



The impact of marine vertebrates on polar terrestrial invertebrate communities

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Received: 3 October 2022 / Revised: 28 March 2023 / Accepted: 4 April 2023
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Abstract

Marine birds and pinnipeds which come to land to breed, rest and moult are widely known to fertilize adjacent terrestrial ecosystems, with cascading effects on vegetation and other trophic levels. We provide a synthesis of the consequences of allochthonous nutrient enrichment for terrestrial invertebrate communities within and around marine vertebrate aggregation sites and nutrient sources in the High Arctic and Continental and Maritime Antarctic, the most nutrient-poor and environmentally extreme parts of the polar regions. Using a combination of literature review (identifying 19 articles from the Arctic Svalbard archipelago and 12 from different Antarctic locations) and new analyses of available datasets of springtail, mite and tardigrade community composition, we confirmed that terrestrial invertebrate abundance and species richness tended to increase, and their community compositions changed, as a result of marine vertebrate fertilisation in both polar regions. These changes were significantly greater on talus slopes enriched by kittiwakes, guillemots and little auks in the Arctic, as compared to the edges of penguin colonies in the Antarctic. Both these habitat areas were typically abundantly vegetated and provided the most favourable microhabitat conditions for terrestrial invertebrates. The most heavily disturbed and manured areas within Antarctic penguin rookeries and seal wallows, generally on flat or gently sloping ground, were typically characterised by extremely low invertebrate diversity. In the Arctic, only sites directly beneath densely-occupied bird cliffs were to some extent comparably barren. Invertebrate responses are dependent on a combination of vertebrate activity, local topography and vegetation development.

Keywords Allochthonous nutrients · Seabird colonies · Seal wallows · Acari · Collembola · Tardigrada

Introduction

Marine vertebrates, primarily birds and pinnipeds, deliver vast amounts of nutrients to terrestrial domains in various regions of the Earth, as they come to land in order to breed, rest or moult (Şekercioğlu 2006; Grant et al. 2022). Allochthonous nutrients typically promote vegetation growth, significantly modify its structure and composition, and have a cascade of impacts through other trophic levels and on various ecosystem processes (e.g. (Mulder et al. 2011;

Otero et al. 2018; De La Peña-Lastra 2021; Almela et al. 2022). Vertebrate fertilisation of terrestrial habitats has been reported from the polar regions (Panagis 1985; Smith 1988, 2008; Smith and Froneman 2008; Zmudczyńska et al. 2012; Zwolicki et al. 2016b; Bokhorst et al. 2019a, b), where low temperatures, and limited nutrient and water availability often constrain physiological and community processes (Thomas et al. 2008). However, an overview of terrestrial invertebrate responses to the influence of marine vertebrates in polar regions is lacking. It might be hypothesised that polar terrestrial ecosystems are likely to be particularly sensitive to input of nitrogen or phosphorus, more so than ecosystems elsewhere, since they are typically characterised by chronically low nutrient availability (Grant et al. 2022). Furthermore, the magnitude of ornithogenic nutrient inputs in polar regions, particularly in parts of Antarctica, has been recognized as being amongst the highest globally (Otero et al. 2018). Here, we set out to provide a clearer perspective

This article belongs to the special issue on the “Pathways and impacts of biotically-mediated marine and other stored nutrient transfer between polar ecosystems”, coordinated by Peter Convey, Katarzyna Zmudczyńska-Skarbek, and Stef Bokhorst.

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on the impact of marine vertebrates on Arctic and Antarctic terrestrial invertebrate communities.

Terrestrial invertebrates are amongst the most abundant and species-rich groups (excluding microorganisms) in both polar regions, and are the only permanent, year-round fauna resident across much of the Antarctic continent (Hodkinson et al. 2013; Hogg et al. 2014; Convey 2017). Among the dominant groups both in terms of species richness and abundance are springtails (Collembola), mites (Acari), flies (Diptera), water bears (Tardigrada), nematodes (Nematoda), rotifers (Rotifera) and enchytraeids (Annelida) (Danks 1981; Jensen and Christensen 2003; Coulson et al. 2014; Hogg et al. 2014; Convey 2017). They provide a wide variety of ecological functions and, in particular, are key players in the decomposition process, and carbon and nutrient cycling (Gillespie et al. 2020). Importantly, the main pathway of energy flow in both Arctic and Antarctic terrestrial food webs runs directly from primary producers to decomposers to organic matter stored in the soil (Davis 1981). Improved understanding of the manner in which these terrestrial invertebrates respond to external nutrient inputs will provide a key contribution to explaining geographical distribution patterns and future modelling of biodiversity.

Distributions of polar soil and limno-terrestrial meso-, meio- and microfauna are characteristically highly patchy, and their population densities vary greatly between habitats and sites over even very short distances (Usher and Booth 1984, 1986; Hertzberg et al. 1994; Coulson et al. 2003; Zawierucha et al. 2015b). Abundances increase substantially at locations with favourable microclimate, nutrient and water status, often influenced by the presence of vegetation, to levels comparable or even higher than typically found in temperate or tropical forests (Potapov et al. 2022). The vicinity of seabird nesting sites and other point sources of nutrients such as beached vertebrate carcasses, provide striking examples of this (Fig. 1; Uvarov and Byzova 1995; Convey 1996; Hodkinson et al. 2013; Zwolicki et al. 2020). However, to date, studies synthesising information on the terrestrial fauna of both polar regions have not generally considered in detail the influence of marine vertebrate fertilisation (Sohlenius et al. 2004; Coulson et al. 2014; Hogg et al. 2014; Russell et al. 2014; Velasco-Castrillón et al. 2014).

