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Research Article

How the small host the small: cryptogam trait-mediated structuring of Antarctic microarthropod communities

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Primary producers shape terrestrial biodiversity, but most research has focused on vascular plants, while the role of cryptogams (mosses, lichens and algae) remains under-explored. Cryptogams dominate Antarctic vegetation and support diverse microarthropod communities. However, how cryptogam traits influence these communities remains poorly understood. We therefore investigated the role of 28 cryptogam species and one vascular plant, via their functional traits, in shaping microarthropod communities across three contrasting sites (Signy Island, Byers Peninsula and Rothera) in the maritime Antarctic. We hypothesized that vegetation nitrogen and moisture content, major microarthropod taxa, and abiotic drivers interact to influence community patterns.

Vegetation type effects on total microarthropod abundance were context-dependent. Mosses hosted more microarthropods than lichens at Signy Island, but these differences diminished further south. Microarthropod richness and springtail abundance were consistently higher in mosses than lichens across all sites, whereas mite abundance did not differ between vegetation types.

Cryptogam nitrogen and moisture content strongly predicted microarthropod community patterns, although their influence varied with vegetation type and location. Among mosses, moisture increased springtail abundance but reduced diversity due to the dominance of *Cryptopygus antarcticus*. In lichens, nitrogen had a stronger influence than in mosses, particularly on mite abundance and Shannon diversity. As hypothesized, moisture was more important at the harshest southern site, while nitrogen had stronger effects at more productive northern locations.

These findings emphasize that the influence of cryptogam traits in structuring Antarctic terrestrial biodiversity is modulated by the environmental context. With future shifts predicted in vegetation composition, the functional traits of emerging dominant species may restructure microarthropod communities and their ecological functions.

Keywords: Antarctica, cryptogam, microarthropod, mite, plant traits, springtail

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Introduction

Primary producers form the foundation of terrestrial ecosystems and determine biodiversity patterns by creating and modifying habitats and regulating resource availability. Their composition and traits can shape the abundance, diversity and composition of consumer communities (Rzanny et al. 2013), with cascading effects on ecosystem functioning (Baiser et al. 2013). However, most understanding to date has been derived from studies of vascular plants, while other important groups of primary producers remain understudied. Cryptogams such as mosses, lichens and algae play important roles in structuring ecosystems where vascular plants are scarce or absent, by buffering against abiotic stress and providing food and habitat for microbial organisms and microarthropods (Lindo and Gonzalez 2010). Plant functional traits, such as water and nutrient content, influence invertebrate abundance and community composition by altering habitat conditions and food availability (Levings and Windsor 1984, Eisenhauer and Powell 2017, Fujii et al. 2020, Sánchez-Galindo et al. 2021). How these relationships extend to cryptogams remains poorly understood, despite their ecological importance. Cryptogams account for roughly 7% of global terrestrial net primary productivity and can cover more than 40% of the ground in tundra and other polar ecosystems, and over 20% in temperate coniferous forests, deserts and boreal forests (Elbert et al. 2012).

Moisture is a key regulator of microarthropod communities (Lindo et al. 2012), but its effects vary among taxa. Springtails (Collembola) are generally more moisture dependent, while some mites (Acari) are more tolerant of drier conditions due to their ability to better regulate water loss (Convey et al. 2003, Tsiafouli et al. 2005, Chikoski et al. 2006, Aupic-Samain et al. 2021). Cryptogams differ in their ability to retain and absorb moisture (Larson 1981, Cornelissen et al. 2007, Gauslaa and Coxson 2011). Although direct comparisons are scarce, mosses generally hold more water than lichens, but considerable variation exists within these two groups (Gimingham 1967, Michel et al. 2013, Wan and Ellis 2020). Terrestrial algae often form thin sheets on the ground surface or overlying vegetation that dry out quickly (Fritsch 1922). These differences in water-holding capacity (WHC) can be attributed in part to morphological traits (Larson 1981). In mosses, colony structure and shoot characteristics (Elumeeva et al. 2011), and cell features such as cell lumen length (Liu et al. 2024) contribute to water retention. In lichens, thallus size (Merinero et al. 2014) and specific thallus mass (Gauslaa 2014), as well as photobiont type (Gauslaa and Coxson 2011) influence WHC and desiccation rate. Terrestrial algae sometimes produce polysaccharides or accumulate low-molecular-weight carbohydrates (e.g. polyols) that help retain water (Medwed et al. 2021). Given these physiological differences, cryptogam water content can influence microarthropod community composition. For instance, a wetter bryosphere in boreal forests has been associated with higher overall microarthropod richness and abundance (Lindo et al. 2012). Similarly, wetter moss layers in boreal peatland hollows support higher microarthropod abundance compared to drier hummocks (Barreto and Lindo 2018). Experimental drought increased oribatid mite abundance, but impaired springtail abundance in the bryosphere (Grau-Andrés et al. 2022). These patterns suggest that wetter cryptogams promote moisture-dependent taxa, whereas drier hosts support communities dominated by more drought-tolerant taxa.

Nutrient availability, particularly nitrogen (N), can further shape microarthropod communities by influencing the nutritional quality and quantity of cryptogamic habitats which, in turn, affects growth and reproduction (Wehner et al. 2014). Lichens with N_2-fixing photobionts typically have higher N contents than lichens without these symbionts (Asplund and Wardle 2017). Mosses also vary in their N contents (Hájek et al. 2014) as determined by species' inherent physiology and environmental N availability. In both mosses and lichens, N deposition strongly influences N content (Boltersdorf et al. 2014, Bokhorst et al. 2019). Previous studies indicated that N content positively influences microarthropod abundance and diversity in lichens and mosses (Bokhorst et al. 2015, 2019), but the extent to which these effects are generalizable across cryptogam groups, microarthropod taxa and environments remains unclear.

Whether the impacts of cryptogam moisture and N content on microarthropod communities are consistent across broader environmental gradients remains largely unknown. Most studies to date have been limited to a single vegetation type or a narrow range of cryptogam species (Bokhorst et al. 2015, 2019, Jonsson et al. 2015, Gwiazdowicz et al. 2023), and few have addressed whether microarthropods respond similarly to cryptogam traits across vegetation types or bioclimatic contexts. That these associations may be context-dependent was shown for mosses, where drought effects on microfauna community composition and nematode abundance were stronger in late-successional forests than in mid- or early-successional forests (Grau-Andrés et al. 2022). Similarly, Ball et al. (2022) showed that Antarctic mite and springtail abundances were influenced by vegetation cover and varied with site and latitude, albeit without a clear link to climate or nutrient limitation. These findings underscore the need for trait-based comparative approaches across gradients, as these can reveal how habitat quality and climatic conditions jointly influence biodiversity (Maron et al. 2014). Whether context-dependent patterns occur for the effects of moisture and N content on microarthropods inhabiting mosses and lichens remains to be determined.

The maritime Antarctic presents an ideal system to study how cryptogam functional traits shape microarthropod communities, as cryptogams dominate primary production (Holdgate 1967) and provide important habitats for taxonomically wide-ranging terrestrial invertebrates in an otherwise harsh environment with low invertebrate diversity (Richard et al. 1994, Ball et al. 2022). The region spans substantial temperature, moisture and radiation gradients (Convey et al. 2014). Although mean air temperatures only modestly change across the maritime Antarctic, water availability decreases with progression southwards (Walton 1984). This is due to declining precipitation and increasing radiation as a result of decreasing cloud cover with latitude (Bokhorst et al. 2008, Schroeter et al. 2010), which can, for instance, increase moss surface temperatures (Perera-Castro et al. 2020). Biodiversity in these ecosystems is closely tied to water availability (Kennedy 1993, Convey et al. 2014). Furthermore, although Antarctic terrestrial ecosystems have low nutrient availability and are generally N-limited (Davey and Rothery 1992), localized but intense nutrient inputs from marine vertebrate colonies or other aggregations alleviate nutrient stress and alter the invertebrate assemblages present (Bokhorst et al. 2019). Although often considered predominantly shaped by abiotic conditions (Convey 1996, Hogg et al. 2006), there is growing recognition of biotic interactions, such as trophic relationships and habitat modification by vegetation, in structuring communities (Caruso et al. 2013, 2019, Lee et al. 2019). Vegetation can buffer extreme environmental conditions through moisture retention, microclimatic stability and nutrient availability (Convey et al. 2018). This buffering capacity mediates some abiotic stressors and creates more stable microenvironments for diverse invertebrate communities (Caruso et al. 2013, Bokhorst and Convey 2016). As such, the relative importance of cryptogam traits for microarthropod communities may shift along the Antarctic Peninsula. Moisture content may be more critical under drier and colder southern conditions. Conversely, N effects might become more influential in milder, more productive northern habitats, where resources may be more limiting for microarthropods.

