

A maritime Antarctic study on the impact of marine vertebrates on terrestrial micro-arthropods via nutrient content of vegetation

Trophic cascades in the Antarctic

Stef Bokhorst^{1,2} and Peter Convey^{3,4}

1 Norwegian Institute for Nature Research (NINA) Department of Arctic Ecology, Tromsø NO-9296, Norway.

2 Department of Systems Ecology, Institute of Ecological Science, VU University Amsterdam, De Boelelaan 1085, NL-1081 HV Amsterdam, The Netherlands

3 British Antarctic Survey, Natural Environmental Research Council, High Cross, Madingley Road, Cambridge CB3 0ET, UK.

4 National Antarctic Research Centre, University Malaya, B303, Level 3, Block B, Lembah Pantai, 50603 Kuala Lumpur, Malaysia

Abstract

Traits of primary producers associated with tissue quality are commonly assumed to play a strong control on higher trophic levels. However, this view is largely based on studies of vascular plants, and cryptogamic vegetation has received far less attention. In this study we utilised natural gradients in nutrient concentrations in cryptogams associated with the proximity of penguin colonies on a maritime Antarctic island, to quantify the impact of nitrogen content for micro-arthropod communities.

Proximity to penguin colonies increased the nitrogen concentration of cryptogams and the penguin source was confirmed by decreasing $\delta^{15}\text{N}$ values at greater distance from colonies. Micro-arthropod abundance, diversity (H') and richness declined with distance from the penguin colonies, and was positively correlated with the nitrogen concentrations of cryptogams. $\Delta^{15}\text{N}$ of micro-arthropods was positively correlated ($r^2 = 0.865$, $P < 0.01$) with $\delta^{15}\text{N}$ of the moss *Andreaea depressinervis*, indicating that penguin-derived nitrogen moves through Antarctic food webs across multiple trophic levels.

Nitrogen content of cryptogams was correlated with associated micro-arthropods indicating that biotic interactions affect community development in Antarctic terrestrial ecosystems. The spatial patterns of Antarctic biodiversity can therefore be affected by local factors, such as marine vertebrates, beyond existing latitudinal patterns of temperature and water availability.

Keywords: Acari; Collembola; Isotope; Lichen; Moss; Nitrogen

Introduction

Functional traits of vascular plant primary producers can be major drivers of the community composition of herbivores and decomposers (Grime et al. 1996; Agrawal and Fishbein 2006; Loranger et al. 2012). Nutrient content of plant tissues, in particular, plays an important role in supporting the diversity and abundance of consumers (Loranger et al. 2012). However, patterns described to date are primarily based on studies of vascular plants (Mattson 1980; Grime 2001). Cryptogams (bryophytes, lichens and algae), in contrast have received less attention despite the large and even dominant role these primary producers play in many ecosystems, especially at higher latitudes and altitudes, and in the global carbon cycle (Davis 1981; Convey 2013; Convey et al. 2014). The few studies examining cryptogam traits in relation to consumption have mainly focused on the inhibitory function of secondary compounds in preventing herbivory (Gauslaa 2005; Asplund and Wardle 2013). The most extensive study to date on the impacts of physiological traits of lichens for invertebrate communities found variable responses from different invertebrate groups to lichen nutrient content which was, in part, due to the variety in lichen growth forms across the different growth locations that were studied (Bokhorst et al. 2015). To overcome the variability caused by differences in growth form and growth location, natural gradients in intra-specific lichen nutrient concentrations are required.

Mosses, lichens and algae are the major macroscopic primary producer components of food webs in many polar terrestrial ecosystems (Convey 2013) and can often be found in the vicinity of penguin colonies. These penguin colonies and other vertebrate aggregations along the coast of the Antarctic Peninsula and many offshore islands provide large quantities of nitrogen that encourage plant growth (Lindeboom 1984; Erskine et al. 1998). Bird-derived nitrogen sources are well known to support vigorous growth of primary producers globally

(Anderson and Polis 1999; Sanchez-Pinero and Polis 2000; Ellis 2005) and to increase ecosystem process rates (Bokhorst et al. 2007a). The impacts generally diminish with increasing distance from the source, creating a nutrient gradient within the vegetation which also includes declines in $\delta^{15}\text{N}$ (Erskine et al. 1998; Zmudczyńska et al. 2012; Crittenden et al. 2015). Such gradients in $\delta^{15}\text{N}$ are useful to determine whether higher trophic levels feed on the penguin-affected vegetation, as $\delta^{15}\text{N}$ levels typically increase by 2-3 units per step in trophic level (Peterson and Fry 1987). To date, the existence or magnitude of any impact of increased nutrient content of primary producers for higher trophic levels in Antarctic terrestrial ecosystems is poorly understood (Davis 1981).