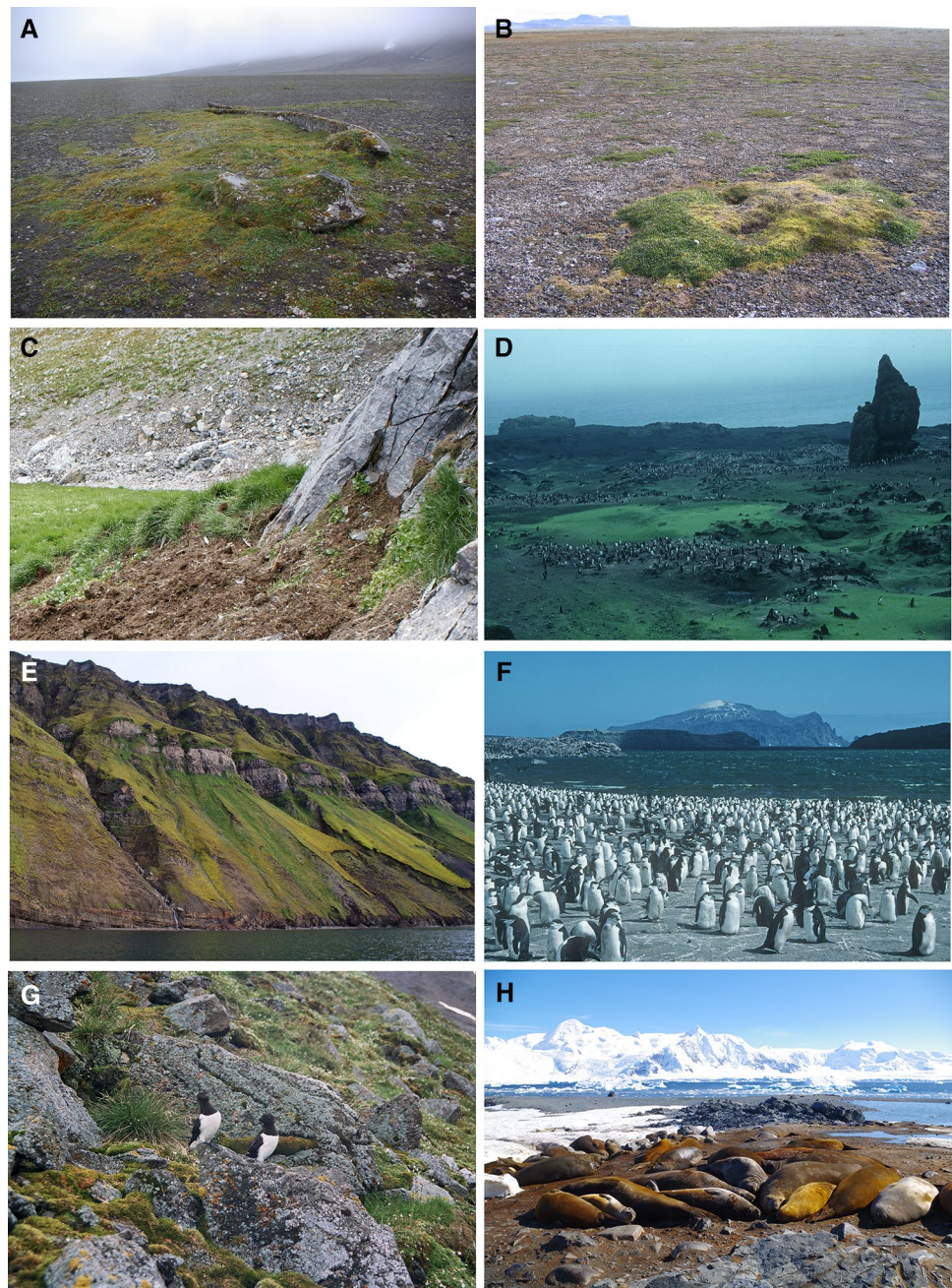
The critical link between marine vertebrate fertilization and terrestrial invertebrates is through nutrient-subsidized vegetation and microbiota. This fertilization effect is often quantified through analyses of nitrogen content of plant material, and causally linked to a marine origin using nitrogen stable isotopes ($\delta^{15}\text{N}$) (Erskine et al. 1998; Crittenden et al. 2015; Bokhorst et al. 2019a, b). Plants and algae, both living and dead, may be directly consumed by invertebrates (Hodkinson et al. 1994; Zawierucha et al. 2019; Almela et al. 2022). Favourable microenvironmental conditions are created amongst foliage (including within macroscopic algal

and other microbial mats) and in the underlying soil, providing shelter from cold, drought, abrasion and excessive solar radiation for both invertebrates and their food including algae, fungi, bacteria and larger prey (Coulson et al. 2003; Bokhorst et al. 2007; Thomas et al. 2008). The type and scale of invertebrate responses to fertilization, such as changes in abundance, species composition and richness, are likely to differ between taxonomic and trophic groups (Zmudczyńska-Skarbek et al. 2017; Bokhorst et al. 2019a; Zawierucha et al. 2019). Different responses may also be hypothesized between northern and southern polar regions due to both differences in invertebrate taxonomic composition, and large-scale differences in the characteristics of the terrestrial locations occupied by different marine vertebrates in the two regions (Fig. 1). In the Arctic, there is particularly strong representation of colonially nesting seabirds, in particular alcids, which occupy high density sites on scree slopes and cliff ledges, while, in the Antarctic, which has no terrestrial vertebrate predators, penguin colonies predominate on coastal flats, with seals hauling out close to shorelines. Although marine mammal aggregations are present in the Arctic (e.g. walrus), their terrestrial impacts have not been investigated.

The Arctic and Antarctic regions contrast in their biodiversity, history, climate and geology, but their terrestrial ecosystems, particularly at higher latitudes, are typically highly nutrient deficient, and any nutrient subsidies are of fundamental importance for the local terrestrial biota (Thomas et al. 2008; Callaghan et al. 2013; Convey 2017). The polar regions are also exposed and exceptionally vulnerable to transformations resulting from current and predicted climate change, including multi-year ice and permafrost melting, air and ocean temperature increases (regionally being the greatest on Earth in recent decades), and fluctuations in the position of the highly productive oceanic Polar Fronts which are key foraging habitats for seabirds (IPCC 2019). The multiple facets of these environmental changes thus impact marine vertebrates (Stempniewicz et al. 2007; Clucas et al. 2014; Sandvik et al. 2014; Furness 2016; Barrett et al. 2017; Bestley et al. 2020) which, in turn, leads to predictions of changed nutrient inputs to neighbouring terrestrial and nearshore marine systems, and consequential alterations in their biodiversity patterns (Bokhorst et al. 2019a).

The primary objective of this study is to provide a synthesis of the possible consequences of allochthonous nutrient enrichment for terrestrial invertebrate communities within and around marine vertebrate aggregation sites in the High Arctic and Continental and Maritime Antarctic, the most environmentally extreme parts of the polar regions (Thomas et al. 2008; Convey et al. 2014; Convey 2017). Using a combination of literature review and new analyses of available datasets, we aim to identify (I) which invertebrate taxonomic groups respond to marine-derived nutrients and how, (II)

Fig. 1 Types of locations influenced by different marine vertebrate aggregations and nutrient sources: **A** vegetation patch around whalebones on raised beaches on Edgeøya, Svalbard, **B** vegetation patch around a great skua nest on Bjørnøya, Svalbard, **C** mechanically damaged base of a bird cliff occupied by black-legged kittiwakes and Brünnich's guillemots in Hornsund, Svalbard, **D** *Prasiola crispa* mats covering areas of intense penguin trampling on Saunders Island, South Sandwich Islands, **E** lush vegetation covering scree slopes beneath bird cliffs occupied by black-legged kittiwakes and Brünnich's guillemots in Isfjorden, Svalbard, **F** centre of a chinstrap penguin colony on Candlemas Island, South Sandwich Islands, **G** scree slope within the colony of little auks in Hornsund, Svalbard, **H** elephant seal wallow on Lagoon Island, Antarctica



whether the same invertebrate responses are seen in both Arctic and Antarctic ecosystems, and (III) identify the role of vegetation and vertebrate activity on polar invertebrate responses to nutrient subsidies.