This study examines how cryptogam traits influence microarthropod abundance and diversity across 1323 plant and lichen samples obtained from three locations in the maritime Antarctic, including 29 native cryptogam species (12 lichens, 17 mosses, 1 macroscopic green alga) and the grass *Deschampsia antarctica*. Using these taxa, we test how vegetation type and variation in moisture and N content influence microarthropod communities. Specifically, we hypothesize that: 1) mosses will support the highest microarthropod abundance/diversity compared to lichens due to their greater WHC; 2) water effects will be stronger for springtails than mites, as the latter are typically more drought-tolerant; and 3) the role of cryptogam moisture for microarthropods will be more important at southern, drier, locations, while N will have a stronger effect on microarthropods at milder, lower-latitude locations. Finally, we use the data to provide a first estimate of the total abundance of mites and springtails in green vegetation and lichens in the maritime Antarctic.

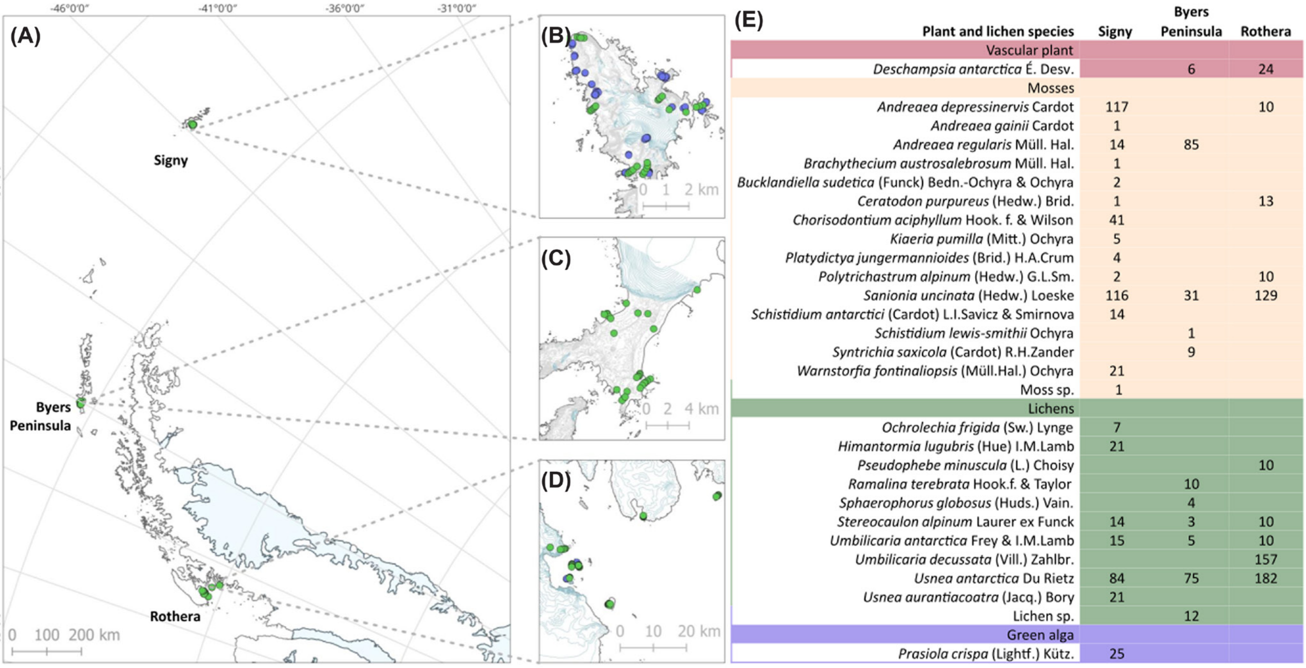
Understanding trait–biodiversity relationships is increasingly urgent given the growing pressures on Antarctic ecosystems from climate change, human activity and invasive species (Convey and Peck 2019). Terrestrial habitats remain under-represented in Antarctica's conservation framework (Hughes et al. 2016, Wauchope et al. 2019), partly due to limited detailed knowledge of species distributions and their ecological roles. Improving our understanding of vegetation–invertebrate linkages will support future biodiversity monitoring and conservation planning in terrestrial Antarctica.

Material and methods

Study sites and data collection

We used a combination of previously published data (Bokhorst and Convey 2016, Bokhorst et al. 2019) and newly collected samples from three locations in the maritime Antarctic: Signy Island (South Orkney Islands), Byers Peninsula (Livingston Island, South Shetland Islands) and islands near Rothera Point (Adelaide Island, western Antarctic Peninsula) (Fig. 1). For simplicity, all samples from the latter are referred to as 'Rothera'. Signy Island (~ 10 km^2; 60°43'4.00"S, 45°37'37.40"W) lies on the Scotia Arc northeast of the Antarctic Peninsula and supports rich and spatially extensive moss and lichen habitats (Smith 1990). Byers Peninsula (62°38'49.99"S, 61°6'37.00"W) hosts some of the highest biological diversity in the region, with extensive moss and lichen carpets (Lindsay 1971). Vegetation near Rothera (67°34'11.36"S, 68°7'19.56"W) is dominated by lichen communities on rocky surfaces, with mosses limited to sheltered, meltwater-fed sites. Due to typically lower cloud cover, Rothera receives up to 50% more summer solar radiation than Signy and Byers Peninsula (Bokhorst et al. 2008).

The dataset of Bokhorst et al. (2019) included microarthropod counts from mosses, lichens and the grass *Deschampsia antarctica* collected at each geographic location. At all three locations, replicate transects (n = 3–6) were established across multiple sites (n = 2–5), both close to and distant from penguin colonies and elephant seal aggregations that influence cryptogam nitrogen (N) content. Distances from the coast ranged between 20 and 1040 m, 3 and 1750 m and 1 and 2100 m for Signy Island, Byers Peninsula and Rothera, respectively. The numbers of marine vertebrate-influenced sites, and less-influenced sites were n = 3 and 3 at Signy Island, n = 2 and 2 at Byers Peninsula and n = 5 and 3 at Rothera. Five points were sampled along each transect, with distance between sampling points influenced by vegetation presence. Due to logistical constraints sampling was carried out across multiple years: Signy Island in 2015, Byers Peninsula in 2017 and Rothera in 2014, 2016 and 2017. Samples of the green algae *Prasiola crispa* from Signy Island were collected across two transects in 2013 and the data published by Bokhorst and Convey (2016). For a complete overview of the sampling years, site-level details, numbers of samples per cryptogam species as well as photographs of most species, see the Supporting information. Our new data comprised 210 moss and lichen samples collected on Signy in the 2022/2023 austral summer, and 90 samples of mosses, lichens and the grass *D. antarctica* around Rothera in the austral summer of 2023/2024. On Signy Island (Fig. 1B), two sampling strategies were applied: 1) four lichen species (*Himantormia lugubris*, *Usnea aurantiaco-atra*, *Stereocaulon alpinum* and *Ochrolechia frigida*) and four moss species (*Warnstorfia fontinaliopsis*, *Andreaea depressinervis*, *A. regularis* and *Chorisodontium aciphyllum*) were collected at