To address these issues we tested whether proximity to penguin colonies was associated with increased nitrogen concentrations and $\delta^{15}\text{N}$ values in cryptogams on Signy Island (maritime Antarctic) and whether this, in turn, correlated with the community composition of the most prominent elements of the terrestrial fauna, springtails and mites (Convey 2013). We hypothesised that: 1) the nitrogen concentrations and $\delta^{15}\text{N}$ values of cryptogams would decrease with increasing distance from penguin colonies; and 2) that, as a consequence, this would be associated with decreased abundance, diversity (H') and species richness of micro-arthropods living among these cryptogams. Confirmation of these hypotheses would provide the first direct evidence for trophic cascades in the Antarctic terrestrial environment, and add support to recent studies (Caruso et al. 2013) challenging the long-held view that abiotic factors are the driving forces underlying spatial patterns and processes in the Antarctic terrestrial biota (Convey 1996; Hogg et al. 2006).

Materials and Methods

Study sites

This study was performed on Signy Island (60°17'S 45°59'W) in the maritime Antarctic region north-east of the Antarctic Peninsula. The island is part of the South Orkney Islands archipelago, has an annual temperature of around -2°C and receives about 400 mm yr⁻¹ of precipitation of which most falls as snow (Walton 1982; Royles et al. 2013). Up to 50% of the island's surface is free of snow and ice during summer (December–February), exposing some of the best-developed and most diverse cryptogam communities in the Antarctic. There are four areas hosting large penguin colonies along the coastline of Signy Island (Fig. 1). The largest of these is at North Point, which is inhabited by Adélie (*Pygoscelis adeliae*), chinstrap (*P. antarctica*) and gentoo penguins (*P. papua*) (total of 13000 breeding pairs). The colony at Gourlay Peninsula is dominated by Adélie and chinstrap penguins (12900 breeding pairs). Smaller colonies are situated along the west coast of the island, with the Cummings Cove area hosting 7000 chinstrap penguin pairs, and Spindrift Rocks 2000 pairs of Adélie penguins.

Sampling regime

During December 2013 we sampled mosses, algae and lichens as close as possible to the four penguin colonies and at four additional sites at increasing distances away from each colony along each of three replicate transects, with sampling points separated by at least 10 m from each other. Due to the differences in vegetation development and topography between the four colonies we were unable to collect all cryptogam species from each transect and sampling distances from the penguin colonies differed (for details see Table 1, Fig. 1). To determine the impact of cryptogam nitrogen concentrations on micro-arthropod communities across larger geographical scales we also sampled lichens along the north-south axis of Signy Island, thereby extending the transect's starting from the North Point penguin colony. In addition, as some of the transects increased in altitude (up to 200 m asl) at greater distance from the penguin colonies, we also included three transects along a hillside remote from any

penguin colonies in order to control for any potential effect of altitude on micro-arthropod community composition (See Fig. 1).

We focussed on the dominant lichen species, *Usnea antarctica* (DuRietz), and *Umbilicaria antarctica* (Frey & I.M. Lamb), the moss *Andreaea depressinervis* (Card.) and the foliose alga *Prasiola crispa* (Lightfoot). Henceforth these species will be referred to by their genus name alone. Sampling from extensive moss carpets or turves was avoided in order to avoid artefacts caused by autocorrelation with the presence or extent of moss, which is known to be a preferred micro-habitat for many micro-arthropods (Davis 1981; Usher and Booth 1984; Bokhorst et al. 2014).

At each sampling site, *Prasiola* was collected with a PVC corer (7 cm diameter) including the underlying soil (at most 1 cm if any present) and stored in a plastic container. Moss and lichen clumps were collected by hand and also stored in individual plastic containers. Mean cryptogam dry mass was: 5.8 g (sd = 2.8) for *Andreaea*, 3.0 g (1.7) for *Umbilicaria*, 3.7 g (1.6) for *Usnea* and 1.8 g (0.9) for *Prasiola*. All samples were kept in the shade at ambient temperatures while in the field and at approximately 5°C in the dark when stored at the station until extraction (within 24 h) in a modified Tullgren extractor for 24 h. Extracted Collembola and Acari were preserved in 70% ethanol and identified to species level, except for the smallest Prostigmata which were grouped together. Micro-arthropod abundance was expressed as the number of individuals per gram moss, algae or lichen. To obtain dry vegetation mass of each sample all soil and rock (if any) were removed and the remaining vegetation weighed when dry after completion of the micro-arthropod extractions. Moisture content of the sample was quantified by weighing each sample before and after placement in the Tullgren funnels.