Methods

Literature review

To identify literature reporting effects of marine vertebrate fertilization on terrestrial invertebrates in the Arctic and

Antarctic we searched Google Scholar using all combinations of the following strings: seabird/penguin/seal/guano/vertebrate/nutrient/ornithogenic AND invertebrate/arthropod/collembola/springtail/acari/mite/mesostigmata/oribatida/prostigmata/araneae/spider/insect/beetle/chironomid/tardigrada/water bear/nematode/enchytraeid/rotifer/protozoa AND arctic/antarctic/polar. We focused on studies reporting data from the High Arctic and Continental and Maritime Antarctic (CA and MA, respectively), and omitted those relating only to the Low or sub-Arctic and the sub-Antarctic, as the former are much more nutrient-limited and, hence, are where the strongest responses to local nutrient input

are expected (Thomas et al. 2008; Convey et al. 2014). We also examined the citation lists from the articles returned in the search to identify omissions. Invertebrate responses to marine vertebrate influence identified or proposed in these articles were tabulated separately for the Arctic (Table 1) and the Antarctic (Table 2). These included changes in taxon abundance, species richness or diversity, community composition, body size, and nitrogen stable isotope ratio ($\delta^{15}\text{N}$), the last of these being the most commonly-used proxy for estimating ornithogenic enrichment and nutrient flow through the food chain (e.g. Kolb et al. 2010; Gillies et al. 2012). Studies describing invertebrate composition around vertebrate colonies but not investigating the effects of the colony on invertebrate communities were not included in the Tables (e.g. Węglarska 1965; Dastyh 1985; Zawierucha et al. 2013). We also excluded studies specifically focusing on the invertebrate fauna of seabird nests, considering this to be a specific habitat not comparable to soil or vegetation due to altered temperature, moisture and access to living and dead bird tissues amongst other factors, although recognising that this habitat is inhabited in part by a distinct commensal or parasitic fauna. For introduction to the specific invertebrate fauna of nests, see Coulson et al. (2009b), Pilskog et al. (2014), Kaczmarek et al. (2018) and Vanstreels et al. (2020).

Meta-analysis of numerical data

To test the general influence of marine vertebrate fertilisation on the variability in community composition of the most abundant invertebrate groups, first, regardless of, and then, with regard to their taxonomic affiliation or polar region we examined several available raw datasets of invertebrate species composition from distinct locations in the High Arctic and Maritime Antarctic regions. These two regions are considered as being comparable to some extent in terms of characteristic climatic conditions and living plant biomass (Thomas et al. 2008). Each dataset covered an area subsidized by vertebrates (primarily seabirds), and a control area, free from allochthonous enrichment. The accessible data encompassed invertebrate communities inhabiting sites within and around seabird nesting grounds located on talus slopes and plateaus in the High Arctic (Svalbard archipelago), and in the vicinities of penguin colonies and seal wallows in the Maritime Antarctic (Antarctic Peninsula, South Shetland Islands and South Orkney Islands). These datasets did not set out to assess the most extreme exposure to vertebrate impact of the very large guano input and strong mechanical disturbance clearly evident within the boundaries of penguin rookeries and seal wallows, and, to a lesser extent, directly at the foot of bird cliffs (e.g. Hodgkinson et al. 1994; Porazinska et al. 2002; Zmudczyńska et al. 2012; Smykla et al. 2018).

Datasets available from the Arctic included the taxonomic composition of springtail communities (35 species) from Hamburgbukta (NW Spitsbergen), Isfjorden (central Spitsbergen) and Bjørnøya (Zmudczyńska-Skarbek et al. 2015, 2017), mites (Oribatida, Mesostigmata, in total 48 species) from Hamburgbukta and Isfjorden (Zmudczyńska-Skarbek et al., unpublished data), and Bjørnøya (Zmudczyńska-Skarbek et al. 2017), and tardigrades (43 species) from Svalbard (Hornsund, Kongsfjorden, Nissenfjella, Nordaustlandet, Amsterdamøya, Danskøya, Fuglesongen, Phippsøya, Parrøya, and Prince Karl Forland, Zawierucha et al. 2015b, 2016, 2017, 2018, unpublished data). The Antarctic datasets contained records of springtails (6 species) and mites (Oribatida, Mesostigmata, Prostigmata, in total 9 species) from Signy Island (South Orkney Islands), Byers Peninsula (Livingston Island, South Shetland Islands), and islands within Ryder Bay (south-east Adelaide Island) (Bokhorst and Convey 2016; Bokhorst et al. 2019a, b). Abundance of individual species of springtails and mites from the Arctic was measured by number of individuals per sample (soil-vegetation core of 6 cm diameter, and ca. 5 cm soil depth). Arctic tardigrade and Antarctic springtail and mite abundances were estimated by number of individuals per 1 g of vegetation. Detailed descriptions of sampling methods and the study locations are given in the original studies cited.

As a measure of the invertebrate community composition change we used sample scores for the first axis of the unconstrained (but containing data from the Vertebrate and Control areas) Detrended Correspondence Analysis (DCA) performed separately for the microarthropods (springtails and mites merged) and tardigrades, and for each location. The length of ordination axes, measured in standard deviation (SD) units, which estimated the heterogeneity in community composition, revealed the non-linear structure of the data (> 3.5 SD in all datasets) for which approximation with a unimodal (weighted-averaging) ordination method like DCA was recommended (Šmilauer and Lepš 2014). In order to skip the within-group variances, and because the compared datasets containing different measures of species abundances for the two invertebrate groups, sample scores for the first axis of each DCA model were standardised, and all data from the separate models were combined into a single data frame. Based on these data, we then compared (i) the magnitudes of invertebrate community composition responses to vertebrate fertilization (i.e. between-group variances) between the two polar regions, and (ii) within the High Arctic alone, vertebrate-influenced changes in composition between the major groups, i.e. soil-dwelling microarthropods and limno-terrestrial tardigrades occupying mainly bryophytes and lichens, but also occurring in litter and soil (Coulson et al. 2014; Zawierucha et al. 2015a, b; no comparable tardigrade data set is available from the Antarctic). ANOVA was performed to identify differences.

Table 1 List of different terrestrial invertebrate taxa responses to seabird colonies presences, measured in the High Arctic localities (all situated within the Svalbard archipelago)

