe or refer to the invertebrate fauna. These have resulted in an inventory listing of over 1000 accepted invertebrate species. Nonetheless, some of these records may represent synonyms or misidentifications and, hence, names extracted from the Svalbard literature require up-to-date taxonomic assessment and confirmation using modern taxonomies (e.g., Kaczmarek et al. 2018; Zawierucha et al. 2020). The "gold-standard" of long term monitoring of a system, with re-sampling that combines traditional morphological identifications based on currently accepted keys with molecular sequencing techniques, is challenging given funding limitations and limited taxonomic expertise. Nonetheless, a realistic and attainable goal is to create a revised inventory based on the existing literature but with critical appraisal of the species gleaned from this literature according to modern understanding. This approach also highlights those elements of the Svalbard invertebrate fauna for which molecular sequence data in the Barcode of Life Data Systems (BOLD) or National Center for Biotechnology Information GenBank are lacking with a view to targeting these species for future study.

The primary aim of this article is, therefore, to present an up-to-date evaluation of the terrestrial and freshwater invertebrate fauna of Svalbard, thereby providing a benchmark resource for current and future research both within the archipelago and in the wider Arctic and globally. We anticipate that this inventory will become a living document that can be regularly updated as knowledge improves and the authors welcome reports of additions or errors.

2. Basis of the inventory

The inventory was created by harvesting the terrestrial and freshwater invertebrate species mentioned in literature appearing between 1869 and 2023. Where relevant, appropriate specialised reports ("grey literature") are also included in the literature base. The complete list of species was then quality checked against the GBIF taxonomic backbone as well as compared with the taxonomic hierarchy in BOLD.

There are a great many taxonomic uncertainties concerning the invertebrate fauna of the Arctic in general and this is also, to some extent, true of the inventory of Svalbard. Although some species were considered in the past as cosmopolitan, in the light of recent findings they are found to be species complexes or morphospecies which, without the use of integrated approaches (combining morphology and molecular studies), cannot be properly identified (e.g., Kihm et al. 2023). Species synonyms have been removed as far as possible in the updated inventory so that only currentlyaccepted species, cross-referenced to the Svalbard literature, are presented. Nonetheless, accurate taxonomic information for some groups described from Svalbard remains based on historical work and no recent taxonomic revisions are available. For these groups it may not presently be possible to determine accurate species names or taxonomic positions. The few vagrant or synanthropic species are not included in the inventory, which focuses on species resident in the natural environment, including parasites. However, nonresident species may be discussed where appropriate in the taxa sections. The majority of observations originate from the accessible western coastal regions of the archipelago, with fewer records from or descriptions of the invertebrate communities of the eastern or northern parts of the archipelago (but see for example de Smet 1993; de Smet and van Rompu 1996; Zawierucha et al. 2013; Coulson et al. 2014*a*; Zawierucha et al. 2017; Ávila-Jiménez et al. 2019).

The inventory for Svalbard currently includes 1091 accepted, or interim, species names. To remove some of the taxonomic uncertainty surrounding the inventory, a sub-list only including species mentioned in the literature since 1990 was also created. This date was selected as it is comparatively recent yet provides a 33 year period for sampling, analysis and publication to take place. We accept, however, that some species records present only in literature from before 1990 may represent rare but bona fide native species. Further, some species records present in the post-1990 inventory may result from mention in the later literature rather than from new observations or descriptions. Fully addressing these caveats is beyond the capacity of this paper. However, we emphasise that this inventory is a living document representing the current state of knowledge, to be updated as new and appropriately quality-controlled information becomes available, and will have an inbuilt "gatekeeper" function enabling quality control of new records.

3. Developments in the inventory of Svalbard since Coulson et al. (2014*a*)

While the review presented by Coulson et al. (2014a) remains largely current, for some taxa there have been corrections or additions to the inventory, often through the identification of new records but also due to taxonomic revision. Below, we briefly highlight selected taxa where knowledge has developed since 2014. Removing species not recorded after 1989 results in a 5% change and reduction of only 51 names suggesting a high level of agreement with current taxonomies (Table 1).

The inventory is available to search and download at GBIF (Coulson et al. 2024).

3.1. Rotifera

The phylum Rotifera sensu stricto includes the predominantly free-living Bdelloidea, Monogononta, and Seisonidea (marine). The Bdelloidea and Monogononta (classis Eurotatoria) consist of approximately 2000 described morphospecies and 34 families. Bdelloidea predominate by species and number of individuals in limnoterrestrial and benthic habitats, whereas Monogononta predominate in plankton and submerged vegetation of inland freshwaters. To date, information on rotifer diversity from Svalbard only relies on classical taxonomy and lacks a molecular approach.

The first mentions of Rotifera for Svalbard concern two unspecified bdelloids genus *Callidina* (now *gen. inq. et inc. sed.*) by von Goes (1862) and *Callidina alpium* Ehrenberg, 1853 (syn. *Pleuretra alpium* (Ehrbg.)) by Ehrenberg (1874) from bryophytes collected from Spitsbergen. In the years following, about 40 publications, generally the result of occasional sampling, added to the knowledge of rotifer diversity of central Spitsbergen (mostly), Prins Karls Forland, Barentsøya, Bjornøya, Edgeøya, Nordaustlandet, and Hopen. The total number of morphospecies from Svalbard currently amounts to 184 species; Bdelloidea 66 and Monogononta 118. The vast majority of these morphospecies are widespread or cosmopolitan. Endemic bdelloid morphospecies could not be demonstrated for Svalbard yet, but their presence cannot be ruled out since Kaya et al. (2010), in a study on moss-dwelling bdelloids from Spitsbergen found that, based solely on morphology, 13 of the taxa were undescribed. Moreover, morphology based identification likely underestimates the true species diversity as shown by applying molecular analysis that also provides increasing evidence of restricted distributions (e.g., Fontaneto et al. 2008; Iakovenko et al. 2015). A single bdelloid, Pleuretra hystrix Bartoš, 1950, appears to be restricted to the Arctic-alpine zone of the northern hemisphere. In the study by Kaya et al. (2010) it was also shown that the difference in bdelloid species composition between samples was quite high. Only geographical location and moisture content had a significant effect on species composition, in contrast with the life-form (turf, carpet, mat) and genus of the moss.

The published number of monogonont morphospecies is also an underestimate (unpublished results W.H.D.S.). Possible endemics are Encentrum murrayi Bryce, 1922, Trichocerca longistyla (Olofsson, 1918), and Synchaeta lakowitziana arctica de Smet, 1988. Notholca latistyla Olofsson, 1918 is restricted to the Arctic zone of the northern hemisphere. As for the Bdelloidea, Monogononta often harbour high levels of cryptic species diversity (e.g., Mills et al. 2017) and cryptic species complexes may be expected for Svalbard. A single study has been conducted on the evolution of zooplankton during the last ice-free period on Spitsbergen (Amrén 1964a, 1964b), and reported temporal variation in the morphology of the highly variable species of Keratella and Notholca. Not all variation could be explained by changing environmental factors and the author considered it to be governed probably by internal factors. Perhaps we may also be dealing with cryptic species. The monogonont species mentioned for plankton and submerged vegetation of Svalbard belong to the same taxa characteristic for these habitats in the temperate palearctic zone; Keratella, Notholca, Kellicottia, and Polyarthra, respectively, Cephalodella, Colurella, Encentrum, Euchlanis, Lepadella, Mytilina, etc. Three species, Encentrum incisum Wulfert, 1936, Encentrum mucronatum Wulfert, 1936, and Lecane arcuata (Bryce, 1891), have also been reported from terrestrial moss samples.

Thanks to the potential of long distance dispersal by, among other mechanisms, dormant anhydrobiotic stages (Bdelloidea) and resting eggs (Monogononta), it is to be expected that global environmental change can have an important impact on the rotifer diversity of Svalbard.

It is now accepted, on the basis of genome analysis, that Acanthocephala are highly derived rotifers. In Svalbard a few species have been reported from the marine realm in seabirds (viz. Arhythmorhynchus longicollis (Villot, 1875), Corynosoma strumosum (Rudolph, 1802)), Polymorphus phippsi (Kostylev, 1902) and seals (viz. Corynosoma semerme (Forssell, 1904), Corynosoma strumosum, Corynosoma villosum Van Cleave, 1953 and Corynosoma sp. 1), whereas from the terrestrial realm only one study reports an unidentified acanthocephalan at low prevalence in Arctic fox.

Table 1. Species richness in Svalbard.

Phylum	Class	Sub-class	Order	Total number of species	Number of species post 1989
Rotifera				184	171
	Eurotatoria			184	171
Gastrotricha				50	50
	Chaetonotida			50	50
Nematoda				136	134
	Adenophorea			4	4
	Chromadorea			95	93
	Enoplea			37	37
Platyhelminthes				29	27
	Cestoda			23	21
	Trematoda			6	6
Annelida				41	41
	Oligochaeta			41	41
Tardigrada				99	99
	Heterotardigrada			17	17
	Eutardigrada			82	82
Chelicerata				212	201
	Arachnida			212	201
		Acari		194	187
		Araneae		18	14
Mandibulata				290	271
	Collembola			67	67
	Insecta			223	204
			Hemiptera	3	3
			Thysanoptera	1	1
			Phthiraptera	35	34
			Coleoptera	16	15
			Hymenoptera	33	23
			Trichoptera	1	1
			Lepidoptera	3	3
			Siphonaptera	2	2
			Diptera	129	122
Crustacea				50	46
	Branchiopoda			16	16
	Copepoda			20	20
	Malacostraca			4	4
	Ostracoda			10	6
			Sum	1091	1040

Note: Numbers in bold font indicate the total number of species in the phylum; in italics the total number of species in the class; in normal font the number of species in the sub-classes or orders. Number of species total = total number of valid species, synonyms removed; post-1989 = only valid species presented in the literature between 1990–2023.

3.2. Gastrotricha

Following recent reviews of the Gastrotricha (Kolicka et al. 2018, 2020), the recorded species diversity of Svalbard has increased from one species (Coulson et al. 2014*a*) to 50. Gastrotrichs have once again become a subject of active study in this region. While older data sets (e.g. de Smet 1993) did not provide sufficient resolution to the species level for Gastrotricha from Spitsbergen and Barentsøya, the newer data gathered since 2013 from the Longyearbyen and Hornsund fjord area led to the discovery of a new genus and eleven new species (both freshwater and marine) that were described and remain endemic to the Arctic region to date (Kolicka

et al. 2018). A further 40 taxa noted from these sampling areas also turned out to be new to science, but they are still waiting for the formal taxonomic description (Kolicka et al. 2020). The potential for further research in the Arctic environment is considerable, and the data obtained from just two regions of one island in the Svalbard archipelago appears to be highly promising. Furthermore, the speciesspecific morphology, phylogenetic positions, and the number of gastrotrichs per 1 cm³ of sediment, which ranges up to approximately 1000 individuals (Kolicka et al. 2018, 2020), indicates that the future of gastrotrich research will likely lead to new discoveries. This could mean that Arctic studies may play a pivotal step in understanding the evolution of the entire Gastrotricha phylum.