Plant and lichen species	Signy	Byers Peninsula	Rothera
Vascular plant			
Deschampsia antarctica É. Desv.		6	24
Mosses			
Andreaea depressinervis Cardot	117		10
Andreaea gainii Cardot	1		
Andreaea regularis Müll. Hal.	14	85	
Brachythecium austrosalebrosum Müll. Hal.	1		
Bucklandiella sudetica (Funck) Bedn.-Ochyra & Ochyra	2		
Ceratodon purpureus (Hedw.) Brid.	1		13
Chorisodontium aciphyllum Hook. f. & Wilson	41		
Kiaeria pumilla (Mitt.) Ochyra	5		
Platydictya jungermannioides (Brid.) H.A.Crum	4		
Polytrichastrum alpinum (Hedw.) G.L.Sm.	2		10
Sanionia uncinata (Hedw.) Loeske	116	31	129
Schistidium antarctici (Cardot) L.I.Savicz & Smirnova	14		
Schistidium lewis-smithii Ochyra		1	
Syntrichia saxicola (Cardot) R.H.Zander		9	
Warnstorfia fontinaliopsis (Müll.Hal.) Ochyra	21		
Moss sp.	1		
Lichens			
Ochrolechia frigida (Sw.) Lynge	7		
Himantormia lugubris (Hue) I.M.Lamb	21		
Pseudophebe minuscula (L.) Choisy			10
Ramalina terebrata Hook.f. & Taylor		10	
Sphaerophorus globosus (Huds.) Vain.		4	
Stereocaulon alpinum Laurer ex Funck	14	3	10
Umbilicaria antarctica Frey & I.M.Lamb	15	5	10
Umbilicaria decussata (Vill.) Zahlbr.			157
Usnea antarctica Du Rietz	84	75	182
Usnea aurantiacoatra (Jacq.) Bory	21		
Lichen sp.		12	
Green alga			
Prasiola crispa (Lightf.) Kütz.	25		

Figure 1. Map of the Antarctic Peninsula (A) showing all sampling locations on Signy Island (B), Byers Peninsula (C) and around Rothera (D), and (E) numbers of samples of moss, lichen, algae and vascular plant species collected at each of the three geographic locations. Dots on the map indicate sampling locations, blue new samples and green previously collected samples.

Backslope (unofficial name), North Gneiss and Foca; and 2) the moss species *Sanionia uncinata* was collected in dry and wet habitats, both close to and distant from penguin colonies. Species were selected to reflect the dominant and most commonly encountered mosses, lichens and algae at each site and across the wider maritime Antarctic, including Signy Island and the Antarctic Peninsula. While not all selected species form continuous colonies, they are representative of the diversity of growth forms and habitat types present in the region. We treated all samples equally in the overall analysis to evaluate general relationships between cryptogam traits and microarthropod communities. Around Rothera, samples of five lichen species (*Usnea antarctica*, *S. alpinum*, *Umbilicaria antarctica*, *U. decussata* and *Pseudophebe minuscula*), three moss species (*S. uncinata*, *A. depressinervis* and *Polytrichastrum alpinum*) and the grass *D. antarctica* were collected across Anchorage Island, Lagoon Island and Léonie Island (Fig. 1D). Moss samples were collected using a 5 cm diameter PVC corer and included entire shoots but excluded underlying soil. Lichen samples were excised from individual rocks. Lichen sample dry mass ranged between 0.5 and 4.0 g, and moss dry mass between 0.8 and 60.0 g. Grass samples consisted of whole plants, including roots with small soil particles attached. Moss species were identified following Ochyra et al. (2008), and lichens according to Øvstedal and Smith (2001). Figure 1E provides details of all vegetation taxa sampled.

Microarthropod extractions

Springtails (Collembola) and mites (Acari) were extracted from vegetation samples into 70% ethanol using Tullgren extractors for 24 h or until the sample was dry. Specimens were identified to species level and counted under a stereomicroscope. We assigned unidentified juvenile mites to a separate group. Initial vegetation fresh mass and post-extraction dry mass were measured, except for Byers Peninsula samples, where field facilities were limited.

Plant and lichen nitrogen and water content measurements

Cryptogam moisture content was calculated as (fresh mass − dry mass)/dry mass × 100. We also quantified WHC of the newly collected plant and lichen samples, by first soaking them in tap water for at least 48 h to reach saturation. After soaking, excess water was allowed to drain off, and samples were air-dried at room temperature and weighed once their weight stabilized. Finally, the samples were oven-dried at 60°C to determine the dry mass. We calculated WHC as (saturated mass − oven-dry mass)/oven-dry mass × 100. While moisture content reflects recent environmental conditions, moss values were strongly correlated with WHC (Supporting information), supporting its use as proxy for WHC. Lichens showed weaker correlations, likely due to more rapid desiccation, thus lichen moisture content is interpreted as a transient habitat condition rather than a trait. Nitrogen content of cryptogam samples was quantified by first oven drying at 70°C for 24 h, then grinding the samples and using dry combustion in an NC 2500 elemental analyzer (Carlo Erba), coupled with a Deltaplus continuous-flow IRMS (Thermo Finnigan). See the Supporting information for mean values and range of sample N and moisture contents.

Topographic and bioclimatic variables

To calculate mean annual temperature and total annual precipitation for each sampling location, we first downloaded modeled macroclimatic data for mean, minimum and maximum temperature and mean precipitation for the period 1981 to 2010 from CHELSA (Karger et al. 2017) with the R package 'climenv' (Tsakalos et al. 2023). CHELSA modeled data have a resolution of 30 arc sec, equating to ~ 1 km^2. Based on these macroclimatic data, bioclimatic variables for each location were calculated in R using 'dismo' (Hijmans et al. 2023) (Table 1).

Statistical analyses

To determine whether the total microarthropod abundance, springtail abundance, mite abundance, microarthropod species richness and Shannon diversity differed between the four major vegetation types (moss, lichen, green alga, grass) and whether vegetation type effects were influenced by geographic location (Signy Island, Byers Peninsula, Rothera), we used generalized linear mixed-effect models (GLMM) via the *glmmTMB* function in the R package 'glmmTMB' (Brooks et al. 2024). For these GLMMs, we fitted models with an interaction between vegetation type and geographic location as a fixed effect and cryptogam species identity as a random effect. Sampling year was included as an additional random effect only if it significantly improved model fit. We tested this using likelihood ratio tests and AIC/BIC criteria. For microarthropod abundance (total, springtail, mite), we used a negative binomial distribution with sample mass as an offset. Richness was modeled using a Poisson distribution and Shannon diversity was modeled using a Gaussian distribution. Model convergence was assessed using Q–Q plots. We used Type II Wald χ2 tests to assess the significance of fixed effects, and estimated marginal means (EMMs) were extracted using the 'emmeans' R package (Lenth 2025). Pairwise contrasts of EMMs were calculated within each geographic region with Sidak corrections for multiple testing.

In addition to vegetation-level comparisons, we used separate GLMMs to test for differences among individual moss and lichen species. For these models, geographic location was included as a random effect and sampling year if it improved model fit. Moss and lichen species with fewer than five replicates were excluded, including *A. gainii*, *B. austrosalebrosum*, *B. sudetica*, *P. jungermannioides*, *S. lewis-smithii* and *S. globosus* (Fig. 1E).

We tested the overall effects of N content and moisture content on microarthropod abundance and diversity metrics using GLMMs for all samples from Signy Island and Rothera, excluding Byers Peninsula due to the lack of availability of moisture data. These models included N content and moisture content as fixed effects, with species identity and geographic location as random factors to account for interspecific and regional variation, and sampling year if it improved model fit. To test if the effects of N and moisture content were consistent for each geographic location, we ran separate GLMMs testing the interaction between N and geographic location (including Byers Peninsula), and moisture content and geographic location separately for mosses and lichens (with cryptogam species as a random factor, and sampling year if it improved model fit). We also tested how the abundances of the most common microarthropod species were influenced by N and moisture content for mosses and lichens separately.

To test whether the different vegetation types hosted distinct microarthropod communities, we conducted a PERMANOVA based on Bray–Curtis dissimilarity matrices using the *adonis2* function from the R package 'vegan' (Oksanen et al. 2013). Geographic location was included as a stratification factor to restrict permutations within each location to ensure that differences in community structure were evaluated independently of regional effects. To assess whether observed differences in microarthropod community composition were influenced by differences in community dispersion, we conducted tests for homogeneity of multivariate

Table 1. Climatic data for the three geographic locations sampled in this study. We show mean annual temperature and total annual precipitation data from the CHELSA climate model for all our sampling locations across Signy, Byers Peninsula and Rothera. Measured air and soil temperatures originate for Signy from Jane Col (60°41'54.97"S, 45°37'41.02"W) from 2007 to 2016 (Convey et al. 2021); those for Rothera originate from Anchorage Island (67°36'11.99"S, 68°12'36.00"W) from 2001 to 2009 (Convey et al. 2020). Measured air temperatures from Byers Peninsula originate from 62°38'49.99"S, 61°6'37.00"W between 2002 and 2010 (Bañón et al. 2013), while measured soil temperatures are from a site adjacent to Limnopolar Lake (62°38'15"S, 61°38'15"W) between 2010 and 2020 (de Pablo et al. 2024). Solar irradiance (all-sky shortwave irradiance, which includes cloud effects) and cloud amount originate from CERES monthly and annual data (Doelling 2017) and are summarized as means over 2013–2024 and for December, January and February. All values show mean [minimum, maximum] values.