Taxa	Abundance	Species richness/diversity	Species composition	Body size	Tissue $\delta^{15}\text{N}$	Seabird species	Location	References
Collembola	Higher	–	–	–	–	BIK, CE	Spitsbergen (Kongsfjorden)	Bengston et al. (1974)
Collembola	–	–	Change ^a	–	–	BIK	Spitsbergen (Kongsfjorden)	Hodkinson et al. (1994)
Collembola	Higher	–	Change	–	–	LA	Spitsbergen (Hornsund)	Byzova et al. (1995)
Collembola	–	–	Change	–	–	BrG, BIK, LA	Spitsbergen (Hornsund)	Uvarov and Byzova (1995)
Collembola	–	Higher	–	–	–	–	Nordautlandet	Fjellberg (1997)
Collembola	–	–	Change	–	–	BrG, BIK	Spitsbergen (Kongsfjorden)	Sømme and Birkemoe (1999)
Collembola	–	Relatively high ^b	–	–	–	AS	Nordautlandet	Lebedeva and Taskaeva (2012)
Collembola	Higher	Lower	Change	–	–	BrG, BIK, LA	Spitsbergen (Hornsund)	Zmudczyńska et al. (2012)
Collembola	–	ns	Change	–	–	GG, GS, LA	Bjørnøya, Spitsbergen (Hamburgbukta, Isfjorden)	Zmudczyńska-Skarbek et al. (2015)
Collembola	–	–	–	–	Higher	AF, BIG, BrG, BIK, CE, NF	Spitsbergen (Kongsfjorden, Krossfjorden)	Kristiansen et al. (2019)
Collembola	No clear effect	Higher	Change	–	–	BIG, GG, LA	Spitsbergen (Grønfjorden)	Lebedeva et al. (2020)
Collembola, Acari	ns	ns ^c	Change	–	Higher ^d	GG, GS, LA	Bjørnøya	Zmudczyńska-Skarbek et al. (2017)
Acari	No clear effect	–	–	–	–	BIK, CE	Spitsbergen (Kongsfjorden)	Bengston et al. (1974)
Acari	No clear effect	–	Change	–	–	LA	Spitsbergen (Hornsund)	Byzova et al. (1995)
Acari	Higher	Higher	Change	–	–	BIG, GG, LA	Spitsbergen (Grønfjorden)	Lebedeva et al. (2020)
Aranei	Higher	Higher	Change	–	–	BIG, GG, LA	Spitsbergen (Grønfjorden)	Lebedeva et al. (2020)
Coleoptera (Staphyllinidae) ^e	Higher	Higher	Change	–	–	BIG, GG, LA	Spitsbergen (Grønfjorden)	Lebedeva et al. (2020)
Diptera (larvae)	Higher	–	–	–	–	BIK, CE	Spitsbergen (Kongsfjorden)	Bengston et al. (1974)

Table 1 (continued)

Taxa	Abundance	Species richness/diversity	Species composition	Body size	Tissue $\delta^{15}\text{N}$	Seabird species	Location	References
Diptera (larvae)	Higher	–	–	–	–	LA	Spitsbergen (Hornsund)	Byzova et al. (1995)
Tardigrada <i>Diaforobiotus islandicus</i>	–	–	–	Higher	–	LA	Spitsbergen (Hornsund)	Zawierucha et al. (2015a)
Tardigrada	–	Change	Change	–	–	LA	Spitsbergen (Hornsund)	Zawierucha et al. (2015b)
Tardigrada	Higher	ns	Change	–	–	LA	Spitsbergen (Hornsund)	Zawierucha et al. (2016)
Tardigrada	No effect	–	–	–	–	LA, BIK, NF	Spitsbergen, Prins Karl Forland, Danskøya, Fuglesongen, Nordaustlandet, Phippsøya, Parryøya	Zawierucha et al. (2017)
Tardigrada <i>Testechiniscus spitsbergensis</i> , <i>Pilatobius recamieri</i>	–	–	–	ns	–	LA	Bjørnøya, Fuglesongen, Nordaustlandet, Phippsøya, Spitsbergen (Hornsund)	Zawierucha et al. (2018)
Tardigrada	Higher: grazers and eutardigrades, the rest ns	–	–	–	–	LA	Spitsbergen (Hornsund)	Zawierucha et al. (2019)
Nematoda	Higher	–	–	–	–	LA	Spitsbergen (Hornsund)	Byzova et al. (1995)
Enchytreidae	No effect	–	–	–	–	LA	Spitsbergen (Hornsund)	Byzova et al. (1995)
Testacea	–	ns	Change	–	–	BIG, GG, LA	Spitsbergen (Grønfjorden)	Mazei et al. (2018)

Seabird species abbreviations: *AP* Atlantic puffin *Fratercula arctica*, *AS* Arctic skua *Stercorarius parasiticus*, *BIG* black guillemot *Cepphus grylle*, *BIK* black-legged kittiwake *Rissa tridactyla*, *BrG* Brünnich's guillemot *Uria lomvia*, *CE* common eider *Somateria mollissima*, *GG* glaucous gull *Larus hyperboreus*, *GS* great skua *Stercorarius skua*, *LA* little auk *Alle alle*, *NF* northern fulmar *Fulmarus glacialis*

Hyphen means the parameter was not studied or data non-available, *ns* non significant response

^aConcluded by us from the given increased *Onychiurus arcticus* abundance below bird cliffs

^bData compared with those presented in (Fjellberg 1997)

^cBut related to vegetation diversity

^d $\delta^{15}\text{N}$ measured in soil and plants, not in the invertebrate tissues

^eLow total abundances (6 *versus* 2 individuals)

Results

Literature review

The literature search identified 19 studies considering invertebrate responses to vertebrate fertilization within the High Arctic, and 12 in the Antarctic (Tables 1 and 2). All Arctic

studies were based on data from the Svalbard archipelago, primarily Spitsbergen, while studies from the southern polar region covered a wider range of distinct locations (Fig. 2).

Studies of the High Arctic region were less diverse as regards to different invertebrate taxa analysed that those from the Antarctic. Twelve of the articles from the Arctic related to springtails, including one collectively with mites

Table 2 List of different terrestrial invertebrate taxa responses to marine vertebrate presences, measured in the Antarctic localities

Taxa	Sampling site against vertebrate aggregation	Abundance	Species richness/diversity	Species composition	Tissue $\delta^{15}\text{N}$	Vertebrate species	Location	References
Collembola	Within	ns	Lower	Change	–	Birds: BS, CP, GP, KP, SGP, SPS mammals: AFS, SES, WS	Barrientos Island (MA)	Enriquez et al. (2018)
Collembola	As close as possible and in increasing distance	Higher	Higher	–	Higher	Birds: AP, CP, GP mammals: SES	Antarctic Peninsula region (MA)	Bokhorst et al. (2019b)
Collembola, Acari	Distance not described	Higher	Higher	Change	–	Birds: AP, BS, KP mammals: AFS, SES, WS	Marguerite Bay, Alexander Island (MA)	Convey and Smith (1997)
Collembola, Acari	Within	Absent	–	–	–	Birds: AP, SPS	Victoria Land (CA)	Sinclair et al. (2006)
Collembola, Acari	As close as possible and in increasing distance	Higher	Higher	–	Higher	Birds: AP, CP, GP	Antarctic Peninsula region (MA)	Bokhorst and Convey (2016)
Acari ^a	Within	Higher	–	–	–	Birds: SP	Dronning Maud Land (CA)	Ryan and Watkins (1989)
Acari	As close as possible and in increasing distance	Higher	Higher	–	Higher	Birds: AP, CP, GP mammals: SES	Antarctic Peninsula region (MA)	Bokhorst et al. (2019b)
Collembola, Prostigmatoda, Nematoda, Tardigrada, Rotifera, Protozoa	Within and around	<i>Panagrolaimus davidi</i> (nematode) higher, no effect for other taxa	–	–	–	Birds: AP	Ross Island (CA)	Sinclair (2001)
Nematoda	From the margin	Absent	–	–	–	Birds: AP	Wilkes Land (CA)	Petz (1997)
Nematoda	Within and adjacent to	<i>P. davidi</i> high ^b , 3 other species absent	–	Change	–	Birds: AP	Ross Island (CA)	Porazinska et al. (2002)
Nematoda	Within	<i>P. davidi</i> higher, 3 other species absent	Lower	Change	–	Birds: AP	Victoria Land (CA)	Raymond et al. (2013)
Nematoda	Within	Lower	Lower	Change	–	Birds: AP, SPS	Victoria Land (CA)	Smykla et al. (2018)
Nematoda	As close as possible and in increasing distance	Higher	–	–	Higher	Birds: AP, CP, GP mammals: SES	Antarctic Peninsula region (MA)	Bokhorst et al. (2019b)
Nematoda	Adjacent to	Lower	–	–	Not clear	Birds: AP, BS, GP, IS, KG, SPS mammals: AFS, SES, WS	Antarctic Peninsula region (MA)	Almela et al. (2022)
Tardigrada	From the margin	Lower than in mosses, slightly higher than in fellfield	–	–	–	Birds: AP	Wilkes Land (CA)	Petz (1997)
Tardigrada	As close as possible and in increasing distance	ns	–	–	Higher	Birds: AP, CP, GP mammals: SES	Antarctic Peninsula region (MA)	Bokhorst et al. (2019b)
Tardigrada	Within	Absent	–	–	–	Birds: AP, SPS	Victoria Land (CA)	Smykla et al. (2018)