3.3. Nematoda

The review of free-living nematodes of the Arctic by Holovachov (2014) is used as the basis for the inventory with the addition of recent descriptions of the nematode parasites of reindeer, polar bear, Arctic fox, and Arctic charr. A total of 136 species are currently recorded from Svalbard (Table 1). This is certainly an underestimate of the true diversity since few faunistic overviews of the nematode diversity of the Arctic exist and knowledge is very incomplete (Holovachov 2014). Since Holovachov's (2014) review, one paper with additional data on species of free-living nematodes from Svalbard has been published (Kerfahi et al. 2017) adding eight confirmed species to the inventory. Around a dozen studies of free-living nematodes have been conducted in Svalbard. The most intensive sampling was carried out by H. van Rossen in 1965, including 65 samples from 17 sites and resulting in 76 species identified by Loof (1971). Most studies before and after that of van Rossen were restricted to smaller areas and lower numbers of samples.

Ostertagia gruehneri Skrjabin, 1929 and Marshallagia marshalli (Ransom, 1907) are the most abundant parasitic nematodes species in the abomasum of Svalbard reindeer (Irvine et al. 2000) and experimental work has indicated negative effects of 0. gruehneri on Svalbard reindeer body condition and fecundity (Stien et al. 2002). By contrast, similar recent experimental work showed no detectable effect of M. marshalli on Svalbard reindeer body mass or pregnancy rate during the winter (Carlsson et al. 2018).

Climate change is expected to impact these parasitic nematodes, which have free-living juvenile stages outside of the host, and hence the impact they have on Svalbard reindeer. A recent review (Moerman et al. 2023) identified key knowledge gaps (specifically combined temperature and moisture effects on parasitic nematodes) that will contribute to understanding the effect of changing climate on parasitic nematodes and hence potentially the dynamics with Svalbard reindeer.

3.4. Annelida

The phylum Annelida is represented primarily by the family Enchytraeidae in Svalbard. The Enchytraeidae worldwide includes about 700 described species from 33 genera (Schmelz and Collado 2023) which are present from the tropics to the polar circles and in terrestrial and aquatic habitats. The enchytraeid fauna of Svalbard currently consists of 39 species (Table 1) representing nine genera. Several species, for example Henlea perpusilla Friend, 1911, Henlea ventriculosa (d'Udekem, 1954), Henlea glandulifera Nurminen, 1970, Bryodrilus diverticulatus Cernosvitov, 1929, and Marionina argentea (Michaelsen, 1889), have been reported as widespread taxa of the Holarctic in the circumpolar and the colder climate temperate zone. It is perhaps unsurprising, therefore, that they are today considered to be species complexes (Schmelz and Collado 2010). Further study applying molecular methods is

therefore necessary and it seems highly likely that recorded species diversity in this group may increase.

Two non-native lumbricid earthworms occur in the anthropogenic soils at Barentsburg (Fig. 1), probably imported with soils for use in the greenhouse, but these do not as yet appear to have established beyond the town limits (Coulson et al. 2013).

The importance of these saprophagous worms in the decomposition of organic matter and the maintenance of the soil structure is indicated by their relatively high abundances in Svalbard soils. Birkemoe et al. (2000) observed ca. 4000 to 10 000 ind./m² in a Salix heath in Adventdalen and ca. 500 to 2000 ind./m² in a *Cassiope* heath at Ny-Ålesund (Fig. 1), while Schlaghamersky and Devetter (2019) recorded densities of up to 9993 individuals/m² \pm 8901 ind./m² at Skansbukta, Billefjord (Fig. 2).

Resulting from human activity in the Russian, formerly Soviet, settlement of Barentsburg, two species not previously identified from Svalbard were observed in anthropogenic soils originally imported from southern Russia or Ukraine (Coulson et al. 2013; Schlaghamerský et al. 2023), Enchytraeus buchholzi (Vejdovsky, 1879) and Enchytraeus dichaetus Schmelz and Collado, 2012. Ongoing climate change may facilitate the survival of such introduced species in the natural soils of Svalbard, particularly in the organic soils and communities below bird colonies that are characteristic of Svalbard.

3.5. Tardigrada

Based on both older and modern literature (before and after 1990) the number of limnoterrestrial tardigrade species of the Svalbard archipelago increased from 92, reported in the checklists published by Zawierucha et al. (2013) and Coulson et al. (2014a), to 99 species (Table 1). The phylum Tardigrada (water bears) includes two classes, Eutardigrada and Heterotardigrada, with the Svalbard inventory being dominated by the former. Limnoterrestrial tardigrades in Svalbard occupy all available habitats and niches spanning from soil through bryophytes and lichens to freshwater reservoirs such as tundra pools and ponds or cryoconite holes on glaciers (Dastych 1985; Zawierucha et al. 2015, 2021). The most detailed inventory of tardigrades is available for the island of Spitsbergen (Fig. 1), whilst knowledge on their occurrence elsewhere in the archipelago is limited to random sampling visits to single or very limited numbers of localities (Zawierucha et al. 2013, 2017). In addition to Spitsbergen, tardigrades have been reported from Phippsøya and Parryøya, Amsterdamøya, Nordaustlandet, Danskøya, Fuglesongen, Edgøya, Barentsøya, Prins Karls Forland, Hopen, and Bjørnøya (Van Rompu and De Smet 1994; Gąsiorek et al. 2016; Zawierucha et al. 2013, 2017, 2018) (Figs. 1 and 2). Developments in knowledge of the tardigrade fauna of Svalbard include redescriptions of old taxa, descriptions of new species, changes in the systematic status of several species and an increase in information available on tardigrade ecology (e.g., Kaczmarek et al. 2018, Zawierucha et al. 2016, 2019a; Stec 2023). The updated inventory includes several species new to science, for example, Diaforobiotus svalbardicus Stec, 2023 from tundra and

Fig. 1. Map of Svalbard indicating the principal islands of the archipelago and the settlements referred to in the text or references. A = Ny-Ålesund, B = Pyramiden, C = Longyearbyen, D = Barentsburg, and E = Hornsund.



Fig. 2. Locations of collecting referred to in the text; (*a*) Phippsøya and Parryøya, (*b*) Nordaustlandet, (*c*) Dellingstupa, (*d*) Petuniabukta, (*e*) Sassendalen, (*f*) Hopen, (*g*) Adventdalen, (*h*) Linnevatn, (*i*) Skansbukta, (*j*) Prins Karls Forland, (*k*) Ossiansarsfjellet, (*l*) Blomstrandhalvøya, (*m*) Dieset catchment, (*n*) Fjortendejulibukta, (*o*) Danskøya, (*p*) Amsterdamøya, and (*q*) Fuglesongen.



Fontouriun glacialis (Zawierucha et al. 2020) from cryoconite holes. There are also new records of species identified exclusively based on molecular sequence evidence, including *Cryoconicus antiarctos* Guidetti et al. 2019, *Hypsibius cf. exemplaris* 1, 2, 3 (Zawierucha et al. 2023), and of species identified based on morphological features, such as *Isohypisbius cf. reticulatius* Pilato, 1973 and *Minibiotus cf. formosus* (Zawierucha et al. 2020, 2023). Finally, some new additions were identified using a combination of molecular and classical approaches (such as *Cryoconicus kaczmareki*; Zawierucha et al. 2023. Some species were removed from the list of Svalbard tardigrades due to uncertain taxonomic status or misidentifications (Kaczmarek et al. 2018).

The most frequently investigated habitats in terms of tardigrade species diversity and distribution in Svalbard are bryophytes and cryoconite holes, while less investigated habitats such as soil, tundra ponds, and streams now require increased future research focus (Dastych 1985; Janiec 1996;

The ecology of tardigrades in the Svalbard archipelago is relatively well studied in comparison with other Arctic regions. Dastych (1985) conducted a comprehensive investigation of the distribution, density and impact of bedrock type on tardigrade assemblages, revealing affinities of some species to acidic or alkaline substrata. However, the crucial role that bird cliffs and allochthonous nutrient deposition play in shaping abundance and species and trophic group distribution in the terrestrial environment of Svalbard is becoming recognised (Zawierucha et al. 2016; Zwolicki et al. 2016; Zmudczyńska-Skarbek et al. 2023). Tardigrades occurring under little auk (Alle alle) colonies reach higher densities and are represented by a higher proportion of microbivore species compared to sites without seabird influence (Zawierucha et al. 2016, 2019a). Additionally, seabird guano indirectly influences, by fertilising the tundra, the body size of these tardigrades (Zawierucha et al. 2018). In terrestrial habitats such as bryophytes, lichens, and soil, altitude also plays an important role in shaping tardigrade abundance, trophic group and species distribution and diversity (Zawierucha et al. 2015, 2019a). On valley glaciers the most important factors determining distribution of tardigrades are stochastic events, such as abrupt ablation at glacier scale, or distance and physical connectivity between glaciers (Zawierucha et al. 2019b, 2023). The maximum densities of tardigrades in Svalbard habitats can reach 28 000 ind./m² of tundra (Dastych 1985), 9.52 ind. $/g^{-1}$ of dry bryophyte material (Zawierucha et al. 2016) and 230 ind./cm³ of wet cryoconite (Zawierucha et al. 2019c).

3.6. Acari

Mites (Acari) are the third most species-rich invertebrate group, after insects and rotifers, in Svalbard. The first records of Acari from Svalbard date to 1871 (Thorell 1871). Since then, the checklist has grown to include more than 150 species (Seniczak et al. 2020).

3.6.1. Mesostigmata

Thirty-eight species of mesostigmatic mites are currently recorded from Svalbard and 35 have been collected recently (Ávila-Jiménez et al. 2011; Coulson et al. 2014b). Some probably valid species, such as Arctoseius laterincisus reported by Thor (1930), have not been observed recently. Unfortunately, after Thor's death a great deal of his material was lost and, while some specimens have recently been discovered at the Natural History Museum (University of Oslo), much is in a poor state of preservation. Amongst the species remaining, Antennoseius oudemansi (Thor, 1930), Neoseiulus magnanalis Thor, 1930 and Proctolaelaps pygmaeus (Müller, 1859), have been redescribed, and the specimens obtained deposited in zoological collections elsewhere in Europe as neotypes (Gwiazdowicz and Rakowski 2009; Kolodochka and Gwiazdowicz 2014; Teodorowicz et al. 2014). The latest newly-described species from Svalbard are Neoseiulus grumantensis Kolodochka and Gwiazdowicz, 2014 and Halolaelaps coulsoni Gwiazdowicz and Teodorowicz, 2017, described from Billefjord (Petuniabukta and Pyramiden) (Figs. 1 and 2) (Gwiazdowicz and Rakowski 2009; Kolodochka and Gwiazdowicz 2014; Gwiazdowicz and Teodorowicz 2017). Recent collections have also generated new species records for Svalbard, including *Dermanyssus hirundinis* (Hermann, 1804), *Neoseiulus ellesmerei* (Chant and Hansell, 1971), *Paragamasus insertus* (Micherdziński, 1969), *Vulgarogamasus immanis* (Berlese, 1904), and *Zercon solenites* Haarløv, 1942 (Gwiazdowicz et al. 2011). Such records indicate that Svalbard, although one of the most thoroughly documented regions in the Arctic for the acarological fauna, is still a source of new and unexpected discoveries.