Analyses of nitrogen and $\delta^{15}N$.

Dried cryptogam samples were transported to Europe for nitrogen and stable isotope $\delta^{15}\text{N}$ analyses. Nitrogen and $\delta^{15}\text{N}$ were analysed using a Fisons NA 1500 elemental analyser coupled to a Finnigan conflo II interface, and a Finnigan MAT Delta S isotope ratio mass spectrometer. In addition, we measured $\delta^{15}\text{N}$ values of adult individuals of the springtail *Cryptogpygus antarcticus* (c. 20 individuals per sample; 210 μg) and the mites *Alaskozetes antarcticus* and *Halozetes belgicae* (both c. 6 individuals per sample; 280 μg) to determine if penguin-derived nitrogen flows from the primary producers to these grazers. The $\delta^{15}\text{N}$ analyses of micro-arthropods were carried out on samples extracted from *Andreaea* as the moss contained the highest micro-arthropod abundance. To remove any ethanol before analyses the micro-arthropods were placed in pre-weighed tin cups and oven dried (60°C) for 24 h. To quantify the biomass of the springtails and mites in each sample the cups were weighed again after drying before analysis of $\delta^{15}\text{N}$ (mass ranged from 89-612 $\mu\text{g}/\text{sample}$).

Calculations and statistical analyses.

To determine differences in nitrogen concentrations, $\delta^{15}\text{N}$, water content, abundance of total micro-arthropods, diversity (H') and species richness along the penguin transects we used a mixed effect model with distance to the penguin colony as fixed factor and site as a random factor for each of the cryptogam species separately. To compare the rate of change of cryptogam traits (%N, $\delta^{15}\text{N}$ and water content) and the micro-arthropod community along transects we compared the slopes of linear regression lines through the transect data points using cryptogam species as fixed factor and site as a random factor. To determine the impact of penguin colonies on the micro-arthropod variables along greater spatial distances we used the same mixed effect model as described above but limited to *Usnea* using data from the North Point and the N-S transects. To account for potential impacts of altitude (as a proxy for temperature) differences along the transects we compared the differences in *Usnea* N

concentrations, $\delta^{15}\text{N}$, water content and micro-arthropod variables with altitude along penguin-influenced transects (North Point, Cummings, and Spindrift Rocks) and non-affected transects (Moraine Valley) with altitude as a fixed factor and site as random factor. Correlation coefficients were calculated between the nitrogen, $\delta^{15}\text{N}$ and water content of cryptogams and the micro-arthropod variables to explore which if any of these was a stronger driver behind observed patterns in community composition. Abundance data were log transformed to achieve homogeneity of variance. All statistical analyses were carried out using SPSS 22.0 (IBM SPSS Statistics version 22.0. Armonk NY, USA).

Results

Cryptogam nitrogen and water content

Nitrogen concentrations of cryptogams declined by nearly two-thirds with increasing distance from penguin colonies (Fig. 2 a-d, Table 2). $\Delta^{15}\text{N}$ declined by between 5 to 15 units as the distance to penguin colonies increased, although the variation between species and different transects was large (Fig. 2e-h). For example, *Prasiola* showed no change in %N or $\delta^{15}\text{N}$ along the Gourlay transect but it did along the North Point transects (Fig. 2b) while *Andreaea* showed declines in N along transects of both sites (Fig. 2a). The horizontal extent of the impact of the penguin colonies on cryptogam N concentrations and $\delta^{15}\text{N}$ was c. 700-1000 m for *Andreaea*, 500-750 m for *Prasiola*, 300-500 m for *Usnea* and 700-1500 m for *Umbilicaria*. Mean nitrogen concentrations and $\delta^{15}\text{N}$ values were highest ($F_{3,133} = 64.1$ and 104.7 respectively; $P < 0.001$) for *Prasiola* (4.1%, 10.4‰), followed by *Andreaea* (2.1%, 2.7‰), *Usnea* (1.1%, -2.4‰) and *Umbilicaria* (1.1%, -5.9‰). There were some differences in water content for individual cryptogams between sites and along transects (Table 2) but not in a consistent pattern along transects (Fig. S1). Mean water content was highest (ANOVA $F_{3,133} = 30.4$ $P < 0.001$) for *Prasiola* (67%), followed by *Umbilicaria* (60%), *Andreaea* (52%) and *Usnea* (25%) (Table 2).