Table 2 (continued)

Taxa	Sampling site against vertebrate aggregation	Abundance	Species richness/diversity	Species composition	Tissue $\delta^{15}\text{N}$	Vertebrate species	Location	References
Tardigrada	Adjacent to	Higher	–	–	Not clear	Birds: AP, BS, GP, IS, KG, SPS mammals: AFS, SES, WS	Antarctic Peninsula region (MA)	Almela et al. (2022)
Rotifera	From the margin	Lower	–	–	–	Birds: AP	Wilkes Land (CA)	Petz (1997)
Rotifera	Within and adjacent to	High ^b	–	–	–	Birds: AP	Ross Island (CA)	Porazinska et al. (2002)
Rotifera	Within	Absent	–	–	–	Birds: AP, SPS	Victoria Land (CA)	Smykla et al. (2018)
Rotifera	Adjacent to	Higher	–	–	Not clear	Birds: AP, BS, GP, IS, KG, SPS mammals: AFS, SES, WS	Antarctic Peninsula region (MA)	Almela et al. (2022)
Ciliophora	From the margin	Lower than in mosses, higher than in fellfield	Lower	–	–	Birds: AP	Wilkes Land (CA)	Petz (1997)

Location abbreviations: CA continental Antarctic, MA maritime Antarctic. Vertebrate species abbreviations: AP Adélie penguin *Pygoscelis adelie*, AFS Antarctic fur seal *Arctocephalus gazella*, BS brown skua *Catharacta leonbergi*, CP chinstrap penguin *P. antarctica*, GP gentoo penguin *P. papua*, IS imperial shag *Phalacrocorax atriceps*, KG kelp gull *Larus dominicanus*, SES southern elephant seal *Mirounga leonina*, SGP southern giant petrel *Macronectes giganteus*, SP snow petrel *Pagodroma nivea*, SPS south polar skua *C. maccornicki*, WS Weddell seal *Leptomychotes weddellii*. Hyphen means the parameter was not studied, 'absent'—in comparison with other site where a taxon was recorded within the study location, 'ns' non significant response

^aNo other arthropods found

^bWithout statistical comparison with areas without seabird influence

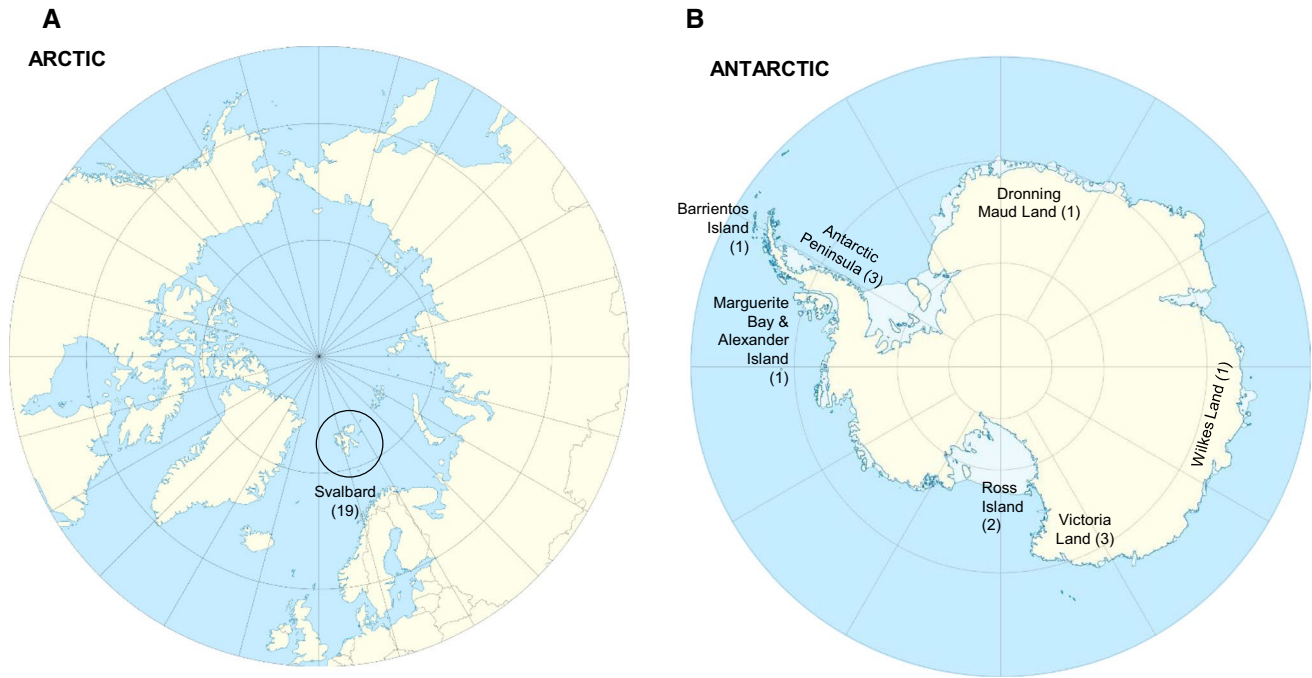


Fig. 2 Maps of **A** the Arctic and **B** the Antarctic, with marked locations of studies described in the literature searched, and number of studies conducted in each location (https://commons.wikimedia.org/wiki/File:Arctic_Ocean_location_map.svg, https://en.wikipedia.org/wiki/File:Antarctica_location_map.svg#filelinks, CC BY-SA 3.0, modified)

(Zmudczyńska-Skarbek et al. 2017) and three also considering mites, spiders, rove beetles, dipteran larvae, nematodes and enchytraeids (Bengtson et al. 1974; Byzova et al. 1995; Lebedeva et al. 2020). Of the remaining seven, six focused solely on tardigrades (Zawierucha et al. 2015a, b, 2016, 2017, 2018, 2019) and one on testate amoebae (Mazei et al. 2018).