3.6.2. Prostigmata

The first records of Prostigmata from Svalbard originate from 1871 when Thorell discovered and described four new species, namely Rhagidia gelida, Penthalaeus insulanus, Bdella arctica, and Bdella decipiens, with the two latter being junior synonyms of Neomolgus littoralis (Linnaeus, 1745) and Bdella longicornis (Linnaeus, 1758), respectively, and Penthalaeus insulanus a junior synonym of Penthaleus major (Dugès, 1834). Trägårdh (1900) recorded Cyta latirostris (Hermann, 1804) and described Penthalodes arcticus (Penthalodidae) from Bear Island (Bjørnøya), erroneously assigning the latter species to Penthaleus (Penthaleidae). The species was subsequently synonymized with Penthalodes ovalis (Dugès, 1834) by Thor (1930), though the synonymy remains to be verified. Oudemans (1928) added another eupodoid species, Cocceupodes clavifrons (Canestrini, 1886) to the fauna of Spitsbergen. The extensive work of Thor (1930) was a major contribution to the knowledge of the prostigmatid mite fauna of Svalbard. It included both new records, such as Eupodes variegatus C.L. Koch, 1838, Penthaleus major (Dugès, 1834), Coccorhagidia clavifrons (Canestrini, 1886), and Nanorchestes arboriger (Berlese, 1904), as well as descriptions of new species, such as Bdella semiscutata, Eustigmaeus oudemansi and Eustigmaeus pulchellus. In subsequent publications (Thor 1931, 1932, 1934) the known prostigmatid diversity was further increased, including nine newly described species. Among them, six species appear to be endemic to Svalbard, namely Bryobia borealis Oudemans, 1930, Podothrombium svalbardense Oudemans, 1930, Eustigmaeus oudemansi (Thor, 1930), Eustigmaeus pulchellus (Thor, 1930), Alicorhagia plumipila (Thor, 1931), Kerdabania arctica (Thor, 1934), while others have their distribution restricted to Arctic regions, e.g., Alicorhagia clavipila (Thor, 1931) (Makarova 2015), and Neoprotereunetes boerneri (Thor, 1934) (Laniecki and Magowski 2023). Subsequently, for a period of almost 100 years, excepting Huhta (1967), no faunistic or taxonomic studies addressed soil-inhabiting Prostigmata in Svalbard. This led to increasing divergence in the level of knowledge available for the Prostigmata and the Oribatida and Mesostigmata. As a result, many of the species described from Svalbard are now hard to interpret because of inadequate original descriptions and lack of modern redescriptions.

Recently, a pilot study of aeroplankton conducted on Spitsbergen in 2022 provided an opportunity to investigate airborne prostigmatid mites (Grewling et al. 2024). Fifteen specimens of Prostigmata were collected, including representa-



tives of one family (species undetermined), two species not recorded from Svalbard, and one potentially undescribed species, although whether any of these are present in the archipelago's terrestrial fauna or were simply carried in the aeroplankton is unknown. The prostigmatid mite fauna of Svalbard, and of the Arctic generally, remains poorly investigated and in need of thorough taxonomic revision. The most recent overview available of the prostigmatid mite fauna of Svalbard is that of Seniczak et al. (2020), but it should be stressed that many of the older records included are of rather historical than scientific significance.

3.6.3. Oribatida

Mites from the suborder Oribatida (Sarcoptiformes) form over half of all known mite species on Svalbard.

As with the Prostigmata and Mesostigmata, the study of the Oribatida has a long history in Svalbard and commenced at the initiation of the early biological investigations in the archipelago. Thorell (1871) was the first to study Svalbard Oribatida and described four species new to science, all of which are still valid. At this time only 126 oribatid species had been described globally (vs. the 11 516 known today; Subías 2023), and most of these 126 are now considered either synonyms or *species inquirendae*.

The known diversity of Svalbard Oribatida has progressively increased from the 20 species known early in the 20th century (Thor 1934), through multiple later studies (Hammer 1946; Karppinen 1967; Niedbała 1971; Karppinen and Krivolutsky 1982; Coulson and Refseth 2004; Lebedeva et al. 2006; Coulson 2007; Bayartogtokh et al. 2011) up to the 93 species listed recently (Seniczak and Seniczak 2020; Seniczak et al. 2020). One further species, Liochthonius simplex (Forsslund, 1942), has been overlooked in previous syntheses and has been reported only once, in a barnacle goose nest (Pilskog et al. 2014). In, addition, one new species, Platynothrus coulsoni A. and S. Seniczak, 2022 has been described recently (Seniczak and Seniczak 2022). Two species, Svalbardia paludicola Thor, 1930 and Oromurcia lucens (L. Koch, 1879), have been synonymised, and a new name, Svalbardia lucens (L. Koch, 1879), has been proposed (Ermilov et al. 2022). After these changes, the known diversity of Svalbard Oribatida comprises 95 species (with three from the cohort Astigmatina) representing 28 families. The richest family is the Brachychthoniidae (15 species), followed by the Ceratozetidae (14 species) and the Crotoniidae (13 species).

Despite its diversity, Svalbard Oribatida still requires baseline survey and research. Almost one third of species have been reported only once, including 17 species only recorded before 1990 (Seniczak and Seniczak 2020; Seniczak et al. 2020). Fourteen species new to science have been described from Svalbard, including four that can be considered endemic (*Kunstidamaeus arcticus* Miko and Monson, 2013, *Autogneta kaisilai* Karppinen, 1967, *Fuscozetes coulsoni* A. and S. Seniczak, 2020, *Platynothrus coulsoni* A. and S. Seniczak, 2022) but, with sampling in previously unsurveyed areas of the archipelago this number will probably increase.

3.7. Araneae

Coulson et al. (2014a) included 17 spider species (16 Linyphiidae and 1 Gnaphosidae) (18 if including the synanthropic species Thanatus formicinus (Clerck, 1757) (Philodromidae) only recorded from within human dwellings (Aakra and Hauge 2003)). The current inventory introduces one additional Hahniidae species, bringing the native species total to 18. However, some uncertainty remains as, although both Walckenaeria karpinskii (O.P. Cambridge, 1873) and Walckenaeria clavicornis (Emerton, 1882) are reported from Svalbard, these are closely related sibling species that are hard to distinguish. Confirmation of species identity using traditional morphometric taxonomy often requires large sample sizes since specific distinguishing characters overlap between the two species. The detailed study of Dahl et al. (2018) included large numbers of W. clavicornis but no W. karpinskii and they suggested, based on this observation, that previous records of W. karpinskii may represent misidentification due to insufficient sample size.

3.8. Collembola

A total of 67 species are recorded from Svalbard. Some appear to be restricted to the eastern coastal region of Edgeøya, Folsomia ciliata Babenko & Bulavintsev, 1993 and Pseudanurophorus psammophilus (Potapov & Stebaeva, 2002) (Fig. 1) (Ávila-Jiménez et al. 2019), suggesting a potential immigration route from the east. Moreover, several new records have been obtained from soils imported in the Soviet era to the towns of Barentsburg (Coulson et al. 2013) and Pyramiden (Coulson et al. 2015) (Fig. 1). In Barentsburg, the five new records included a known invasive alien species (IAS), Deuteraphorura variabilis (Stach, 1954) (Coulson et al. 2013). The soils sampled were on the slope below the town's abandoned greenhouses and consist of a mixture of soils imported from Ukraine during Soviet times to be used in the greenhouse and manure from the cattle and pig house. They therefore represent an unusual environment compared with most of Svalbard's natural soils. Nonetheless, the species found could potentially colonise nutrient-rich soils below the bird cliffs considered characteristic of Svalbard (Jónsdóttir 2005). Soil was similarly imported to Pyramiden (Fig. 1) with the aim to create a green lawn in the central square. Less information is available concerning the origin of this soil but it is likely to also have been sourced from Ukraine. In the soils here and between the buildings within Pyramiden two new Collembola records were obtained, Thalassaphorura debilis (Moniez, 1889) and Desoria tigrina Nicolet, 1842 (Coulson et al. 2015). Of the total of 26 species of Collembola recorded from Pyramiden by Coulson et al. (2015), 12 had not been previously observed in the vicinity of the town and potentially could have been imported with the soils. Many of the Collembola (and mites) now reported from this location have wide geographical distributions and might be expected to occur in the regions the imported soils were obtained from, even if they also occur naturally on Svalbard. Such species would not be identified in a study focusing simply on species presence or absence, raising the potential for conspecific individuals being

introduced that are genetically distinct from the native Svalbard population and result in genetic homogenisation.

Vertagopus pseudocinereus Fjellberg, 1975 has been removed from the inventory. This species was originally described from specimens collected from under bark on conifer logs imported for mining construction at Ny-Ålesund (Fjellberg 1980) (Fig. 1). This species lives on tree bark (a corticole species) and does not occur, or reproduce, in Arctic environments. *Megalothorax minimus* (Willem, 1900) may have been confused in earlier records and, if so, these records may refer to *Megalothorax svalbardensis* Schneider and D'Haese, 2013.

3.9. Insecta

3.9.1. Phthiraptera

There have been no recent changes to the inventory for parasitic lice recorded from Svalbard, and the number of phthirapteran species (of all suborders) remains 35 (two Anoplura, eight Amblycera, 25 Ischnocera).

3.9.2. Hemiptera

Three resident aphid species are known. Acyrthosiphon svalbardicum Heikinheimo, 1968 is the most studied of the Hemiptera on Svalbard, occurring along the west coast associated with Dryas octopetala in locations where there is a long summer snow-free period (Strathdee and Bale 1995). Simon et al. (2019) demonstrated close genetic similarities between Acyrthosiphon svalbardicum and Acyrthosiphon brevicorne from the Norwegian mainland but made no attempt to synonymise them. Wieczorek et al. (2020) compared the structure of the reproductive system of the sexual generation of Acyrthosiphon svalbardicum and its temperate counterpart, Acyrthosiphon pisum (Harris 1776). Sitobion (Metobion) calvulum (Ossiannilsson, 1958), associated with Salix polaris, is to date only recorded from Adventdalen and Sassendalen (Fig. 2). Acyrthosiphon svalbardicum and S. (M.) calvulum are currently regarded as species endemic to the archipelago both representing the Aphidinae family. A third species, Pemphigus sp. (Eriosomatinae) which awaits formal identification, is known from Longyearbyen (Isfjorden) as well as Fjortendejulibukta (Krossfjorden) (Figs. 1 and 2). Because this species feeds on grass roots, most often hidden under stones, it is rarely searched for and its distribution in Svalbard is highly likely to be underestimated. Myzus (Nectarosiphon) persicae (Sulzer, 1776) has been collected in Longyearbyen. An alien and potentially invasive aphid species, large numbers were observed on three imported ornamental plants which were on display outside the main supermarket in the town (Wieczorek and Chłond 2019). While it is unknown whether the species was able to migrate to local plants and survive under the natural conditions in Svalbard, further studies are required to confirm the status of this species. Several windborne vagrants have also been recorded, including Cinara confinis (Koch, 1856), Cavariella salicis (Monell, 1879) and an unidentified species of the genus Aphis (Coulson and Refseth 2004), but their continued presence is unknown. For such species a barrier to colonization is likely to be the lack of specific host plants.