Micro-arthropod communities in relation to distance from penguin colonies, cryptogam nitrogen and water content

There were consistent declines in Acari abundance (3.9 ind./100 m), species richness (0.2 species/100m) and diversity (H') (0.07/100 m) across cryptogam species and sites (Fig. 3, Table 2) resulting in lower (Tukey HSD $P < 0.01$) values at the furthest transect points compared to points closest to the penguin colonies. Change in Collembola abundance was

variable between species and sites with larger changes along Gourlay compared to North Point transects among *Prasiola* and *Umbilicaria* resulting in no overall change in Collembola abundance along transects within the *Prasiola* samples (Fig. 3e). These variable Collembola patterns were also responsible for the significant species-site interactions for changes in total micro-arthropods (Table 2).

Micro-arthropod communities were positively correlated with nitrogen concentrations of the cryptogam species but not with that of *Prasiola* (Fig. 4). Acari abundance was significantly correlated with the nitrogen concentrations of all cryptogam species while Collembola abundance was significantly correlated with the nitrogen concentrations of *Andreaea* only (Fig 4a). There were positive correlations between micro-arthropod diversity (H') and the nitrogen concentrations of the cryptogams (but not that of *Prasiola*), and of species richness and nitrogen concentrations of the two lichens (Fig. 4). $\Delta^{15}N$ for the collembolan *Cryptopygus antarcticus* was positively correlated with the $\delta^{15}N$ values of *Andreaea* (Fig. 5a), and on average 3.6‰ (± 0.47) higher than the $\delta^{15}N$ of the moss they were extracted from. Positive correlations were also found for $\delta^{15}N$ of the mites *Alaskozetes antarcticus* and *Halozetes belgicae* with that of *Andreaea* (Fig. 5b), and $\delta^{15}N$ was 5.8‰ (± 0.3) higher compared to the moss they were extracted from. There was no correlation between micro-arthropods (total abundance, Acari and Collembola) and tissue water content within cryptogam species. However, when compared across all samples ($n = 166$), total micro-arthropod and Collembola abundance were positively correlated ($r^2 = 0.15$ and 0.24 respectively $P < 0.05$) with cryptogam water content, reflecting the potential impact of the different cryptogam growth forms and water holding capacity.

Micro-arthropod communities across Signy Island and in relation to altitude

There were no differences in micro-arthropod abundance, diversity (H') or species richness along the N-S transect across the island (Fig. 6). Nitrogen concentrations and $\delta^{15}N$ did not differ along the N-S transect and the penguin impact on *Usnea* N concentrations was limited to c. 300-500 m distance (Fig. 6c). There were no correlations between *Usnea* N concentrations and the micro-arthropod community along the N-S transect (data not shown). The penguin colony impact on micro-arthropod abundance, diversity (H') and species richness in *Usnea* appears limited to c. 300-500 m distance as all more distant sampling sites showed no further differences (Fig. 6a,b). There was no difference in the micro-arthropod abundance or species richness across transects from Moraine Valley to Green Gable (Fig. 6d,e) indicating that there was no effect of altitude on the micro-arthropod community along the study transects. $\delta^{15}N$ of *Usnea* did not change with altitude along the Moraine Valley transects (Fig. 6f) and there was no correlation with the micro-arthropod abundance or species richness. In comparison with the penguin colony-associated transects the micro-arthropod abundance, diversity (H') and richness were consistently lower (Tukey HSD $P < 0.05$) along the Moraine Valley transect (Table 2, Fig. 6).

Micro-arthropod communities across cryptogam species

Species richness was highest (Tukey HSD $P < 0.01$) in *Andreaea* (4 species on average) compared to the other cryptogams (2 to 3 species) (Table 2). The lowest micro-arthropod diversity (H') was found among *Prasiola* (mean H' of 0.3 across all samples) while the other cryptogam species had higher (Tukey HSD $P < 0.05$) mean values ranging from 0.5 to 0.7. In contrast, total micro-arthropod abundance was highest (Tukey HSD $P < 0.05$) in *Prasiola* followed by *Andreaea*, *Umbilicaria* and *Usnea* (data not shown). Acari abundance did not differ between cryptogam species. Collembola abundance was consistently higher

(Tukey HSD $P < 0.001$) in *Prasiola* compared to the other cryptogam species, and *Andreaea* supported more Collembola than the two lichen species.