Property	Source	Signy	Byers Peninsula	Rothera
Mean annual temperature (°C)	CHELSA	−3.4 [−3.6, −2.5]	−1.7 [−3.8, −1.4]	−6.3 [−7.1, −3.7]
	Measured	−4.8 [−32.7, 22.4]	−2.8	−4.6 [−34.0, 7.4]
Soil temperature (5 cm) (°C)	Measured	−2.1 [−15.5, 10.0]	−0.4 [−8.2, 14.1]	−2.3 [−15.1, 22.9]
Total annual precipitation (mm)	CHELSA	996 [725, 1221]	1488 [1221, 1681]	1456 [825, 2171]
Annual all-sky surface shortwave irradiance (W m^{-2})	CERES	102.0 [95.8, 107.4]	95.1 [91.8, 98.4]	107.4 [99.4, 113.1]
Cloud cover (%)	CERES	90.3 [88.9, 92.2]	88.7 [87.0, 91.4]	89.4 [87.0, 91.4]
Summer all-sky surface shortwave irradiance (W m^{-2})	CERES	187.0 [178.3, 198.6]	192.5 [178.6, 209.1]	220.9 [201.4, 237.7]
Summer cloud cover (%)	CERES	92.7 [88.2, 95.0]	90.0 [83.4, 92.4]	87.3 [82.7, 93.1]

dispersions (using betadisper) based on Bray–Curtis dissimilarities. These tests were run for all samples combined and separately per geographic region (Signy, Byers, Rothera), followed by permutation tests (permutest) and pairwise comparisons using Tukey HSD post hoc tests. To estimate total regional abundance of mites and springtails, we calculated mean densities (± SD) per m^2 for green vegetation (algae, moss, grass) and lichens. We assumed lichen samples covered the same area as moss cores. These densities were combined with satellite-based vegetation area estimates from Walshaw et al. (2024). All statistical analyses were conducted in R ver. 4.4.2 (www.r-project.org).

Results

A total of 247 620 microarthropod individuals were extracted from 1323 vegetation samples, with a mean abundance 27.4 ± 6.1 individuals g^{-1} dry mass, equivalent to a density of 95 780 ± 6402 individuals m^{-2}.

Microarthropod abundance and community composition across major vegetation types

Microarthropod abundance varied significantly between vegetation types and species (Table 2, Supporting information). Across all sites, the green alga *Prasiola crispa* supported the highest total microarthropod abundances, while lichens generally supported the lowest. Mosses harbored 3–20× more microarthropods than lichens, though this pattern was strongest at Signy Island and Byers Peninsula. At Rothera, no significant difference in microarthropod abundance was found between mosses and lichens (Fig. 2).

Springtail abundance was consistently higher in mosses than in lichens across all three regions (Table 2, Fig. 2). In contrast, mite abundance did not differ significantly between vegetation types, although the difference was location-specific (Table 2).

Microarthropod community composition also differed between vegetation types (PERMANOVA: $R^2=0.10$, $p=0.003$; Fig. 3), with this difference remaining consistent across sampling locations (PERMANOVA: Signy: $R^2=0.09$, $p=0.003$; Byers Peninsula $R^2=0.10$, $p=0.003$; Rothera $R^2=0.09$, $p=0.003$). However, differences in microarthropod community composition were partially accompanied by differences in community dispersion across vegetation types (betadisper: overall $F(31\ 167)=69.58$, $p < 0.001$; Signy $F(2469)=13.61$, $p < 0.001$; and Rothera $F(2471)=6.80$, $p=0.001$; but not at Byers Peninsula $F(2222)=2.40$, $p=0.093$). Therefore, overall observed differences in community composition and at Signy and at Rothera, may be partly driven by differences in beta diversity (i.e. within-group variability), rather than only by shifts in community structure.

Microarthropod abundance and community composition across moss and lichen species

Mite and springtail abundance varied substantially across moss and lichen species (Fig. 4, Supporting information). For example, no springtails were found in the lichens *Ochrolechia frigida*, *Pseudophebe miniscula*, *Ramalina terebrata* and *Usnea* spp., while the highest springtail abundances were recorded in *Umbilicaria antarctica* (7.77 individuals g^{-1} of sample dry mass), *Stereocaulon alpinum* (8.74 g^{-1}) and *Sphaerophorus globosus* (8.75 g^{-1}). Likewise, *O. frigida* did not host any mites, while mite abundances in lichens were highest in *Pseudophebe minuscula* (71.97 g^{-1}), *Umbilicaria decussata* (89.15 g^{-1}) and Lichen sp. (116.93 g^{-1}) (Fig. 4, Supporting information).

Among moss species, *Syntrichia saxicola* (18.3 g^{-1} of sample dry mass) and *Chorisodontium aciphyllum* (7.36 g^{-1} of sample dry mass) hosted the lowest numbers of springtails, while *Andreaea gainii* (138.75 g^{-1}), *Schistidium antarctici* (119.61 g^{-1}), *Brachythecium austrosalebrosum* (341.92 g^{-1}) and *Ceratodon purpureus* (193.73 g^{-1}) supported the highest numbers (Fig. 4, Supporting information). For mites, the lowest abundances were observed in *Bucklandiella sudetica* (0.37 g^{-1}) and *C. aciphyllum* (0.86 g^{-1}). The highest mite densities were recorded in *Sanionia uncinata* (23.44 g^{-1}) and *S. saxicola* (29.62 g^{-1}) (Fig. 2, Supporting information).

Table 2. Type II Wald $\chi 2$ test results for generalized linear mixed-effect models (GLMMs) testing effects of vegetation type, geographic location and their interaction on microarthropod abundance, springtail abundance, mite abundance, richness and Shannon diversity.

Response variable	Effect	Chisq	Df	p-value
Microarthropod abundance	Vegetation type	12.2	3	**0.007**
	Geographic location	4.83	2	0.09
	Vegetation type × geographic location	17.4	3	**< 0.001**
Springtail abundance	Vegetation type	26.3	3	**< 0.001**
	Geographic location	44.5	2	**< 0.001**
	Vegetation type × geographic location	30.1	3	**< 0.001**
Mite abundance	Vegetation type	3.23	3	0.36
	Geographic location	29.3	2	**< 0.001**
	Vegetation type × geographic location	23.6	3	**< 0.001**
Microarthropod richness	Vegetation type	20.0	3	**< 0.001**
	Geographic location	61.7	2	**< 0.001**
	Vegetation type × geographic location	7.00	3	0.07
Microarthropod Shannon diversity	Vegetation type	2.40	3	0.49
	Geographic location	9.17	2	**0.01**
	Vegetation type × geographic location	23.1	3	**< 0.001**