In the southern polar region, five of the studies focused solely on springtails and/or mites (Ryan and Watkins 1989; Convey and Smith 1997; Sinclair et al. 2006; Bokhorst and Convey 2016; Enríquez et al. 2018). One study focused exclusively on nematodes (Raymond et al. 2013). The remaining six studies included multiple invertebrate groups, including those mentioned previously as well as tardigrades, rotifers and the microfaunal groups of ciliates and testate amoebae (Petz 1997; Sinclair 2001; Porazinska et al. 2002; Smykla et al. 2018; Bokhorst et al. 2019a; Almela et al. 2022).

Meta-analysis of numerical data

Based on data assessing springtails, mites and tardigrades from sites affected by marine vertebrates and non-impacted control sites (Zawierucha et al. 2015b, 2016, 2017, 2018; Zmudczyńska-Skarbek et al. 2015, 2017; Bokhorst and Convey 2016; Bokhorst et al. 2019a, b),

we found significant vertebrate influence on terrestrial invertebrate community composition regardless of their taxonomic affiliation or geographic location (Model 1, factor: VERTEBRATES; $F = 111.65$, $df = 1$, $p < 0.001$; Suppl. Table 1, Fig. 3). This factor was also significant when only data from the Arctic (Model 2, $F = 106.31$, $df = 1$, $p < 0.001$) or only representing arthropods were considered (Model 3, $F = 95.10$, $df = 1$, $p < 0.001$). Within the Arctic, the magnitude of these differences was similar for both arthropod and tardigrade communities (Model 2, factor: VERTEBRATES*GROUP; $F = 1.37$, $df = 1$, $p = 0.24$), irrespective of differences between habitats studied (soil vs. bryophyte/mixed bryophyte and lichen substrates). However, the magnitude of change in arthropod communities differed between the Arctic and the Antarctic, with significantly larger changes observed in the Arctic (Model 3, factor: VERTEBRATES*LOCATION; $F = 37.88$, $df = 1$, $p < 0.001$).

Discussion

Synthesis of the information presented in the existing literature identified together with new analyses of available datasets have enabled us to address important questions regarding the impact of marine vertebrates on Arctic and Antarctic terrestrial invertebrate communities:

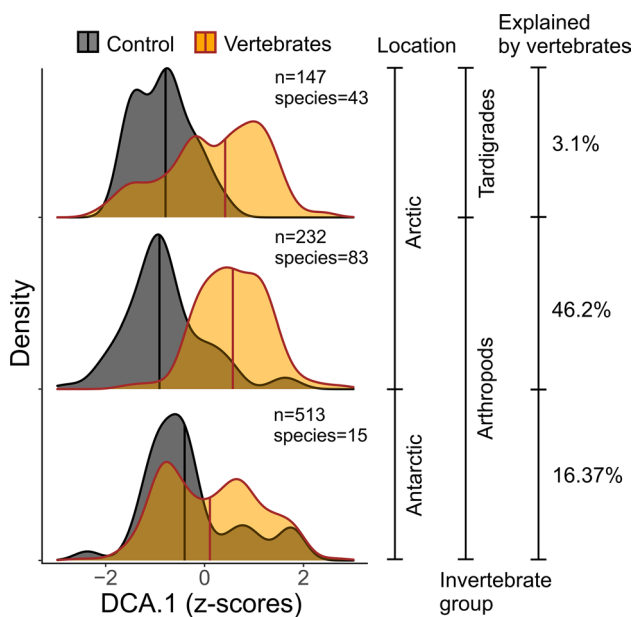


Fig. 3 Differences in species composition shown as density functions of the 1st DCA axes of the vertebrate-influenced (Vertebrates) and non-influenced (Control) areas disaggregated by major invertebrate groups (arthropods, i.e. springtails and mites, merged, vs. tardigrades) and location (Arctic vs. Antarctic), with percent of variability explained by VERTEBRATES factor in each model (detailed results of the ANOVAs shown in Suppl. Table 1)

Which terrestrial invertebrate groups respond to marine-derived nutrients?

In the Arctic, densities of nematodes, dipterans and tardigrades were higher in the vicinity of bird nesting concentrations than in other habitats examined (Byzova et al. 1995; Zawierucha et al. 2016, 2017, 2019), while mites, enchytraeids and testate amoebae showed no clear effects (Byzova et al. 1995; Zmudczyńska-Skarbek et al. 2017; Mazei et al. 2018). Tardigrade trophic groups differed between areas influenced by little auk breeding colonies and control sites at Hornsund, with higher abundance of microbivorous (grazing on biofilms) and herbivorous (feeding mainly on mosses and green algae) taxa close to the former (Zawierucha et al. 2019). In studies of springtails, three reported substantial increases in their abundance in response to ornithogenic fertilization (Bengtson et al. 1974; Byzova et al. 1995; Zmudczyńska et al. 2012), while the remaining nine found no evidence of change (Table 1). Higher densities of mites, spiders and beetles, and numbers of species of these groups and springtails, were reported under a bird cliff as compared to a coastal tundra terrace in a single study (Lebedeva et al. 2020).

Springtail richness response to external nutrient input was reported in three studies (Table 1). Comparison of

springtail communities across various sites, including those near a bird cliff, in northern Svalbard indicated that species richness was highest near bird cliffs (Fjellberg 1997; Lebedeva et al. 2020). However, springtail diversity was lower in bird-influenced sites compared to control sites at Hornsund, reflecting a shift in dominance of the most abundant species under bird influence (Zmudczyńska et al. 2012). A systematic comparison of bird-influenced and non-influenced sites in Isfjorden, Hamburgbukta and on the island of Bjørnøya identified no significant differences in springtail species richness (Zmudczyńska-Skarbek et al. 2015, 2017). Currently available data therefore suggest that, typically, Arctic terrestrial invertebrate abundance is increased by ornithogenic nutrient input, but there is limited and inconsistent evidence for direct impacts on species richness. However, it is clear that invertebrate community composition is altered near seabird colonies, and there are also examples of both species recorded solely from ornithogenically-influenced sites and others recorded only in non-influenced control sites.

Mite and springtail abundances were consistently higher in areas receiving ornithogenic fertilisation compared to non-affected areas across Antarctic sites, while nematodes, tardigrades and rotifers showed highly variable responses (Table 2). Where reported, species richness values of mites and springtails were again higher in bird-influenced areas while nematode richness declined (hence, species composition of those communities changed, Table 2). The consistent response by mites and springtails is in line with expectations from their generally assumed role as microbivores/detritivores in polar communities (Hogg et al. 2006). The apparently variable responses of other micro-invertebrate groups may relate to differences in sampling strategy applied across studies, feeding preferences of individual species (which have rarely if ever been explicitly documented in polar species), or their dispersal mode, while other limiting factors such as water availability and salinity may have differed between studies (Sinclair 2001; Porazinska et al. 2002). To address some of these issues, Bokhorst et al. (2019b) only sampled equivalent substrates (the same moss species) from sites with and without ornithogenic influence, reporting increased abundance of nematodes. Studies reporting lower nematode abundance in fertilised areas often included different vegetation types between ornithogenically-influenced and non-influenced sites (Smykla et al. 2018), or were based on work at sites separated by several hundred kilometres (Almela et al. 2022). These differences highlight that, at present, insufficient comparable studies are available to enable the role that nutrients can play in shaping Antarctic terrestrial communities to be assessed with confidence.