The predatory mite *Gamasellus racovitzai* was found across all cryptogams but abundances were higher in *Andreaea* and *Prasiola* (data not shown). Abundance of the predatory mite *G. racovitzai* was positively correlated with Collembola (prey) abundance across all ($n = 126$) cryptogam samples along transects ($r^2 = 0.113$, $P < 0.05$) but this correlation improved ($r^2 = 0.585$, $P < 0.01$) when only the *Usnea* data ($n = 42$) were used, as no significant correlations were present among the other cryptogams individually (data not shown).

Discussion

This is one of the first studies to examine the role of cryptogam nutrient traits in relation to micro-arthropod communities, and the first to do this in the Antarctic. Our data provide clear support for the role of primary producers, as distinct from abiotic interactions, as a factor contributing to ecosystem development in terrestrial ecosystems of the maritime Antarctic region (Hogg et al. 2006; Caruso et al. 2013). Although the spatial distribution of Antarctic terrestrial biodiversity is heavily influenced by temperature and water availability (Convey et al. 2014), marine vertebrates clearly have a strong impact at local scales (Erskine et al. 1998; Ellis 2005). Our findings are consistent with general patterns observed for vascular plants in more temperate regions (Loranger et al. 2012) and therefore extend general understanding of the drivers of invertebrate abundance and diversity through traits of other important primary producers such as cryptogams (Bokhorst et al. 2015).

Hypothesis 1 was supported by the decrease in nitrogen concentrations and $\delta^{15}\text{N}$ of cryptogams with increasing distance from penguin colonies. These findings are consistent with other studies from polar regions, where plant productivity increased closer to penguin colonies (Lindeboom 1984) and the stable isotope nitrogen signature of the primary producers was directly linked to the trophic level of the animals producing the faecal matter (Erskine et al. 1998; Crittenden et al. 2015). Like many plants in Arctic and temperate regions, Antarctic primary producers also tend to be nitrogen-limited in their growth (Davey and Rothery 1992; Wasley et al. 2006) and penguin colonies greatly increase the availability of nitrogen for cryptogams. The direct impact of penguin colonies here on the nitrogen content (% N and $\delta^{15}\text{N}$) of cryptogams varied greatly between species and sites, ranging from 300-1500 m distance, which is within the range of observations from Marion Island (Erskine et al. 1998),

although Crittenden et al. (2015) reported detectable impacts of penguin-derived ammonia on lichen physiological activity at distances of up to 10 km.

The variation in N concentrations between species and sites with distance to penguin colonies was most likely caused by site specific factors. For instance, N concentrations of *Andreaea* and *Prasiola* both declined along North Point transects but along the Gourlay transects this pattern was only found for *Andreaea*. This lack of response by *Prasiola* to the obvious N gradients that exist along the Gourlay transects, as shown by N concentration in *Andreaea* and *Umbilicaria*, may be caused by the decaying moss bank that underlies these transects (Smith 1988) from which *Prasiola* may receive additional N, while *Andreaea* and *Umbilicaria* were sampled from rock and therefore not so open to influence by N sources from below. However, there is no good explanation available for the differences in N content changes between *Usnea* and *Umbilicaria* along the Cummings Cove transects. Despite Signy Island being a relatively small island and nutrient inputs from sea spray and marine vertebrates generally being assumed to reach across the island (Allen et al. 1967) there were clear changes and limits (c. 300-1500 m horizontal distance) detected here to the impact of penguin colonies on the nitrogen concentrations or $\delta^{15}\text{N}$ of cryptogams. Additional factors that may have affected cryptogam $\delta^{15}\text{N}$ values include the penguin population size, dominant penguin species within the colony and overall wind direction that carries the nitrogen towards the vegetation. A larger comparative study than that presented here would be required to take these factors into account.