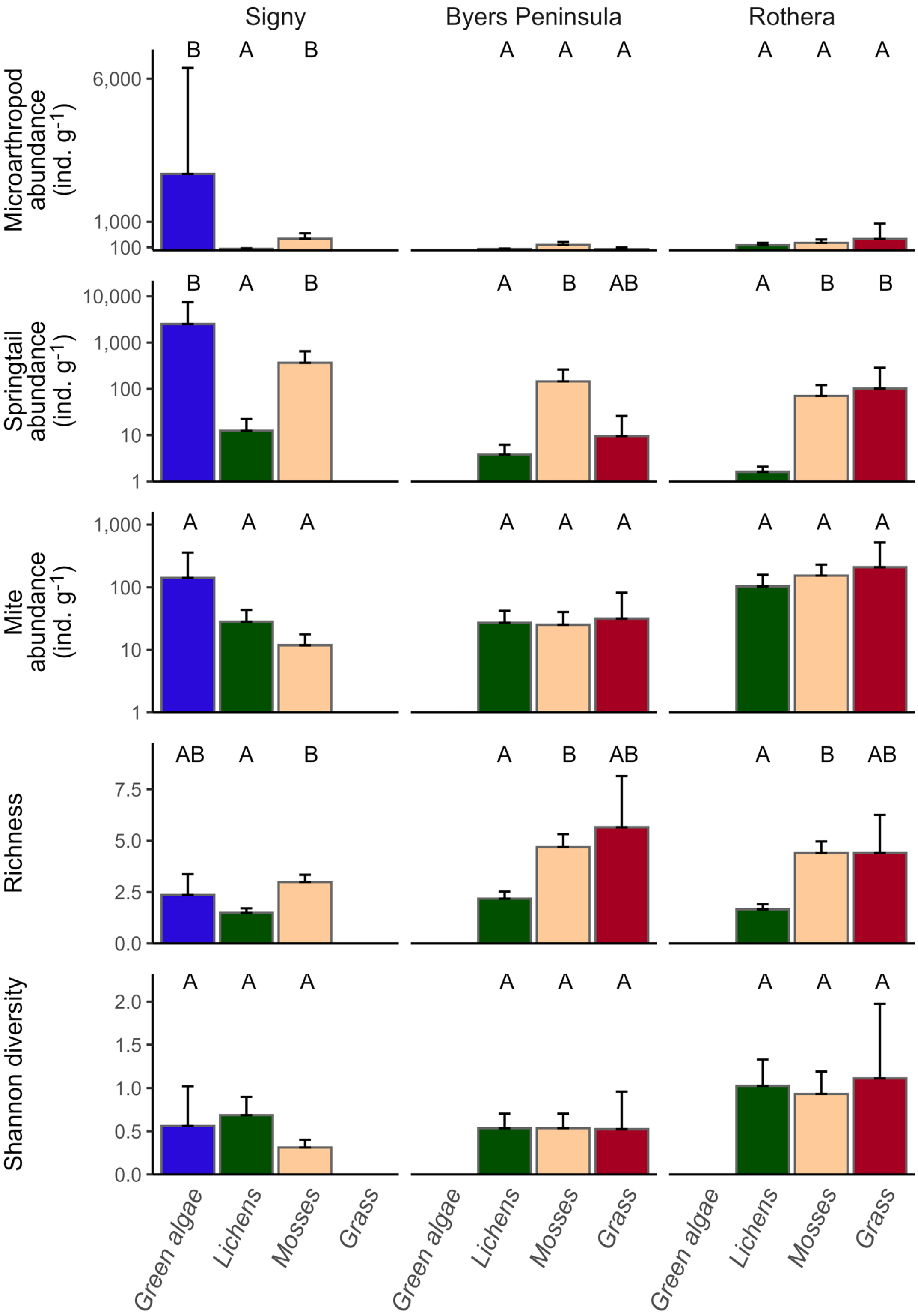


Figure 2. Total microarthropod abundance, springtail abundance, mite abundance, microathropod richness, and Shannon diversity in green alga, lichens, mosses and grass across three geographic locations. Bars represent estimated marginal means (± SE) from generalized linear mixed-effect models (GLMMs) including a vegetation type × geographic location interaction and species identity as a random effect. Different letters above bars indicate statistically significant pairwise differences between vegetation types within each location (Sidak-adjusted).

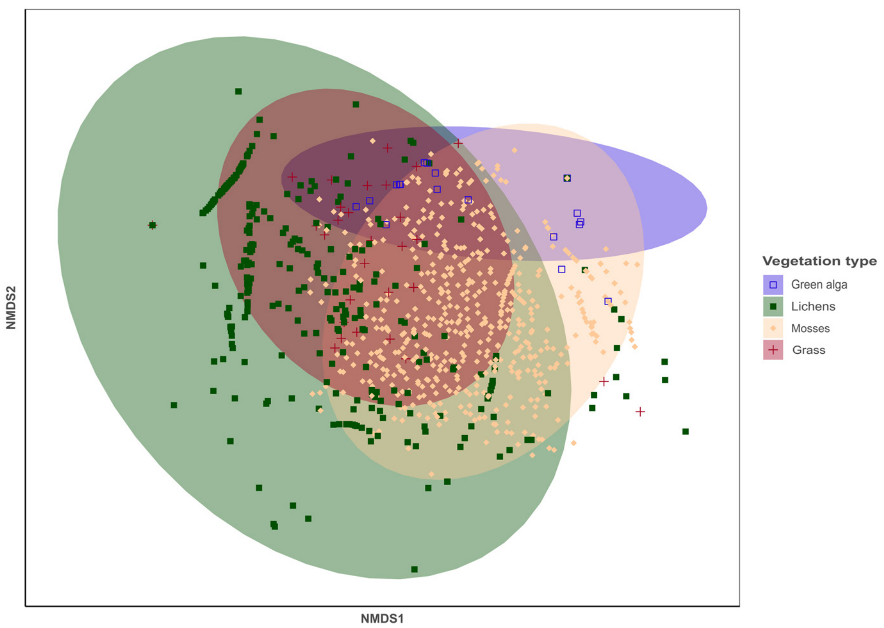


Figure 3. Non-metric multidimensional scaling (NMDS) analysis of microarthropod community composition across multiple transects in three sites remote from each other in the maritime Antarctic (Signy, Byers Peninsula, Rothera). Colours and shapes indicate major vegetation types: the green alga *Prasiola crispa* (n = 24), lichens (n = 640), mosses (n = 629) and the grass *Deschampsia antarctica* (n = 30). NMDS stress: 0.18.

Springtail and mite abundance patterns generally aligned with vegetation type preferences, with springtails favoring mosses and mites favoring lichens. The only exception was the predatory mite, *Gamasellus racovitzai*, which was more abundant in mosses than in lichens (Supporting information). The mites *Halozetes belgicae* and *Alaskozetes antarcticus* showed similar abundance patterns in moss and lichen species (Supporting information).

Richness and diversity across vegetation types and moss and lichen species

Microarthropod species richness varied significantly by vegetation type ($\chi^2 = 20.0$, $p < 0.001$), with mosses supporting higher richness than lichens (Table 2, Fig. 2). Shannon diversity did not differ between vegetation types overall ($p = 0.49$), but it showed a significant vegetation type × location interaction ($\chi^2 = 23.1$, $p < 0.001$). However, within-location patterns were non-significant.

At moss and lichen species level, moss species with a high springtail abundance tended to have lower mite abundance and lower Shannon diversity, and vice versa for lichens (Fig. 5).

Moss and lichen trait effects on microarthropod abundance and diversity indices

Nitrogen (N) content was consistently positively associated with microarthropod abundance and diversity indicators across mosses and lichens (Fig. 6A). However, the influence of N content on microarthropod abundance was 1.64× stronger in mosses than in lichens. While springtail and mite abundance responded similarly to N across vegetation types, microarthropod richness showed a 1.2× stronger response in lichens, and Shannon diversity increased 24× more with N content in lichens than in mosses. Nitrogen effects were weaker at Rothera than at Byers Peninsula or Signy (Fig. 6B, Supporting information).

Moisture content had contrasting effects across vegetation types (Fig. 6A). In mosses, higher moisture increased total abundance and springtail abundance but reduced mite abundance, richness and diversity. In lichens, moisture had no effect on total microarthropod abundance, species richness or Shannon diversity, except for springtails, where the positive effect of moisture was 1.4× stronger than in mosses. However, effects of moisture on microarthropod abundances and diversity indices were stronger at Rothera than at Signy (Fig. 6C, Supporting information).

While N content consistently increased total microarthropod abundance across mosses and lichens, responses differed across individual microarthropod species (Supporting information). *Friesea* sp. (springtail) and *Gamazellus racovitzai* (mite) abundance responded differently depending on vegetation type. Moisture effects were even more variable across microarthropod species and vegetation types. In mosses, springtail abundance increased with moisture content, particularly for *Cryptopygus antarcticus*, whereas *Folsomotoma octooculata* and *Friesea* sp. showed negative responses. In lichens, moisture content increased springtail abundance, except for *F. octooculata*. Mite abundance responses to moisture content were negative for *Alaskozetes antarcticus* in lichens and *G. racovitzai* in mosses, but otherwise non-significant.