Are terrestrial invertebrate responses consistent between Arctic and Antarctic ecosystems?

Terrestrial invertebrate abundance and richness tended to increase, and community composition change, with marine vertebrate fertilisation in both polar regions (Fig. 2). However, the comparison of the arthropod taxonomic composition change explained by the influence of vertebrates between the High Arctic and Maritime Antarctic showed that the magnitude of this change was significantly greater in the Arctic. This may reflect the greater overall number of species recorded across the different Arctic studies (83 species) than those in the Antarctic (15 species). It must also be recognised that areas facing the most extreme exposure to vertebrate faeces input and strong mechanical disturbance (within the boundaries of penguin rookeries and seal wallows, and directly at the foot of bird cliffs; Hodkinson et al. 1994; Porazinska et al. 2002; Zmudczyńska et al. 2012; Smykla et al. 2018) were excluded from this analysis as they were not comparable between the two regions, and clearly dependent on vertebrate activity, local topography and vegetation.

What are the roles of vegetation and vertebrate activity on invertebrate responses in the context of nutrient subsidies?

Vertebrate-sourced enrichment of invertebrate communities was proved in both polar regions by using $\delta^{15}\text{N}$ stable isotope signatures of invertebrates and substrates of their habitats (soil and/or vegetation; Kristiansen et al. 2019, Bokhorst and Convey 2016; Bokhorst et al. 2019b). The vertebrate impact on the invertebrates increased closer to the vertebrate aggregations (Bokhorst and Convey 2016; Bokhorst et al. 2019b), and also with vertebrate aggregation size (Kristiansen et al. 2019).

However, soil invertebrate communities may not directly respond to enhanced soil nutrients but, rather, population increases may be associated with higher primary production or increased food quality (Ryan and Watkins 1989; Zmudczyńska et al. 2012; Zawierucha et al. 2016). Temperature and water availability play a strong limiting role on invertebrate growth, reproduction and survival in the polar regions (Convey 1996). Any consequential benefits from ornithogenically-derived nutrients for invertebrate communities need to be placed in the context of other biotic and abiotic factors. Vegetation forms an important resource for invertebrates, providing microhabitats that can buffer against ambient temperature and desiccation stress fluctuations, as well as providing food (often in the form of epiphytic and underlying soil microbiota, as well as detritus). Within dry and barren tundra/fellfield habitats invertebrates will aggregate in association with

even the smallest vegetation patches (Usher and Booth 1984, 1986; Hertzberg et al. 1994; Coulson et al. 2003). Although polar primary producers tend to benefit from increased nutrient availability (Smith 1988, 2008; Smith and Froneman 2008; Zwolicki et al. 2020) few can cope with the extremely high nutrient loading and physical trampling experienced within the boundaries of dense marine bird or mammal aggregations (Convey and Hughes 2022). The topography surrounding such aggregations also strongly affects nutrient run-off and distribution, thereby affecting how the vegetation develops and, in turn, the associated invertebrate communities.

Most studies on Svalbard have explored the talus slopes within and around little auk colonies, and below cliffs occupied by Brünnich's guillemots and black-legged kittiwakes (Fig. 1). Complete and lush vegetation cover is commonly observed along such slopes, apart from sites very close to the base of the bird cliffs or within the colony itself, where mechanical disturbance by falling rock debris and nest material, trampling activity and excess guano input is experienced (Eurola and Hakala 1977; Hodkinson et al. 1994; Zmudczyńska et al. 2008; Zmudczyńska-Skarbek et al. 2013; Zwolicki et al. 2020). A band of unstable ground immediately adjacent to the base of large, densely-occupied bird cliffs may be completely devoid of vegetation (the zone described as 'sterile' by Odasz 1994), or only sparsely colonised by a very few nitrophilous, relatively fast-growing vascular plant species such as *Cochlearia groenlandica* and *Poa alpina* (Zwolicki et al. 2016a), and patches of algae and cyanobacteria (Richter et al. 2018). Such poorly vegetated habitat found at the foot of Gnålberget cliff (Hornsund) was colonised by a single springtail species, *Megaphorura arctica* (Zmudczyńska et al. 2012). Hodkinson et al. (1994) considered that the species' dense populations were locally supported by relatively abundant supply of food in the form of damaged or dead plant material crushed by the falling stones. In contrast, Sømme and Birkemoe (1999) recorded the highest springtail diversity in the steep slope directly below the bird cliff and even on rock shelves within the colony at Krykkjefjellet (Kongsfjorden) in comparison with the area between the cliff and the neighbouring beach. Such differences may result from colony-specific features, such as the much smaller population of birds nesting at Krykkjefjellet (less than 1000 breeding pairs, Coulson et al. 2009a), resulting in less intense manuring, and perhaps more stable ground in comparison with the colony and the area beneath it in Hornsund (colony size 20–30,000 breeding pairs, Stempniewicz et al. 2021). Together such factors may encourage the development of more diverse vegetation, in turn influencing the composition and development of the terrestrial invertebrate community (Byzova et al. 1995; Coulson et al. 2003). For example, in Hornsund, tardigrades reach higher densities in mosses, which dominate under the little auk

colony, in comparison with lichens which dominate in non-influenced control sites (Zawierucha et al. 2016).

Unlike the High Arctic bird cliff habitats described above, Antarctic penguin colonies (and, similarly, seal aggregations) are generally located on accessible flat or gently sloping ground, although may still reach some way above sea level (Fig. 1) (e.g. Convey and Hughes 2022). This results in accumulation of faeces, substantial retention of the allochthonous nutrients, and over-fertilization to levels toxic for most organisms within such sites (during the breeding season penguins may deliver up to 10 kg dry mass of excreta per square metre, Tatur and Myrcha 1984). Together with intensive trampling by the flightless birds, which are also much larger than their Arctic counterparts, or mechanical damage by seals, this almost completely prevents development of vegetation within the occupied area, with only some nitrophilous algae such as *Prasiola crispa* occurring sporadically, along with nitrophilous lichens on local rock outcrops (Smykla et al. 2007; Favero-Longo et al. 2011; Zwolicki et al. 2015). However, when growing in its foliose form, *P. crispa* provides a habitat in which springtails, rotifers and tardigrades may reach their peak abundances (as high as 510,000 ind m⁻² of the widespread maritime Antarctic species *Cryptopygus antarcticus*, or in excess of 8000 rotifer ind. per 100 mg dry sample mass; Convey and Smith 1997; Enríquez et al. 2018; Lukashanets et al. 2022). In Victoria Land (CA), where microarthropods and microinvertebrates are generally represented by very few species and occur at low abundances (Adams et al. 2006), a nematological study of the most nutrient-affected soils within penguin rookeries identified a high population density of a single nematode species, *Panagrolaimus davidi* (Raymond et al. 2013). Likewise, two nematodes, *P. davidi* and *Plectus murrayi*, were the only invertebrates detected within penguin colonies (though both at lower densities than elsewhere) out of all the terrestrial invertebrates recorded by Smykla et al. (2018) in Victoria Land. Sinclair et al. (2006) similarly recorded no microarthropods within Victoria Land penguin rookeries. At the same time Porazinska et al. (2002) noted abundant *P. davidi* and rotifers, with tardigrades and other nematodes being virtually absent in penguin colonies on Ross Island (CA). Within and around snow petrel colonies on Dronning Maud Land nunataks (CA), Ryan and Watkins (1989) recorded higher densities of prostigmatid mites (but no other arthropods), relating their abundance to plant cover, primarily that of *P. crispa*. However, higher abundance of one mite species, *Nanorchestes antarcticus* was recorded within the petrel colony where the vegetation cover was limited, suggested to be a result of increased abundance of microbial food, in turn a result of ornithogenic influence. Another example of varied, yet primarily related to trophic strategy, responses of invertebrate species to strong impact of marine vertebrates is given by Enríquez et al. (2018). In