The decreases in micro-arthropod abundance, diversity (H') and species richness as distance to the penguin colonies increased provide support for Hypothesis 2. The micro-arthropod community values also showed strong correlations with cryptogam nitrogen concentrations indicating that this may be a driving force for community assembly at higher

298 trophic levels in these Antarctic ecosystems. Water availability and temperature are typically
299 considered as strong drivers of biological patterns in the Antarctic (Kennedy 1993; Convey et
300 al. 2014), but we did not observe any effect of intra-specific cryptogam water content or site
301 temperature (as altitude proxy) on the micro-arthropod community along the sampling
302 transects. Although site temperature was only studied for *Usnea*, the Gourlay transects
303 (including other cryptogams) showed strong declines in Acari abundance while only reaching
304 a third of the altitude of other transects, indicating that altitude/temperature differences along
305 these transects play a minor role for the studied species. The current data indicate that water
306 and temperature are of less importance than nutrient availability at closer proximity (c. 500
307 m) to penguin colonies for Antarctic micro-arthropods at this maritime Antarctic island. This
308 suggests that, at relatively small geographical scales, different drivers of community assembly
309 exist in maritime Antarctic terrestrial ecosystems. The existence of such smaller-scale
310 gradients in driving forces behind community development allows for further detailed
311 unravelling of these factors by manipulations of nutrient availability (Wasley et al. 2006) and
312 micro-climate (Bokhorst et al. 2011). Further work should ideally also include other
313 physiological variables such as phosphorus and defence compounds (Bokhorst et al. 2015;
314 Crittenden et al. 2015).

315 The strong correlation between the $\delta^{15}\text{N}$ of the micro-arthropods and that of the moss
316 *Andreaea* (Fig. 5) indicates that the penguin-derived nitrogen is taken up by the moss and
317 transferred to the micro-arthropods. The mean increase from moss to springtails was 3.6‰
318 and is consistent with changes generally associated between trophic levels (Peterson and Fry
319 1987). However, with the current data it is not possible to determine if the springtails feed on
320 the live moss, the epiphytic micro-flora living among the moss shoots, or on decaying moss
321 shoots. The 5.8‰ increase found for the mites compared to the moss (Fig. 5b) is higher than a

single trophic level step, suggesting that the mites also feed from other food sources with higher $\delta^{15}\text{N}$ values such as penguin faecal matter and dead animals (Goddard 1982; Schneider et al. 2004). Despite these uncertainties the $\delta^{15}\text{N}$ values showed a clear pattern along transects away from penguin colonies in both primary producers and consumers, with consistent declines in nitrogen concentrations and abundance, diversity and species richness of micro-arthropods. These results provide strong support for the existence of biotic interactions between primary producers and higher trophic levels in Antarctic terrestrial ecosystems.

The abundance of micro-arthropods, notably Collembola, was not always related to the nitrogen concentrations of the primary producers and, particularly, the *Prasiola* communities showed very poor correlations despite the large range in nitrogen concentrations measured (N: 1.6% - 6.2%). This indicates that other characteristics of cryptogams, such as phosphorus, defence compounds against herbivory and growth form affecting the micro-habitat conditions, may also have played a role (Asplund and Wardle 2013; Bokhorst et al. 2015). Overall, the highest micro-arthropod abundance and diversity were found among *Andreaea* and *Prasiola* compared to the lichens. These differences most likely reflect the differences in nitrogen concentrations, growth form and water content (there were significant correlations with water content when compared across all sampled cryptogams, as opposed to the low variation within species). The compact growth of moss shoots provides a more stable micro-environment than the open structure of the lichen thallus, and moss has been shown to have a strong positive effect on the abundance of micro-arthropods in other parts of the world (Salmane and Brumelis 2008; Bokhorst et al. 2014). The collembolan *Cryptopygus antarcticus* is known to have poor control over its body water content (Block and Harrisson 1995; Convey et al. 2003) and, therefore, would be less prone to desiccation when within the moss profile. Similarly, the foliose alga *Prasiola*, whose 3D structure is typified by much

folding and many small protected cavities, provides a continuous moist environment optimal for these micro-arthropods. The high abundance of micro-arthropods among *Prasiola* compared to the cryptogams was most likely driven by the preference for algae as a food source by at least some of these micro-arthropods (Worland and Lukešová 2000; Bokhorst et al. 2007b) and the availability of optimal moisture conditions. The main driving forces underlying the distribution of consumers within Antarctic terrestrial ecosystems may therefore depend on the specific requirements for growth and avoidance of adverse abiotic conditions of individual species of micro-arthropod. Further work comparing a larger range of cryptogam growth forms than used in this study would be required to determine the role of these for the invertebrate communities in the Antarctic.