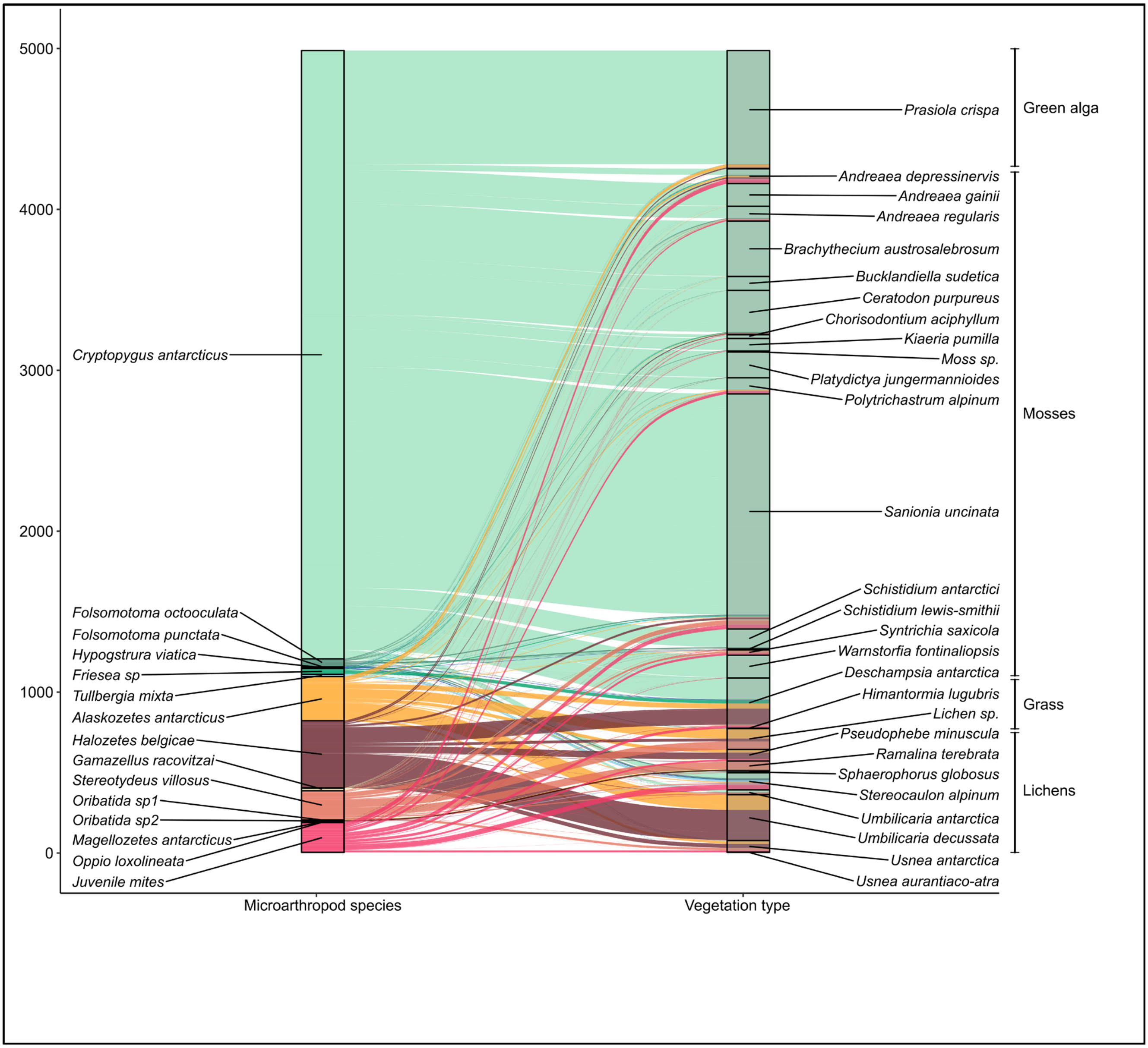


Figure 4. Alluvial diagram showing associations between microarthropod species (left) and plant, lichen and green alga species (right) at three geographically distant sites in the maritime Antarctic. The width of the flows indicates mean abundance (individuals per gram dry mass). The colours represent microarthropod species, with springtail species in green and mite species in brown colors.

Estimation of total microarthropod abundance in the maritime Antarctic

Based on our microarthropod abundance data, we estimated an average density of 130 380 ± 11 027 springtails m^{-2} and 21 302 ± 2275 mites m^{-2} of green vegetation (green alga, grass, moss). For lichens, average springtail density was 1598 ± 322 m^{-2} and mite density 34 984 ± 4059 m^{-2}. Applying these densities to recent satellite imagery-derived area estimations of green vegetation (27.2 km^2) and lichen cover (7.9 km^2) in the maritime Antarctic taken from Walshaw et al. (2024), we estimate 3.55×10^9 springtails and 5.79×10^8 mites in green vegetation, and 1.26×10^7 springtails and 2.76×10^8 mites in lichens across the maritime Antarctic (Supporting information).

Discussion

Vegetation type and geographic location interactively shape microarthropod communities

Primary producers shape terrestrial biodiversity through habitat modification and resource provisioning. Our results showed that microarthropod abundance differed significantly across vegetation types (mosses, lichens, a green alga and a

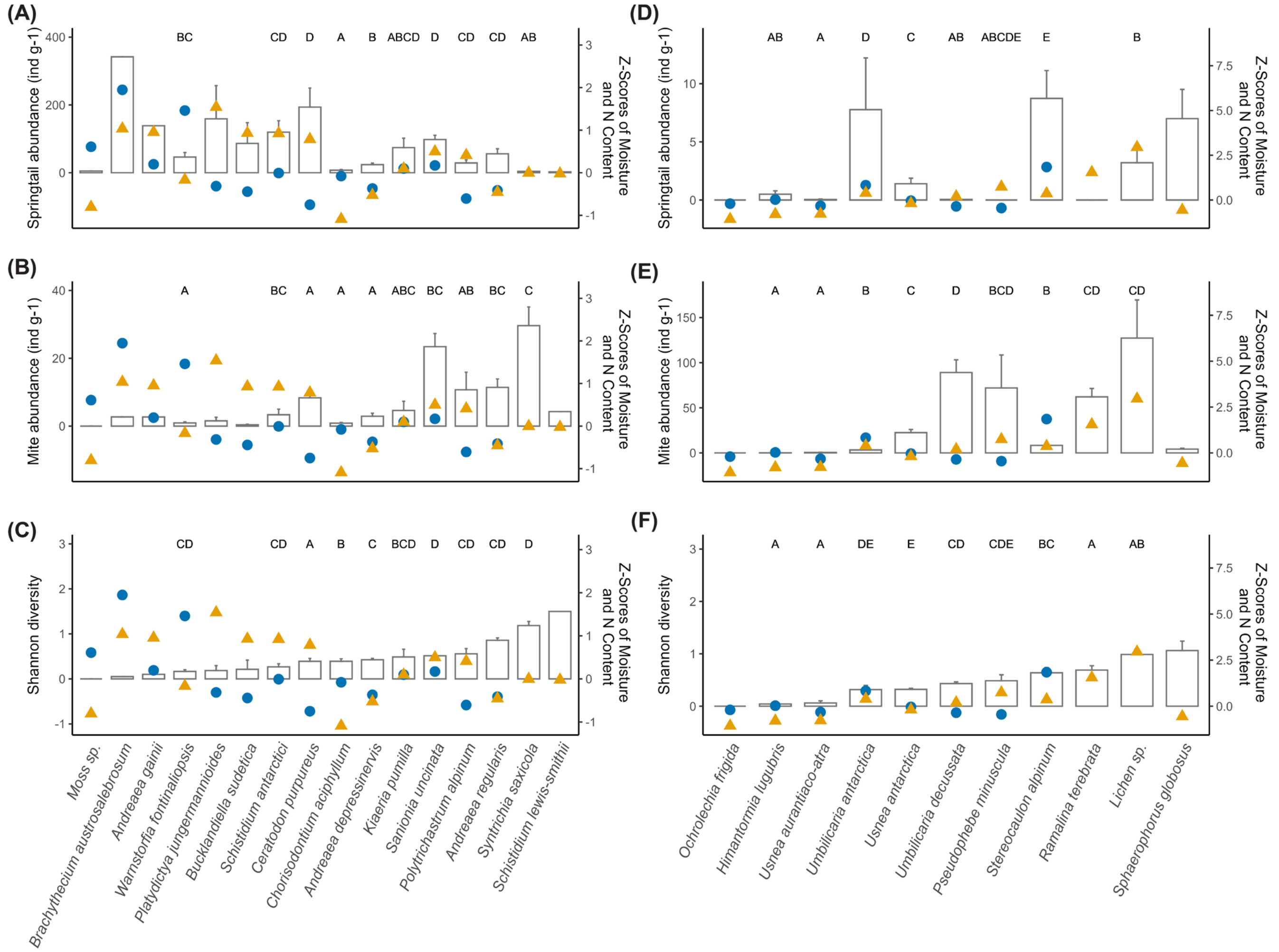


Figure 5. Barplots of overall abundance and diversity of microarthropods across multiple transects in three geographically distant sites in the maritime Antarctic. (A) springtail abundance, (B) mite abundance, (C) microarthropod Shannon diversity in all sampled moss species, and (D) springtail abundance and (E) mite abundance and (F) microarthropod Shannon diversity in all sampled lichen species. Error bars indicate standard errors. Differences between species are indicated with letters, based on generalized linear mixed-effect models (GLMMs) with geographic locations as a random factor (bars without letters were excluded due to limited replication). Blue dots indicate mean moisture content and orange triangles show mean nitrogen contents for each moss and lichen species.