3.9.3. Coleoptera

Coulson et al. (2014*a*) listed 19 species from 11 families but only 16 species are in the current review considered to be native, and of these only three being commonly recorded in surveys outside settlements (*Boreophilia subplana* (J. Sahlberg, 1880), *Atheta graminicola* (Gravenhorst, 1806) and *Isochnus flagellum* (Erichson, 1902)). Of the commonly recorded species, *I. flagellum* has recently been extracted from soil samples exposed to different winter temperature regimes on Svalbard, including to below -25 °C, highlighting their ability to withstand these winter conditions as adults (Convey et al. 2015).

3.9.4. Hymenoptera

Several new discoveries of species representing this group in Svalbard have been made recently. In a study on the flower visiting insects in Adventdalen (Fig. 2), Gillespie and Cooper (2022) observed and captured individuals of the families Megaspillidae and Diapriidae feeding from flowers of Silene acaulis and Stellaria longipes subsp. longipes, respectively, although the specimens have not yet been identified to species level. In addition, DNA metabarcoding of faecal samples of snow bunting chicks in Adventdalen have revealed the first record of Nematus caeruleocarpus Hartig, 1837 (Tenthredinidae) and an undescribed species of the genus Amauronematus (Tenthredinidae) (Stoltz 2019). Finally, Diaeretellus svalbardicum Chaubet and Tomanović, 2013 was reported as new species to science in 2012, and is a parasitoid of the endemic aphid A. svalbardicum (Chaubet et al. 2013), but was omitted from the 2014 inventory. Given the reliance of hymenopterans on other species for parasitism or adult food, future studies are likely to provide further new species records.

3.9.5. Trichoptera

There has been no recent change to the inventory for Trichoptera (which remains a single species, *Apatania zonella* Zetterstedt, 1840).

3.9.6. Lepidoptera

Of the 10 Lepidoptera species recorded from Svalbard, only three are considered resident, *Apamea exulis* (Lefèbvre, 1836), *Pyla fusca* (Haworth, 1811) and *Plutella polaris* Zeller, 1880 (Coulson et al. 2014*a*), the last of which was not recorded since its first collection in 1873 until rediscovery in 2015 at Dellingstupa in Wijdefjord (Søli et al. 2018) (Fig. 2). Individuals of *P. polaris* were collected from the Altai mountains in Russia in 2016 (Huemer et al. 2017), and results from DNA barcoding (COI) demonstrated these to be conspecific with material from Svalbard, thus showing a highly disjunct global distribution (Søli et al. 2018). *Apamea exulis* appears to



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be scarce but rather widespread in western coastal areas of the archipelago, whereas *P. fusca* has appears to have a more restricted distribution, with a few known locations, in particular Ossiansarsfjellet close to Ny-Ålesund (Coulson et al. 2003) (Fig. 2). Of the remaining species recorded from Svalbard, four are considered to be vagrants (*Syngrapha interrogationis* (L., 1758), *Vanessa cardui* (L., 1758), *Loxostege sticticalis* (L., 1761) and *Plutella xylostella* (L., 1758), while three are synanthropic species associated with human settlements (*Pieris napi* (L., 1758), *Hofmannophila pseudospretella* (Stainton, 1849) and *Ephestia kuehniella* Zeller, 1879) (e.g., Coulson 2015). The vagrants and synanthropic species are not listed in the inventory.

3.9.7. Diptera

Diptera is the most diverse group of insects on Svalbard and in the present inventory we list 129 resident species compared with the 122 species listed by Coulson et al. (2014a). As numerous new records and species have been included in the present inventory, this modest increase in species number can be ascribed to the high number of previous uncertain and dubious records that have been deleted from the 2014 inventory. Chironomidae form a large and important part of the fauna, with 66 species listed in 2014, increasing to 72 species at present (thereof 54 with Linnean names and 18 with interim names) (Stur and Ekrem 2020). Another nematoceran family constitutes the second largest group in terms of species number, the Sciaridae with 18 species (Menzel et al. 2020), increased from 13 in the 2014 inventory. The remaining 39 species are distributed across 15 families, of which the two most species-rich are Mycetophillidae and Muscidae, each with 7 species. In addition to the resident species two well known vagrant species have been recorded, Syrphus ribesii (L., 1758) and Syrphus torvus Osten-Sacken, 1875, and do not appear in this inventory, while at least three species are considered accidentally introduced, associated with human settlements, viz. Drosophila funebris (Fabricius, 1787), Calliphora vicina Robineau-Desvoidy, 1830 and Protophormia atriceps (Zetterstedt, 1845), and also do not appear in the inventory. An interesting recent addition was the record of the syrphid Eupeodes vockerothi (Fluke, 1952) at Blomstrandhalvøya (Fig. 2) in 2018 (see Nielsen and Gammelmoe 2017), a species not previously recorded outside Greenland and the Nearctic. More intensive sampling from new and poorly studied areas of Svalbard, together with extensive use of DNA barcoding and metabarcoding, as demonstrated by Stur and Ekrem (2020), will undoubtedly add new species in the future, and will certainly improve our understanding of species distributions in Arctic regions (e.g., Ekrem et al. 2018).

3.10. Freshwater habitats

During the last decade there has been an increased focus on documenting terrestrial and aquatic biodiversity in the Arctic as a basis for future monitoring, especially in the light of the rapid environmental changes that Arctic ecosystems are experiencing (Dimante-Deimantovica et al. 2018; Walseng et al. 2018; Brittain et al. 2020). This focus was initiated by the Arctic Council's Circumpolar Biodiversity Monitoring Program (Conservation of Arctic Flora and Fauna) (Culp et al. 2012). For freshwater systems this has resulted in an extensive report on the state of Arctic freshwater biodiversity (Lento et al. 2019; Culp et al. 2022) which also includes suggestions for abiotic and biotic variables to measure and protocols to monitor Arctic biodiversity. This is also explored by Goedkoop et al. (2022). The extensive database built up during this program has formed the basis for analyses of diversity patterns throughout the circumpolar Arctic. For example, the freshwater macroinvertebrate fauna of island archipelagos such as Svalbard is limited by virtue of their geographic position and isolation, with island faunas representing a subset of those of the mainland (Lento et al. 2022). Increases in both species and functional diversity as a result of global warming will also be limited, or slowed, by biogeographical constraints on the colonisation of archipelagos such as Svalbard (Lento et al. 2022, 2023). However, the three-spined stickleback, Gasterosteus aculeatus, a freshwater fish species new for Svalbard has recently been recorded (Svenning et al. 2015), indicating that some level of connectivity exists.

Studies of freshwater invertebrate populations can also reveal differences in production and growth at a local scale, exemplifying the importance of recording multiple abiotic and biotic variables when setting up long term monitoring programs. For example, populations of two aquatic Diamesa species, Diamesa aberrata Lundbeck, 1889 and Diamesa bohemani Goetghebuer, 1932 (Chironomidae) were studied in three contrasting streams near Ny-Ålesund (Schütz et al. 2022). Differences in water temperature led to diverging development patterns on local spatial scales. The lowest larval growth was in a rain/snowmelt fed stream with low food availability and quality. Surprisingly, food quality was better in a glacially influenced stream and was comparable with a groundwater-fed stream enriched by nesting sea birds. Thus, despite lower temperatures, the glacier-fed stream had comparable secondary production to rain/snowmelt streams.

3.11. Anthropogenic disturbance and invasive alien species (IAS)

With human activity, including industry and increasing intensity of scientific research and tourism, there follows a risk of accidental introduction of IAS (Coulson 2015), and altered community compositions. As noted above, there are newly recorded species that could potentially become invasive under current environmental scenarios, for example the several introduced Collembola species occurring in the nutrient-rich and deep organic soils in Barentsburg which may have the potential to colonise similar natural habitats occurring beneath bird cliffs (Coulson et al. 2013). The physical alteration of these soils is also likely impacting the community composition of native species, for example, high nutrient dung heaps seem to be favouring unusually high density, low-diversity Dipteran communities of Calliphora and Scathophaga. Moreover, the consequences of introduction of new genotypes of existing species are less well appreciated for native Svalbard populations. Many species of terrestrial invertebrate present

in Svalbard have distributions that extend far beyond the Arctic. It is likely that regional differences in genotypes exist, but that importation of these new genotypes to Svalbard goes unnoticed since monitoring focuses on the appearance of new species rather than individuals of native species.

4. Knowledge gaps evident from the inventory and supporting literature

The inventory, and its underlying literature base, reveal several significant gaps concerning the understanding of the terrestrial and freshwater species diversity of Svalbard.

Species lacking sequence data in BOLD. The species inventory was reduced to taxa with Linnean names at the genus and species level, but keeping interim names if present in BOLD and uploaded as the checklist CL-INVSV "Invertebrates of the Svalbard archipelago." A gap analysis against the BOLD database 27 February 2024, identified 51.05% of the species with sequence data and 46.18% with formal barcodes (Table S1 Supplementary Material). Thus, there are 522 named species from Svalbard that lack sequence data in BOLD. Undoubtedly, the taxonomic coverage would be higher if including other markers and data hosted in GenBank, but the results show that an effort is needed to provide reference barcodes for a higher percentage of Svalbard invertebrates if molecular tools such as metabarcoding are to be used in biomonitoring.

Gaps in knowledge of specific groups and taxonomic confusion. The level of detailed knowledge is not consistent across the different groups of invertebrate fauna. Certain groups have traditionally received more attention and revision from taxonomists and ecologists than others (e.g., Diptera, Collembola, Oribatida). This has resulted in an imbalance, as also seen for other geographical regions, in our knowledge of species biodiversity.

Limitations in geographic coverage of Svalbard. The majority of studies address only the Isfjord or Kongsfjord regions around Longyearbyen or Ny-Ålesund (Fig. 1), respectively. Both these fjord systems lie on the west coast of Spitsbergen and few studies have sampled the invertebrate communities of the northern or eastern regions of the archipelago. This is despite previously noted indications that their invertebrate faunas may be distinct from the milder western regions due to likely differing immigration and colonisation histories (Coulson et al. 2014*a*; Ávila-Jiménez et al. 2019).