The current findings indicate a strong link between the nitrogen concentrations of Antarctic primary producers such as mosses and lichens and the community composition of associated micro-arthropods. These data extend the general understanding of the influence of nutrient concentrations in cryptogams on community assembly of invertebrates. Although the data indicate that the impact of marine vertebrates on cryptogam nutrients and micro-arthropod community development is important, it also declines at relatively short distances (c. 300-1500 m) from the source. Micro-arthropod biodiversity patterns in the maritime Antarctic are driven by availability of water and temperature when considered across large geographical scales, but biotic interactions can clearly become more important at the local scale.

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Figures

Figure 1. Map of Signy Island indicating the major penguin colonies. The lines represent the sampling transects along which samples of cryptogams and micro-arthropods were collected. The dashed line represents transects without penguin presence from the bottom of Moraine Valley to the top of Green Gable.

Figure 2. Nitrogen concentrations (%) and $\delta^{15}\text{N}$ values of *Andreaea depressinervis* (a), *Prasiola crispa* (b), *Usnea antarctica* (c) and *Umbilicaria antarctica* (d) along transects away from penguin colonies on Signy Island. Note that not all species were present along each transect. Different letters indicate significant differences (Tukey HSD $P < 0.05$) in N or $\delta^{15}\text{N}$ values between sampling sites. For clarity these differences are only presented for one transect but the other transects show similar patterns. Data points are the mean of $n = 3$ with SE as error bars. ●: North Point, ○: Gourlay, ▼: Cummings Cove, ■: Spindrift rocks.

Figure 3. Micro-arthropod abundance, diversity (H') and species richness along transects away from penguin colonies on Signy Island. Regression lines are drawn through the mean of the presented data points. Significant r^2 are indicated by: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$. Data points are the mean of $n = 3$ with error bars as SE. ●: North Point, ○: Gourlay, ▼: Cummings Cove, ■: Spindrift rocks.

Figure 4. Regressions between micro-arthropod abundance, diversity (H'), richness with the nitrogen (%) concentration of *Andreaea depressinervis*, *Prasiola crispa*, *Usnea antarctica* and *Umbilicaria antarctica*. Data points are individual moss, alga and lichen samples collected along transects away from penguin colonies. Significant r^2 are indicated by: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Figure 5. Regressions between $\delta^{15}\text{N}$ of *Andreaea depressinervis* and $\delta^{15}\text{N}$ of micro-arthropods. a) $\delta^{15}\text{N}$ of *Cryptopygus antarcticus* from the North Point and Gourlay transects. The upper dashed regression line through the springtail data points was 3.5‰ higher ($Y = 1.028 X + 3.54$) than that of the moss ($Y = X$). b) $\delta^{15}\text{N}$ of *Alaskozetes antarcticus* and *Halozetes belgicae* from the Gourlay transects. The upper dashed regression line through the mite data points was 5.8‰ higher ($Y = 0.974 X + 6.0$) than that of the moss ($Y = X$). Significant r^2 are indicated by: * $P < 0.05$, ** $P < 0.01$ and *** $P < 0.001$.

Figure 6. Micro-arthropod abundance and richness in *Usnea antarctica* across Signy Island and in relation to altitude. a) Micro-arthropod abundance, b) species richness, c) Nitrogen (‰N) and $\delta^{15}\text{N}$ of *Usnea* along the North Point transects away from the penguin colony (grey shaded area) and the north-south transect across Signy Island. Data points with different letters are significantly different (Tukey HSD $P < 0.05$). Note that, for clarity, in c) only the Tukey differences for $\delta^{15}\text{N}$ are shown but the ‰N follows the same pattern. d) Micro-arthropod abundance, e) species richness, f) $\delta^{15}\text{N}$ of *Usnea* along the slopes of the penguin-affected North Point transects and that of Moraine Valley (without penguins). ‰N of *Usnea* shows the same pattern as for $\delta^{15}\text{N}$ but is not shown. Different letters indicate significant differences (Tukey HSD $P < 0.05$) for each site separately. ANOVA statistics are presented in Table 2. Data points are the mean of $n = 3$ with SE as error bars.

517 Table 1. Details of cryptogam sampling transects in relation to penguin colonies across Signy Island. For the exact location of each penguin
518 colony and the locations of the N-S transect and Moraine Valley see Figure 1. Distances from penguin colonies for the N-S transect were
519 measured from North Point for Robin Peak, Springtail Spur and Jane Col, while Snow Hills and Garnet Hill were measured from the Gourlay
520 Peninsula. -: not present at site.