grass), and that these patterns varied with geographic location. Different vegetation types thus contribute differently to Antarctic terrestrial biodiversity (Ball et al. 2022). These observed patterns are likely linked to species-specific traits of the vegetation types, such as differences in moisture retention, nutrient content and structural complexity, which we discuss in the next section.

These differences were largely driven by consistently higher springtail abundance in mosses than in lichen across Signy, Byers Peninsula and Rothera. While differences in mite abundance across vegetation types depended on geographic location, they were not significantly different between vegetation types. Total microarthropod abundance differed between vegetation types, but this pattern was only significant at Signy Island. This suggests that these patterns are modulated by local environmental conditions (Nielsen et al. 2010, Bokhorst et al. 2017). At Byers Peninsula and Rothera, differences in microarthropod abundance between mosses and lichens disappeared suggesting that, under harsher climatic conditions, microarthropod host preferences may be overridden by abiotic constraints (Bokhorst et al. 2024). Notably, Rothera moss samples were dominated by juvenile or unidentified mites, which may indicate a role for mosses in providing microclimatic buffering for early life stages under extreme conditions. Whether similar patterns also occur in cryptogam-dominated ecosystems beyond Antarctica is unclear, although the contrasting pattern in springtail abundances between mosses and lichens partly mirror findings from Arctic ecosystems in Svalbard, where springtails were ten times more abundant than mites in wet moss tundra

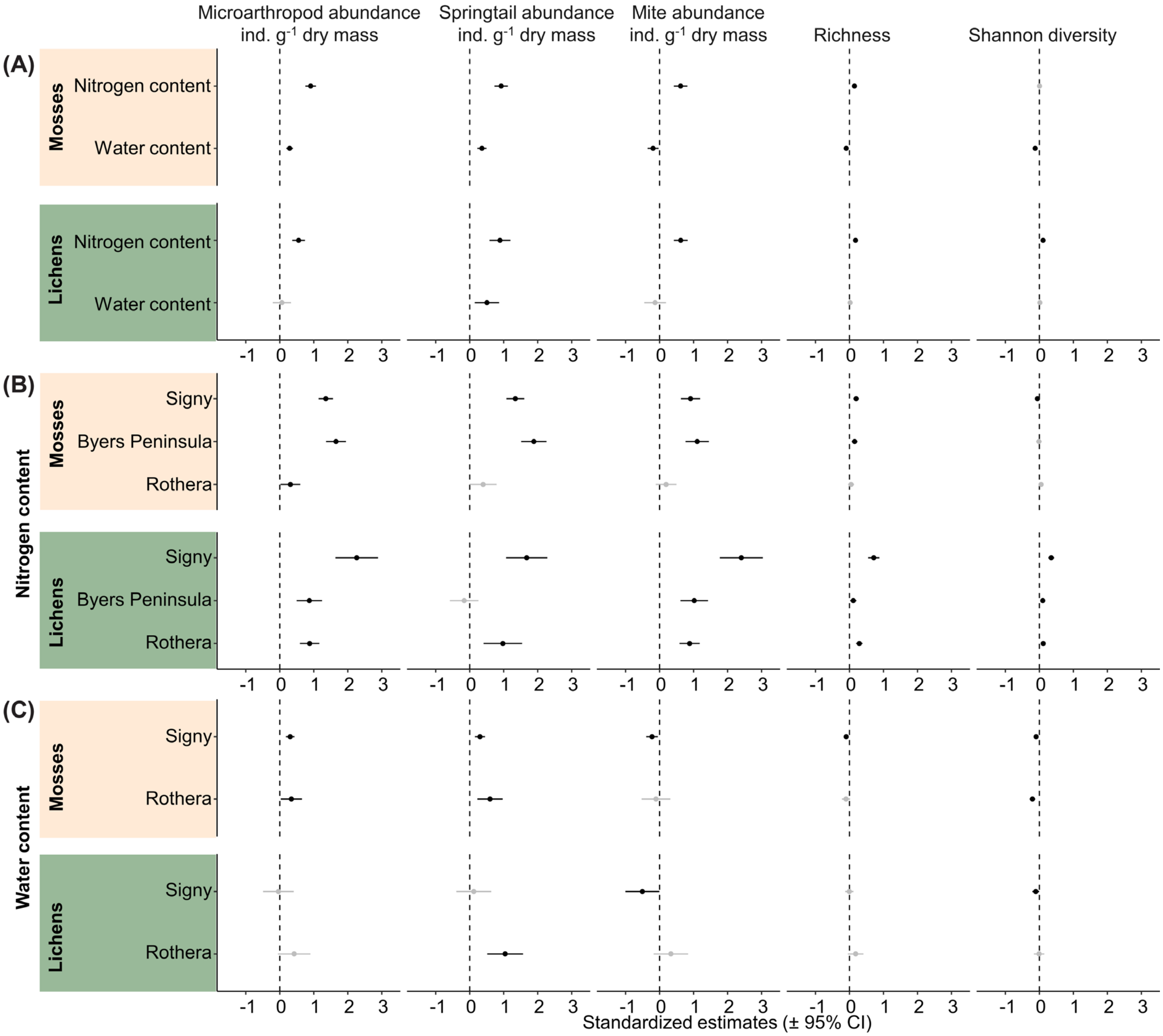


Figure 6. (A) Standardized effect sizes of terms included in generalized linear mixed models for microarthropod abundance, springtail abundance, mite abundance, richness and Shannon diversity associated with mosses (n = 466) and lichens (n = 369). Samples include both Signy and Rothera. Geographic location and moss and lichen species identity were treated as random factors in these models. (B) Standardized effect sizes of nitrogen content in generalized linear mixed models (GLMMs) for microarthropod abundance, springtail abundance, mite abundance, richness and Shannon diversity associated with mosses (n = 586) and lichens (n = 636). Moss and lichen species identity were treated as random factors in these models. (C) Standardized effect sizes of sample water content in GLMMs for microarthropod abundance, springtail abundance, mite abundance, richness and Shannon diversity associated with mosses (n = 489) and lichens (n = 486) in Signy and Rothera. Moss and lichen species identity were treated as random factors in these models. Points indicate the estimate and bars represent 95% confidence intervals. Significant effects are shown in black, non-significant effects in grey.

(Bengtson et al. 1974). Coulson et al. (2003), in another High Arctic study, showed close connections between plant species and soil fauna.

Beyond the clear differences between mosses and lichens, the green alga *Prasiola crispa* supported exceptionally high microarthropod abundances, likely reflecting its dual role as both food source and habitat (Bokhorst et al. 2007). However, since *P. crispa* was sampled only on Signy Island, we cannot generalize this result across the maritime Antarctic. The grass *Deschampsia antarctica*, the only vascular plant sampled, supported relatively similar abundances of mites and springtails, but it did not differ significantly in terms of richness or Shannon diversity from lichens or mosses. Sample sizes for *D. antarctica* were lower than for mosses and lichens, and geographically limited, making definitive conclusions difficult. However, at Rothera, *D. antarctica* hosted more springtails than lichens, which we did not observe at Byers Peninsula. This raises the possibility that its future expansion in colder southern areas (Cannone et al. 2022) in the maritime Antarctic under climate warming may disproportionally impact local microarthropod communities.