Time series data are largely absent. Most available data concern community composition at one moment in time. This means that there is little understanding of the effects of environmental variability and change on, for example, species abundance, phenology, and ecosystem functions/services performed such as pollination, decomposition, and as prey items. The lack of such data are a significant handicap for our understanding of the system as a whole and ability to identify trajectories as compared to interannual variation. This limitation bedevils invertebrate research in many polar regions (but see the Greenland Monitoring Programme for an exception; https://g-e-m.dk/). Few ecological studies on ecosystem functioning. The majority of reports consist of community composition and there are few multi-year studies focussing on functions of this fauna in the ecosystem, for example, decomposition and nutrient cycling. There is a need to identify trophic connections, carbon and nutrient fluxes, and energy flow. We also highlight the lack of cross-over studies, for example that of Stoltz (2019), which focused on the diet of breeding birds, revealed useful information on the invertebrate fauna.

Colonisation of Svalbard and immigration history. Few studies address the immigration history (and, conversely, endemism), colonisation of or dispersal routes to and around Svalbard. This is in stark contrast to understanding of the immigration history of vascular plants (Brožová et al. 2023). It is likely that much of the invertebrate community observed is the result of colonisation events since the retreat of the ice following the last glacial maximum (Coulson et al. 2014a). Yet the source populations and the timing of arrival to Svalbard remain unclear. Uncertainty also applies to immigration routes, although oceanic currents and air masses have been postulated to be involved (Coulson et al. 2002a, 2002b) as well as via zoochoric association with migrating birds (Lebedeva and Lebedev 2008). The existing of terrestrial refugia during glacial periods for invertebrates in Svalbard still require investigation.

Threat or otherwise of invasive alien species (IAS). This has not been considered for the invertebrate fauna with the exception of the parasite *Echinococcus multilocularis* Leuckart, 1863 (Cestoda; Taeniidae). Plans exist for the threat of this parasite, its alien host, and Svalbard's vegetation (Governor of Svalbard 2017). However, the impacts of other non-native invertebrates on the archipelago's ecosystems have not yet been considered despite there being a long and increasing history of terrestrial alien invertebrate species being recorded (Coulson 2015).

Lack of information on effects of environmental change and anthropogenic disturbance. There is a particular need for an improved mechanistic understanding of the impacts of current and projected future environmental changes on invertebrate communities and ecosystem functioning. The lack of comprehensive monitoring and reporting programmes remains a considerable handicap (Lento et al. 2019; Gillespie et al. 2020; Aronsson et al. 2021; Goedkoop et al. 2022). Moreover, the sparsity of studies of ecophysiological responses of these faunas precludes accurate projection of future community trajectories.

Few studies addressing pan-Arctic diversity. This was again highlighted recently in the Conservation of Arctic Flora and Fauna (CAFF) report, Status and Trends of Arctic Terrestrial Biodiversity (Aronsson et al. 2021), where the focus of the analysis was forced to be restricted to the North Atlantic region since a lack of data and inconsistencies in taxonomies invalidated any broader analysis (Gillespie et al. 2020).

Few sequencing studies. Recent advances in sequencing methodologies have opened opportunities for studies on hidden genetic diversity (often termed cryptic diversity) and environmental DNA (Zawierucha et al. 2020), especially in the context of enhancing monitoring programmes. For some taxa (see Section 3.1 Rotifera) a molecular approach for the



Svalbard fauna has not begun. Whilst not all species present in Svalbard are represented in sequence libraries, this technology opens up clear opportunities in diversity studies. The broad genetic diversity of Arctic plants is now appreciated, however few studies have addressed molecular diversity in the Arctic invertebrate fauna.

5. Svalbard as a field location for Arctic terrestrial biology research

Svalbard provides an excellent "natural laboratory" to study phenomena such as primary succession (e.g., Hodkinson et al. 2003, 2004), and to explore the impacts of environmental changes in the absence of other anthropogenic stressors such as land use change and fragmentation (Høye et al. 2021; Pedersen et al. 2022). Located in the European High Arctic (Fig 1), the archipelago includes the three coldest botanical Arctic sub-zones, A, B, and C (Walker et al. 2005) and their associated invertebrate faunas. As a result of the international science community active in the archipelago and the establishment of the SIOS initiative there is an increasingly comprehensive resource of time-series data (e.g., meteorological, including biologically relevant soil temperatures, e.g., Convey et al. 2018) with additional projects commencing such as increased high resolution drone mapping (Research in Svalbard Database, 2024). The invertebrate inventory presented in this article will also eventually become accessible from NIRD and via the SIOS Data Portal (SIOS 2024). The establishment of SIOS and Svalbard Science Forum have facilitated access to Svalbard for researchers as well as increased collaboration. This includes the SIOS organised biennial Svalbard Science Conference that provides a meeting place for researchers working in Svalbard and the Ny-Ålesund Flagship Programmes, including the Terrestrial Ecosystems Flagship (Ny-SMAC 2024), that assists in coordinating terrestrial science and developing common infrastructure in the vicinity of the Ny-Ålesund Research Station (Fig. 1). Although improving, funding for invertebrate monitoring and research needs strengthening-with most focus currently on the more charismatic vertebrates. Freshwater monitoring has recently started on a limited scale in Dieset catchment and Linnévatn (NINA- Miljødirektoratet) (Fig. 2).

Despite the High Arctic location and environment, the presence of a sizable settlement in Longyearbyen and at the Ny-Ålesund research station provide logistical solutions to many of the challenges encountered with remote Arctic fieldwork. These include regular scheduled flights to the mainland (Oslo and Tromsø), local transport (small boats, ships, or helicopter), power for instrumentation, back-up and technical services, and accommodation. This provides logistical services for researchers to explore the impacts of environmental changes in the absence of other anthropogenic stressors such as land use change and fragmentation. As a result, locations such as Ny-Ålesund have developed a long history of terrestrial biological research (Pedersen et al. 2022).

Furthermore, regular flights now take place between Longyearbyen and Villum Research Station (close to the military unit Station Nord) in Greenland, enhancing possibilities for comparative studies between these two key Arctic locations. Finally, the establishment of the University Centre in Svalbard (UNIS) in 1994 and its subsequent rapid development provides a base for permanent staff resident in Longyearbyen to study the entire polar year along with laboratory facilities and logistical support, and, not least, skilled and enthusiastic students.

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Data availability

As described in the text the inventory is available as a searchable download from GBIF or the corresponding author. Inventory of the terrestrial and freshwater fauna of the Svalbard archipelago. Version 1.3. The University Centre in Svalbard. Checklist dataset https;//doi.org/10.15468/mfcetc accessed via GBIF.org on 14 February 2024.

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Competing interests

The authors know of no competing interests.

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Supplementary material

Supplementary data are available with the article at https://doi.org/10.1139/as-2024-0017.

References

- Aakra, K., and Hauge, E. 2003. Checklist of Norwegian spiders (Arachnida: Araneae) including Svalbard and Jan Mayen. Norwegian Journal of Entomology, 50: 109–129.
- Amrén, H. 1964a. Temporal variation of the rotifer Keratella quadrata (Müll.) in some ponds on Spitsbergen. Zoologiska Bidrag Från Uppsala, 36: 93–208.
- Amrén, H. 1964b. Ecological and taxonomical studies on zooplankton from Spitsbergen. Zoologiska Bidrag Från Uppsala, 36: 209–276.
- Aronsson, M., Heiðmarsson, S., Jóhannesdóttir, H., Barry, T., Braa, J., Burns, C.T., et al. 2021. State of the Arctic Terrestrial Biodiversity Report. Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland. ISBN 978-9935-431-94-3.
- Ávila-Jiménez, M.L., Gwiazdowicz, D.J., and Coulson, S.J. 2011. On the gamasid (Acari: Parasitiformes) mite fauna of Svalbard: a revised checklist of a high Arctic archipelago. Zootaxa, **3091**: 33–41. doi:10. 11646/zootaxa.3091.1.2.
- Ávila-Jiménez, M.L., Solhøy, T., Gwiazdowicz, D.J., Fjellberg, A., Dózsa-Farkas, K., Monson, F., et al. 2019. The invertebrate fauna of Edgeøya, Svalbard: Arctic landscape community composition reflects pan-Arctic biogeography patterns Polar Biology, 42: 837–850. doi:10.1007/ s00300-019-02471-x.
- Bayartogtokh, B., Schatz, H., and Ekrem, T. 2011. Distribution and diversity of the soil mites of Svalbard with redescriptions of three known species (Acari: Oribatida). International Journal of Acarology, **37**: 467– 484. doi:10.1080/01647954.2010.525525.
- Birkemoe, T., Coulson, S.J., and Sømme, L. 2000. Life cycles and population dynamics of enchytraeids Oligochaeta from the High Arctic. Canadian Journal of Zoology, 78: 2079–2086. doi:10.1139/z00-148.
- Brittain, J.E., Schartau, A.K., and Svenning, M.A. 2020. Biologisk mangfold i ferskvann på Svalbard: kunnskapsgrunnlag, påvirkning og forslag till framtidig overvåkning. NINA Rapport 13/2020. (in Norwegian).
- Brožová, V., Bolstad, J.S., Seregin, A.P., and Eidesen, P.B. 2023. From everywhere all at once: several colonization routes available to Svalbard in the early Holocene. Ecology and Evolution, 13: e9892. doi:10.1002/ ece3.9892.
- Böcher, J., Kristensen, N., Pape, T., and Vilhelmsen, L. 2015. The Greenland Entomofauna. An Identification Manual of Insects, Arachnids and their Allies. Fauna Entomologica Scandinavica, 44. doi:10.1163/ 9789004261051.
- Carlsson, A.M., Albon, S.D., Coulson, S.J., Ropstad, E., Stien, A., Wilson, K., et al. 2018. Little impact of over-winter parasitism on a freeranging ungulate in the high Arctic. Functional Ecology, **32**: 1046– 1056. doi:10.1111/1365-2435.13037.
- Chaubet, B., Derocles, S.A.P., Hulle, M., Le Relec, A., Outreman, Y., Simon, J-C., and Tomanovic, Z. 2013. Two new species of aphid parasitoids (Hyemnoptera, Braconidae, Aphidiinae) from the High Arctic (Spitsbergen, Svalbard). Zoologischer Anzeiger—A Journal of Comparative Zoology, 252: 34–40. doi:10.1016/j.jcz.2012.03.001.
- Convey, P., Abbandonato, H.D.A., Bergan, F., Beumer, L.T., Biersma, E.M., Bråthen, V.S., et al. 2015. Survival of rapidly fluctuating natural low winter temperatures by Arctic soil invertebrates. Journal of Thermal Biology 54: 111–117. doi:10.1016/j.jtherbio.2014.07.009smet.
- Convey, P., Coulson, S.J., Worland, M.R., and Sjöblom, A. 2018. Implications of annual and shorter term temperature patterns and variation in the surface levels of polar soils for terrestrial biota. Polar Biology, 41: 1587–1605. doi:10.1007/s00300-018-2299-0.
- Coulson, S.J. 2007. Terrestrial and freshwater invertebrate fauna of the high Arctic archipelago of Svalbard. Zootaxa, **1448**: 41–58. doi:10. 11646/zootaxa.1448.1.2.
- Coulson, S.J. 2015. The alien terrestrial invertebrate fauna of the High Arctic archipelago of Svalbard: potential implications for the native flora and fauna. Polar Research, 34: 27364, doi:10.3402/polar.v34. 27364.