Sampling sites	North Point	Gourlay	Cummings	Spindrift rocks	N-S transect	Moraine Valley
	Distance from penguin colony (m) and altitude (m asl.)					altitude (m asl.)
Penguin species	<i>P. adeliae</i> , <i>P. antarctica</i> , <i>P. papua</i>	<i>P. adeliae</i> <i>P. antarctica</i>	<i>P. antarctica</i>	<i>P. adeliae</i>		
Breeding pairs (n)	13000	12900	7000	2000		
1	0 (30)	0 (10)	20 (20)	150 (20)	Robin Peak	1000 (220) 40
2	300 (50)	150 (20)	100 (50)	200 (40)	Springtail Spur	1700 (160) 60
3	500 (100)	300 (20)	300 (80)	300 (60)	Jane Col	2700 (160) 90
4	700 (150)	700 (60)	600 (150)	500 (100)	Snow Hills	3600 (265) 120
5	800 (200)	1300 (70)	-	700 (150)	Garnet Hill	2100 (227) 206
Species sampled						
<i>Andreaea</i>	+	+				
<i>Prasiola</i>	+	+				
<i>Usnea</i>	+		+	+	+	+
<i>Umbilicaria</i>	+	+	+			

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523 Table 2. Mixed effects ANOVA results of cryptogam differences in N content, $\delta^{15}\text{N}$, water content and micro-arthropods in relation to distance
524 to penguin colonies. The comparison of change in arthropods along transects compares the slopes of linear regression through the data points (as
525 shown in Fig. 3). The North-South transect statistics show the comparison of the micro-arthropod community among *Usnea* from the North
526 Point penguin colony to the southern tip of the island (see Table 1). The altitude statistics represent a comparison of the micro-arthropod
527 community among *Usnea* along three penguin-associated transects (see Table 1) to that of non-penguin affected transects (Moraine Valley).
528 There were three replicate transects per site and site was used as a random factor in the analyses. Significant differences are indicated by * $P <$
529 0.05, ** $P < 0.01$, *** $P < 0.001$.

		Cryptogam			Micro-arthropod abundance			Species richness	Diversity
		%N	$\delta^{15}\text{N}$	Water content	Total	Acari	Collembola	R	(H')
<i>Andreaea</i>	Distance (8,20)	12.2 ***	5.7 ***	1.9	0.1	5.7 **	2.4	6.2 ***	7.8 ***
	Site (1,20)	14.4 ***	0.3	3.9	0.5	0.4	1.6	2.5	0.0
<i>Prasiola</i>	Distance (7,18)	2.0	3.1 *	2.3	2.2	2.4	2.6	2.8 *	4.3 **
	Site (1,18)	0.2	5.5 *	6.9 *	0.1	0.1	6.5 *	0.3	7.5 *
<i>Usnea</i>	Distance (9,30)	5.5 ***	8.4 ***	7.3 ***	13.1 ***	10.3 ***	10.9 ***	6.5 ***	3.1 **
	Site (2,30)	2.4	6.3 **	12.0 ***	2.6	2.5	1.7	2.0	0.3
<i>Umbilicaria</i>	Distance (10,29)	5.2 ***	1.1	3.9 **	1.5	2.3*	1.3	3.7 **	4.5 **
	Site (2,29)	9.3 **	5.6 **	36.5 ***	0.7	1.6	8.8 **	0.3	1.1
Rate of change in micro-arthropods along transects									
	Species (3,20)	1.0	1.1	10.8 *	0.7	1.0	0.2	9.0	0.8
	Site (3,20)	2.4	0.7	2.6	0.3	1.5	0.5	1.7	0.3
	Site×Species (3,20)	9.7 ***	8.9 ***	1.4	9.3 ***	1.9	10.0 ***	0.2	1.3
N-S transect across Signy Island									
<i>Usnea</i>	Distance (8,20)	4.9 **	4.5 **	3.4 *	9.6 ***	4.4 **	18.2 ***	2.1	0.7
	Site (1,20)	0.0	1.6	4.8 *	0.1	0.2	0.7	0.1	0.6
Altitude comparison									
<i>Usnea</i>	Altitude (12,41)	6.3 ***	7.6 ***	2.7 **	8.6 ***	8.3 ***	7.3 ***	6.0 ***	2.2 *
	Site (2,41)	2.4	11.0 ***	20.1 ***	2.4	4.1 *	2.6	0.1	1.3