that study, among eight different substrate types studied on Barrientos Island (MA), the algivorous springtail *C. antarcticus* occurred most abundantly on *P. crispa* mats (on average 55,053 ind per m²) and within penguin colonies (48,576 ind m⁻²) but was least numerous immediately adjacent to southern elephant seal wallows (73 ind m⁻²). The latter observation may reflect extreme compaction of the soil preventing the build-up of springtail communities despite abundance of food, although this has not been studied specifically (but see Greenslade et al. (2012) for an example of soil compaction by human activity being associated with lower soil microarthropod densities on maritime Antarctic Deception Island). Conversely, the highest density of the nematophagous springtail *Friesea grisea* (now classified as *F. antarctica*; Greenslade 2018) was detected in nutrient-rich seal wallows (1019 ind m⁻²) where the probability of finding prey (nematodes) was high, while in penguin colonies the species' abundance was relatively low (55 ind m⁻²). Locally the seal wallows, and not the penguin colonies, were also some of the most favourable habitats for the springtails *Cryptopygus badasa* and *Folsomotoma octooculata*. The invertebrate responses documented in these studies indicate that the conditions in the centres of marine vertebrate aggregations are extremely challenging if not intolerable for most species, while small patches of even the simplest vegetation can provide shelter and support extremely high invertebrate densities (Ryan and Watkins 1989; Convey and Smith 1997; Enríquez et al. 2018).

Notwithstanding the type and location of vertebrate aggregation, nutrients originating from their faeces do not remain within the area but can enrich ecosystems even up to many kilometres away (Erskine et al. 1998; Crittenden et al. 2015; Bokhorst et al. 2019a). As the nutrient loading diminishes with distance from the vertebrate aggregation, vegetation can benefit from the additional nutrients and flourish (Sinclair et al. 2006; Smykla et al. 2007; Zwolicki et al. 2015; Almela et al. 2022) with beneficial consequences for associated fauna.

The large differences in faunal community composition found along the gradient of distance from a single seabird colony or seal wallow are generally also matched by changes in vegetation community composition or structure (Ryan and Watkins 1989; Sømme and Birkemoe 1999; Sinclair et al. 2006; Zmudczyńska et al. 2012; Zawierucha et al. 2016). This suggests that marine vertebrates may drive increased beta diversity (species turnover; Whittaker 1977) of terrestrial invertebrates over relatively short distances even if, at some points along those gradients alpha (local) diversity can be much lower than elsewhere (Zmudczyńska et al. 2012; Zawierucha et al. 2015b).

Furthermore, the response of the invertebrate community to allochthonous nutrient subsidies is likely to be less clear than that of vegetation (e.g. Odasz 1994; Zwolicki

et al. 2015, 2016b; Zmudczyńska-Skarbek et al. 2017) as it involves further transfers through the trophic web and integration with multiple components in invertebrate diets. There may be multiple feeding strategies present in one invertebrate community, and even in one taxonomic group, such as specific or general microbivory, herbivory, decomposition or predation (Ryan and Watkins 1989; Zmudczyńska-Skarbek et al. 2017; Bokhorst et al. 2019a; Zawierucha et al. 2019).

Conclusions

At present, all studies of marine vertebrate impact on terrestrial invertebrate communities in the Arctic have taken place on the Svalbard archipelago, and explicit studies are lacking from other Arctic regions such as Siberia, Canada, Greenland, Alaska or the Russian Arctic Ocean archipelagos, where extensive bird colonies are also present (www.birdlife.org; Table 1). The geographic extent of Antarctic studies is much wider even though there are fewer studies overall (Table 2, Fig. 2).

The data collated from the available literature and new analyses presented here indicate that invertebrate communities benefit from the enhanced nutrient availability provided by marine vertebrates in both polar regions. However, there are typically reduced invertebrate abundance levels within areas of ‘toxic’ nutrient levels and extreme physical disturbance within colonies or aggregations, while at the edge and within the wider dispersed nutrient footprint the invertebrates thrive. The mechanisms leading to increased invertebrate abundance are not fully confirmed, despite some studies identifying a direct links through tracing stable isotopes (^{15}N). Given well documented microbial and vegetation community responses to nutrient loading by birds in both polar regions, and that invertebrate communities in turn rely on these for both food and shelter, it is plausible that there is causal connection between vertebrate-derived nutrients and increased invertebrate population sizes.

Studies of the consequences of the marine vertebrate fertilization on terrestrial invertebrate communities in polar regions are still sparse. Future research will benefit from widening the geographic range considered, along with the types of impacted terrain, manuring intensity and/or substrate types. It will also be important to apply comparable sampling strategies and measures of abundance and diversity across studies. The general knowledge gap relating to detailed autecological studies of polar invertebrates, in particular relating to their feeding strategies and diets also needs to be addressed. Nonetheless, this study clearly demonstrates that the responses of terrestrial invertebrate communities to external nutrient inputs are complex.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00300-023-03134-8>.

Acknowledgements We thank Arne Fjellberg for taxonomic examination of Svalbard Collembola samples. This study was supported by the Polish Ministry of Science and Higher Education (Grant Numbers 1883/P01/2007/32, IPY/25/2007, and 3290/B/P01/2009/36), and the Polish-Norwegian Research Fund (PNRF-234-AI-1/07) to KZS and AZ; PC is supported by NERC core funding to the BAS ‘Biodiversity, Evolution and Adaptation’ Team.

Author contributions KZS reviewed literature, collected springtails and mites from Svalbard, and drafted the original manuscript. PC and SB edited the original draft and contributed additional text, and sampled invertebrates from the Antarctic. DJG identified specimens of mesostigmatid, and PS of oribatid, mites. KZ collected and identified specimens of tardigrades from Svalbard, and reviewed tardigrade literature. AZ collected springtails and mites from Svalbard, and performed statistical analyses of numerical data. All authors read, commented on and approved the final manuscript.

Declarations

Competing interest The authors declare no competing interest.

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