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- Coulson, S.J., Hodkinson, I.D., Webb, N.R., Mikkola, K., Harrison, J.A., and Pedgley, D. 2002a. Aerial colonisation of high Arctic islands by invertebrates: the Diamondback moth, *Plutella xylostella* (Lepidoptera: Yponomeutidae) as a potential indicator species. Diversity and Distributions, **8**: 327–334. doi:10.1046/j.1472-4642.2002.00157.x.
- Coulson, S.J., Hodkinson, I.D., Webb, N.R., and Harrison, J.A. 2002b. Survival of saltwater immersion by terrestrial invertebrates. Implications for the colonisation of Arctic islands. Functional Ecology, **16**: 353–356. doi:10.1046/j.1365-2435.2002.00636.x.
- Coulson, S.J., Hodkinson, I.D., Webb, N.R., and Convey, P. 2003. A high Arctic population of *Pyla fusca* (Lepidoptera, Pyralidae) on Svalbard? Polar Biology, 26: 283–285. doi:10.1007/s00300-002-0475-7.
- Coulson, S.J., and Refseth, D. 2004. The terrestrial and freshwater invertebrate fauna of Svalbard (and Jan Mayen). *In* A catalogue of the terrestrial and marine animals of Svalbard. *Edited by* P. Prestrud, H. Strøm and H. Goldman Skrifter **201**. Norwegian Polar Institute, Tromsø. pp. 57–122.
- Coulson, S.J., Fjellberg, A., Gwiazdowicz, D.J., Lebedeva, N.V., Melekhina, E.N., Solhøy, T., et al. 2013. Introduction of invertebrates into the High Arctic via imported soils: the case of Barentsburg in Svalbard. Biological Invasions, 15: 1–5. doi:10.1007/ s10530-012-0277-y.
- Coulson, S.J., Convey, P., Aakra, K., Aarvik, L., Ávila-Jiménez, M.L., Babenko, A., et al. 2014a. The terrestrial and freshwater invertebrate biodiversity of the archipelagoes of the Barents Sea: Svalbard, Franz Josef Land and Novaya Zemlya. Soil Biology and Biochemistry, 68: 440–470. doi:10.1016/j.soilbio.2013.10.006.
- Coulson, S.J., Schatz, H., Gwiazdowicz, D.J., and Solhøy, T. 2014b. The oribatid and mesostigmatid mite fauna (Acari) of the High Arctic island of Hopen. Polish Polar Research, **35**: 133–139. doi:10.2478/popore-2014-0002.
- Coulson, S.J., Fjellberg, A., Melekhina, E.N., Taskaeva, A.A., Lebedeva, N.V., Belkina, O., et al. 2015. Microarthropod communities of disturbed or imported soils in the High Arctic: the abandoned coal mining town of Pyramiden, Svalbard. Biodiversity and Conservation, 24: 1671–1690. doi:10.1007/s10531-015-0885-9.
- Coulson, S.J., Bartlett, J., Boström, S., Brittain, J., Christoffersen, K.S., Convey, P., et al. 2024. Inventory of the terrestrial and freshwater fauna of the Svalbard archipelago. Version 1.3. The University Centre in Svalbard. Checklist dataset. Available from https://www.gbif.org/dataset /443d4938-8d5a-4e2e-a5b8-53fd139bb1d6.
- Culp, J.M., Lento, J., Goedkoop, W., Power, M., Rautio, M., Christoffersen, K.S., et al. 2012. Developing a circumpolar monitoring framework for Arctic freshwater biodiversity. Biodiversity, 13: 215–227. doi:10.1080/ 14888386.2012.717526.
- Culp, J.M., Goedkoop, W., Christensen, T., Christoffersen, K.S., Fefilova, E., Liljaniemi, P., et al. 2022. Arctic freshwater biodiversity: establishing baselines, trends, and drivers of ecological change. Freshwater Biology, 67: 1–13. doi:10.1111/fwb.13831.
- Dahl, M.T., Yoccuz, N.G., Aakra, K., and Coulson, S.J. 2018. The Araneae of Svalbard: landscape scale spider community diversity in the High Arctic. Polar Biology, 41: 839–853. doi:10.1007/s00300-017-2247-4.
- Dastych, H. 1985. West Spitsbergen Tardigrada. Acta Zoologica Cracoviensia, **28**: 2–8.
- De Smet, W.H. 1993. Report on rotifers from Barentsøya, Svalbard (78° 30' N). Fauna Norvegica A, 14: 1–26.
- De Smet, W.H., and Van Rompu, E.A. 1996. Freshwater tardigrades from Hopen, Svalbard (76° 31' N). Fauna Norvegica Series A, **17**: 1–9.
- Devetter, M., Háněl, L., Raschmanová, N., Bryndová, M., and Schlaghamerský, J. 2021. Terrestrial invertebrates along a gradient of deglaciation in Svalbard: long-term development of soil fauna communities. Geoderma, **383**: 114720. doi:10.1016/j.geoderma.2020.114720.
- Dimante-Deimantovica, I., Walseng, B., Chertoprud, E., and Novichkova, A. 2018. New and previously known species of Copepoda and Cladocera (Crustacea) from Svalbard, Norway—who are they and where do they come from? Fauna Norvegica, **38**: 18–29. doi:10.5324/fn.v38i0. 2502.
- Disko Island. 2024. Avaialble form https://arktiskstation.ku.dk/english/a bout/ [accessed 15 January 2024].
- Ekrem, T., Stur, E., Orton, M.G., and Adamowicz, S.J. 2018. DNA barcode data reveal biogeographic trends in Arctic non-biting midges. Genome, 61: 787–796. doi:10.1139/gen-2018-0100.

- Ehrenberg, C.G. 1874. Das unsichtbar wirkende Leben der Nordpolarzone. Die Zweite Deutsche Nordpolarfahrt in den Jahren 1869 und 1870, Band II, Leipzig.
- Ermilov, S.G., Makarova, O.L., and Behan-Pelletier, V.M. 2022. Taxonomy and ecology of the Arctic oribatid mite *Svalbardia lucens* comb. nov. (Acari, Oribatida, Ceratozetidae): resolving a longstanding confusion. Systematic and Applied Acarology **27**: 497–510. doi:10.11158/saa.27. 3.8.
- Fjellberg, A. 1980. Identification keys to Norwegian Collembola. Norsk Entomologisk Forening, (Norwegian Entomology Society).
- Fontaneto, D., Barraclough, T.G., Chen, K., Ricci, C., and Herniou, E.A. 2008. Molecular evidence for broad-scale distributions in bdelloid rotifers: everything is not everywhere but most things are very widespread. Molecular Ecology, 17: 3136–3146. doi:10.1111/j. 1365-294X.2008.03806.x.
- Gąsiorek, P., Stec, D., Morek, W., Zawierucha, K., Kaczmarek, Ł., Lachowska-Cierlik, D., and Michalczyk, Ł. 2016. An integrative revision of *Mesocrista* Pilato, 1987 (Tardigrada: Eutardigrada: Hypsibiidae). Journal of Natural History, **50**: 2803–2828. doi:10.1080/00222933. 2016.1234654.
- Gillespie, M.K.A., Alfredsson, M., Barrio, I.C., Bowden, J., Convey, P., Culler, L.E., et al. 2020. Status and trends of Arctic terrestrial arthropod diversity of the North Atlantic region. Ambio, 49: 718–731. doi:10.1007/s13280-019-01162-5.
- Gillespie, M.K.A., and Cooper, E.J. 2022. The seasonal dynamics of a High Arctic plant–visitor network: temporal observations and responses to delayed snow melt. Arctic Science, **8**: 786–803. doi:10.1139/ as-2020-0056.
- Goedkoop, W., Culp, J.M., Christensen, T., Christoffersen, K.S., Fefilova, E., Guðbergsson, G., et al. 2022. Improving the framework for assessment of ecological change in the Arctic: A circumpolar synthesis of freshwater biodiversity. Freshwater Biology, 67: 210–223. doi:10.1111/fwb.13873.
- Governor of Svalbard. 2017. Handlingsplan mot fremmede arter på Svalbard. Sysselmannen på Svalbard. Rapportserie Nr. 1/2017(in Norwegian).
- Grewling, Ł., Laniecki, R., Jastrzębski, M., Borkowska, J., Marek, Z., Kondrat, K., et al. 2024. Dispersal of pollen and invertebrates by wind in contrasting Arctic habitats of Svalbard. Polish Polar Research.
- Gwiazdowicz, D.J., Teodorowicz, E., and Coulson, S.J. 2011. Redescription of Zercon solenites Haarløv, 1942 (Acari, Zerconidae) with a key to the Svalbard species of the genus Zercon. International Journal of Acarology, 37: 135–148. doi:10.1080/01647954.2010.543699.
- Gwiazdowicz, D.J., and Rakowski, R. 2009. Redescription of Proctolaelaps parvanalis (Thor, 1930) (Acari: Ascidae) from Spitsbergen. Entomologica Fennica, 20: 281–286. doi:10.33338/ef.84491.
- Gwiazdowicz, D.J., and Teodorowicz, E. 2017. Description of *Halolaelaps coulsoni* n. sp. (Acari, Halolaelapidae) from the High Arctic. Acarologia, 57: 393–406. doi:10.1051/acarologia/20174164.
- Hammer, M. 1946. The zoology of East Greenland oribatids.. Meddelelser om Grønland, 122: 1–39.
- Hodkinson, I.D., Coulson, S.J., and Webb, N.R. 2003. Community assembly on proglacial chronosequences in the high Arctic: vegetation and soil development in north-west Svalbard. Journal of Ecology, 91: 651– 663. doi:10.1046/j.1365-2745.2003.00786.x.
- Hodkinson, I.D., Coulson, S.J., and Webb, N.R. 2004. Invertebrate community assembly along proglacial chronosequences in the high Arctic. Journal of Animal Ecology, 73: 556–568. doi:10.1111/j.0021-8790. 2004.00829.x.
- Holovachov, O. 2014. Nematodes from terrestrial and freshwater habitats in the Arctic. Biodiversity Data Journal, **2**: e1165. doi:10.3897/BDJ.2. e1165.
- Huemer, P., Wieser, C., Wiesmair, B., Sergey, Y.S., Wieser, C., and Yakovlev, R.V. 2017. Schmetterlinge (Lepidoptera) des Altai-Gebirges (Südsibirien, Russland)—Eindrücke einer internationalen Expedition im Spätsommer 2016. Carinthia II, 207: 27–564.
- Huhta, V. 1967. Notes on the arthropod fauna of Spitsbergen. I. 3. Some notes of the spider fauna of Spitsbergen. Annales Entomologicae Fennicae, **33**: 27.
- Høye, T., Loboda, S., Koltz, A.M., and Schmidt, N.M. 2021. Nonlinear trends in abundance and diversity and complex responses to climate change in Arctic arthropods. Proceedings of the National Academy of Sciences, **118**: e2002557117. doi:10.1073/pnas.2002557117.