While our study focused on vegetation itself, other habitats, such as bare or sparsely vegetated soils, substrates underlying cryptogams or bird nests, and rock aggregates, provide alternative microhabitats (Richard et al. 1994, Block and Convey 1995, Block et al. 2009) that may shape invertebrate communities and contribute to population numbers in ways not captured by our vegetation-focused approach.

Moss and lichen traits as drivers of microarthropod communities

The patterns we found across vegetation types can arise due to shared abiotic preferences between vegetation and microarthropods, or vegetation shaping microarthropod communities through physiochemical traits, or biotic interactions (e.g. trophic relationships). To assess the role of vegetation traits in structuring microarthropod communities, we examined how two key traits (moisture and N content) link to microarthropod abundances and diversity indicators in mosses and lichens. Moisture and N content strongly influence microarthropod abundance and diversity, albeit with differential effects across taxa and vegetation types. Mosses with higher moisture content supported greater springtail abundances, reaffirming the role of water in sustaining moisture-sensitive taxa (Convey et al. 2003) and partly supporting our first hypothesis. However contrary to our first hypothesis, mosses with higher moisture content showed reduced Shannon diversity, due to the dominance of *Cryptopygus antarcticus*, a springtail species that thrives in moist conditions (Hayward et al. 2004). The positive relationship between moss moisture content and microarthropod abundance aligns with findings from boreal forests (Lindo et al. 2012), but was not consistently observed in earlier studies of wet and dry moss carpets on Signy Island (Block 1982), potentially due to interactions with other environmental factors or differing moisture optima among microarthropod species (Verhoef and van Selm 1983, Hayward et al. 2004). In contrast, in lichens, moisture content had no effect on total microarthropod abundance or diversity, although moisture content did positively influence springtail abundance in lichens, but not mite abundance. These findings support our second hypothesis, that mites will react less strongly to moisture than springtails. While our findings underscore the importance of moisture content for springtail distributions, we recognize that moisture was measured only at the time of sampling. For mosses, moisture content was strongly correlated with WHC, supporting its interpretation as a trait metric. But, in lichens, this relationship was absent. Therefore, the correlation found between springtail abundance and lichen moisture content more likely reflects short-term environmental moisture conditions and is not related to inherent lichen characteristics. Given the seasonal and microhabitat variability of Antarctic moisture conditions (Bokhorst et al. 2007), future studies should incorporate repeated moisture measurements over time to more accurately describe habitat suitability.

Although rarely mechanistically tested (Davey and Rothery 1992), Antarctic terrestrial ecosystems are considered N limited. Moss and lichen tissue N content indeed emerged as a consistent driver of microarthropod abundance and diversity across both mosses and lichens. Higher N levels likely enhance habitat quality, either of the host or of the associated microbial community, or both, supporting greater microarthropod diversity, with mites appearing particularly adept at exploiting N-enriched lichens (Bokhorst et al. 2015). These patterns were reflected in species-level variation. N-rich lichen species such as *Umbilicaria antarctica* and N-fixing *Stereocaulon alpinum* supported greater microarthropod diversity than N-poor species like *Ochrolechia frigida*. Similarly, mosses such as *Brachythecium austrosalebrosum* and *Schistidium antarctici* supported high springtail abundances and showed high N content, while species like *Andreaea depressinervis* hosted fewer microarthropods and had lower levels of N and moisture. In the maritime Antarctic, moss and lichen N contents are strongly influenced by nutrient inputs from marine bird and seal aggregations, and our analyses of a broader set of cryptogam species confirm the positive correlation between cryptogam N content and microarthropod abundance and species richness reported by Bokhorst et al. (2019). The high abundances of springtails in *Prasiola crispa*, which is often well developed in and around vertebrate aggregations, is likely also due to high N content. Unlike N, phosphorus (P) is not typically considered a biologically limiting factor in the maritime Antarctic (Chacón et al. 2013). However, in more extreme Antarctic environments such as cryoconite holes (Schmidt et al. 2022) or lakes, P can be limiting. While marine vertebrates also strongly influence P input in the maritime Antarctic (Wasley et al. 2006, Rodrigues et al. 2021), their role in shaping microarthropod communities remains unclear. Given that N and P frequently co-limit, further research is warranted to study the potential influence of P availability on microarthropods via vegetation P content.

The relative impact of cryptogam N and moisture content on microarthropods varied between locations. Nitrogen content had a stronger positive effect on microarthropod abundance at the more northern sites (Signy and Byers Peninsula) than at Rothera, the southernmost site. In contrast, the positive influence of cryptogam moisture content on springtail abundance was more pronounced at Rothera, suggesting that desiccation stress may amplify the importance of cryptogam water content and thus WHC under harsher conditions. This is consistent with findings from alpine systems, where cushion plants more strongly facilitate invertebrate abundance under more stressful microclimates (Molina-Montenegro et al. 2006). These patterns support our hypothesis that moisture becomes a more limiting factor in southern, drier environments, while N may play a greater role in more productive northern habitats.

Interestingly, N and moisture content did not affect all microarthropod taxa equally. For instance, the springtails

Friesea sp. and *Folsomotoma octooculata* decreased in abundance with increasing moisture in mosses. This aligns with previous suggestions that differential desiccation tolerances and behavioral strategies to drought of *F. griesea* and *C. antarcticus* determine their distribution patterns (Hayward et al. 2004). Such contrasting responses highlight that cryptogam traits interact with species-specific life-history strategies of microarthropods. This supports the recognition of traits that mediate interactions across trophic levels, i.e. 'interaction traits', as proposed by Lavorel et al. (2013).

Microarthropod population sizes in the maritime Antarctic

Our study provides the first quantitative estimates of microarthropod abundance across Antarctic vegetation types. Extrapolating from average densities across our 1323 samples, we estimated that mosses, *P. crispa* and *D. antarctica* collectively support over 3.5 billion springtails and nearly 600 million mites across the maritime Antarctic. Lichens are estimated to host around 13 million springtails and 280 million mites. These numbers highlight the scale of invertebrate biomass associated with Antarctic vegetation. Our estimates are based on average abundances from our sampled sites and do not account for the spatial distribution and total coverage of different vegetation types across the maritime Antarctic, nor habitats that our dataset does not include. Given the unknown extent of specific moss and lichen species in the maritime Antarctic, total abundance estimates remain subject to uncertainty. Future research should integrate high-resolution vegetation mapping with microarthropod sampling to improve Antarctic-wide abundance assessments.

Conclusions and future research directions

As climate change accelerates, ice-free areas are predicted to expand in the maritime Antarctic (Lee et al. 2017) and consequential shifts in vegetation composition are likely to alter microhabitat availability and associated biodiversity. For example, the increasing abundance of the native vascular plant *D. antarctica* (Cannone et al. 2016, 2022) may on the one hand enhance springtail abundance in the more abiotically extreme regions in the short term. On the other hand, it may in the long run outcompete cryptogams and lead to homogenization of habitats, thereby reducing the heterogeneity that underpins microarthropod diversity. This study supports the growing recognition that Antarctic ecosystems are not solely abiotically driven but also shaped by biotic interactions, including habitat modification and trophic relationships (Hogg et al. 2006, Caruso et al. 2013, 2019, Convey et al. 2018). Antarctic vegetation also supports diverse microbial communities and other invertebrate taxa, such as nematodes and tardigrades (Schwarz et al. 1993, Nielsen et al. 2011). This opens opportunities for integrative research that examines how cryptogam-associated microarthropod communities interact with microbial decomposers and other soil invertebrates to influence nutrient cycling and ecosystem functioning.

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Author contributions

Ingeborg J. Klarenberg: Conceptualization (lead); Data curation (equal); Formal analysis (lead); Investigation (lead); Visualization (lead); Writing – original draft (lead). **Rong Liu**: Investigation (equal); Methodology (equal); Writing – review and editing (equal). **Peter Convey**: Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Johannes H. C. Cornelissen**: Conceptualization (equal); Funding acquisition (equal); Supervision (equal); Writing – review and editing (equal). **Stef Bokhorst**: Conceptualization (equal); Data curation (equal); Funding acquisition (equal); Investigation (equal); Supervision (equal); Writing – review and editing (equal).

Data availability statement

Data are available from the Zenodo Digital Repository: https://doi.org/10.5281/zenodo.17112197 (Klarenberg et al. 2025).

Supporting information

The Supporting information associated with this article is available with the online version.

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