- Iakovenko, N.S., Smykla, J., Convey, P., Kašparová, E., Kozeretska, I.A., Trokhymets, V., et al. 2000. Antarctic bdelloid rotifers: diversity, endemism and evolution. Hydrobiologia Parasitology, **120**: 297–311. doi:10.1007/s10750-015-2463-2.
- Irvine, R.J., Stien, A., Halvorsen, O., Langvatn, R., and Albon, S.D. 2000. Life-history strategies and population dynamics of abomasal nematodes in Svalbard reindeer *Rangifer tarandus platyrhynchus*. Parasitology, **120**: 297–311. doi:10.1017/S0031182099005430.
- Janiec, K. 1996. The comparison of freshwater invertebrates of Spitsbergen (Arctic) and King George Island (Antarctic). Pol. Polar Res. 17: 173–202.
- Jorna, J., Vandenbrink, B., Hogg, I.D., Wall, D.H., and Adams, B.J. 2023. Metabarcoding inventory of an arctic tundra soil ecosystem reveals highly heterogeneous communities at a small scale. Polar Biology, **46**: 461–471. doi:10.1007/s00300-023-03131-x.
- Jónsdóttir, I.S. 2005. Terrestrial ecosystems on Svalbard: heterogeneity, complexity and fragility from an Arctic island perspective. Proceedings Royal Irish Academy, **105**: 155e165.
- Kaczmarek, Ł., Zawierucha, K., Smykla, J., and Michalczyk, Ł. 2012. Tardigrada of the Revdalen (Spitsbergen) with the descriptions of two new species: *Bryodelphax parvuspolaris* (Heterotardigrada) and *Isohypsibius coulsoni* (Eutardigrada). Polar Biology, **35:** 1013–1026. doi:10.1007/ s00300-011-1149-0.
- Kaczmarek, Ł., Zawierucha, K., Buda, J., Stec, D., Gawlak, M., Michalczyk, Ł., and Roszkowska, M. 2018. An integrative redescription of the nominal taxon for the *Mesobiotus harmsworthi* group (Tardigrada: Macrobiotidae) leads to descriptions of two new *Mesobiotus* species from Arctic. PLoS ONE, 13: e0204756. doi:10.1371/ journal.pone.0204756.
- Karppinen, E. 1967. Data on the oribatids (Acari) of Spitzbergen. In: notes on the arthropod fauna of Spitzbergen. Annales Entomologici Fennici, 33: 18–26.
- Karppinen, E., and Krivolutsky, D.A. 1982. List of oribatid mites (Acarina, Oribatei) of the Northern Paleoarctic region. I. Europe Acta Entomologici Fennici, 41: 1–18.
- Kaya, M., De Smet, W.H., and Fontaneto, D. 2010. Survey of moss-dwelling bdelloid rotifers from middle Arctic Spitsbergen (Svalbard). Polar Biology, 33: 833–842. doi:10.1007/s00300-009-0761-8.
- Kerfahi, D., Park, J., Tripathi, B.M., Singh, D., Porazinska, D.L., Moroenyane, I., and Adams, J.M. 2017. Molecular methods reveal controls on nematode community structure and unexpectedly high nematode diversity, in Svalbard high Arctic tundra. Polar Biology, 40: 765–776. doi:10.1007/s00300-016-1999-6.
- Kihm, J.H., Zawierucha, K., Rho, H.S., and Park, T.Y.S. 2023. Homology of the head sensory structures between Heterotardigrada and Eutardigrada supported in a new species of water bear (Ramazzottiidae: *Ramazzottius*). Zoological Letters, **9**: 22. doi:10.1186/ s40851-023-00221-w.
- Kolicka, M., Kotwicki, L., and Dabert, M. 2018. Diversity of Gastrotricha on Spitsbergen (Svalbard Archipelago, Arctic) with a description of seven new species. Annales Zoologici, 68: 609–739. doi:10.3161/ 00034541ANZ2018.68.4.001.
- Kolicka, M., Dabert, M., Olszanowski, Z., and Dabert, J. 2020. Sweet or salty? The origin of freshwater gastrotrichs (Gastrotricha, Chaetonotida) revealed by molecular phylogenetic analysis. Cladistics, 36: 458–480. doi:10.1111/cla.12424.
- Kolodochka, L.A., and Gwiazdowicz, D.J. 2014. A new species of predaceous mite of the genus *Neoseiulus* Hughes (Acari, Phytoseiidae), with redescriptions of *N. magnanalis* (Thor) and *N. ellesmerei* (Chant & Hansell), from Svalbard, High Arctic. Zootaxa, **3793**: 1–452. doi:10. 11646/zootaxa.3793.4.3.
- Laniecki, R., and Magowski, W.L. 2023. New definition of Neoprotereunetes Fain et Camerik, its distribution and description of the new genus in Eupodidae (Acariformes: Prostigmata: Eupodoidea). Animals, 13(2213). doi:10.3390/ani13243761.
- Lebedeva, N.V., Lebedev, V.D., and Melekhina, E.N. 2006. New data on the oribatid mite (Oribatei) fauna of Svalbard. Doklady Biological Sciences, **407**: 182–186. doi:10.1134/S0012496606020207.
- Lebedeva, N.V., and Lebedev, V.D. 2008. Transport of oribatid mites to the polar areas by birds. Integrative Acarology, Integrative Acarology, Proceedings of the 6th European Congress. doi:359–367. doi:13140/2. 1.1428.3207.

- Lento, J., Goedkoop, W., Culp, J., Christoffersen, K.S., Lárusson, K.F., Fefilova, E., et al. 2019. State of the Arctic Freshwater Biodiversity. Conservation of Arctic Flora and Fauna International Secretariat, Akureyri, Iceland. ISBN 978-9935-431-77-6.
- Lento, J., Culp, J.M., Levenstein, B., Aroviita, J., Baturina, M.A., Bogan, D., et al. 2022. Temperature and spatial connectivity drive patterns in freshwater macroinvertebrate diversity across the Arctic. Freshwater Biology, 67: 159–175. doi:10.1111/fwb.13805.
- Lento, J., Lau, D.C., Brittain, J.E., Culp, J.M., and Goedkoop, W. 2023. Macroinvertebrate traits in Arctic streams reveal latitudinal patterns in physiology and habits that are strongly linked to climate. Frontiers in Ecology and Evolution, **11**: 1209612. doi:10.3389/fevo.2023. 1209612.
- Loof, P.A.A. 1971. Freeliving and plant parasitic nematodes from Spitzbergen collected by Mr. H. von Rossen. Mededelingen Landbouwhogeschool Wageningen 71: 1–86.
- Makarova, O.L. 2015. The fauna of free-living mites (Acari) of Greenland. Entomological Review, 95: 108–125. doi:10.1134/ S0013873815010133.
- Menzel, F., Gammelmo, Ø., Olsen, K.M., and Köhler, A. 2020. The Black Fungus Gnats (Diptera, Sciaridae) of Norway—Part I: species records published until December 2019, with an updated checklist. ZooKeys, 957: 17–104. doi:10.3897/zookeys.957.46528.
- Mills, S., Alcántara-Rodríguez, J.A., Ciros-Pérez, J., Gómez, A., Hagiwara, A., and Galindo, K.H. 2017. Fifteen species in one: deciphering the *Brachionus plicatilis* species complex (Rotifera, Monogononta) through DNA taxonomy. Hydrobiologia, **796**: 39–58. doi:10.1007/ s10750-016-2725-7.
- Moerman, T.M., Albon, S., Coulson, S.J., and Loe, L.E. 2023. Climate change effects on parasitic nematodes—where are the knowledge gaps? Journal of Helminthology, 97: e94,1–e9411. doi:10.1017/ S0022149X23000652.
- Niedbała, W. 1971. Oribatei (Acari) of Spitsbergen. Bulletin of the Polish Academy of Sciences Biological Sciences, **19**: 737–742.
- Nielsen, T.R., and Gammelmoe, Ø. 2017. Sjekkliste over norske blomsterfluer (Diptera, Syrphidae). Insekt-Nytt, 42: 15–42.
- Nowosad, D., Hogg, I.D., and Adamowicz, S. 2020. Using DNA barcoding to inventory and track changes in the distribution and diversity of freshwater invertebrates in the Canadian Arctic. Polar Knowledge: Aqhaliat Report, **3**: Polar Knowledge Canada, p. 15–17.
- Ny-SMAC. 2024. Ny-Ålesund Science Managers Committee. Available from https://nyalesundresearch.no/research-and-monitoring/terrest rial-ecosystems/15/01/24.
- Oudemans, A.C. 1928. Acari von Svalbard (früher Spitzbergen). Archiv für Naturgeschichte, **92**: 106–127.
- Pedersen, Å.Ø., Convey, P., Fuglei, E., Ravolainen, V., Newsham, K.K., Augusti, A., et al. 2022. High Arctic terrestrial research in Ny-Ålesund, Svalbard: a synthesis. Polar Research. 41: 6310. doi:10.33265/polar. v41.6310.
- Pilskog, H.E., Solhøy, T., Gwiazdowicz, D.J., Grytnes, J.A., and Coulson, S.J. 2014. Invertebrate communities inhabiting nests of migrating passerine, wild fowl and sea birds breeding in the High Arctic, Svalbard. Polar Biology. 37: 981–998. doi:10.1007/s00300-014-1495-9.
- Research in Svalbard Database. 2024. Available from https://www.resear chinsvalbard.no/ [accessed 14 January 2024].
- Schlaghamersky, J., and Devetter, M. 2019. Enchytraeid assemblages at the foot of a talus slope in Skansbukta on the Arctic island of Spitsbergen. Soil Organisms 91: 97–105.
- Schlaghamerský, J., Bílková, M., Tóthová, A.S., and Devetter, M. 2023. Enchytraeids in imported soil and organic deposits in Pyramiden, an abandoned mining town on Spitsbergen in the High Arctic. Applied Soil Ecology, **192**: 105069. doi:10.1016/j.apsoil.2023.105069.
- Schmelz, R.M., and Collado, R. 2010. A guide to European terrestrial and freshwater species of Enchytraeidae (Oligochaeta). Soil Organisms, 82: 1–176. Available from https://soil-organisms.org/index.php/SO/ar ticle/view/203.
- Schmelz, R.M., and Collado, R. 2023. Checklist of taxa of Enchytraeidae (Oligochaeta): an update. Soil Organisms, 87: 149–152. Available from https://soil-organisms.org/index.php/SO/article/view/326.
- Schütz, S.A., Brittain, J.E., and Füreder, L. 2022. Diverging life cycle patterns of two Diamesa species (Diptera, Chironomidae) in High Arctic streams, Svalbard. Polar Biology. 45: 285–296. doi:10.1007/ s00300-021-02987-1.



- Seniczak, A., and Seniczak, S. 2020. Diversity of oribatid mites (Acari: Oribatida) in the Svalbard archipelago: a historical overview. Zootaxa, 4834.1.3.
- Seniczak, A., Seniczak, S., Schwarzfeld, M.D., Coulson, S.J., and Gwiazdowicz, D.J. 2020. Diversity and distribution of mites (Acari: Ixodida, Mesostigmata, Trombidiformes, Sarcoptiformes) in the Svalbard Archipelago. Diversity, 12: 323. doi:10.3390/d12090323.
- Seniczak, A., and Seniczak, S. 2022. Morphological ontogeny of Platynothrus coulsoni sp. nov. (Acari, Oribatida, Camisiidae) from Spitsbergen (Norway). Systematic and Applied Acarology, 27: 1436–1453.
- Simon, J.-C., Mahéo, F., Mieuzet, L., Buchard, C., Gauthier, J.-P., Maurice, D., et al. 2019. Life on the Edge: Ecological Genetics of a High Arctic Insect Species and Its Circumpolar Counterpart. Insects, 10: 427. doi:10.3390/insects10120427.
- SIOS. 2024. Available from https://sios-svalbard.org/Data [accessed 9 February 2024].
- Stec, D. 2023. Integrative taxonomy helps to revise systematics and questions the purported cosmopolitan nature of the type species within the genus *Diaforobiotus* (Eutardigrada: Richtersiusidae). Organisms Diversity & Evolution, 23: 309–328. doi:10.1007/s13127-022-00592-6.
- Stien, A., Irvine, R.J., Ropstad, E., Halvorsen, O., Langvatn, R., and Albon, S.D. 2002. The impact of gastrointestinal nematodes on wild reindeer: experimental and cross-sectional studies. Journal of Animal Ecology, **71**: 937–945. doi:10.1046/j.1365-2656. 2002.00659.x.
- Stoltz, C. 2019. The nestling diet of Svalbard snow buntings identified by DNA metabarcoding. Masters report. University of Tromsö, Norway, 33pp.
- Strathdee, A.T., and Bale, J.S. 1995. Factors limiting the distribution of Acyrthosiphon svalbardicum (Hemiptera: Aphididae) on Spitsbergen. Polar Biology, 15: 375–380. doi:10.1007/BF00238489.
- Stur, E., and Ekrem, T. 2020. The Chironomidae (Diptera) of Svalbard and Jan Mayen. Insects, 2020, **11**: 183.
- Subías, L.S. 2023. Listado sistemático, sinonímico y biogeográfico de los Ácaros Oribátidos (Acariformes, Oribatida) del mundo (1758–2002). Graellsia 2004, 60 (número extraordinario), 3-305. Updated 2023–18 actualization, 540pp., [accessed December, 2023].
- Svenning, M.A., Aas, M., and Borgstrøm, R. 2015. First records of threespined stickleback *Gasterosteus aculeatus* in Svalbard freshwaters: an effect of climate change? Polar Biology, **38**: 1937–1940. doi:10.1007/ s00300-015-1752-6.
- Søli, G.E.E., Aarvik, L., and Magnussen, T. 2018. *Plutella polaris* Zeller, 1880 (Lepidoptera, Plutellidae) rediscovered at Svalbard, Norway, with comments on its taxonomic position. Nota Lepidopterologica, 41: 129–137. doi:10.3897/nl.41.22423.
- Teodorowicz, E., Gwiazdowicz, D.J., and Coulson, S.J. 2014. Redescription of Antennoseius (Vitzthumia) oudemansi (Acari, Mesostigmata) from Spitsbergen, Svalbard. Entomologica Fennica, 25: 27–42. doi:10. 33338/ef.41467.
- Thor, S. 1930. Beiträge zur Kenntnis der Invertebraten fauna von Svalbard. Skrifter om Svalbard Ishavet, **27**: 1–156.
- Thor, S. 1931. Norwegische Alycidae I-VII. Zoologischer Anzeiger, **94**: 229–238.
- Thor, S. 1932. Norwegische Tydeidae VIII-XV, mit Bemerkungen über die Gattung Tydeus und über Augen, Trachées usw. Zoologischer Anzeiger, 98: 69–91.
- Thor, S. 1934. Neue Beiträge zur Kenntnis der Invertebraten-Fauna vin Svalbard. Zoologischer Anzeiger, **107**: 114–139.
- Thorell, T. 1871. Om Arachnider från Spetsbergen och Beeren-Eiland. Öfvers. K. Vet. Akad. Forhandl. 6: 683–702.
- Trägårdh, I. 1900. Beiträge zur Fauna der Bären-Insel. K. Svenska Vet. Akademien Handlingar, **26**: 1–24.
- Van Rompu, E.A., and De Smet, W.H. 1994. Freshwater tardigrades from Hopen, Svalbard (76°31′N). Fauna Norvegica Series A, **17**: 1–9.
- Von Goes, A. 1862. Om Tardigrader Anguillulae m.m. fr\u00e4n Spetsbergen. Öfvers. K. Vet. Akad. Forhandl. 1862: 18.
- Walker, D.A., Raynolds, M.K., Daniëls, F.J.A., Einarsson, E., Elvebakk, A., Gould, W.A., et al. 2005. The circumpolar Arctic vegetation map. Journal of Vegetation Science. 16: 267–282. doi:10.1111/j.1654-1103.2005. tb02365.x.
- Walseng, B., Jensen, T., Dimante-Deimantovica, I., Christoffersen, K.S., Chertoprud, M., Chertoprud, E., et al. 2018. Freshwater diversity in

Svalbard: providing baseline data for ecosystems in change. Polar Biology, **41**: 1995–2005. doi:10.1007/s00300-018-2340-3.

- Wieczorek, K., and Chłond, D. 2019. The first detection of the alien species: green-peach aphid Myzus (Nectarosiphon) persicae (Insecta, Hemiptera, Aphididae) in the Svalbard archipelago. Polar Biology, 42: 1947–1951. doi:10.1007/s00300-019-02562-9.
- Wieczorek, K., Chłond, D., Junkiert, Ł., and Świątek, P. 2020. Structure of the reproductive system of the sexual generation of the endemic Arctic species Acyrthosiphon svalbardicum and its temperate counterpart Acyrthosiphon pisum (Hemiptera, Aphididae). Biology of Reproduction, 103: 1043–1053. doi:10.1093/biolre/ioaa147.
- Zackenberg. 2024. Available from https://g-e-m.dk/gem-localities/zacken berg [accessed 15 January 2024].
- Zawierucha, K., Coulson, S.J., Michalczyk, Ł.U, and Kaczmarek, Ł.U. 2013. Current knowledge of the Tardigrada of Svalbard with the first records of water bears from Nordaustlandet (High Arctic). Polar Research, 32: 20886. doi:10.3402/polar.v32i0.20886.
- Zawierucha, K., Smykla, J., Michalczyk, Ł., Gołdyn, B., and Kaczmarek, Ł. 2015. Distribution and diversity of Tardigrada along altitudinal gradients in the Hornsund, Spitsbergen (Arctic). Polar Research, 34: 24168. doi:10.3402/polar.v34.24168.
- Zawierucha, K., Zmudczyńska-Skarbek, K., Kaczmarek, Ł., and Wojczulanis-Jakubas, K. 2016. The influence of a seabird colony on abundance and species composition of water bears (Tardigrada) in Hornsund (Spitsbergen, Arctic). Polar Biology, **39**: 713–723. doi:10.1007/s00300-015-1827-4.
- Zawierucha, K., Węgrzyn, M., Ostrowska, M., and Wietrzyk, P. 2017. Tardigrada in Svalbard lichens: diversity, densities and habitat heterogeneity. Polar Biology, 40: 1385–1392. doi:10.1007/ s00300-016-2063-2.
- Zawierucha, K., Podkowa, P., Marciniak, M., Gasiorek, P., Zmudczyńska-Skarbek, K., Janko, K., and Włodarska-Kowalczuk, M. 2018.
 Temperature (latitude) and nutrient (seabird guano) effects on limno-terrestrial Tardigrada (*Testechiniscus spitsbergensis* and *Pilatobius recamieri*) body size. Polar Research, 37: 1492297. doi:10.1080/ 17518369.2018.1492297.
- Zawierucha, K., Zmudczyńska-Skarbek, K., Guil, N., and Bogdziewicz, M. 2019a. Seabirds modify trophic groups, while altitude promotes xeric-tolerant species of Tardigrada in the high Arctic tundra (Svalbard archipelago). Acta Oecologica, **98:** 50–58. doi:10.1016/j.actao. 2019.05.007.
- Zawierucha, K., Buda, J., and Nawrot, A. 2019b. Extreme weather event results in the removal of invertebrates from cryoconite holes on an Arctic valley glacier (Longyearbreen, Svalbard). Ecological Research, 34: 370–379. doi:10.1111/1440-1703.1276.
- Zawierucha, K., Buda, J., Fontaneto, D., Ambrosini, R., Franzetti, A., Wierzgoń, M., and Bogdziewicz, M. 2019c. Fine-scale spatial heterogeneity of invertebrates within cryoconite holes. Aquatic Ecology, 53: 179–190. doi:10.1007/s10452-019-09681-9.
- Zawierucha, K., Buda, J., Jaromerska, T.N., Janko, K., and Gasiorek, P. 2020. Integrative approach reveals new species of water bears (*Pilatobius, Grevenius*, and *Acutuncus*) from Arctic cryoconite holes, with the discovery of hidden lineages of *Hypsibius*. Zoologischer Anzeiger, 289: 141–165. doi:10.1016/j.jcz.2020.09.004.
- Zawierucha, K., Porazinska, D.L., Ficetola, G.F., Ambrosini, R., Baccolo, G., Buda, J., et al. 2021. A hole in the nematosphere: tardigrades and rotifers dominate the cryoconite hole environment, whereas nematodes are missing. Journal of Zoology, **313**: 18–36. doi:10.1111/jzo. 12832.
- Zawierucha, K., Kašparová, E.Š., McInnes, S., Buda, J., Ambrosini, R., Devetter, M., et al. 2023. Cryophilic Tardigrada have disjunct and bipolar distribution and establish long-term stable, low-density demes. Polar Biology, 46: 1011–1027. doi:10.1007/s00300-023-03170-4.
- Zmudczyńska-Skarbek, K., Bokhorst, S., Convey, P., Gwiazdowicz, D.J., Skubała, P., Zawierucha, K., and Zwolicki, A. 2023. The impact of marine vertebrates on polar terrestrial invertebrate communities. Polar Biology. doi:10.1007/s00300-023-03134-8.
- Zwolicki, A., Zmudczyńska-Skarbek, K., Matuła, J., Wojtuń, B., and Stempniewicz, L. 2016. Differential responses of Arctic vegetation to nutrient enrichment by plankton-and fish-eating colonial seabirds in Spitsbergen. Frontiers in Plant Science, 07: 1959. doi:10.3389/fpls.2016. 01959.

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